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THE CLADISTIC RELATIONSHIPS OF THE CHARADRIIFORMES

by

Joseph George Strauch, Jr.

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Zoology)
in The University of Michigan
1976

Doctoral Committee

Professor Robert W. Storer, Chairman
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INTRODUCTION

I have been dissatisfied for some time with the methods and evidence used in the past to estimate the relationships among birds, especially among the higher categories. While Stresemann (1959) thought that there was an "absence of trustworthy information on the relationships of the higher categories of birds," concluding that such groupings are merely "a matter of convention," I do not think that the failures of the past indicate that there is no hope for the future. In recent years there has been a theoretical and methodological revolution in the estimation of phylogenetic relationships (Camin and Sokal 1965; Hennig 1966; Fitch and Margoliash 1967; Kluge and Farris 1969; Estabrook 1972). Unfortunately few of these new ideas have been used in avian systematics (Selander 1971; Cracraft 1972); this study is an attempt to rectify that situation.

Ornithologists often have not distinguished between systematics ("the study of the kinds and diversity of organisms and the relationships among them") and taxonomy ("the theory and practice of classifying organisms") (Simpson 1961; Mayr 1969; Selander 1971). Thus in much of the literature of avian systematics systematic decisions are often expressed as classifications.

The currently accepted classification of birds dates from the work of Gadow (1892, 1893). While several authors (Wetmore 1930, 1934, 1940, 1951, 1960; Mayr and Amadon 1951; Stresemann 1959; Storer 1971) have made minor changes in Gadow's classification using new evidence for realignment of some families or genera, the only proposal for a radical change in Gadow's classification (Verheyen 1961) has been almost universally rejected as unsound. A detailed history of bird classification has been presented by Sibley (1970) and by Sibley and Ahlquist (1972).

Bird classification has been and continues to be based on a more or less subjective judgment of phenetic or "overall" resemblance among taxa. The problems of using phenetic resemblance to estimate phylogenetic relationship has been discussed by Pratt (1972a, b) and Griffiths

(1974). Before 1867 birds which looked alike, such as auks and penguins, gulls and shearwaters, or plovers and sandpipers, were often placed together. As new characters, especially internal ones, were discovered, or as old characters were reinterpreted, new classifications were proposed. Huxley's analysis of the avian skull (1867) marks the genesis of modern bird classification; his order Schizognathae contained all the birds now included in the Charadriiformes as well as almost all the birds which later authors believed to be related to one or another family in the Charadriiformes.

The major debates among bird systematists concerning charadriiform birds since Huxley's work have centered around several problems: possible relationships among the Laridae, Procellariiformes, Gaviidae, and Alcidae (Coues 1868; Sclater 1880; Stejner 1885; Shufeldt 1891), relationships among the Gruiformes and Charadriiformes, especially that between the Otididae and Burhinidae (Garrod 1873; Sclater 1880; Sharpe 1891; Low 1931; Lowe 1931b; Boetticher 1934; Stresemann 1959) and that between the Rallidae and the Jacanidae (Forbes 1881; Lowe 1925; Stresemann 1959), the relationships of the Thinocoridae (Seebohm 1895; Shufeldt 1891; Mathews and Iredale 1921; Lowe 1922, 1923; Hanke and Niethammer 1955; Sibley, Corbin, and Ahlquist 1972), and the question of whether the Pteroclidae are Charadriiformes (Huxley 1868; Garrod 1874; Sclater 1880; Gadow 1893; Beddard 1898; Mayr and Amadon 1951; Maclean 1967, 1969; Stegmann 1968, 1969; Olson 1970; Storer 1971). Although Stresemann (1959) preferred to separate the Jacanidae, Thinocoridae, and Burhinidae from the Charadriiformes, all other modern classifications include them. There is, however, no consensus regarding the relationships of the Pteroclidae. Recent evidence has again suggested a relationship between the Charadriiformes and the Procellariiformes (Sibley and Ahlquist 1972) and another between the former and the Gaviidae (Storer 1956, 1971; Sibley and Ahlquist 1972).

Seebohm (1888, 1895), Fürbringer (1888), Sharpe (1891), Shufeldt (1903), Lowe (1931b, c), Boetticher (1934), Mayr and Amadon (1951), Timmerman (1957b), Wetmore (1960), and Storer (1971) all presented classifications of charadriiform birds much like Gadow's (1892). The significance of Gadow's classification is that he used many more characters than did his predecessors in forming his conclusions. His

classification is thus more robust than those previously proposed.

Between 1914 and 1933 Percy R. Lowe published a series of papers on the anatomy and relationships of the Charadriiformes, especially shorebirds. Lowe's contributions include descriptions of the anatomy of several previously unstudied forms and discussions of the states of several characters in many different species. His decisions regarding relationships, however, are suspect because he relied too heavily on a few characters, such as color pattern, supraorbital grooves, and the morphology of the quadrato-tympanic articulation.

Kozlova (1961) and her collaborator Yudin (1965) proposed a phylogeny of the Charadriiformes based on their "ecologico-morphology" method. Using information on the behavior, ecology, and morphology of the head and wing, they begin with the assumption that the genus Pluvialis represents the archetype of the Charadriiformes from which more specialized charadriiform groups radiated. The vagueness of their methods for inferring relationships and their use of much fragmentary and anecdotal evidence make many of their conclusions of doubtful value.

In a survey of 24 orders of birds Kitto and Wilson (1966) found that charadriiform birds have a unique S malate dehydrogenase, the mobility of which is 55% that of most other birds. Their results indicate that the Jacanidae and Burhinidae are members of the Charadriiformes while the Pteroclidae are not.

Jehl (1968b) surveyed the plumage patterns of the downy young of shorebirds, much as did Lowe (1915a). His conclusions, based on subjective estimates of similarity of overall patterns and the relationships implied by them, are in need of a more objective reevaluation.

Burton (1974) made an extensive survey of the feeding apparatus of shorebirds but did not use his findings to suggest relationships. Ahlquist (1974) used the IFPA (isoelectric focusing in polyacrylamide) of egg-white proteins and two-dimensional electrophoresis maps of ovalbumin peptide digests to estimate relationships among the Charadriiformes. Unfortunately his conclusions can be accepted only as suggestive, since he made dubious assumptions concerning the homologies between the spots found on the peptide maps for different species and used analytical methods inappropriate to his data.

In this study I have used the method of character compatibility to estimate the cladistic relationship among the Charadriiformes. This approach is based on current evolutionary theory, and its methods of analysis have been shown to be mathematically exact (Estabrook 1972; Estabrook, Johnson, and McMorris 1975, 1976a, b; McMorris 1975). Unlike the Wagner Tree parsimony methods (Kluge and Farris 1969) and the methods used by the followers of Hennig (e.g., Cracraft 1974), character compatibility allows one to identify precisely and objectively the best characters used in a study.

Nomenclature

The nomenclature used in the text is basically that of Peters (1934) with the exception that the generic and specific names used by Jehl (1968b) are followed for almost all the shorebirds (see Appendix III). The classification and nomenclatural changes I recommend as a result of this study are given in Appendix VII.

Character names follow Bock and McEvey (1969), supplemented by Bams (1956), Burton (1971, 1974), Cracraft (1968), George and Berger (1966), Holman (1961), Howard (1929), Lebedinsky (1913), Rand (1954), and Zusi and Jehl (1970).

WHAT IS A CHARADRIIFORM?

Before the evolutionary history of a group of organisms can be estimated, its membership must be determined. An investigator must choose a group of organisms which he believes to represent the living descendants of a single ancestor which gave rise to no other extant forms. Thus even before an evolutionary history can be estimated, some estimate of evolutionary history is already assumed at a higher taxonomic level. I agree with Colless (1967, 1969a, b) that one must always start with some sort of phenetic classification as a beginning evolutionary estimate.

Present avian classification is based on an essentially phenetic clustering of similar birds, which may be traced to the work of Gadow (1892). The phylogenetic relationships of the orders of birds remain obscure, although many authors have suggested relationships among some of them. On the basis of overall resemblance, the Gruiformes and Columbiformes are probably more closely related to the Charadriiformes than are any other orders of birds (the traditional thought). The Gruiformes, however, probably represent a polyphyletic group, only some of which are close to Charadriiformes. Suggestions that the Procellariiformes (Sibley and Ahlquist 1972) and Gaviiformes (Storer 1956; Sibley and Ahlquist 1972) are closely related to the Charadriiformes seem plausible but require further investigation. Placement of the families Jacanidae, Thinocoridae, Burhinidae, and Pteroclidae among the Gruiformes, Charadriiformes, and Columbiformes is still in dispute (Stresemann 1959; Storer 1971; Sibley and Ahlquist 1972; Maclean 1967; Stegmann 1959; Olson 1970).

I thus had the choice of arbitrarily following one of the modern classifications of the Charadriiformes or of making an independent determination of which families belong in the order. I decided to define the Charadriiformes by comparing representatives of families in the three orders: Gruiformes, Charadriiformes, and Columbiformes. Representatives of the Gaviiformes and Podicipediformes were also included to investigate the possibility that loons belong in the

Charadriiformes. A list of the species used in this preliminary study and their character states is presented in Appendix II. These species represent almost all the families in the five orders and much of the diversity within them. Representatives of all families which have been assigned to the Charadriiformes by recent workers were included.

Forty-four skeletal and two integumental characters were used in comparing the species (Appendix I). Homologies for the characters were determined according to their relative positions in the skeleton. (See Jardine (1969) for a formal method.) Since the avian skeleton is extremely uniform throughout the class, homology based on relative position is probably the same as the evolutionary homology which would be obtained if the phylogeny of each structure could be followed from a structure found in the most recent common ancestor of the birds to the structures found in presently living species (Simpson 1961). This assumption might fail in the case of some of the complex structures of the skull and the hypotarsus, however, especially since the ontogeny of these structures has been studied in only a few birds (Jollie 1957; Cracraft 1968).

To determine similarity based on common ancestry rather than on adaptation to a common selective force, characters must be obtained from as much of the phenotype as possible. Birds adapted to a particular type of food, for example, may show considerable convergence in their bills and skulls. The seed-eating members of the Ploceidae, Estrildidae, Fringillidae, and Emberizidae were once thought to belong to a single family which included all finches, but consideration of characters other than the finch-like bill has led to the conclusion that several different phyletic lines have led to morphologically similar seed-eaters (Sibley 1970 and references therein).

In the first part of this study the characters (Appendix I) were distributed over the phenotype as follows: 19 characters of the skull and mandible, 4 characters of the axial skeleton, 15 characters of the pectoral girdle and skeleton of the wings, 6 characters of the pelvic girdle and skeleton of the hind limbs, and 2 characters of the integument. Three of the characters were meristic (actual counts of structures such as vertebrae) while the rest were qualitative. The characters were scored as the actual counts for the meristic characters and

as a series (0,1,2...n) for as many states as were identified for the qualitative characters. Of the qualitatives characters, 25 were scored as having only two states, 0 and 1; the remaining 18 qualitative characters were multistate and were scored in a plausible sequence, as from simple to more complex.

The Prim Network cluster analysis (Prim 1957) was used to analyze the skeletal characters of this assemblage (Appendix II). The Prim Network program produces a single-linkage phenetic clustering with no assumptions of directionality. The longest internodes in the Prim Network obtained (Fig. 1) occur between the Columbidae and the Otididae, between the Otididae and the Podicipedidae, between the Gaviidae and the Rallidae, between the Rallidae and the Eurypygidae, between the Gaviidae and the Alcidae, and between the Haematopodidae and the Burhinidae. These results support the hypothesis that the Gruiformes are polyphyletic, that the Pteroclidae and Columbidae are closer to each other than either is to any charadriiform, and, most important for this study, that the Charadriiformes (sensu Wetmore 1960) represent a monophyletic assemblage. There is no evidence that the Jacanidae are similar to the Rallidae, that the Thinocoridae are close to any of the Gruiformes, or that the Burhinidae are close to the Otididae. The Gaviidae fall about midway between the Podicipedidae and the Alcidae; they were not included in the Charadriiformes in this study.

This analysis indicates that the Charadriiformes are a monophyletic assemblage consisting of the following families: Jacanidae, Rostratulidae, Haematopodidae, Charadriidae, Scolopacidae, Recurvirostridae, Phalaropodidae, Dromadidae, Burhinidae, Glareolidae, Thinocoridae, Chionididae, Stercorariidae, Laridae, Rynchopidae, and Alcidae.

Fig. 1. Prim network of representative species of the Gruiformes, Charadriiformes, and Columbiformes based on 44 qualitative and meristic characters (see text).

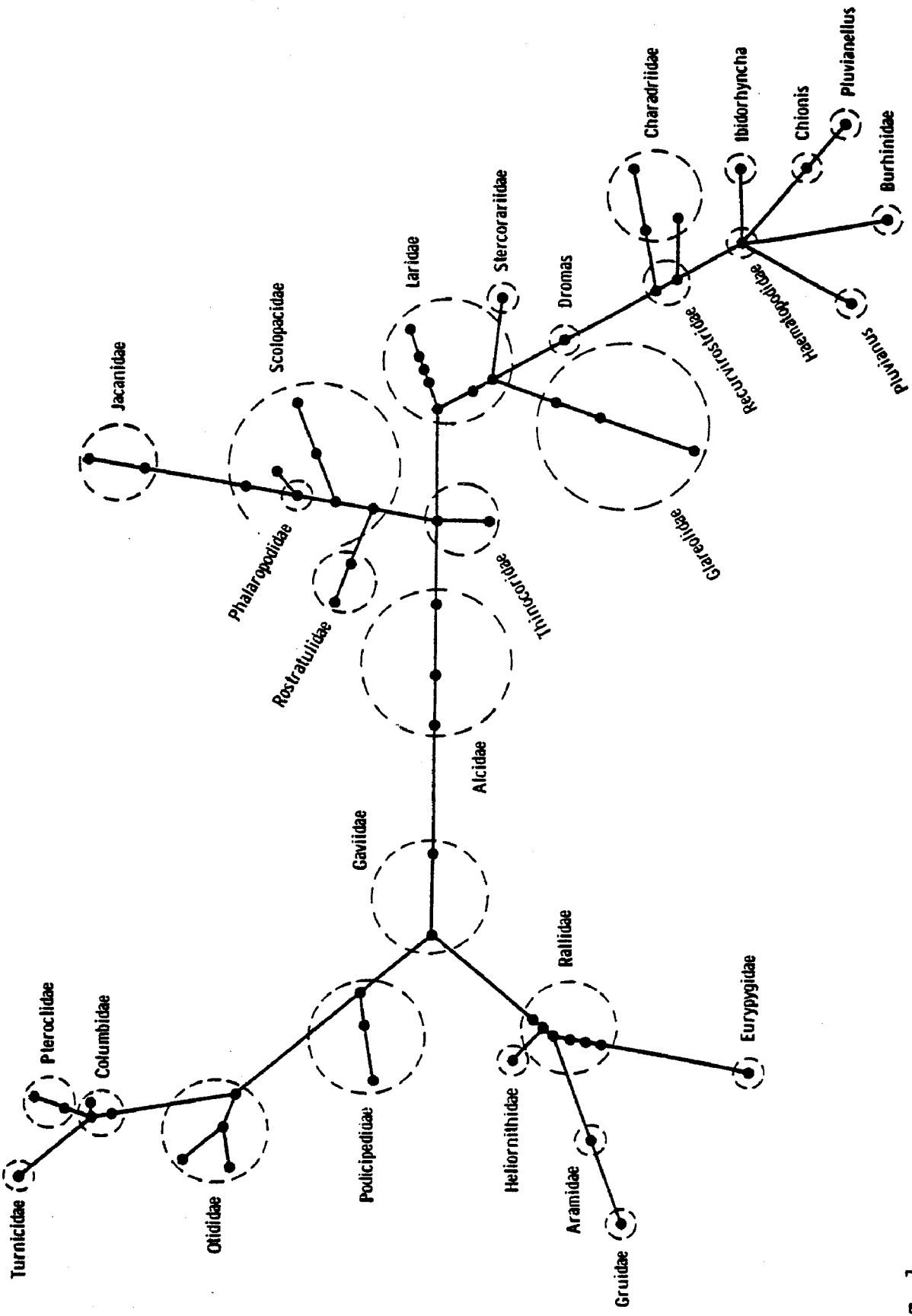

Turnicidae
Pteroclidae
Columbidae
Otididae
Podicipedidae
Heliornithidae
Aramidae
Gruidae
Rallidae
Eurypygidae
Gaviidae
Alcidae
Thinocoridae
Rostratulidae
Phalaropodidae
Scolopacidae
Jacanidae
Glareolidae
Recurvirostridae
Dromas
Stercorariidae
Laridae
Charadriidae
Haematopodidae
Ibidorhyncha
Chionis
Pluvianellus
Burhinidae
Pluvianus

Fig. 1

THE METHOD OF CHARACTER COMPATIBILITY FOR PHYLOGENETIC INFERENCE

Much of the literature of systematics deals with the identification of characters which are good estimators of evolutionary history. Early systematists had little more than their own insights to help them choose the characters which best indicate relationship. The subjectivity of the intuitive method has led many systematists to reject classical phylogenetic studies and to accept phenetic methods (Sneath and Sokal 1972). Pheneticists argue that classifications should be based on overall resemblance without regard to phylogeny. Those interested in estimating evolutionary history, on the other hand, have long held that some characters are better than others for reconstructing phylogenies and that the major problem is to identify them.

Character compatibility is a method for identifying cladistically useful characters. Since this approach is unfamiliar to most investigators, a brief and simplified summary of the underlying theory is given below. (See Estabrook 1972; Estabrook, Johnscn, and McMorris 1975, 1976a, b; McMorris 1975.)

When a worker assembles specimens of organisms whose evolutionary history he wishes to estimate, he makes certain assumptions about the degrees of relatedness among them and about their evolutionary history. The assumptions made here are that the organisms being studied are members of a set of evolutionary units (EUs) whose cladistic history can be represented by a tree.

There is disagreement about what the set of evolutionary units should be. Hennig (1965, 1966) argued that a set of evolutionary units consists of groups of organisms alive at the same time. The concept of a set of evolutionary units used here, however, is broadened to include the set's own most recent common ancestor and all the units arising from that common ancestor, contemporary or ancestral. It is therefore necessary to make estimates of the unrepresented units, just as hypothetical intermediates must be estimated in the Wagner Tree parsimony methods (Kluge and Farris 1969). A hypothetical representation of the

evolutionary history of a set of evolutionary units is illustrated in Figure 2A. Each phyletic line segment of the tree represents a discrete (monophyletic) evolutionary unit; it represents genetic continuity through time. To satisfy the requirements that each unit be discrete and that no two units have any organism in common, a few generations close to a branching point of a phyletic line, or joining distinct units consecutive along the same phyletic line, are excluded from evolutionary units.

One advantage of recognizing discrete evolutionary units is that it permits the cladistic relationships among the units to be represented by algebraic relationships. The hypothetical evolutionary history in Fig. 2C is not a set of evolutionary units. The history is not divergent, there are no discrete units except for the ancestor, a, and it is not a tree since the branches reunite. The true set of evolutionary units will be called S' and the set of organisms (recent or fossil) for which there are samples in the form of specimens, S.

The term evolutionary unit (EU) differs significantly from the already established operational taxonomic unit (OTU) of Sneath and Sokal (1972). The OTU implies no historical pattern among the units under study. Any collection of objects or abstractions whose similarities and differences may be quantified may serve as a set of OTUs. The definition of a set of EUs, on the other hand, assumes that the set under study has only one true history, which can be estimated.

Once the units under study have been defined, it is necessary to define the relationship among them that we wish to study. The algebraic relationship A, "is an ancestor of," defined for S', the set of evolutionary units described above, is of special significance. This relationship is defined so that for any units in S' the following are always true:

1. aAa (read a is an ancestor of a), i.e., a is its own ancestor;
2. if aAb and bAa are both true, then a is the same unit as b;
3. if aAb and bAc are both true, then aAc is also true. The relationship A forms what is known mathematically as a tree partial order (Estabrook 1968, 1972).

The relationship A can be illustrated with a Hasse diagram. (A Hasse diagram in abstract algebra is a diagram which represents a

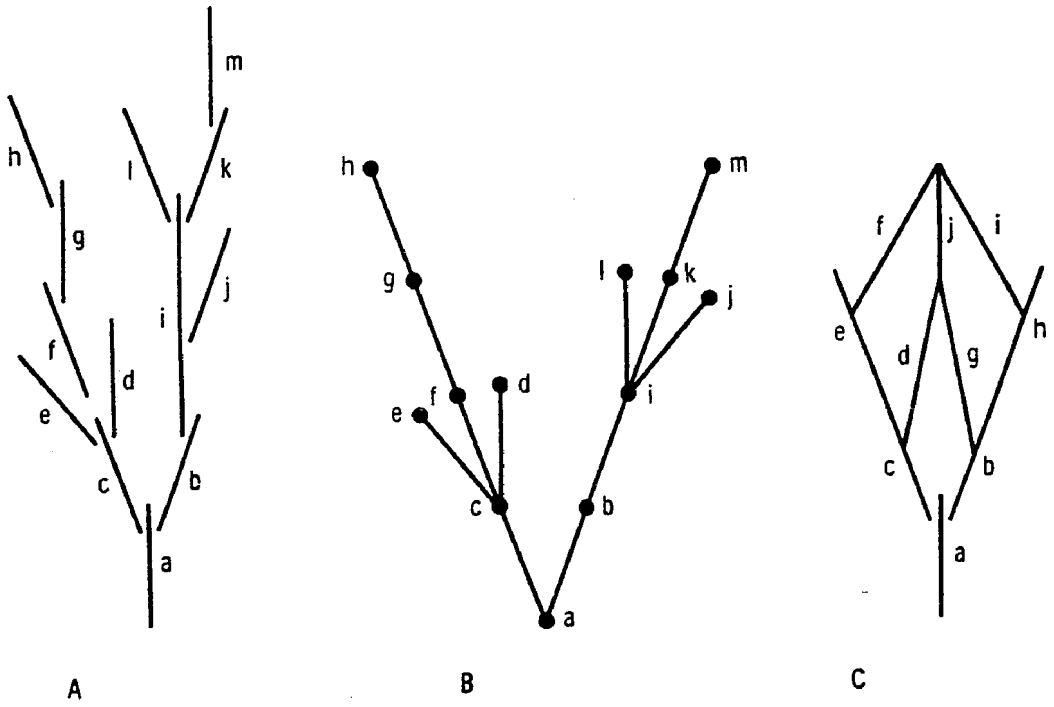


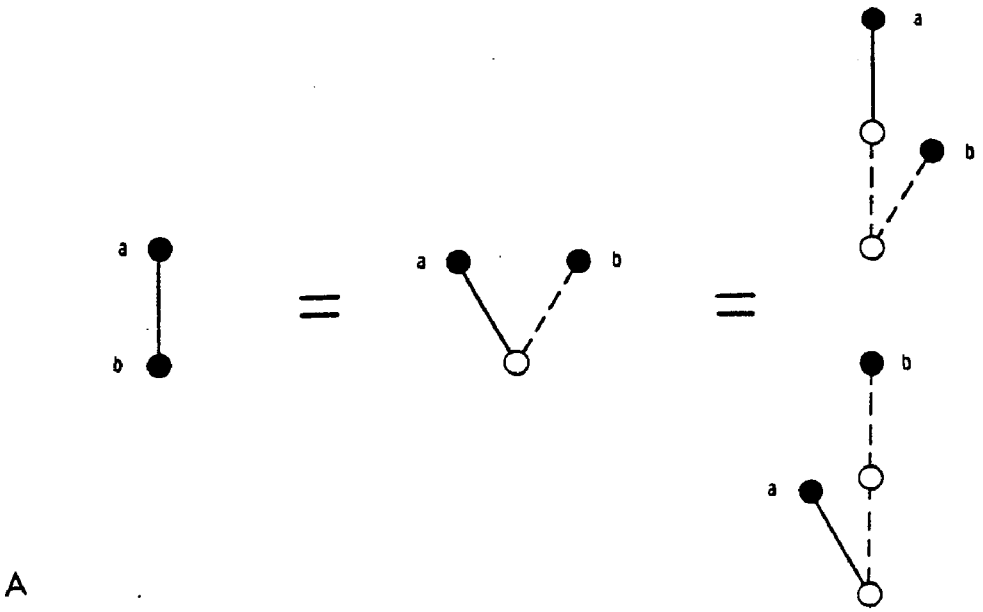
Fig. 2. Representations of evolutionary history. A. a tree representing the evolutionary history of a hypothetical set of evolutionary units; B. a Hasse diagram for the relationship <u>is an ancestor of</u> among the set of evolutionary units in A; C. the evolutionary history for a group which is not divergent.

partially ordered set (Moore 1967).) Figures which resemble Hasse diagrams are often used to represent phylogenetic trees, but, strictly speaking, Hasse diagrams are graphic representations of the relationship for the set of units placed on them. The nodes on a Hasse diagram represent phyletic units; these nodes are connected by lines (called edges), which signify that the nodes are related in a specific manner. Fig. 2B is the Hasse diagram of the tree partial order A for the set of EUs S' shown in Fig. 2A. The partially ordered elements of S' are connected by lines such that whenever aAb, a path leads from a, possibly through other elements which lie between a and b in the diagram, to b, in a direction which is always toward the top of the diagram. The line between a and c is read, "a is an ancestor of c."

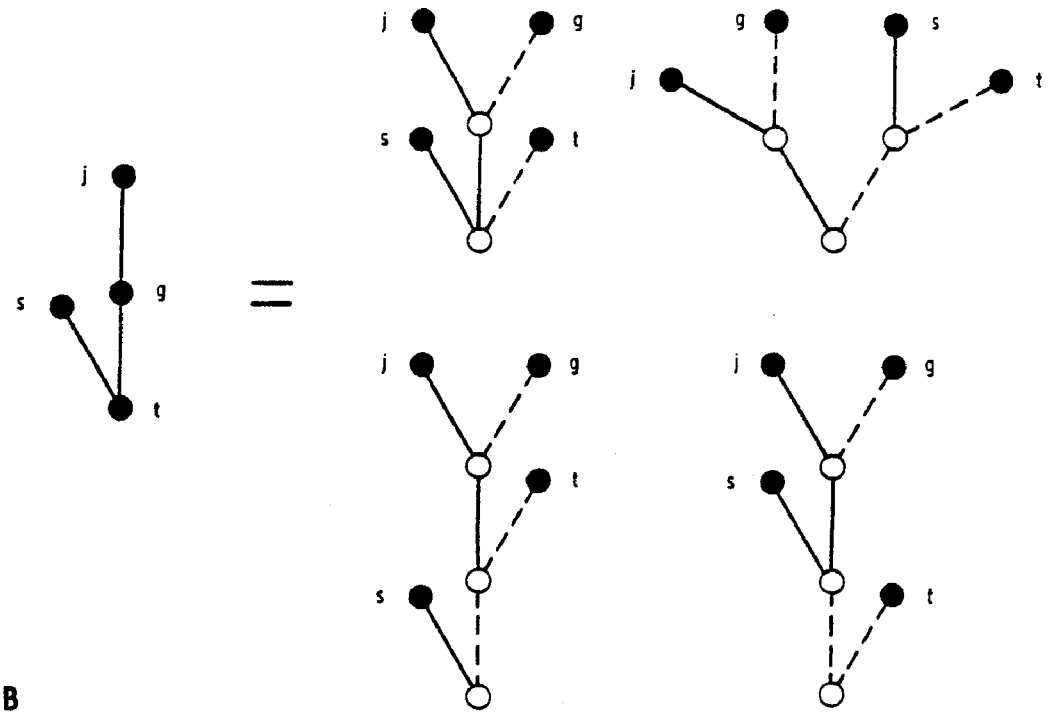
All the trees presented in this study are in the form of Hasse diagrams. The phylogenetic implications of these diagrams are illustrated in Fig. 3. On these diagrams solid circles represent real EUs (a and b in Fig. 3A), and open circles represent hypothetical EUs generated by the analyses. When a real EU is connected directly to another real EU on the tree, such as a connected to b in Fig. 3A, it does not imply that one EU is the ancestor of the other but only that the characters defining the tree do not distinguish some EUs from their ancestors. Thus in Fig. 3A a and b share a common ancestor, but none of the characters used to devise the tree distinguish b from the ancestor it shares with a. The middle figure in Fig. 3A shows this relationship with a dashed line for the internode between b and the ancestor it shares with a. The figures on the right in Fig. 3A show other possible phylogenetic interpretations of the figure on the left. A more complex tree and four of the possible phylogenies it could represent are shown in Fig. 3B. This tree is found for the Laroidea in this study (Fig. 56).

Central to estimating the evolutionary history of a set of EUs is finding a basis for comparison and then structuring a comparative scheme which translates statements of similarities and differences into statements about the relative recency of common ancestry of the EUs. A basis for such a comparison is called a "character." A character is a function defined for the study collection S, or, ideally for the set of EUs, S', for which the values are descriptions. The members of

Fig. 3. Phylogenetic implications of Hasse diagrams. A. A Hasse diagram on which real EU b is shown to be the ancestor of real EU a. Such a diagram is best interpreted as indicating that EUs a and b share a common ancestor but none of the characters used in the study distinguish b from the most recent common ancestor it shares with a (middle figure). The two figures on the right are more complex interpretations of the possible relationship between a and b which would be of interest only if a third EU had to be included on the diagram. B. The figures on the right represent possible phylogenetic histories which are consistent with the Hasse diagram on the left. Solid circles represent real EUs, open circles represent hypothetical ancestral EUs, solid internodes represent character state transitions defined by characters included in a study, and dashed internodes represent possible transitions but are not defined by any character in the study.



A



B

Fig. 3

the set descriptions are called "character states." Thus the character "toe webbing" might have character states "toes not webbed" and "toes webbed." Thus if the character K is a character for S, and a is contained in S, K(a) is the description of a based on or made by character K. For example, for the EU "American Avocet (Recurvirostra americana)" contained in the set "Charadriiformes," the character "toe webbing" would have the description "toes webbed." A character may be construed as an equivalence relation on S (or S'). An equivalence relation asserts that two things are equivalent with respect to some consideration. Thus the four living species of avocets are equivalent with respect to toe webbing.

If a, b, and c are EUs and E is an equivalence relation on S or S', then E is defined as having the following properties:

1. aEa is always true;
2. if aEb is true, them bEa must be true;
3. if aEb and bEc are true, then aEc must also be true.

By placing a and b in the same class whenever aEb, E determines a nonhierarchical classification of S or S'. These are the equivalence classes of E. Character K determines an equivalence relation aEb if and only if K(a) = K(b). The equivalence classes of K are called character states.

Characters useful for estimating the true evolutionary history should be divergent, that is, all the EUs belonging to a given state K(a) must have evolved from a most recent common ancestor with K(a) with no change in the property characteristic of K(a) (no reversals), and changes in the states of K must have occurred only on phyletic lines leading directly to the recent common ancestors of the states of K themselves (unique origin). Thus for the character "toe webbing" to be divergent, all avocets with webbed toes must have evolved from a most recent common ancestor with webbed toes, all the organisms along the phyletic lines leading from the common ancestor of avocets to the recent species of avocets must also have had webbed toes, and finally, the change in the character "toe webbing" which gave rise to webbed toes occurred only on the phyletic line leading directly to the most recent common ancestor of all avocets.

To use characters to estimate evolutionary history the properties

of characters which are ideally related to true history must be specified. A cladistic character is a character which includes estimates of evolutionary trends and is therefore itself an estimate of evolutionary history. A relationship P, is more primitive than, is defined for the set of character states of K. P is a tree partial order which estimates the evolutionary trends among the states of K. The Hasse diagram of P is a character state tree (Fig. 4). If K is to be used to estimate evolutionary history, then there must be a relationship between the relationship A, is an ancestor of, and the relationship P, is more primitive than. For A to be ideally related to P, each equivalence class of K should have the following properties:

1. Each equivalence class of E should contain its own most recent common ancestor (should contain a unique minimal element).

2. If a first EU is an ancestor of a second EU, then the state of which the first is a member should be equal or primitive in the character state tree of P to the state of which the second is a member.

3. If one character state is primitive to another in the character state tree of P, then the most recent common ancestor for the one state should be ancestral in A to the most recent common ancestor of the other.

If the relationship between A and P is ideal, then the partial order induced by A onto the subset of S' made up of the respective character-state minimal elements will be isomorphic to (the same as) P, whose Hasse diagram is the character state tree. Estabrook, Johnson, and McMorris (1975) prove as a theorem that a cladistic character with this relationship to A is a true cladistic character if the character state tree is true.

Fig. 4 illustrates the ideal relationship between the Hasse diagrams of A and P. In the figure each element of P corresponds to an element in A which is the minimal element in that state; thus K(b) corresponds to b, K(f) corresponds to f, etc. Note that if certain edges of the Hasse diagram of A are greatly stretched, the Hasse diagram for P results. A character is true if all the statements it makes about A are true; a false character makes statements about A which are false. The Hasse diagram for a true character and the Hasse diagram for A will have one fewer edge than there are states in the character,

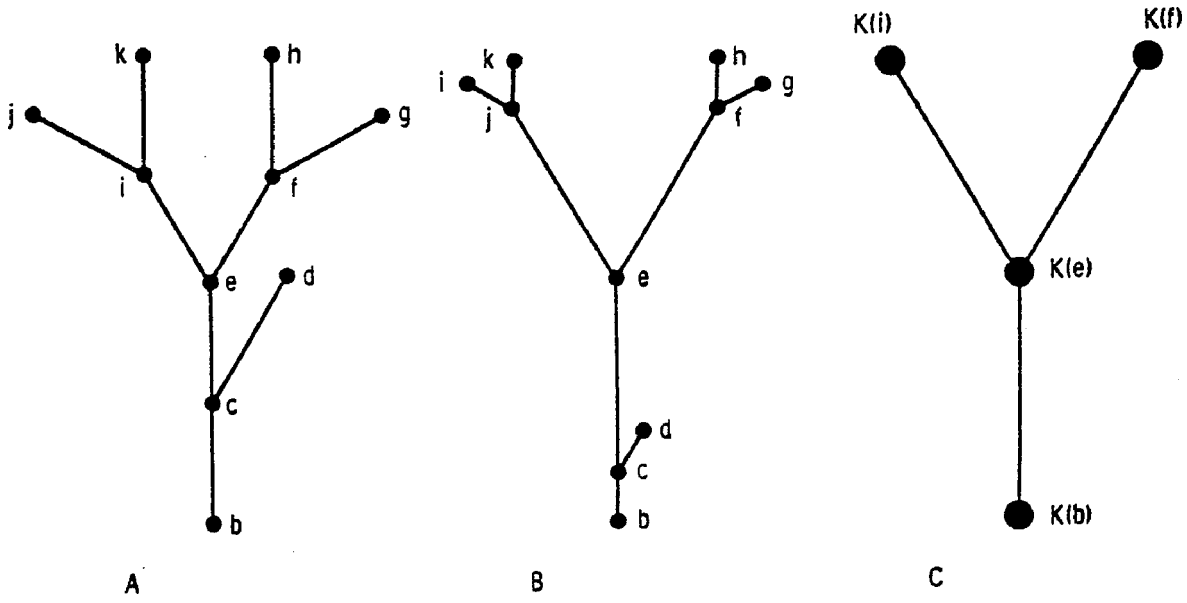


Fig. 4. The ideal relationship between the Hasse diagram for a set of evolutionary units and a character state tree. A. a Hasse diagram for a hypothetical set of evolutionary units; B. the same Hasse diagram as in (A) with the internodes between the equivalence classes defined by the character whose character state tree is shown in (C) stretched; C. a character state tree. The cladistic patterns for the equivalence classes (B) are the same as those for the character states (C).

while a false character will specify edges of A which do not exist.

Once the concept of an ideal cladistic character has been defined, a method of finding among the collection of real characters those characters which are most likely to be true is needed. Under the assumption that there are only bifurcations in true evolutionary history, there are $\prod_{i=1}^{N-1}(2i-1)$ possible estimates of evolutionary history for any set of N EUs. This is a very large number for a study collection of even moderate size; even if many are highly unlikely, there still remains a large set of possible estimates. Characters help to reduce the number of likely possibilities to a small set, which ideally is the one most likely estimate. Remember that each character divides the set of EUs into a set of equivalence classes, which for cladistic characters is a set of tree partial orders. Among all the possible evolutionary histories for a set of EUs only one is true. Each character in effect divides all the possible estimates into two groups. The first consists of those partial orders which, if any of them be true, result in the character's being true; the second contains those which, if any be true, result in the character's being false. Unfortunately there is no technique for determining which characters are true. The concept of compatibility of characters (LeQuesne 1964; Camin and Sokal 1965; Estabrook 1972), however, determines which characters may be true. Two true characters may make different statements about A, but they never contradict each other. Two characters are compatible if it is logically possible for both to be true simultaneously. Two characters are incompatible if they logically contradict each other; at least one of them is false. They may both be false, and two compatible characters may also both be false. Thus, given two partial orders defined by two different characters, compatibility means that the mathematical intersection of the two sets is non-empty, that is, it contains all the estimates of evolutionary history which are logically possible and for which the estimates made by each character do not contradict each other. Usually this group of estimates is much smaller than for any character alone. An intersection which is empty implies that no estimate of evolutionary history allows both characters to be true simultaneously.

In order to test characters for compatibility a character state tree must be created for each character used in the study. Short of

knowing true evolutionary history, there is no sure way of doing this. Regardless of the complexity of the tree, the first step in creating a character state tree is to identify the primitive state represented in the study collection. Suggestions on how to do this are discussed by Sporne (1956), Wagner (1961), Kluge and Farris (1969), and Estabrook (1972), among others. The principal method used in this study is that of the ground plan or correlation. The problems of using this method are discussed by Colless (1969b) and Stebbins (1974). It is assumed that more primitive character states are more likely to be distributed throughout other groups similar to, and supposedly related to, the group under study (outgroups), are more likely to be widespread within the group than is any derived state, and are therefore likely to be associated in the same evolutionary units with the primitive states of other characters. For simple two-state characters, defining the primitive state fixes the character state tree. For characters with more than two states, the number of possible trees is only partially determined when a primitive state is identified. Construction of the character state tree must in this case be based on whatever evidence is available to predict the evolutionary relationship among the character states. Sometimes evidence from patterns found in other groups, such as the loss of parts or increased complexity of a structure, can be used. Often one must guess.

There are several reasons why many characters lead to incorrect historical inferences. Specimens may not all represent EUs; there may be hybrids, polyploids (Wagner 1970), or specimens which are atypical because of disease, stress, or genetic abnormalities. The character may be constructed on the basis of false homology. Characters being compared may represent differences in life cycle or maturity. Finally, the character may show homoplasy; similar-appearing states may not share a common most recent ancestor.

What evidence is there that the set of characters is compatible because of a shared evolutionary history and is not just a chance result? Intuitively, it would be expected that few characters from a character set would be compatible over many EUs. Since there are many chances for errors in devising character state trees, many trees are probably false, and the number of incompatibilities in a data set is

usually large. Statistical methods for testing the significance of the size of a set of compatible characters are currently unavailable, but it seems reasonable that finding a large set of mutually compatible characters is unlikely. My preliminary simulation experiments show that there are usually no compatibilities in a completely random data set, and it is only when some structure in the distribution of character states is imposed upon the EUs that compatibilities of about 3% of the total number of characters are found. The structure in real data sets is thought to be the result of an historical process. Thus the larger the set of mutually compatible characters (the larger the clique) found in a study, the greater the confidence that the compatibilities represent true history.

Fortunately it is easy to determine the compatibilities in a set of characters by means of a computer. The cartesian product of two characters (a lattice containing a vertex for every possible combination of the character states of the two original characters) can be thought of as a new character (Estabrook 1968, 1972). The cartesian product of two characters I and II, written I $\otimes$ II, is illustrated in Fig. 5 for two simple characters. If I and II are compatible, their cartesian product is a tree order; if incompatible, their cartesian product is not a tree order. Fig. 5B and 5C represent the cartesian products of compatible characters, while Fig. 5D represents the cartesian product of incompatible characters.

The procedure for determining compatibilities can be greatly simplified by factoring a character state tree into its binary factors. (Farris, Kluge, and Eckardt (1970) call this process additive binary coding.) A binary character has only two states, 0 and 1. Any complex character of n states can be factored into a set of n-1 binary characters. Fig. 6 shows how each state is recoded for each factor. Note that each factor represents one transition in the original character state tree. Although calculating the cartesian product for complex characters is difficult, calculating cartesian products for binary characters is simple. Most important, two characters are compatible if and only if each of the binary factors of the first is compatible with each of the binary factors of the second (Estabrook, Johnson, and McMorris 1975). The process of factoring characters into their binary

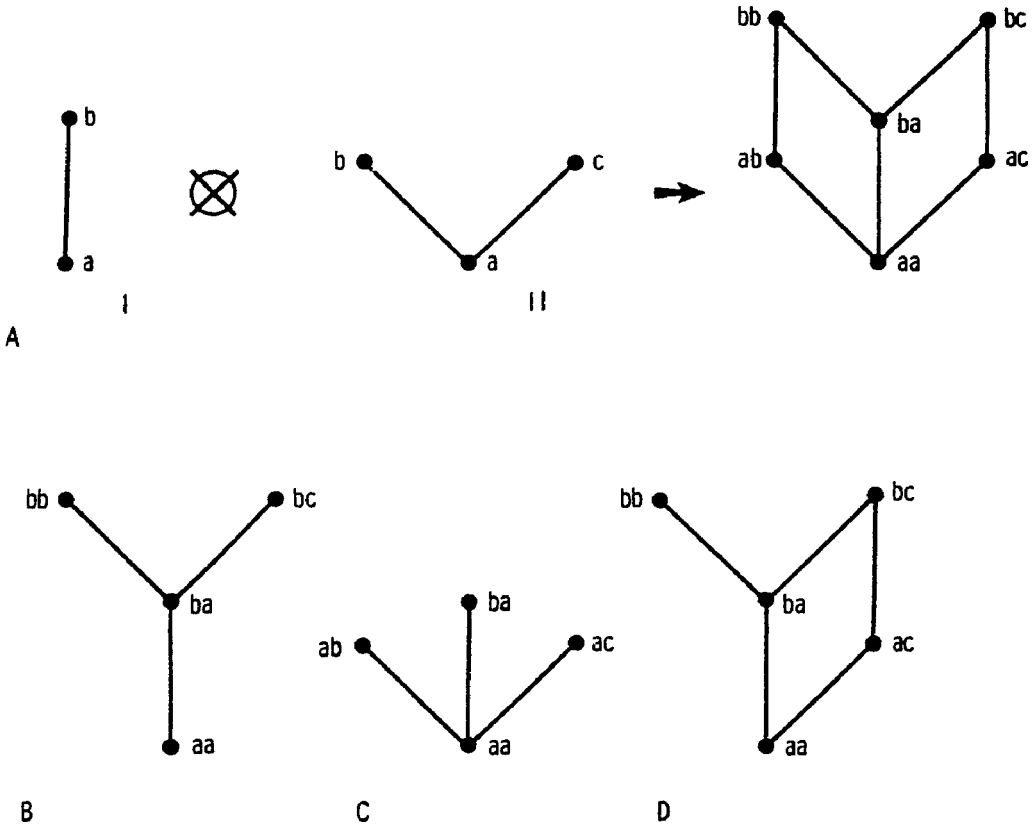


Fig. 5. Character compatibility. A. the cartesian product of two characters (I and II) whose character state trees are shown on the left is represented by the lattice on the right. If the nodes on this lattice which represent character state combinations not found in the study collection are discarded (along with unnecessary internodes) and the resulting diagram is a tree ((B) and (C)), the characters are compatible; if the resulting figure is not a tree (D), the characters are incompatible.

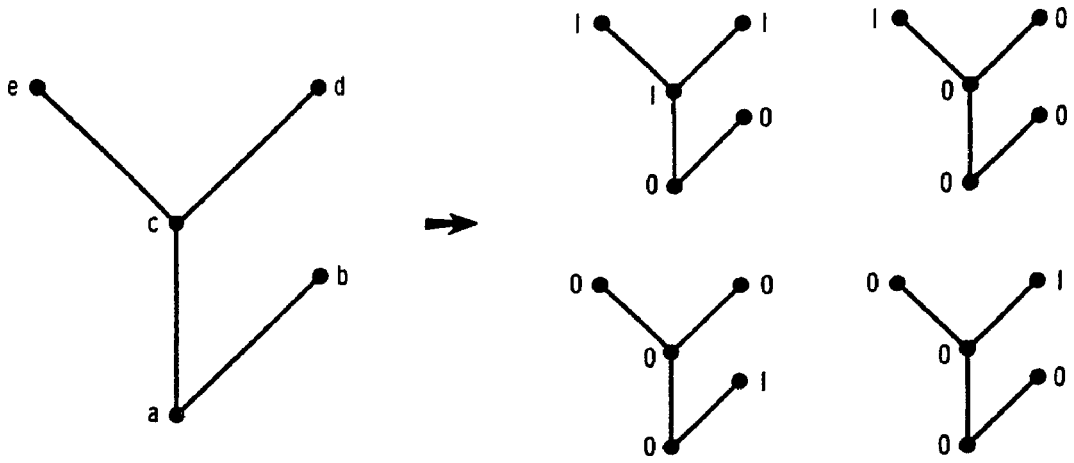


Fig. 6. Binary factors. The ordering among the N states on the character state tree on the left can be represented as N-1 binary characters. For each transition on the original character state tree the state 0 of the binary factor indicates that the transition has not taken place, and the state 1 indicates that the transition has taken place. The four figures on the right represent the binary factors of the character state tree on the left. Thus an EU with character state d would be coded (starting at the left top binary factor) as having binary states 1, 0, 0, 1, while an EU with character state e would be coded as having binary states 1, 1, 0, 0.

factors and testing these factors for compatibility also identifies which states of a character cause the incompatibilities. Information on exact trouble spots may be used in logical revision of character state trees.

The characters which define the basic, or primary, phyletic lines of the group under study are called primary characters for that group. In the early analyses of a large group the relationships on the primary phyletic lines usually are only partially resolved. To resolve the relationships of these lines further the analysis may be repeated on each line separately. Usually several additional characters are found to be compatible with the original primary characters. These additional characters are called secondary characters for the overall study or local primary characters for the line in which they are primary. This process may be repeated in smaller and smaller groups until all the local primary characters have been found. As the size of the group becomes smaller, however, the chance that characters will be included randomly in the largest cliques increases.

Sometimes more than one largest clique is found in a given analysis. Either all the largest cliques may be accepted as defining equally probable estimates of relationships, or their intersections (set of characters included in all the cliques) may be accepted as defining the best estimate of relationships, or a choice may be made among them. A choice among the cliques may be made only if a choice among the conflicting characters can be made. Characters in the clique which defined the monophyletic line are usually more reliable, since they have already passed a more rigorous test. Occasionally, only a clique smaller than the largest clique can pass this test. Characters which make more complex statements about relationships, either because of the shape of their character state trees or because of the distribution of their states over the EUs, may be chosen over characters which make simple statements about relationships because it is less probable that they are included in a largest clique by chance alone. A character whose biology is well known may be chosen over a character whose biology is poorly known if the biological knowledge supports the character state trees. In some cases the conflicting characters may be involved only in the branching patterns at the tips of some branches

and thus do not affect the major branching patterns of the overall tree. In those cases a decision on the value of a character may be postponed until the smaller monophyletic groups have been analyzed.

Some characters may be rejected in a compatibility analysis because they are homoplastic on a restricted part of the phylogenetic tree. If the instances of homoplasy for some characters have taken place early in the history of the group, these characters may be true cladistic characters for some of the branches of the phylogenetic tree. The technique of finding locally compatible characters in smaller and smaller monophyletic groups identifies such characters. If the instances of homoplasy, however, have occurred late in the history of the group, some characters may be rejected by all the compatibility analyses in which they are examined. In instances where the early branching patterns of the tree being reconstructed are poorly resolved, it may be of value to identify the latter type of characters and use them to increase the resolution of the tree.

The following procedure may be used for finding characters of the latter type in a study using compatibility analyses. After the smaller monophyletic groups have been identified and analyzed, the EUs in each group which are least derived are identified, or the character states of the most recent common ancestor of the group are estimated. A compatibility analysis using only the "more conservative" EUs, or the reconstructed ancestors, is then made to find additional characters compatible with the original clique. This procedure has the effect of removing instances of homoplasy which occur at the tips of the branches and objectively identifies additional characters for reconstructing the early branching pattern of the phylogenetic tree. Since they are based on characters with known homoplasy, the transitions defined in this manner are less certain than those identified in the original analysis of the group. While this method may be used to extract the maximum amount of information from a particular data set, it is inferior to the addition of new characters to the data set.

The characters found to be true in a study may always be tested against new characters. This is particularly important for analyzing small monophyletic groups in which only a few characters vary, since such analyses usually yield several largest cliques. Because it is

often impossible to decide among these cliques, it is best to increase the character set and perform a new analysis. Often many characters which could not be coded satisfactorily for the entire study collection can be introduced at this stage. Plumage characters in birds are an example.

CHARACTERS

Skull Characters

Character 1: position of the lacrimal-ectethmoid complex (Fig. 7, 8, 9). The lower end of the lacrimal-ectethmoid complex is usually far from the jugal bar. In Pluvianus and the Burhinidae, however, it abuts the jugal bar. In the snipes and woodcocks the end of the complex is joined by a thin ribbon of bone to the postorbital and zygomatic processes, a condition which is clearly derived. Based on the distribution of states within the Charadriiformes, the condition in which the complex is far from the jugal bar is probably the primitive state.

Coding: primitive: complex not abutting jugal bar nor connected with postorbital process (A) (Fig. 8, 9A, 9C); derived from primitive: complex abutting jugal bar (B) (Fig. 7, 9B); derived from primitive: complex connected with postorbital process (C) (not illustrated).

Character 2: fusion of lacrimal and ectethmoid (Fig. 7, 8, 9). In most Charadriiformes and Columbiformes the lacrimals and ectethmoids are touching and usually fused. In a few of the Charadriiformes and in most of the Gruidae the two structures are not in contanct, usually because the ectethmoids are reduced or absent. On the basis of the distribution of the states within the Charadriiformes, the fused or touching condition is probably the primitive state.

Coding: primitive: lacrimal and ectethmoid touching or fused (A) (Fig. 7, 8, 9A, 9C); derived: lacrimal and ectethmoid not in contact (B) (Fig. 9B).

Character 3: fusion of the ectethmoid and frontals (Fig. 7, 8, 9). The most widely distributed condition for this character in the Gruiformes, Charadriiformes, and Columbiformes is for there to be no connection or fusion between the ectethmoids and frontals; this is assumed to be the primitive state.

Coding: primitive: ectethmoid and frontal not in contact (B) (Fig. 7, 8, 9); derived: ectethmoid and frontal in contact and often fused (A) (not illustrated).

Character 4: angle between jugal bar and lateral nasal bar

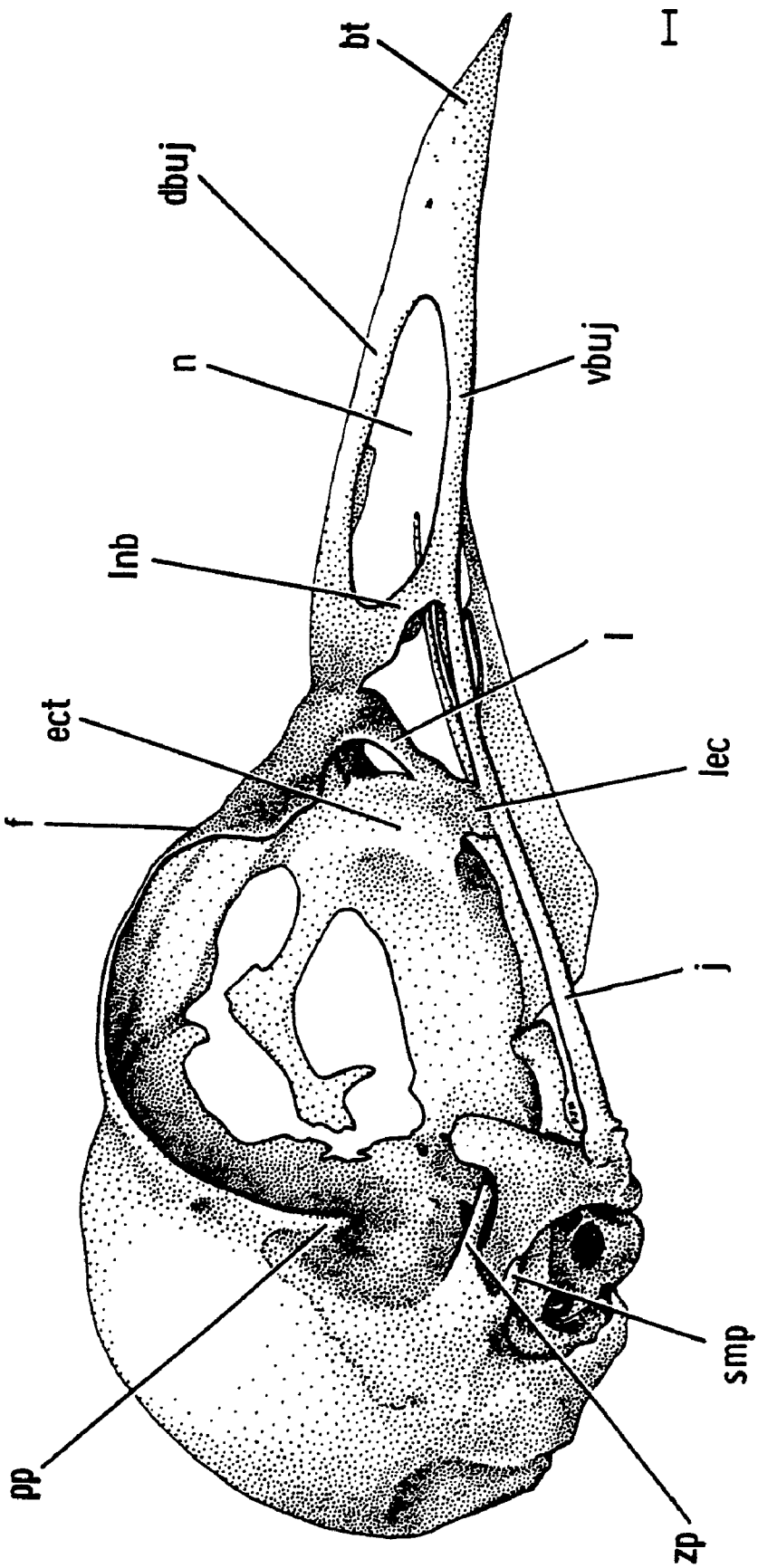


Fig. 7. Right lateral view of the skull of Pluvianus aegyptius (FMNH 93449). Abbreviations: bt, bill tip; dbuj, dorsal bar of the upper jaw; ect, ectethmoid; f, frontal; j, jugal bar; l, lacrimal; lec, lacrimal-ectethmoid complex; lnb, lateral nasal bar; n, nostril; pp, postorbital process; smp, suprameatic process; vbuj, ventral bar of the upper jaw; zp, zygomatic process. Scale represents 1 mm.

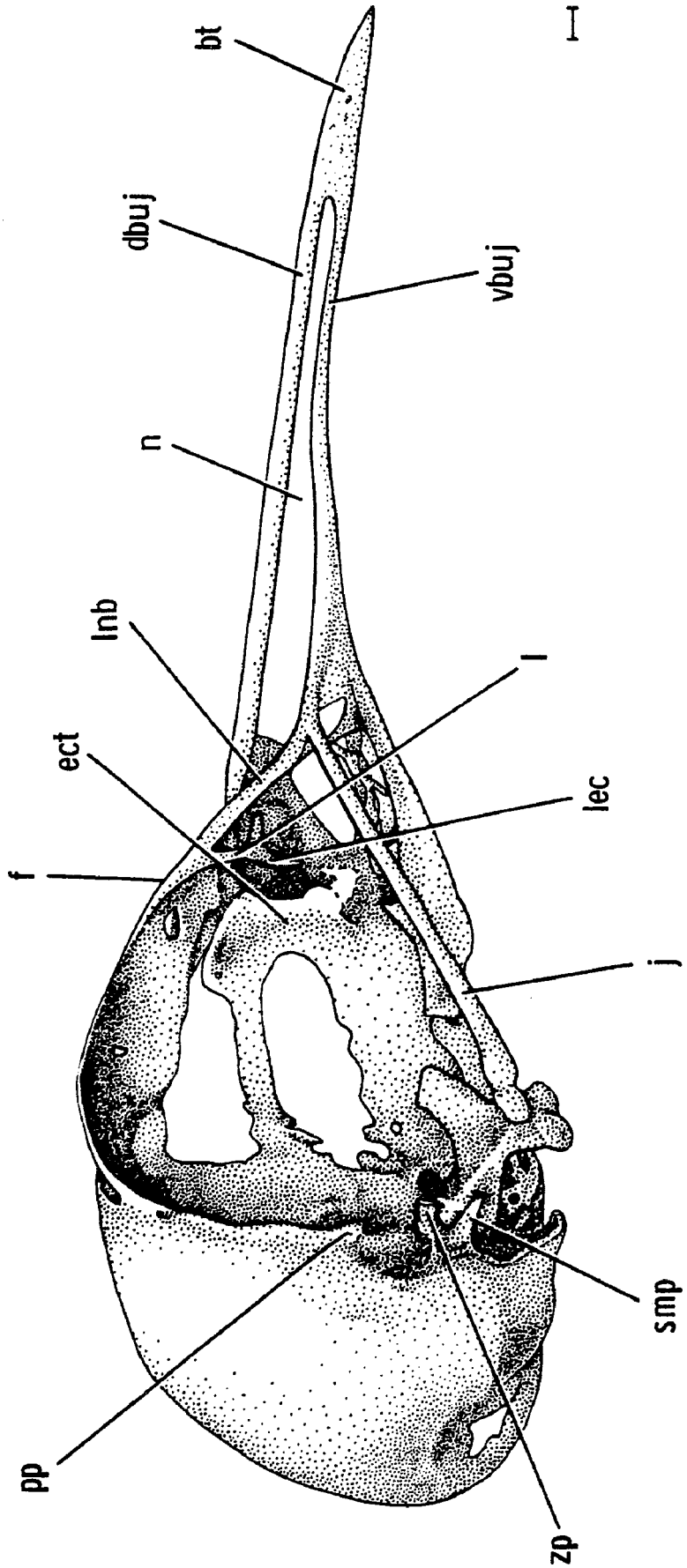


Fig. 8. Right lateral view of the skull of Thinornis novaeseelandiae (NZNM 1403). Abbreviations as in Fig. 7. Scale represents 1 mm.

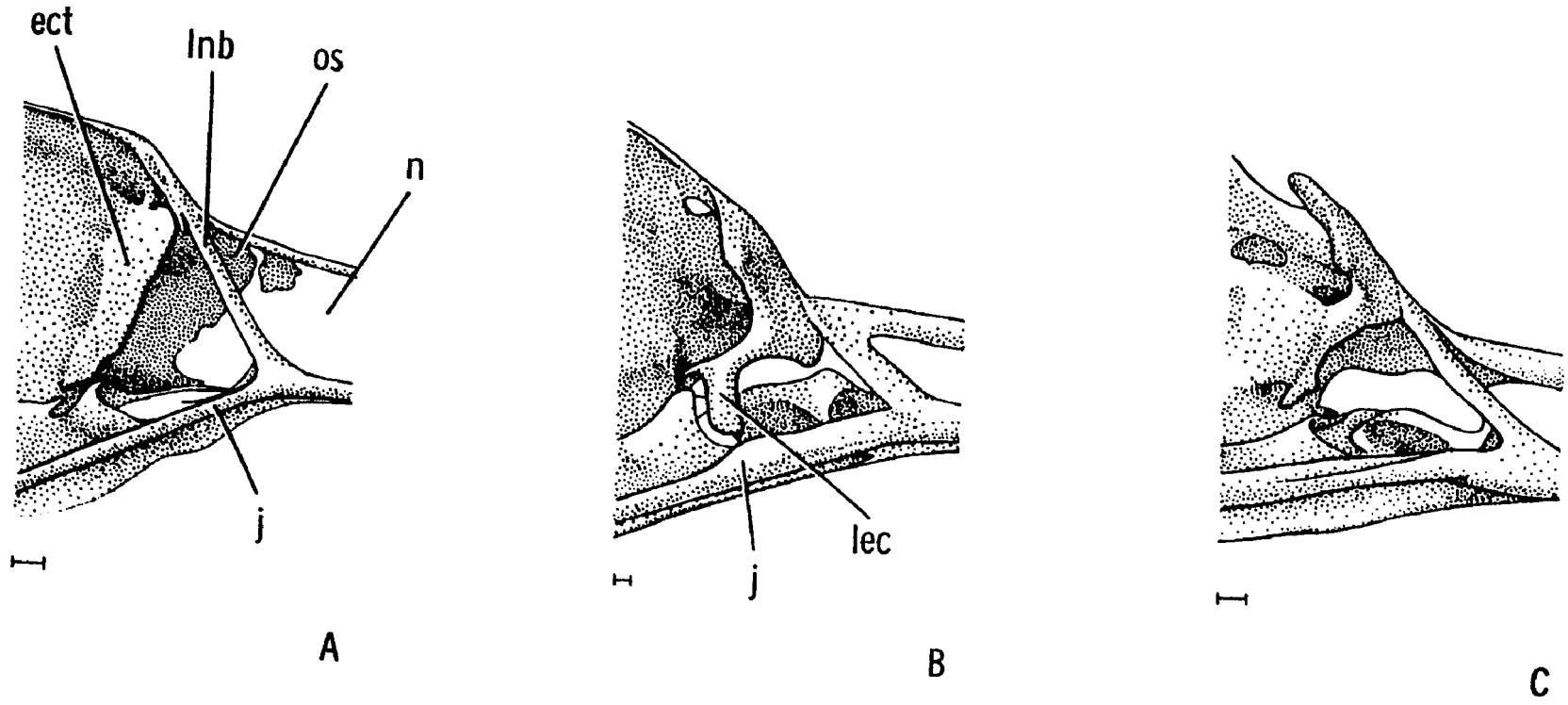


Fig. 9. Right lateral view of the skulls of three species. A. Attagis gayi (UMMZ 209968); B. Burhinus magnirostris (UMMZ 214183); C. Stercorarius pomarinus (UMMZ 153518). Abbreviations: ect, ectethmoid; j, jugal bar; lec, lacrimal-ectethmoid complex; lnb, lateral nasal bar; n, nostril; os, orbital septum. Scales represent 1 mm.

(Fig. 7, 8, 9, 15). Lowe (1915b) used several angles between elements of the skull to separate his subfamilies Eroliinae and Tringinae of the Scolopacidae. One of these, the angle between the jugal bar and lateral nasal bar, or the angle between the jugal bar and the ventral bar of the upper jaw, as Lowe defined it, was used in this study. Two states were recognized, one in which the lateral nasal bar is relatively long, forming an angle of about 60 degrees or less with the jugal bar, and one in which the lateral nasal bar is relatively short, forming an angle of about 70 degrees or more with the jugal bar. Only the first state was found in the Gruiformes and Columbiformes and is probably the primitive state.

Coding: primitive: angle between lateral nasal bar and jugal bar about 60 degrees or less (A) (Fig. 7, 9B, 9C, 15B, 15C); derived from primitive: angle between lateral nasal bar and jugal bar about 70 degrees or more (B) (Fig. 8, 15A, 15D); derived from primitive: like (B), found in Thinocoridae, assumed to be a result of the short, finch-like bill and possibly of independent origin (C) (Fig. 9A).

Character 5: length of the zygomatic process relative to that of the suprameatic process (Fig. 7). In most charadriiform birds the zygomatic process is longer than the suprameatic process; this condition is probably the primitive state. The condition in the snipes and woodcocks, in which this process is connected with the lacrimal-ectethmoid complex, is probably derived.

Coding: primitive: zygomatic process longer than suprameatic process (B) (Fig. 7); derived from primitive: zygomatic process shorter than suprameatic process (A) (not illustrated); derived from primitive: zygomatic process connected with lacrimal-ectethmoid complex (C) (not illustrated).

Character 6: anterior development of the orbital septum (Fig. 8, 9). In some Charadriiformes the orbital septum is poorly developed anterior to the region of the ectethmoid plate, while in others it extends far into the nostril and acts as a brace for the dorsal bar of the upper jaw. This condition in which the orbital septum extends anterior to the junction of the jugal bar and lateral nasal bar does not occur in the Gruiformes, Columbiformes, nor in most of the Charadriiformes and is thus probably a derived condition.

Coding: primitive: orbital septum not extending anterior to the junction of the jugal bar and lateral nasal bar (A) (Fig. 8, 9A, 9B, 9C); derived: orbital septum extending anterior to junction of jugal bar and lateral nasal bar (B) (not illustrated).

Character 7: nostril type (Fig. 7, 8, 9). It is probable from the distribution of nostril types among the Gruiformes, Charadriiformes, and Columbiformes that the schizorhinal nostril is the primitive condition for the Charadriiformes.

Coding: primitive: nostril schizorhinal (A) (Fig. 8, 9A, 9C); derived: nostrils holorhinal (B) (Fig. 7, 9B).

Character 8: form of the bill tip (Fig. 10). Lowe (1915b) used the morphology of the bill tip as a character to differentiate between his subfamilies Eroliinae and Tringinae of the Scolopacidae. I found his simple classification of two states inadequate to describe the diversity found throughout the Charadriiformes. In the Gruiformes, Columbiformes, and most of the Charadriiformes the dorsal and ventral bars of the upper jaw are separate for most of the length of the bill, fusing for only a short distance at the tip. This generalized state is taken to represent the primitive condition. At the beginning of this study the only derived state recognized was that in which the tip of the bill is relatively long, with the dorsal and ventral bars fused for about half the length of the bill. Within these two states there is still a considerable diversity of bill types. Later I recognized additional derived states for this character to describe better the diversity observed. I have assumed that all the derived types arose independently from the primitive state.

Coding: primitive: bill tip short, dorsal and ventral bars of upper jaw fused only near tip of bill (B) (Fig. 10B, 10E); derived from primitive: bill tip long, dorsal and ventral bars of upper jaw fused for about one-half length of bill (A) (Fig. 10C, 10F, 10H); derived from primitive: unique to Rostratula, generally like (A) but dorsal bar flattened with a distinctive ridge along top (C) (Fig. 10A); derived from primitive: short, stubby, finch-like tip, unique to Thinocoridae (D) (Fig. 10G); derived from primitive: generally like primitive states but tip a sharp, short cone, unique to Arenaria (E) (Fig. 10D); derived from primitive: like primitive state but

Fig. 10. Bill of eight species. A. Rostratula benghalensis (MVZ 120048); B. Larus philadelphia (UMMZ 153791); C. Gygis alba (UMMZ 210367); D. Arenaria interpres (UMMZ 216124); E. Actitis macularia (UMMZ 85037); F. Tringa glareola (UMMZ 219076); G. Attagis gayi (UMMZ 209968); H. Himantopus h. mexicanus (UMMZ 74110). Each scale division represents 1 mm.

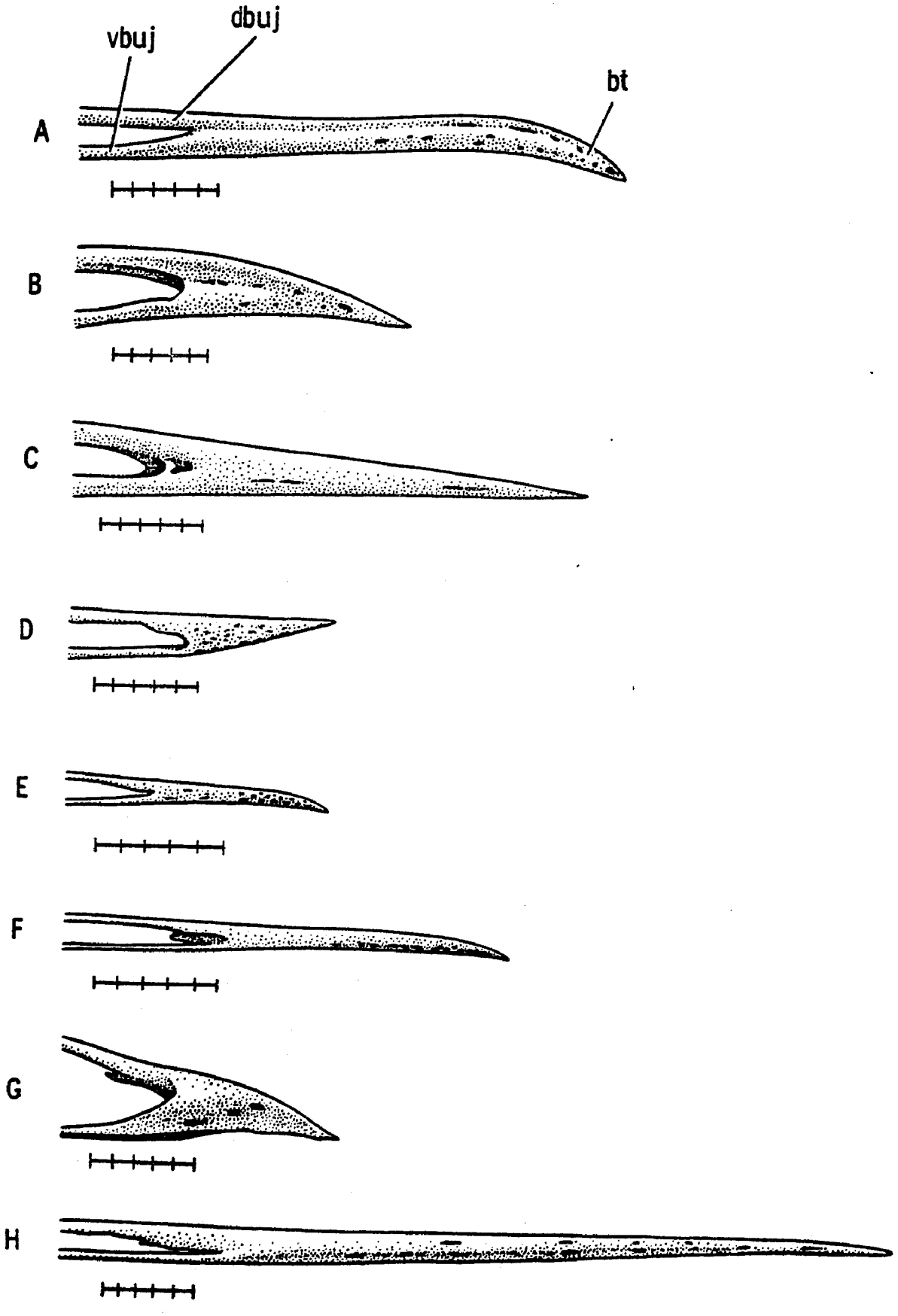


Fig. 10

with a distict flange of bone on both sides of dorsal bar of upper jaw covering the nostril for about one-half length of bill, meeting but not fused to ventral bar of upper jaw; found only in phalaropes (F) (not illustrated).

Character 9: shape of the cross-section of the dorsal bar of the upper jaw (Fig. 11). The dorsal bar of the upper jaw of most Charadriiformes (and of all Gruiformes and Columbiformes) is a simple, unreinforced bar; this condition is probably the primitive state. Several species, especially members of the Scolopacidae, have bars which are distinctly reinforced. This reinforcement is correlated with a forward shift in the zone of bending in the rhynchokinetic skull of charadriiform birds (Schumacher 1929; Burton 1974), allowing the birds to open just the tip of the bill. This reinforcement appears to have evolved several times, since several distinctive morphologies exist for it. The typical peep (Calidris sp.) shows a slight thickening in the middle of the dorsal bar which in many species is hardly distinguishable from the primitive condition. I have coded all the species of Calidris, as well as the snipes and woodcocks, as belonging to the primitive condition regardless of the extent of the reinforcement. In many sandpipers and the curlews the cross-section of the bar is distinctly oval (Fig. 11B), in the snipes it is more or less teardrop-shaped (Fig. 11C), and in the woodcocks it is shaped like a haystack (Fig. 11D). These conditions were coded as primitive because other coding I considered would necessitate making a priori judgments about relatedness among the Scolopacidae. The derived states recognized are as follows: cross-section distinctly T-shaped (Fig. 11E), unique to Limnodromus (An alternative hypothesis would be that this shape evolved from or gave rise to the teardrop shape found in snipe.); cross-section broad and flat with a narrow reinforcing rod down the center, shaped somewhat like a thumbtack (Fig. 11F), unique to Limicola (This condition may be related to the Limnodromus condition.); cross-section in the form of an inverted U (Fig. 11G), unique to Limosa. (Since completing this study I have found this condition present in some specimens of Xenus.)

Coding: primitive: cross-section of dorsal bar of upper jaw simple and unreinforced or, if reinforced, cross-section oval, teardrop- or haystack-shaped (A) (Fig. 11A, 11B, 11C, 11D); derived from

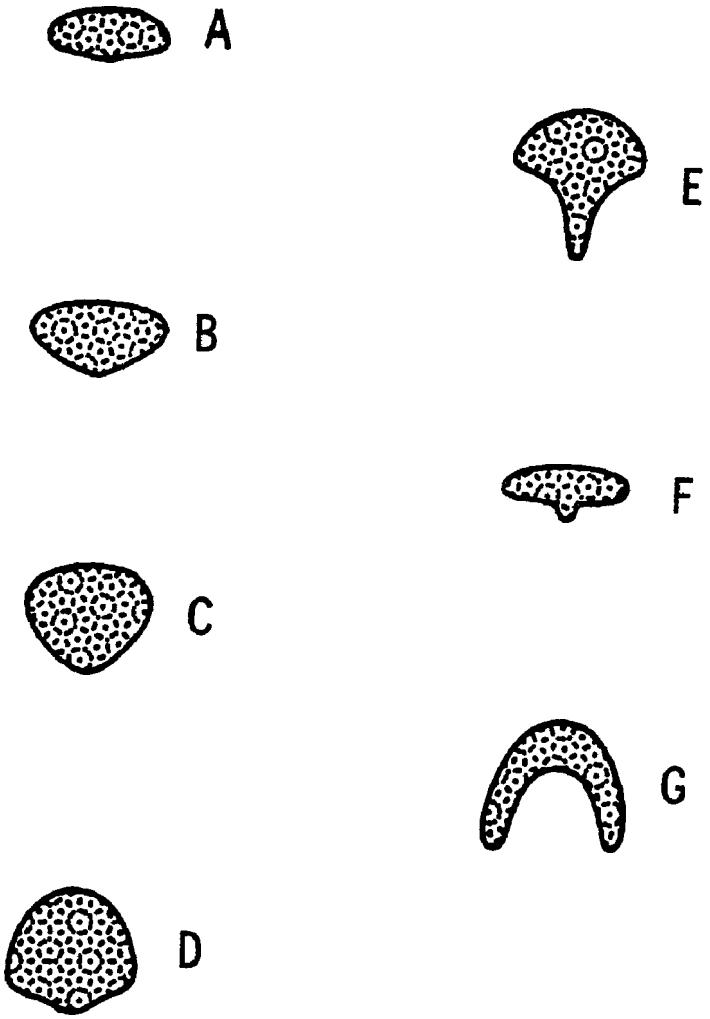


Fig. 11. Cross-sections of the dorsal bar of the upper jaw of representative charadriiform birds. A. and B. extremes of the condition found in most species (see text); C. Gallinago; D. Scolopax; E. Limnodromus; F. Limicola; G. Limosa.

primitive: cross-section T-shaped (B) (Fig. 11E); derived from primitive: cross-section like a thumbtack (C) (Fig. 11F); derived from primitive: cross-section like inverted U (D) (Fig. 11G).

Character 10: basipterygoid articulation of pterygoid and basipterygoid processes on basisphenoid rostrum (Fig. 12). A well-developed basipterygoid process on the basisphenoid rostrum and a corresponding process located on the posterior edge of the pterygoid are present in many birds. In this study such processes were found in the skulls of adult Turnicidae, Rostratulidae, Jacanidae, Scolopacidae, Charadriidae, Pteroclidae, and Columbidae; they were absent in the adult skulls of Podicipedidae, Gaviidae, Rallidae, Heliornithidae, Eurypygidae, Gruidae, Aramidae, Otididae, Thinocoridae, Chionididae, Glareolidae (except Peltohyas), Burhinidae, Dromadidae, Laroidea, and Alcae.

Jollie (1957) reports that many birds have basipterygoid processes early in development which are later enclosed by the parasphenoid. Such a process is illustrated in Uria by Parker (1890). Very young chicks of Chionis, Dromas, Rynchops, and some Laridae have such a process, though it is absent in the adults (Lowe 1916a, b; Maillard 1948; personal obs.).

It is not clear from the distribution of the states in the outgroups or within the Charadriiformes which state is primitive. I have chosen the absence of the process in the adult as primitive because that state appears in most of the families examined in this study.

Coding: primitive: processes absent (A) (not illustrated); derived: processes present in adult (B) (Fig. 12).

Character 11: medial condyle of quadrate (Fig. 12). Bock (1964) used the differences in the morphology of the three articular condyles of the quadrate as qualitative taxonomic characters to separate plovers and glareolids. In this study I use states of only the medial condyle. In the most widely distributed condition in the Charadriiformes there is a distinct groove on the anterolateral face of the condyle; this is probably the primitive state for the order. The groove is present in the Gruiformes but absent in the Columbiformes. While Bock found no groove in the Glareolidae, some specimens I have examined show a distinct dimple on the condyle. The position of the condyle in the Glareolidae, however, is very distinctive, with the condyle somewhat raised and

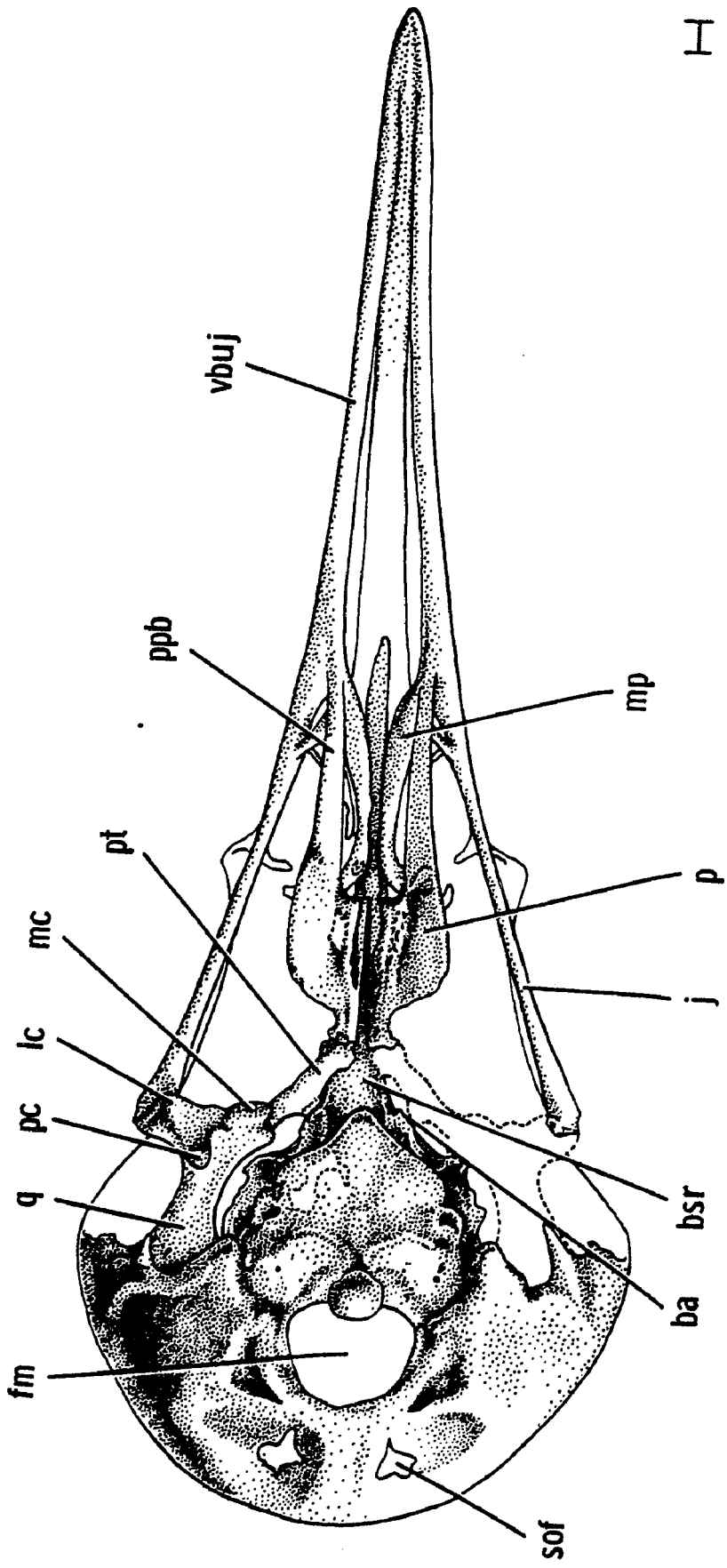


Fig. 12. Ventral view of the skull of Thinornis novaeseelandiae (NZNM 1403). Abbreviations: ba, basipterygoid articulation; bsr, basisphenoid rostrum; fm, foramen magnum; j, jugal bar; lc, lateral condyle of quadrate; mc, medial condyle of quadrate; mp, maxillopalatine; p, palatine; pc, posterior condyle of quadrate; ppb, prepalatine bar; pt, pterygoid; q, quadrate; sof, supraoccipital foramen; vbuj, ventral bar of upper jaw. Scale represents 1 mm.

twisted so that it faces outward.

Coding: primitive: distinct groove on anterolateral face of medial condyle of quadrate (A) (Fig. 12); derived from primitive: no groove on anterolateral face of medial condyle of quadrate (B) (not illustrated); derived from primitive: medial condyle of quadrate raised and twisted so that it faces outward; little or no grooving on anterolateral face (C) (not illustrated).

Character 12: degree of fusion of the maxillopalatine-palatine complex (Fig. 12, 13, 14). The degree of fusion of the maxillopalatines and the palatines varies considerably among the species in the three orders examined. The most widespread and thus most likely primitive condition within the Charadriiformes is for the maxillopalatines to be delicate structures having little or no fusion with the palatines. I have recognized two derived states which appear to have developed sequentially from the primitive state, a state in which there is considerable but not complete fusion between the maxillopalatines and palatines and a state in which the two structures are completely fused, often with complete loss of an identifiable maxillopalatine.

Coding: primitive: maxillopalatines and palatines with little or no fusion (A) (Fig. 12, 13A, 13C, 14A); derived from primitive: maxillopalatines and palatines considerably but not completely fused (B) (Fig. 14B, 14C, 14D); derived from (B): two structures completely fused (C) (Fig. 13B, 13D).

Character 13: configuration of the junction of the jugal bar, prepalatine bar, and ventral bar of the upper jaw (Fig. 12, 13, 14). A groove on the ventral surface of the ventral bar of the upper jaw extends anteriorly from the area where the jugal bar, prepalatine bar, and ventral bar of the upper jaw meet in all Charadriiformes except Numenius, Bartramia, and Prosobonia. In the latter three a flat sheet of bone extends across this region. This sheet of bone is considerably reduced in Prosobonia.

Coding: primitive: no sheet of bone over area where jugal bar, prepalatine bar, and ventral bar of upper jaw meet (A) (Fig. 12, 13A, 13B, 13C, 13D, 14D); derived: a sheet of bone over this area (B) (Fig. 14A, 14B, 14C).

Characters 14, 15, 16, 17: maxillopalatine struts (Fig. 15).

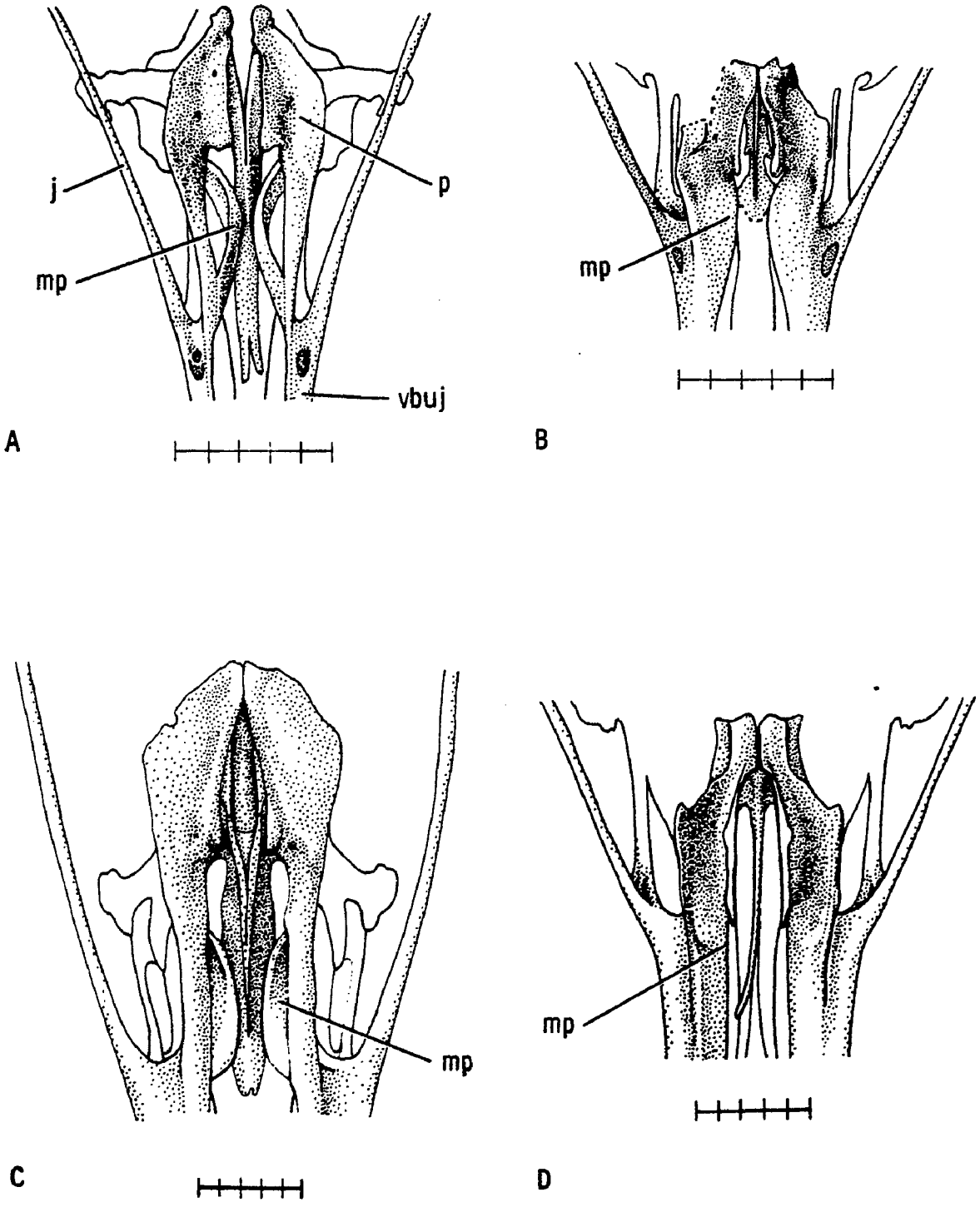


Fig. 13. Ventral view of the palates of four species. A. Nycticryphes semicollaris (UMMZ 157022); B. Coenocorypha aucklandii (NZNM 1406); C. Cephus grylle (UMMZ 151022); D. Scolopax rusticola (UMMZ 156165). Abbreviations as in Fig. 12. Each scale unit represents 1 mm.

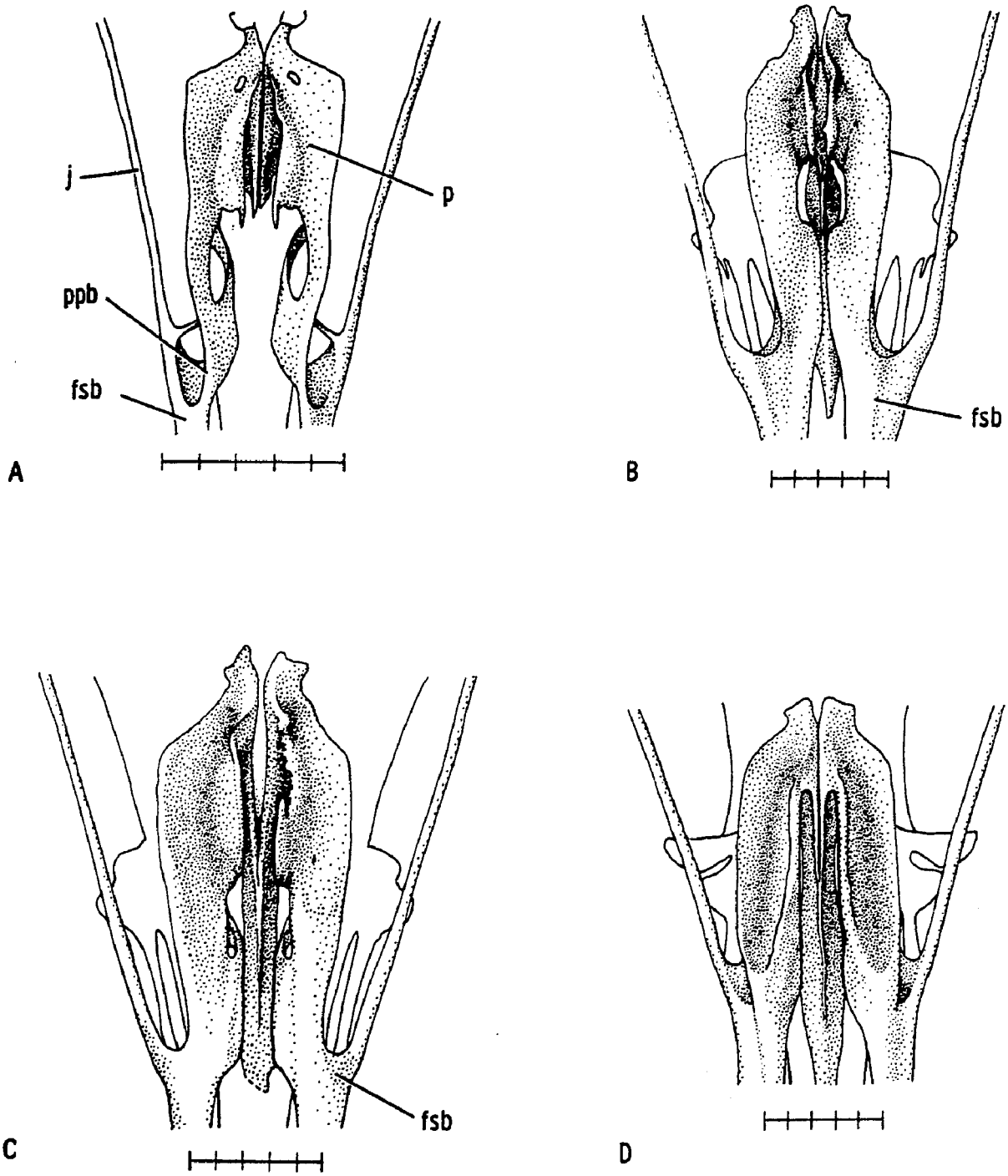


Fig. 14. Ventral view of the palates of four species. A. Prosobonia cancellatus (AMNH 6592); B. Bartramia longicauda (UMMZ 151204); C. Numenius minutus (USNM 347648); D. Limosa haemastica (UMMZ 154491). Abbreviations: fsb, flat sheet of bone; j, jugal bar; p, palatine; ppb, prepalatine bar. Each scale unit represents 1 mm.

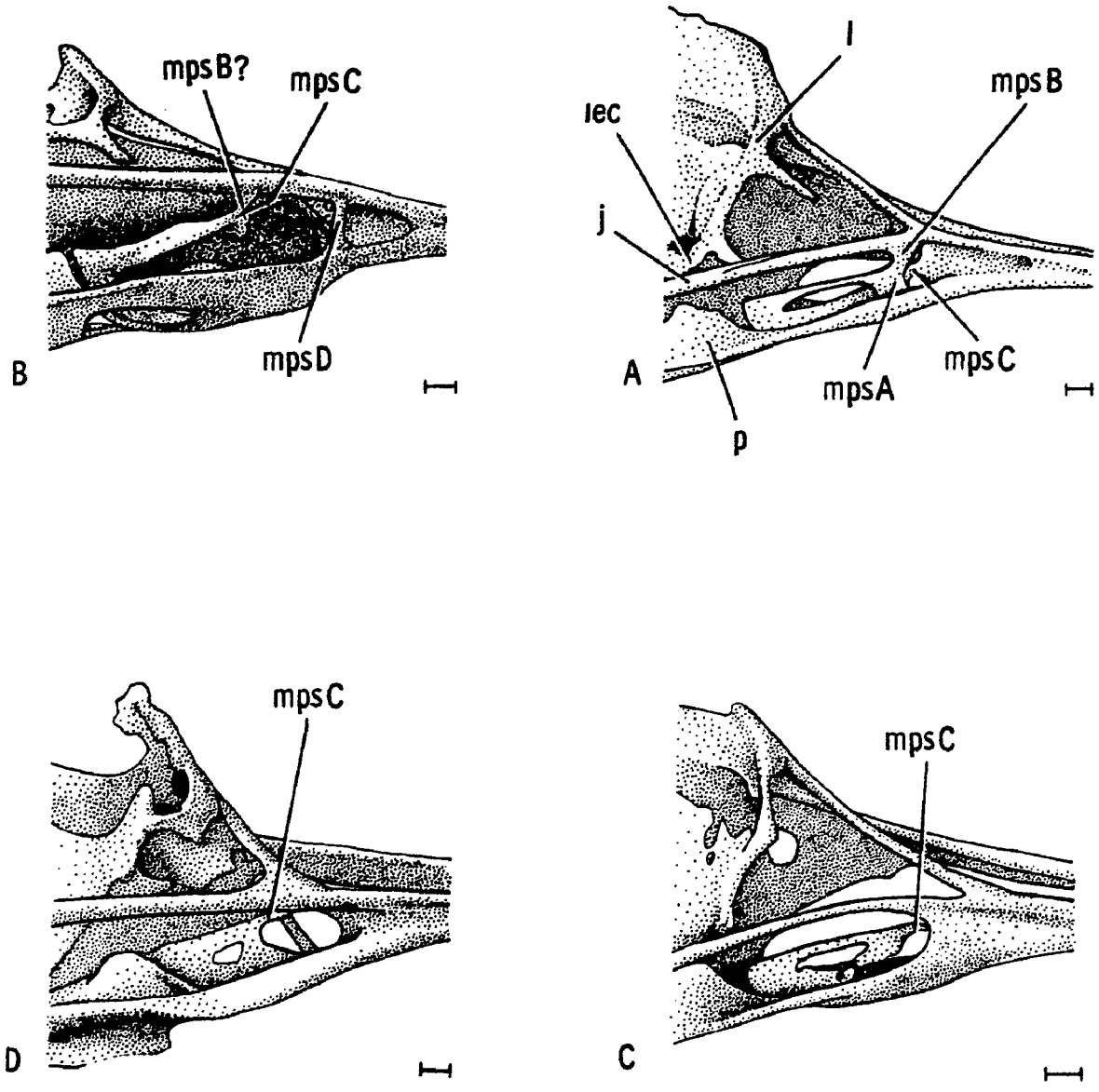


Fig. 15. Ventrolateral view of the skulls of four species. A. Charadrius montanus (UMMZ 220120); B. Heteroscelus incanus (UMMZ 151698); C. Numenius minutus (USNM 347648); D. Aphriza virgata (UMMZ 215473). Abbreviations: j, jugal bar; l, lacrimal; lec, lacrimal-ectethmoid complex; mpsA, maxillopalatine strut A; mpsB, maxillopalatine strut B; mpsC, maxillopalatine strut C; mpsD, maxillopalatine strut D; p, palatine. Scales represent 1 mm.

The complex architecture of the maxillopalatine in the Charadriiformes is characterized by the presence or absence of at least four different bony struts. Lowe (1931b) and Zusi and Jehl (1970), whose designations A, B, C, and D are followed here, used these struts as qualitative taxonomic characters to separate the Scolopacidae and Charadriidae but did not speculate on which conditions might be primitive or derived. In many but not all of the Gruiformes and Columbiformes the maxillopalatine is hollow and egg-shaped; it is similar in some Glareolidae and Laridae but is usually perforated in several places. The primitive condition in the Charadriiformes is thus probably that of an almost entire maxillopalatine with the degree of ossification decreasing during evolution of the group. The presence of struts A and C is therefore primitive, representing the remnants of a more complete ossification of the maxillopalatine.

Some specimens of Charadrius cucullatus and those of species of the Haematopodidae, Ibidorhynchidae, and Recurvirostridae appear to lack strut A. Other specimens, however, have a distinct raised arch of bone on the lateral-facing medial wall of the maxillopalatine. This arch probably represents strut A in those species where the maxillopalatines have become compressed during development such that the lateral and medial surfaces of the maxillopalatines have fused.

Strut B, which connects the maxillopalatine with the jugal bar, is present in the Gruiformes and Columbiformes; on the basis of this distribution, the presence of strut B is probably the primitive condition. As noted by Zusi and Jehl (op. cit.), some specimens of Tringa have a strut similar to B while other specimens of the same species lack it. It is impossible to determine from adult skulls whether B and C are both present in Tringa but lie so close together that they sometimes fuse and cannot be distinguished, or whether B is absent in Tringa and C sometimes sends a branch out to the jugal bar. All species of Tringa were coded as having strut B. While it is unclear whether strut D, which is unique to the Tringinae, is actually a maxillopalatine structure, its presence, however, is clearly a derived condition.

Coding: Character 14 (strut A): primitive: present, either as a distinct strut or as an ossified ridge on lateral surface of maxillopalatine (B) (Fig. 15A); derived: absent (A) (Fig. 15B,

15C, 15D);

Character 15 (strut B): primitive: present (B) (Fig. 15A, 15B); derived: absent (A) (15C, 15D);

Character 16 (strut C): primitive: present (B) (Fig. 15A, 15B, 15C, 15D); derived: absent (A) (not illustrated);

Character 17 (strut D): primitive: absent (A) (Fig. 15A, 15C, 15D); derived: present (B) (Fig. 15B).

Character 18: supraoccipital foramina (Fig. 12, 16). A pair of supraoccipital foramina just posterior to the foramen magnum is present in some birds. In this study the condition was found in the Gruidae, Rostratulidae, Scolopacidae, Charadriidae, Glareolidae, and Alcae, though not necessarily in every species. On the basis of the distribution of the states within the Charadriiformes, absence of such foramina is probably the primitive condition.

Coding: primitive: supraoccipital foramina absent (A) (not illustrated); derived: a pair of supraoccipital foramina present (B) (Fig. 12, 16).

Character 19: shape of the foramen magnum (Fig. 12, 16). The shape of the foramen magnum for most of the Charadriiformes is essentially the same. In some species of Scolopacidae, however, it is distinctly heart-shaped.

Coding: primitive: foramen magnum not distinctly heart-shaped (A) (Fig. 12, 16B); derived: foramen magnum distinctly heart-shaped (B) (Fig. 16A).

Character 20: position of the nasal glands (Fig. 17). All birds possess distinctive head glands known as nasal glands (Shoemaker 1972). In marine birds particularly these glands have been demonstrated to excrete salt (Schmidt-Nielsen 1960) and thus are often called salt glands. Staaland (1967) has shown a strong correlation among ecology, nasal gland anatomy, and function for several species of charadriiform birds. In these birds the glands usually lie in supraorbital grooves in the skull; in some species with well-developed glands these grooves are so large that the supraorbital rims are absent. Lowe (1922) used the extent of ossification of the supraorbital rims of plover skulls as a generic character. Bock (1958) showed that the correlation between skull ossification and plumage color which Lowe used is better explained

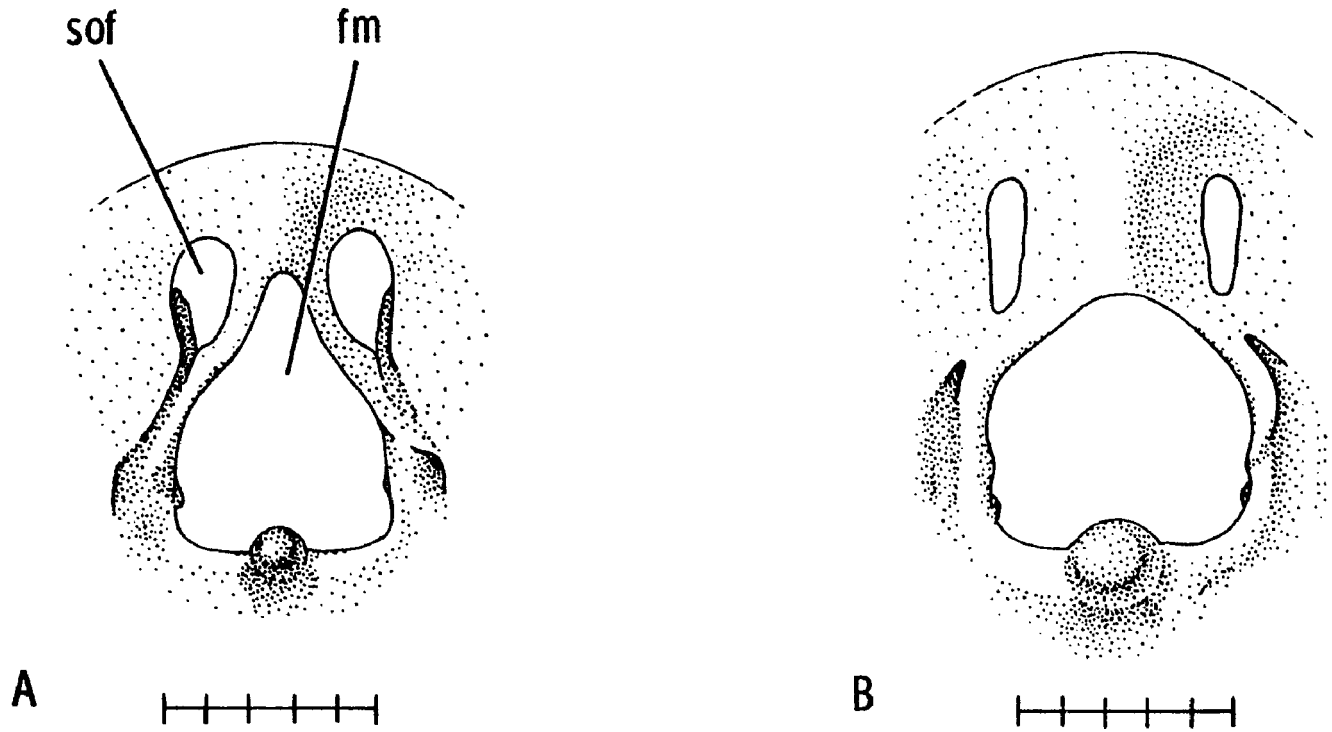


Fig. 16. Occipital region of the skulls of two species. A. Calidris melanotos (UMMZ 70485); B. Arenaria interpres (UMMZ 216124). Abbreviations: fm, foramen magnum; sof, supraoccipital foramen. Each scale unit represents 1 mm.

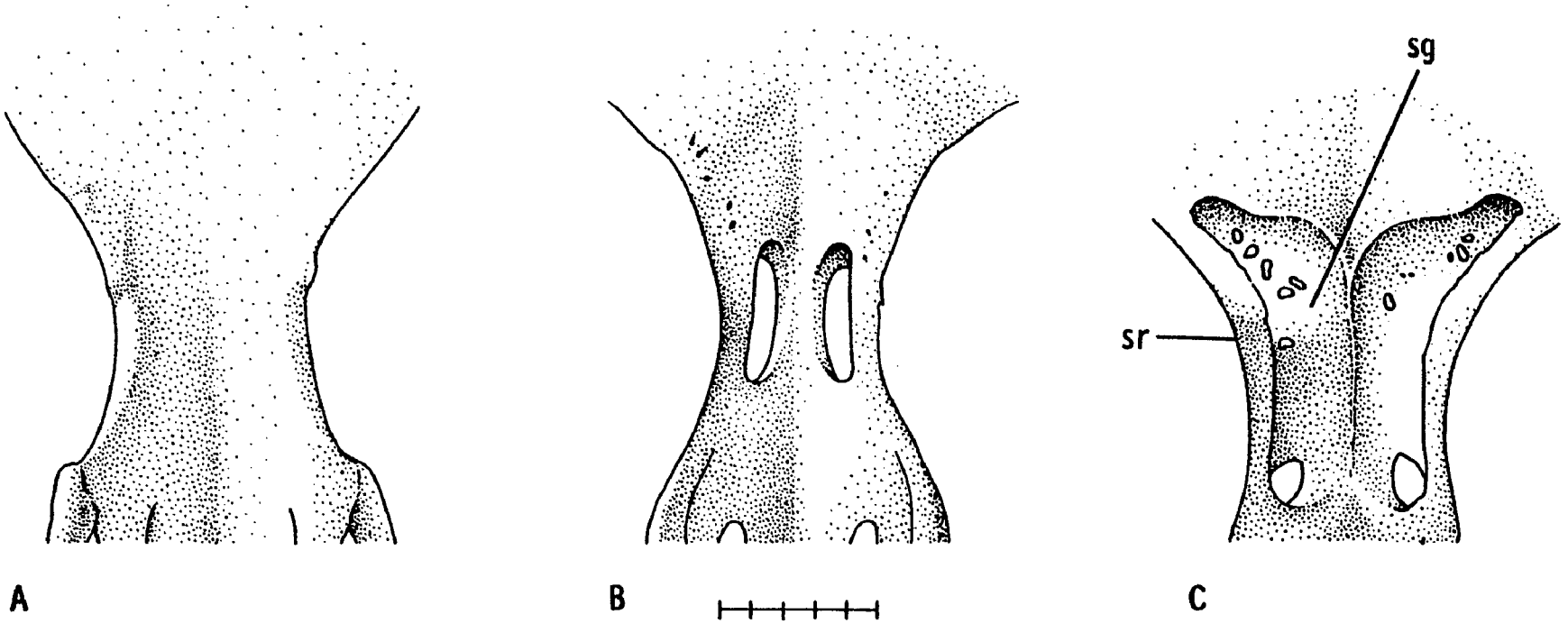


Fig. 17. Dorsal view of the frontal region of the skulls of three species. A. Ibidorhyncha struthersii (USNM 292767); B. Cursorius cursor (UM 2964); C. Thinornis novaeseelandiae (NZNM 1403). Abbreviations: sg, supraorbital groove; sr, supraorbital rim. Each scale unit represents 1 mm.

as adaptations to similar environments rather than as indicators of phylogenetic relationship. Yudin (1965) believed that "well-developed nasal glands are a primordial feature of the family Charadriidae, which to some extent are reduced independently and at different times in the various members of this group under the influence of changes in mode of life...all Charadriidae with weakly developed nasal glands are specialized forms." Apparently, Yudin, like Lowe, equated phylogenetic development of the glands with the relative size of the glands found in the supraorbital position, since he was uncertain about the significance of the apparent interorbital position of the gland in Pluvianus.

Studying the ontogeny of the gland might be a better method of elucidating phylogenetic relationship. This has been described for a few birds by Marples (1932) and Technau (1936). Technau classified birds on the basis of the location of the nasal gland; his schematic representation (Technau op. cit., Fig. 23) could be taken as a possible evolutionary series. The positions described by Technau are preorbital, preorbital-interorbital, interorbital, interorbital-exorbital, exorbital, exorbital-supraorbital, and supraorbital. Correct identification of these states, however, requires fresh or well-preserved intact specimens, which were unavailable for most of the species I studied. I was able to distinguish at least three different states from skulls: supraorbital, in which a distinct groove is present; exorbital, in which the supraorbital rim is missing even though there is no supraorbital groove (This state was verified in a preserved specimen of Jacana, in which a small nasal gland is present, replacing the supraorbital rim.); and neither of the above, in which case the gland was assumed to be either inter- or preorbital. There is no indication of the position of the nasal gland on the skull of Scolopax, nor could I locate a gland in three poorly-preserved heads of Philohela minor. Technau lists S. rusticola as having a preorbital gland. The three skulls of Pluvianus I examined show a small, shallow, supraorbital nasal gland groove. The distribution of the states of the gland among the Gruiformes and Columbiformes was not helpful in determining the primitive state of this character; the distribution of states among the Charadriiformes indicates that the primitive condition is supraorbital.

Coding: primitive: supraorbital nasal gland (C) (Fig. 17C);

derived from primitive: exorbital nasal gland (B) (not illustrated); derived from (B): nasal gland neither supraorbital nor exorbital (A) (Fig. 17A); derived from primitive: like primitive state but groove for gland has become a foramen in top of skull; found only in some species of Cursorius (D) (Fig. 17B).

Mandible Characters

Character 21: prearticular process of mandible (Fig. 18). The prearticular process of the mandible in Charadriiformes is variable. In the most widely distributed and probably primitive state there is a flange on the upper side of the distal end of the process. In the snipes and woodcocks the process is expanded and hollowed, and the flange is absent; in the Glareolidae the flange is absent; and in the Charadriidae the flange extends to and is usually fused with the supraangular except for Anarhynchus frontalis, in which the flange is absent.

Coding: primitive: flange on prearticular process but not fused to supraangular (A) (Fig. 18A, 18B, 18D); derived from primitive: flange on prearticular process fused to supraangular (B) (Fig. 18F); derived from (B): no flange on prearticular process; unique to A. frontalis (D) (not illustrated); derived from primitive: no flange on prearticular process (C) (Fig. 18E); derived from primitive: prearticular process expanded and hollow, no flange (E) (Fig. 18C).

Character 22: posterior process of mandible (Fig. 18). At the attachment of aponeurosis XI of M. pseudotemporalis superficialis pt. 1 to the mandible is located the posterior process of the mandible (point R of Bams 1956). In most charadriiform birds the process arises on the prearticular; this is assumed to be the primitive state. In some of the Scolopacidae the process is found on the supraangular, but there is a corresponding bump on the prearticular. In the snipes and woodcocks the position of the process is shifted posteriad on the mandible.

Coding: primitive: posterior process on prearticular in normal position (A) (Fig. 18A, 18B, 18E, 18F); derived from primitive: process normal with corresponding bump on supraangular (B) (Fig. 18D); derived from primitive: process shifted posteriad on mandible (C) (Fig. 18C).

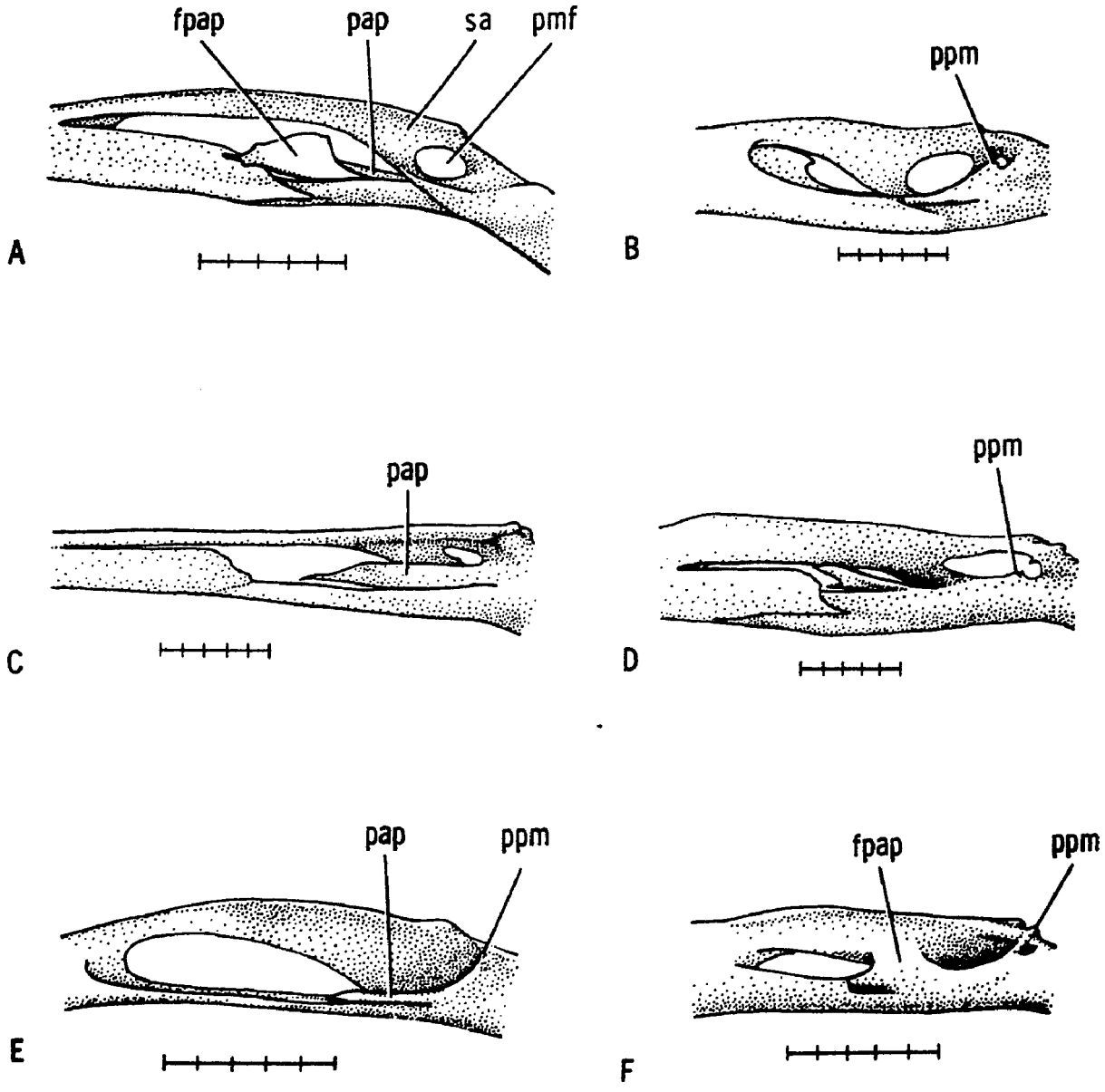


Fig. 18. Medial view of the mandibles of six species. A. Nycticryphes semicollaris (UMMZ 157021); B. Metopidius indicus (UMMZ 214551); C. Coenocorypha aucklandii (NZNM 1406); D. Catoptrophorus semipalmatus (UMMZ 156426); E. Pluvianellus socialis (SDSNH 37901); F. Thinornis novaeseelandiae (NZNM 1403). Abbreviations: fpap, flange of prearticular process; pap, prearticular process; pmf, posterior mandibular fossa; ppm, posterior process of mandible; sa, supraangular. Each scale unit represents 1 mm.

Character 23: posterior mandibular fossa (Fig. 19). Most of the Gruiformes and Charadriiformes examined have a posterior fossa in the mandible; it is absent in the Columbiformes.

Coding: primitive: posterior mandibular fossa present (A) (Fig. 19A); derived: posterior mandibular fossa absent (B) (Fig. 19B, 19C).

Head and Neck Muscle Characters

Characters 24, 25, 26, 27, 28, 29, and 30 (not illustrated). These characters are based on tabulations of the positions of attachment on the neck vertebrae of three neck muscles which insert on the cranium, as published by Burton (1971, 1972a, 1974). Since I had no information on the states found in the Alcae and information on only four species of the Laridae (Zusi 1962), the alcids examined were coded as if they had the primitive state for these characters, and the characters were ignored in the analysis of the Laroidea. I also had to estimate the states for some species for which I had skeletons but which Burton (1974) did not examine. The state of a presumed closest relative was used. Usually all the species in a genus had the same state.

Coding: Character 24: presence of an origin of M. complexus on vertebra 3: primitive: present (A); derived: absent (B);

Character 25: presence of an origin of M. complexus on vertebra 4: primitive: present (A); derived: absent (B);

Character 26: presence of an origin of M. complexus on vertebra 5: primitive: present (A); derived: absent (B);

Character 27: presence of an origin of M. complexus on vertebra 6: primitive: present (A); derived: absent (B);

Character 28: presence of an origin of M. complexus on vertebra 7: primitive: present (A); derived: absent (B);

Character 29: sites of origin of M. splenius capitis: primitive: origin only on vertebra 2 (A); derived: origin on vertebrae 2 and 3 (B);

Character 30: sites of origin of M. rectus capitis: primitive: origins of M. rectus capitis on vertebrae 1-5 (A); derived from primitive: origins on vertebrae 1-4 only (B); derived from primitive: origins on vertebrae 1-3 only (C).

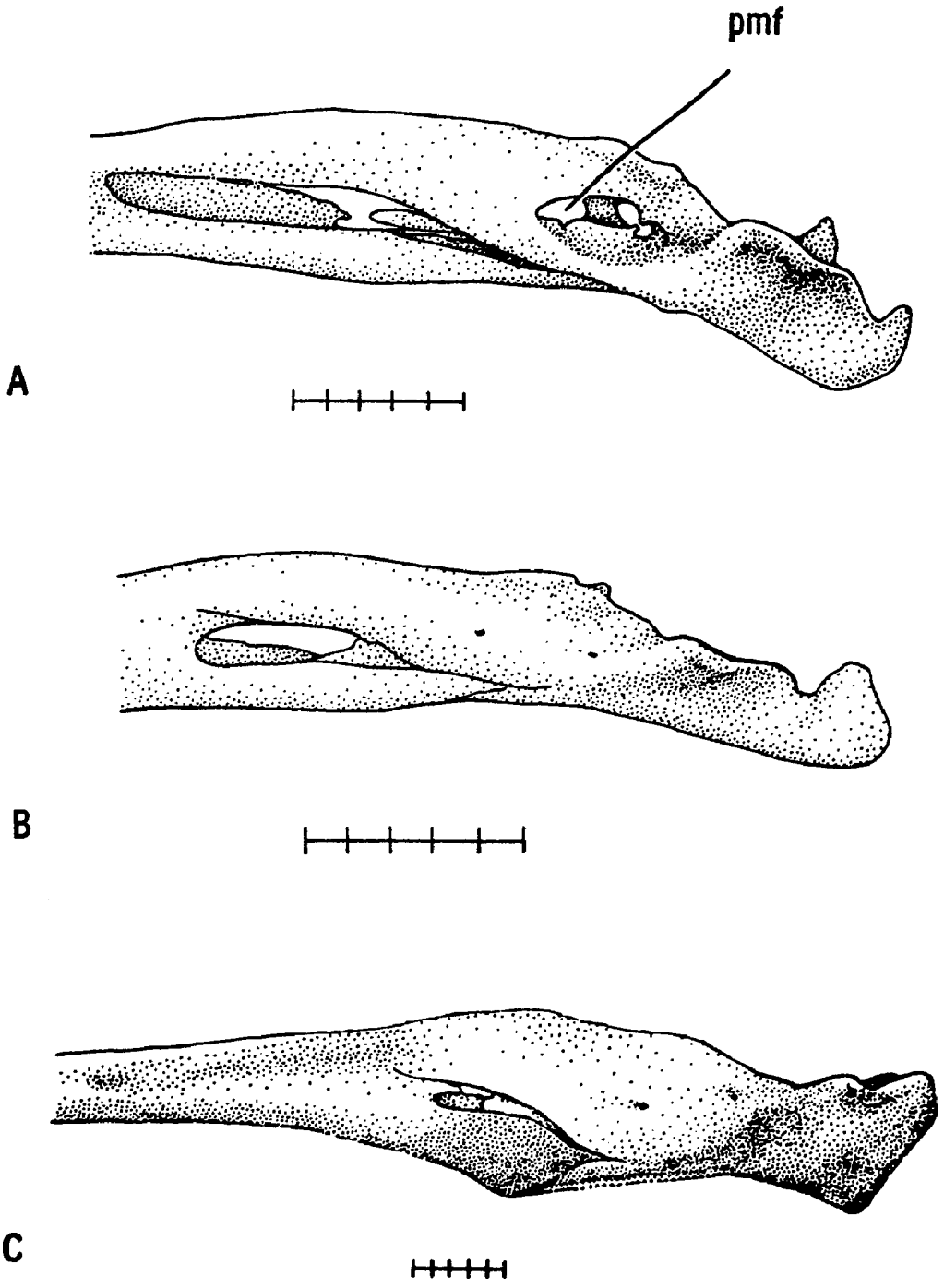


Fig. 19. Lateral view of the mandibles of three species. A. Aphriza virgata (UMMZ 219 182); B. Thinornis novaeseelandiae (NZNM 1403); C. Stercorarius pomarinus (UMMZ 153518). Abbreviations: pmf, posterior mandibular fossa. Each scale unit represents 1 mm.

Axial Skeleton Characters

Character 31: number of caudal vertebrae, omitting the pygostyle (not illustrated). The number of caudal vertebrae in the Charadriiformes varies from five to nine. The most widely distributed state in the order is eight; this is probably the primitive state. It is assumed that the evolution of this character has proceeded with a loss or gain of only one vertebra at a time. All Jacanidae have five vertebrae except Hydrophasianus chirurgus, which has six. The sixth caudal vertebra in chirurgus is assumed to be derived, along with the greatly elongated tail of the species, from the normal five of the Jacanidae.

Coding: primitive: eight caudal vertebrae (B); derived in single steps of vertebrae, increasing or decreasing from eight: 9 (C), 7 (A), 6 (D), 5 (E), and 6 in Jacanidae (G).

Character 32: number of neck vertebrae, omitting those with unfused cervical ribs (not illustrated). The most common and probably primitive state in Charadriiformes is 13 neck vertebrae.

Coding: primitive: 13 neck vertebrae (A); derived from primitive: 12 neck vertebrae (B); derived from primitive: 14 neck vertebrae (C).

Character 33: cervical vertebral strut (Fig. 20). The presence of a distinctive strut on the cervical vertebrae of vanelline plovers was first described by Zusi and Jehl (1970). A similar strut is on the cervical vertebrae of the Burhinidae and on a few vertebrae of one of three skeletons of Pluvianus which I examined. No such strut is found in the Gruiformes or Columbiformes; its presence in the Charadriiformes is probably a derived state. I originally coded the presence of a strut as the same state for the lapwings and the thickknees, 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.

Coding: primitive: no cervical vertebral strut (A) (not illustrated); derived from primitive: cervical vertebral strut in Vanellinae (B) (Fig. 20A); derived from primitive: cervical vertebral strut in Burhinidae (C) (Fig. 20B).

Character 34: type of dorsal vertebrae (not illustrated). Two types of dorsal vertebrae are found in the Charadriiformes, heterocoelous (articular surfaces saddle-shaped) and opisthocoelous

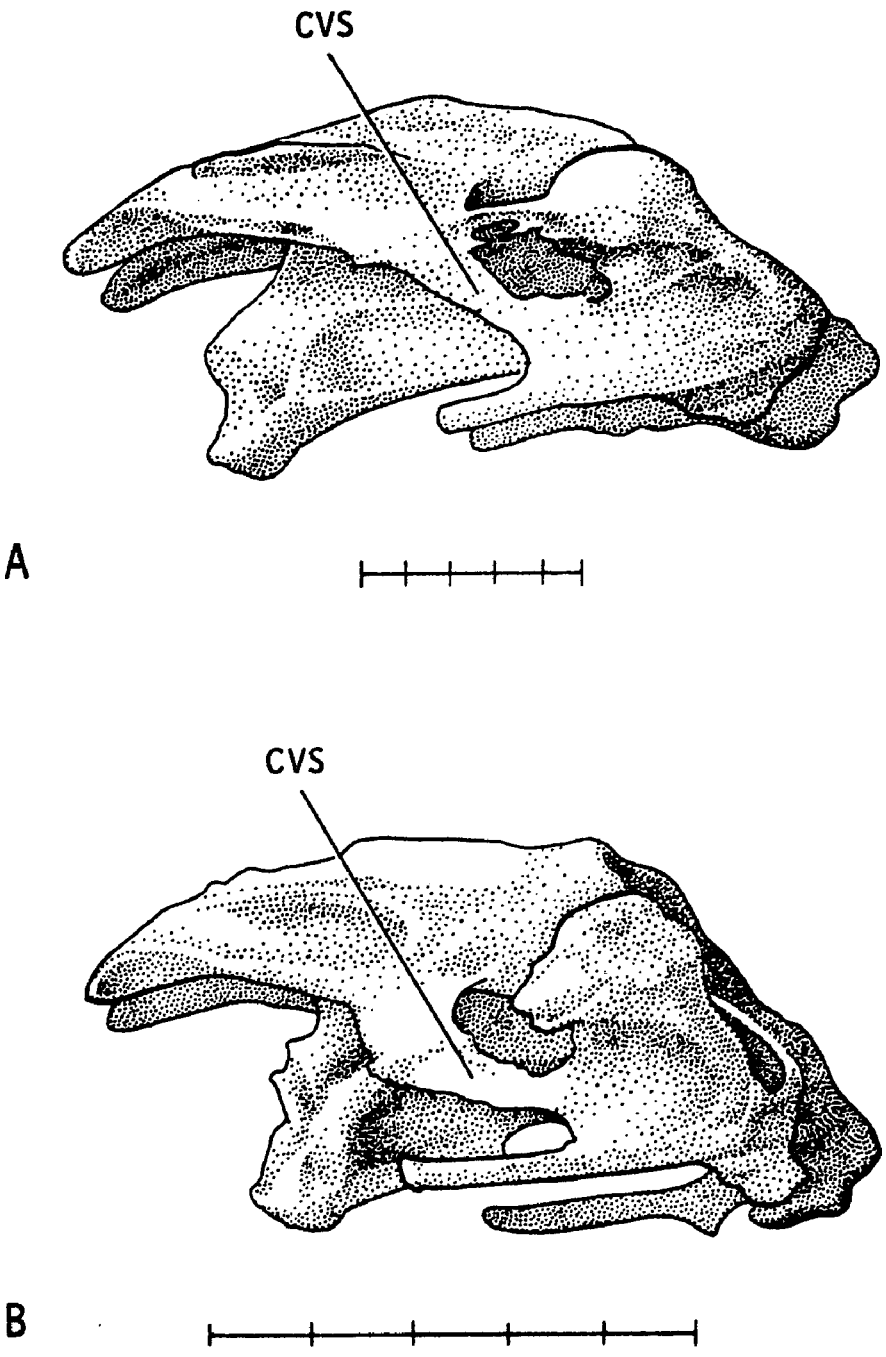


Fig. 20. Eighth cervical vertebra of two species. A. Vanellus melanopterus (UMMZ 220264); B. Burhinus magnirostris (UMMZ 214183). Abbreviation: cvs, cervical vertebral strut. Each scale unit represents 1 mm.

(anterior articular surface convex and posterior articular surface concave). The heterocoelous condition is the most widespread in all birds and is the only condition found in the Gruiformes and Columbiformes. It is thus probably the primitive condition in the Charadriiformes.

Coding: primitive: dorsal vertebrae heterocoelous (A); derived: dorsal vertebrae opisthocoelous (B).

Pectoral Girdle Characters

Character 35: number of sternal costal processes (Fig. 21, 22). The number of sternal costal processes is variable within the Gruiformes, Charadriiformes, and Columbiformes, with five and six being the most widely distributed states. Within the Charadriiformes the six-process condition is the most widely distributed and probably primitive state.

Coding: primitive: six costal processes on sternum (A) (Fig. 21); derived from primitive: five costal processes (B) (Fig. 22); derived from (B): four costal processes (C) (not illustrated); derived from primitive: seven costal processes (D) (not illustrated).

Character 36: medial sternal notch (Fig. 21, 22). The sternum of all Charadriiformes is notched, all species having a lateral notch and some species having both a lateral and a medial notch. Except in the Otididae the medial notch is absent in the Gruiformes; it is present in the Columbiformes. Based on its distribution within the order, the absence of a medial notch is probably primitive in the Charadriiformes. This character, however, is not stable within the Scolopacidae, both states occurring in a series of specimens of some species. In addition, some specimens were intermediate, with a medial notch on only one side or with medial notches present only as foramina. Any species in which at least some of the specimens had a medial notch was coded as having the notch.

Coding: primitive: medial sternal notch absent (A) (Fig. 22); derived: medial sternal notch present (B) (Fig. 21).

Character 37: relative lengths of the posterior lateral sternal process and xiphial area (Fig. 21, 22). The posterior lateral sternal process does not extend posteriad as far as the xiphial area in most Charadriiformes; this is probably the primitive state.

Coding: primitive: posterior lateral sternal process not

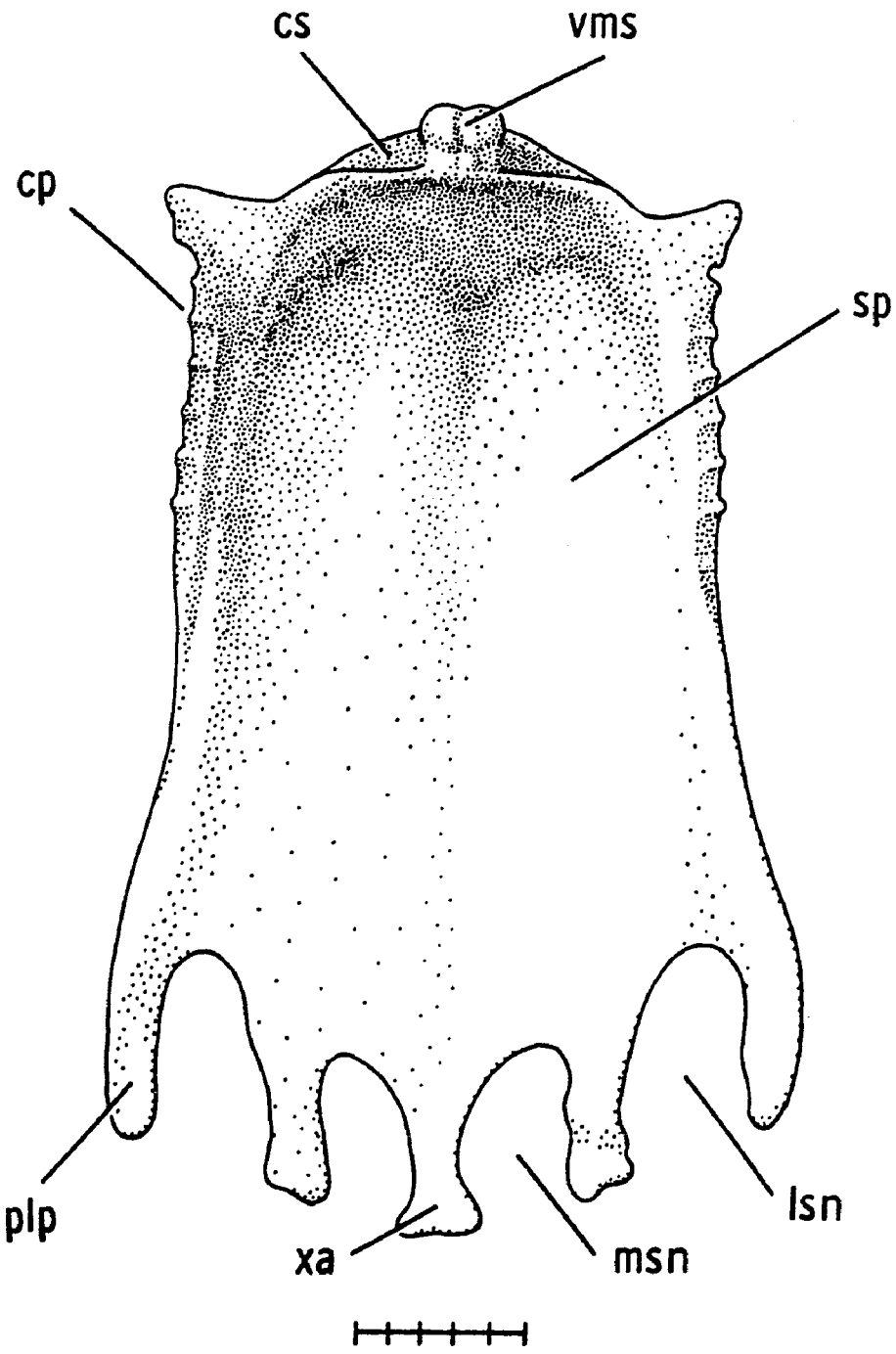


Fig. 21. Dorsal view of the sternum of Thinornis novaeseelandiae (NZNM 1403). Abbreviations: cp, costal process; cs, coracoidal sulcus; lsn, lateral sternal notch; msn, medial sternal notch; plp, posterior lateral process; sp, sternal plate; vms, ventral manubrial process; xa, xiphial area. Each scale unit represents 1 mm.

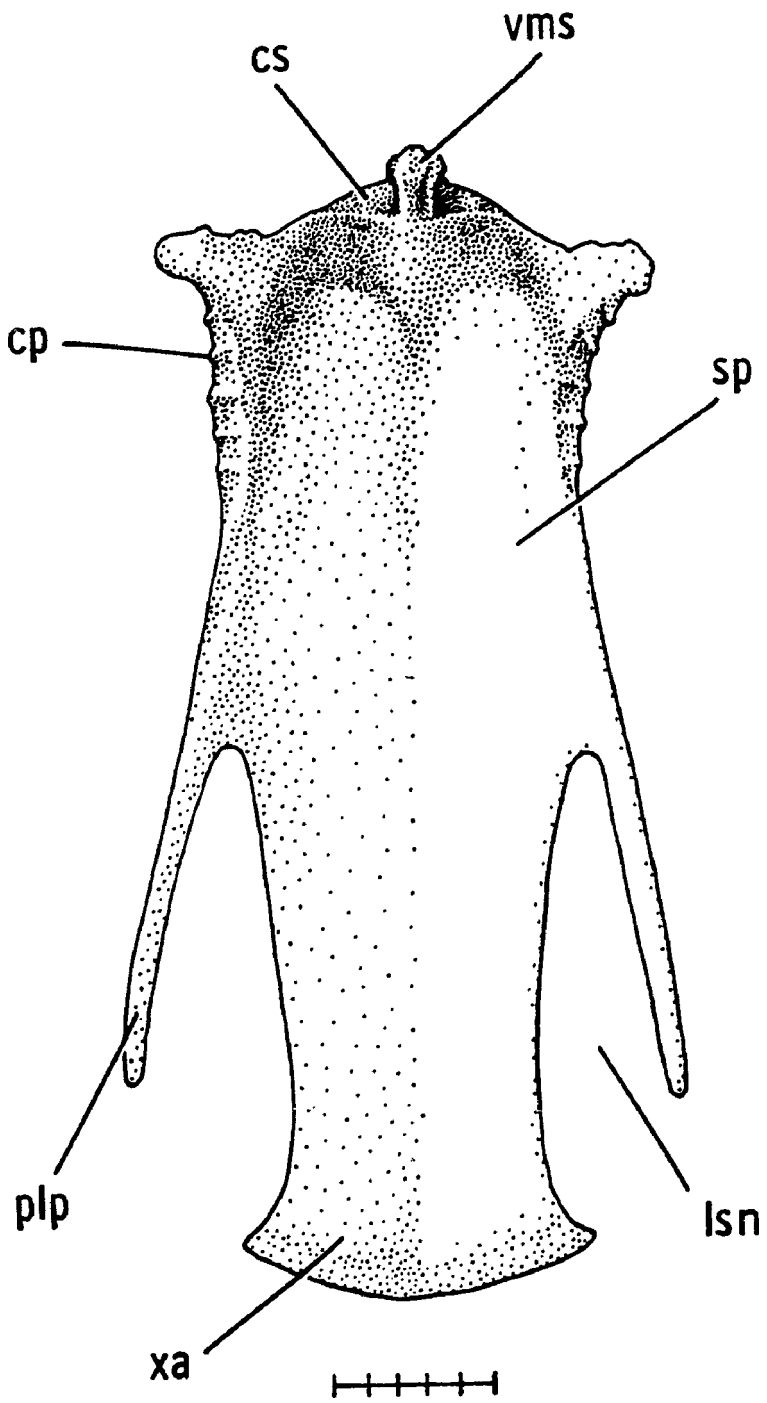


Fig. 22. Dorsal view of the sternum of Nycticryphes semicollaris (UMMZ 157021). Abbreviations as in Fig. 21. Each scale unit represents 1 mm.

extending as far posteriad as the xiphial area (C) (Fig. 21, 22); derived from primitive: posterior lateral sternal process and xiphial area extending about equal distance posteriad (A) (not illustrated); derived from (A): posterior lateral sternal process extending farther posteriad than xiphial area (B) (not illustrated). (No charadriiform had this state.)

Character 38: ventral manubrial spine of sternum (Fig. 21, 22). A well-developed ventral manubrial spine is characteristic of the Charadriiformes but is generally absent in the Gruiformes and Columbiformes. Usually in the Charadriiformes a distinct ridge from the spine to the sternal plate forms a wall between the medial ends of the coracoidal sulci. This is probably the primitive state.

Coding: primitive: distinct ridge from ventral manubrial spine to sternal plate forming a wall between medial ends of coracoidal sulci (A) (Fig. 21, 22); derived: ridge absent (B) (not illustrated).

Character 39: coracoidal foramen (Fig. 23). A distinct foramen is present in the coracoid of many birds. Its distribution among the Gruiformes, Charadriiformes, and Columbiformes indicates that its presence is primitive. Zusi and Jehl (1970) report that the foramen is present in all plovers except Charadrius melanops. But the foramen is present in one of the four specimens of this species that I examined. The specimen with the foramen is clearly an adult, based on gonad measurements. The other three specimens were collected during the latter part of the breeding season but have small gonads; one is clearly immature, as shown by the unossified condition of the tarsometatarsus. Since a series of skeletons of adults will probably show the foramen present in individuals with fully ossified skeletons, I scored this species as having a coracoidal foramen.

The coding of this character in the Glareolidae was difficult. The foramen is present in Glareola but absent in Cursorius. In Rhinoptilus the foramen is present in two skeletons of cinctus, in three of four specimens of chalcopterus, but in only one of four specimens of africanus which I examined. All three species of Rhinoptilus were coded as having the foramen. After preliminary analyses indicated that the species of the three genera cited above form a monophyletic group, the absence of a foramen in Cursorius was

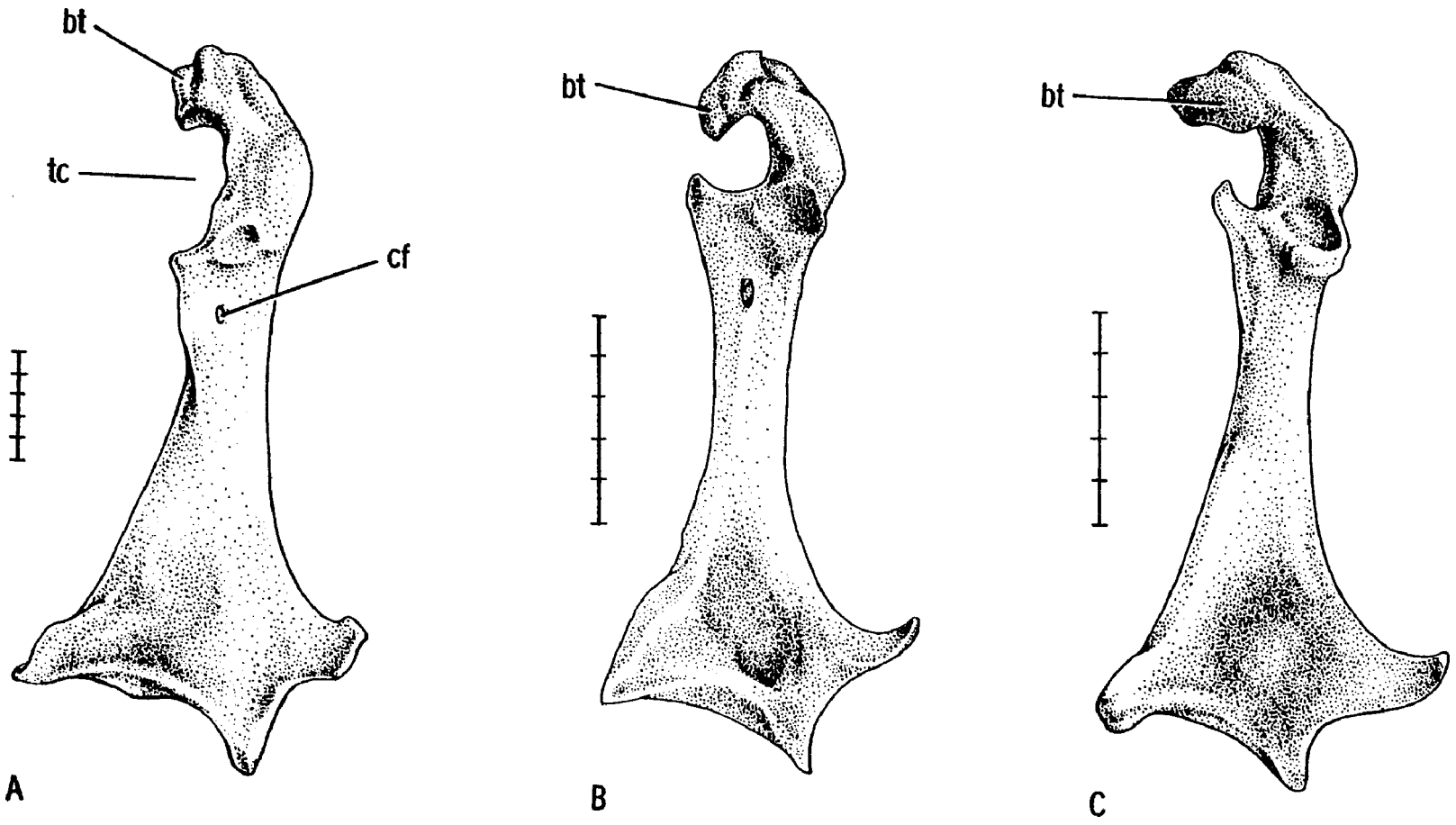


Fig. 23. Posterior view of the coracoids of three species. A. Cepphus grylle (UMMZ 151779); B. Thinornis novaeseelandiae (NZNM 1403); C. Nycticryphes semicollaris (UMMZ 157021). Abbreviations: bt, brachial tuberosity; cf, coracoidal foramen; tc, triosseal canal. Each scale unit represents 1 mm.

coded as a uniquely derived state.

Coding: primitive: coracoidal foramen present (A) (Fig. 23A, 23B); derived from primitive: coracoidal foramen absent (B) (Fig. 23C); derived from primitive: coracoidal foramen absent in Glareolidae (C) (not illustrated).

Character 40: brachial tuberosity of coracoid (Fig. 23). In most of the Charadriiformes the brachial tuberosity of the coracoid roofs the triosseal canal; it is probably the primitive condition. In the Alcidae, however, the head of the coracoid is twisted ventrally so that the tuberosity no longer roofs the canal.

Coding: primitive: brachial tuberosity of coracoid roofing triosseal canal (A) (Fig. 23B, 23C); derived: brachial tuberosity twisted, not roofing canal (B) (Fig. 23A).

Character 41: symphysis of furcula (Fig. 24). The outward-facing surface of the symphysis of the furcula in Charadriiformes usually has no distinct grooving, or it has a very shallow groove which does not extend into the furcular process. This is believed to be the primitive condition. In the Laroidea a distinct groove extends into the furcular process, while in some plovers and auks there is a distinct ridge at the bottom of the groove.

Coding: primitive: no groove or only a very shallow groove on outward-facing surface of symphysis of furcula (A) (Fig. 24B, 24D); derived from primitive: distinct groove extending into furcular process (B) (Fig. 24A); derived from primitive: distinct ridge at bottom of groove (C) (Fig. 24C).

Wing Characters

Character 42: ridge in capital groove of humerus (Fig. 25). Some charadriiforms have a ridge in the capital groove of the humerus. Absence of the ridge is probably the primitive state, since no ridge is found in the Gruiformes, most Charadriiformes, and the Columbiformes.

Coding: primitive: no ridge in capital groove of humerus (A) (Fig. 25B, 25C); derived: ridge present in capital groove of humerus (B) (Fig. 25A, 25D, 25E).

Character 43: shape of the deltoid crest of the humerus (Fig. 25). Zusi and Jehl (1970) observed that the shape of the anconal

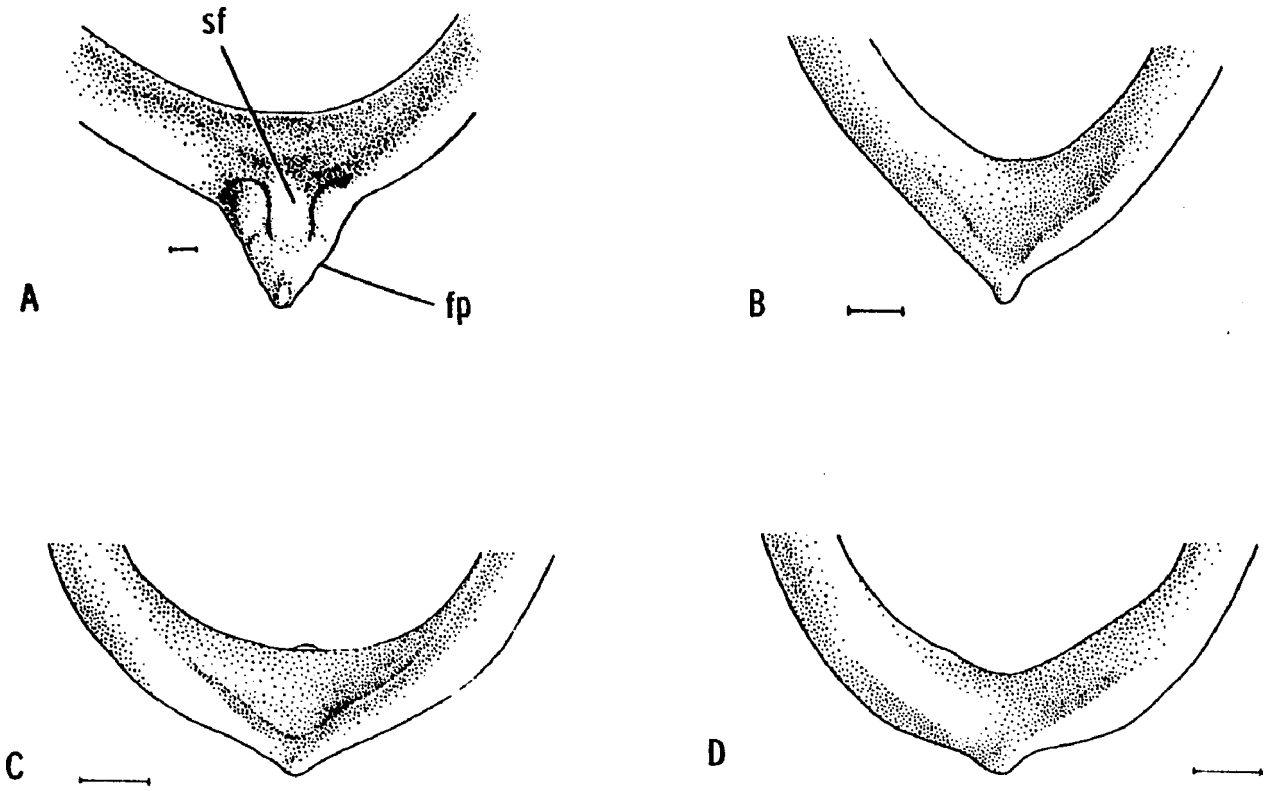


Fig. 24. Anterior view of the furculae of four species. A. Stercorarius pomarinus (UMMZ 153518); B. Pluvianus aegyptius (FMNH 93450); C. Charadrius placidus (USNM 318989); D. Thinornis novaeseelandiae (NZNM 1403). Abbreviations: fp, furcular process; sf, symphysis of furcula. Scales represent 1 mm.

Fig. 25. Anconal view of the humeri of five species. A. Rhinoptilus chalcopterus (UMMZ 156673); B. Metopidius indicus (UMMZ 219843); C. Catoptrophorus semipalmatus (UMMZ 156426); D. Burhinus magnirostris (UMMZ 214183); E. Thinornis novaeseelandiae (NZNM 1403). Abbreviations: asdc, anconal surface of deltoid crest; cg, capital groove; cgr, capital groove ridge; dc, deltoid crest; ecp, ectepicondylar prominence; h, head of humerus; pfII, pneumatic fossa II. Each scale unit represents 1 mm.

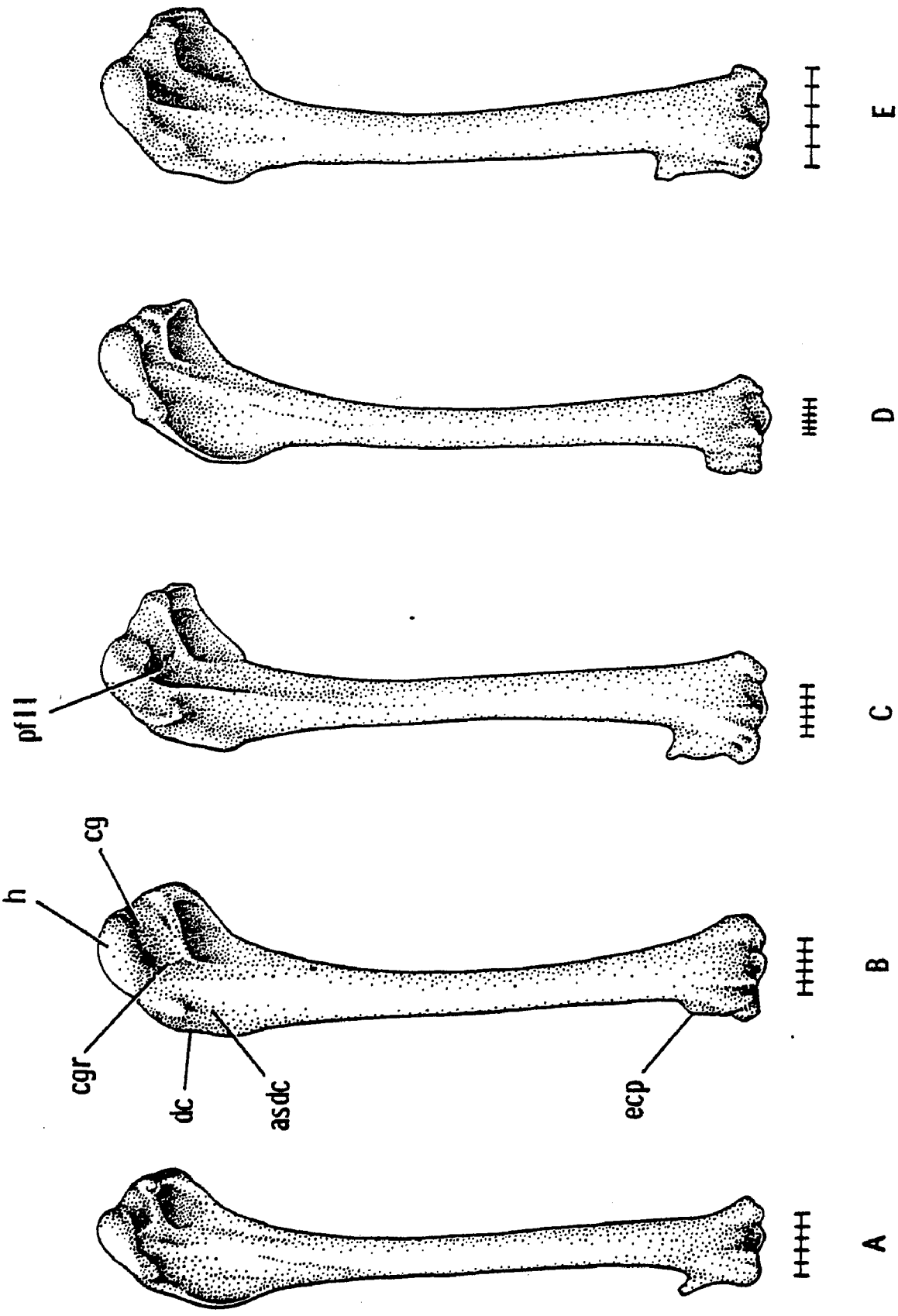


Fig. 25

surface of the deltoid crest is concave in plovers and convex in sandpipers. Since the surface is convex in the Gruiformes, some Charadriiformes, and the Columbiformes, this condition is probably the primitive condition.

Coding: primitive: anconal surface of deltoid crest of humerus convex (A) (Fig. 25B, 25C); derived: anconal surface of deltoid crest of humerus concave (B) (Fig. 25A, 25D, 25E).

Character 44: pneumatic fossa II of humerus (Fig. 25). A well-developed pneumatic fossa II of the humerus is characteristic of the Charadriiformes and presumably represents the primitive condition.

Coding: primitive: pneumatic fossa II of humerus well-developed (A) (Fig. 25C, 25D, 25E); derived: pneumatic fossa II of humerus poorly-developed (B) (Fig. 25A, 25B).

Character 45: ectepicondylar prominence of humerus (Fig. 25). Almost all charadriiform birds have a well-developed ectepicondylar prominence on the humerus. This prominence was absent from the humeri of all the members of the Gruiformes and Columbiformes examined. Since the prominence is so widespread in the Charadriiformes and since its absence is correlated with other advanced states, presence of the prominence is probably the primitive state of the order.

Coding: primitive: well-developed ectepicondylar prominence on humerus (Fig. 25A, 25C, 25E); derived: ectepicondylar prominence absent (A) (Fig. 25B, 25D).

Character 46: extensor process of the metacarpus (not illustrated). The extensor process of the metacarpus of the carpometacarpus is unmodified in the Gruiformes, most Charadriiformes, and the Columbiformes. Some species of Charadriiformes, on the other hand, have well-developed wing spurs or horny knobs on the process, the function of which has never been demonstrated. Several authors have debated the value of wing spurs in classifying the Vanellinae (Boetticher 1954; Bock 1958; Wolters 1974). The wing spurs of plovers and jacanas are well-known (Rand 1954), but several less spectacular modifications of the process have been overlooked. I found a distinct wing knob in Pluvianellus socialis, Chionis alba, and Pluvianus aegyptius, and a possible knob in some plovers and oystercatchers. Sharpe (1896) reported a wing spur for Chionis minor.

The coding of this character was modified during the course of the study. The spurs of jacanas and plovers are quite different (Rand op. cit.), those of the former being short cones while those of the latter are more claw-like and somewhat flattened. These two types of spurs appear to be independently derived and were coded thus. The jacanas which do not have well-developed spurs all have wing knobs and highly modified radii (Rand op. cit.). Since the evolutionary relationship between the jacana knobs and spurs is unclear, an unspecified process for the jacans has been assumed; this could logically be an unmodified process, a knob, or a spur; it assumes an unmodified radius which gave rise to two independently derived conditions: a well-developed spur with an unmodified radius and a wing knob with a modified radius. The wing knobs in Pluvianellus, Chionis, and Pluvianus were originally coded as the same state. Later it became clear that all the evidence from other characters indicated that the knob in Pluvianus had been independently derived, and the character coding was changed accordingly. In addition, all other evidence indicated that Hoploxypterus cayanus is not a member of the Vanellinae and that its wing spur had been derived independently of that found in the lapwings. Coding was changed to reflect this conclusion. Finally, the low, flat process found in some of the Alcidae is probably an independent derivation from the primitive state.

Coding: primitive: unmodified extensor process of metacarpus of carpometacarpus (A); derived from primitive: wing knob of Pluvianus (B); derived from primitive: wing knobs of Chionis and Pluvianellus (I); derived from primitive: wing spurs of Vanellinae (C); derived from primitive: wing spur of Hoploxypterus (F); derived from primitive: low, flat process of Alcidae (D); derived from primitive: hypothetical ancestral state for Jacanidae (G); derived from (G): jacana wing spurs (E); derived from (G): jacana wing knobs (H).

Character 47: position of intermetacarpal tuberosity on metacarpal II of carpometacarpal (not illustrated). The intermetacarpal tuberosity is a large scar on the edge of the dorsal surface of metacarpal II of the carpometacarpus facing into the intermetacarpal space. This is the location of attachment for M. flexor metacarpi posterior (George and Berger 1966). The most widespread and presumably primitive

state for this character is for the scar to be located outside the groove where metacarpals II and III join.

Coding: primitive: intermetacarpal tuberosity outside groove where metacarpals II and III join (A); derived: intermetacarpal tuberosity within groove formed where metacarpals II and III join (B).

Character 48: distal metacarpal symphysis of carpometacarpus (Fig. 26). A small ossified bridge over the distal metacarpal symphysis of the carpometacarpus is unique to the Jacanidae and is probably a derived condition.

Coding: primitive: no ossified bridge over the distal metacarpal symphysis of the carpometacarpus (A) (Fig. 26B); derived: bridge present (B) (Fig. 26A).

Character 49: proximal phalanx, digit III (not illustrated). A strongly perforated proximal phalanx, digit III is unique to the Laroidea within the Charadriiformes; it probably represents a derived condition. Some specimens of the Phalaropodinae and the Glareolidae seem to have the derived state, but in all cases the perforation is a hole in a thin sheet of bone and appears to represent incomplete ossification or a damaged specimen. The thin sheet of bone is always absent in the Laridae. The states of this character are well-illustrated by Stegmann (1963).

Coding: primitive: proximal phalanx, digit III not perforated (A); derived: proximal phalanx, digit III perforated (B).

Synsacrum Characters

Character 50: synsacral strut (Fig. 27, 28). Most charadriiform birds have a strut or brace extending from the fused sacral-caudal vertebrae to the acetabulum. In the most widely distributed and presumably primitive state for the Charadriiformes this strut arises from the fifth vertebra from the posterior end of the synsacrum. In the derived states the strut lies one vertebra proximal or distal to the end of the synsacrum or is absent.

Coding: primitive: synsacral strut extending from fifth vertebra (A) (Fig. 27, 28); derived from primitive: synsacral strut extending from sixth vertebra (B) (not illustrated); derived from primitive: synsacral strut extending from fourth vertebra (D) not

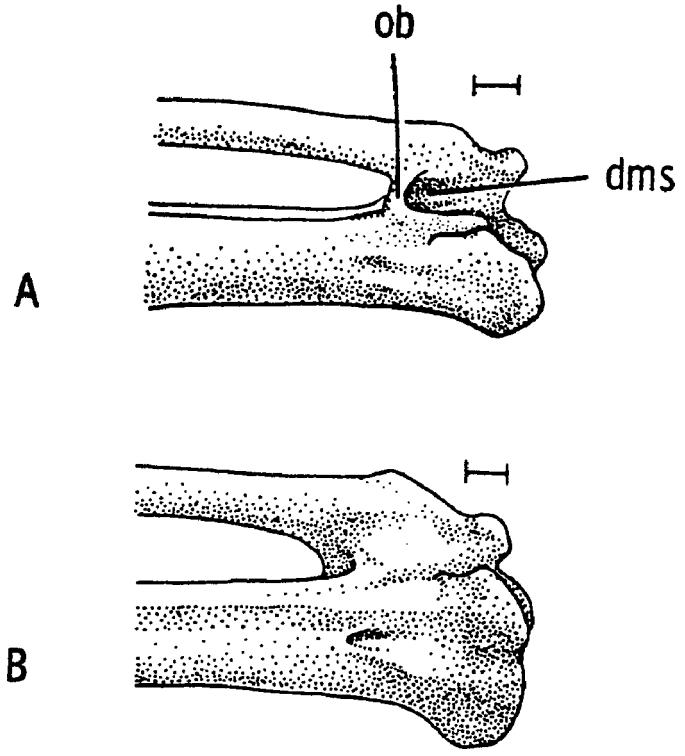


Fig. 26. Dorsal view of the distal end of carpometacarpi of two species. A. Metopidius indicus (UMMZ 219846); B. Vanellus macropterus (RVNH b). Abbreviations: dms, distal metacarpal symphysis; os, ossified bridge. Scales represent 1 mm.

Fig. 27. Ventral view of the synsacrum of Thinornis novaeseelandiae (NZNM 1403). Abbreviations: ipf, interapophyseal foramen; isa, ischial angle; lss, lateral synsacral strut; lvp, lumbar vertebral parapophysis; ppil, posterior projection of ilium; pu, pubis; rd, renal depression; scv, sacral-caudal vertebrae; vsi, ventral surface of ilium. Scale represents 1 mm.

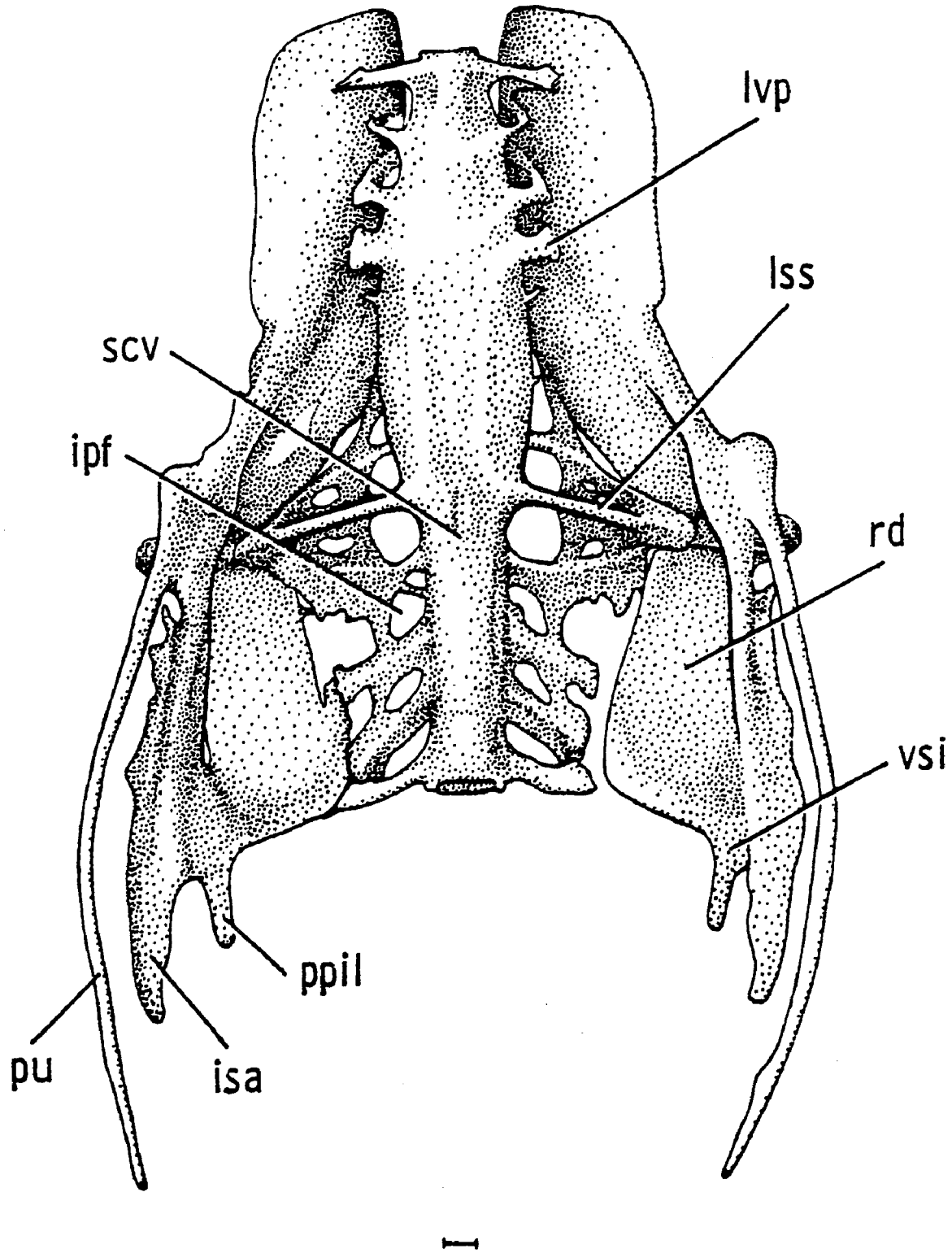


Fig. 27

Fig. 28. Ventral view of the synsacrum of Metopidius indicus (UMMZ 214551). Abbreviations as in Fig. 27. Scale represents 1 mm.

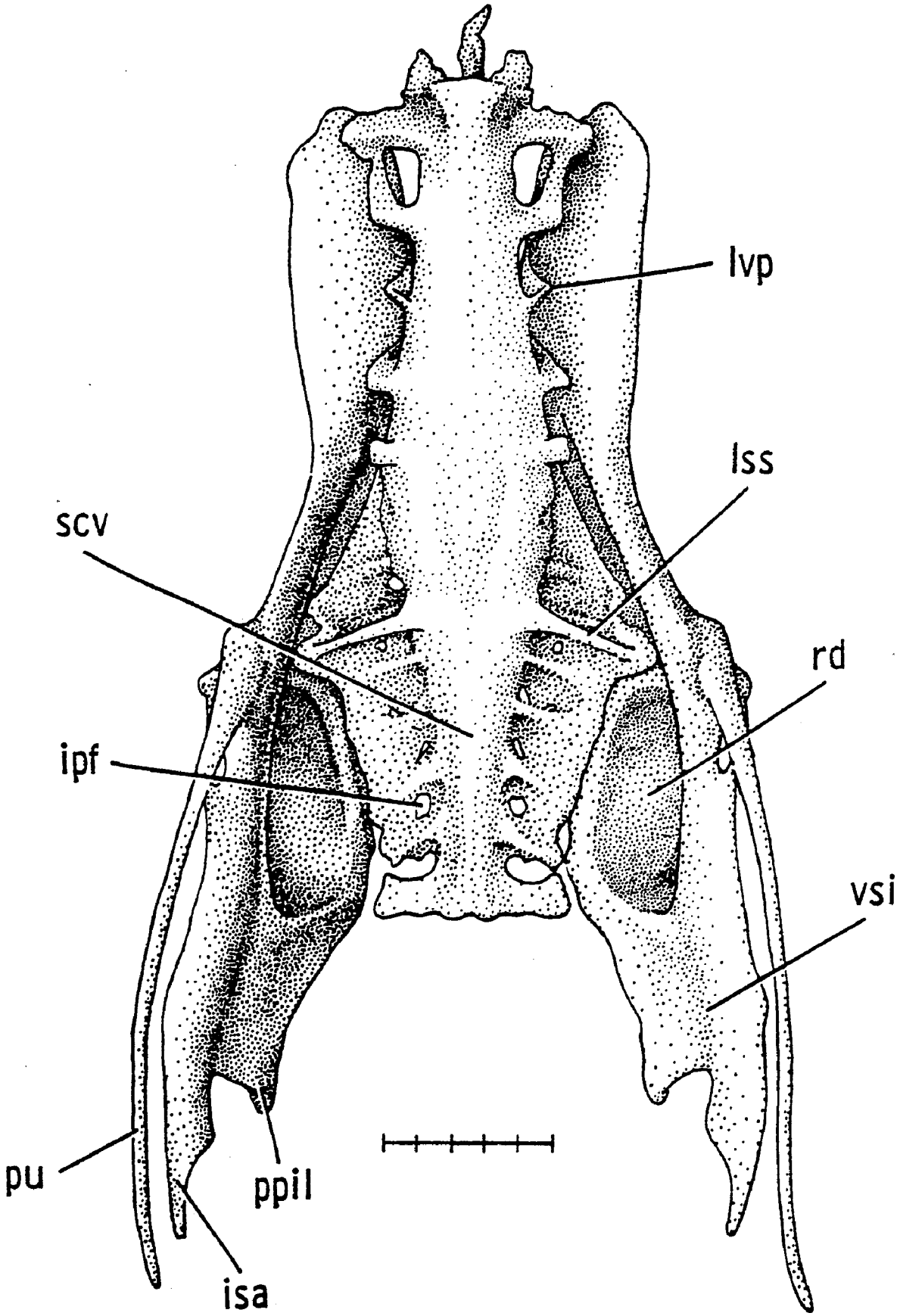


Fig. 28

illustrated); derived from primitive: synsacral strut absent (C) (not illustrated).

Character 51: second synsacral strut (not illustrated). A few species of Charadriiformes have a second synsacral strut either posterior or anterior to the first strut. The value of this character is doubtful because the second strut is present in some specimens of several species but absent in other specimens. Some specimens also have an additional strut on one side but not on the other.

Coding: primitive: no second synsacral strut (A); derived from primitive: second strut posterior to first strut (B); derived from primitive: second strut anterior to first strut (C).

Character 52: position of lateral synsacral strut (Fig. 27, 28). The lateral synsacral strut extends from the fused sacral-caudal vertebrae to the acetabulum in the Gruiformes and most of the Charadriiformes but falls short of the acetabulum in the Columbiformes. The most widely distributed condition within the Charadriiformes, in which the strut extends to the acetabulum, is probably primitive. The condition in the Alcidae, in which the strut is completely absent, is probably an independently derived state.

Coding: primitive: lateral synsacral strut extending from fused sacral-caudal vertebrae to acetabulum (A) (Fig. 27, 28); derived from primitive: strut falling short of acetabulum (B) (not illustrated); derived from primitive: strut absent (C) (not illustrated).

Character 53: number of lumbar vertebral parapophyses (Fig. 27, 28). Most charadriiform birds have three parapophyses on the lumbar vertebrae; this is probably the primitive state for the order.

Coding: primitive: three parapophyses on lumbar vertebrae (A) (Fig. 27, 28); derived: four parapophyses on lumbar vertebrae (B) (not illustrated).

Character 54: condition of posterior end of the renal depression (Fig. 27, 28). The posterior end of the renal depression of the synsacrum of most charadriiform birds is almost flat, and there is little or no discontinuity between the end of the depression and the ventral surface of the ilium; this condition is probably the primitive state. In some species the end of the depression is abrupt, deep, and partially roofed by the inner posterior surface of the ilium; in others

a strut defines the end of the depression.

Coding: primitive: posterior end of the renal depression flat with little or no discontinuity between end of depression and ventral surface of ilium (A) (Fig. 27); derived from primitive: distinct strut at end of depression (B) (not illustrated); derived from primitive: end of depression deep and abrupt (C) (Fig. 28).

Character 55: foramina on ventral surface of ilium (Fig. 27, 28). There are foramina on the ventral surface of the ilium (= renal bar of Holmann (1961)?) in some species of Stercorarius. While some species of gulls and terns have depressions in this area, the foramina are found only in the skuas.

Coding: primitive: no foramina in ventral surface of ilium (A) (Fig. 27, 28); derived: foramina present in ventral surface of ilium (B) (not illustrated).

Character 56: interapophyseal foramina of synsacrum (Fig. 27, 28). A large number of interapophyseal foramina is characteristic of the charadriiform synsacrum. Almost all the Gruiformes and Columbiformes have two or fewer such foramina on each side of the synsacrum. In the Charadriiformes only two species of Jacanidae and the woodcocks consistently have fewer than three foramina on each side of the synsacrum, a condition which is probably derived.

Coding: primitive: three or more interapophyseal foramina on each side of synsacrum (A) (Fig. 27, 28); derived: fewer than three foramina (B) (not illustrated).

Character 57: shape of the posterior medial edge of the ilium (Fig. 27, 28). The posterior edge of the ilium of most Charadriiformes meets its medial edge at nearly a right angle. In some species the edge forms a smooth curve, while in others the medial edge is straight all the way to the ischial angle.

Coding: primitive: posterior medial and medial edge of ilium forming abrupt right angle (B) (Fig. 27); derived from primitive: posterior medial and medial edge of ilium forming smooth curve (A) (Fig. 28); derived from primitive: medial edge of ilium straight all the way to ischial angle (C) (not illustrated).

Character 58: extent of the ischium (Fig. 29). In most Charadriiformes the ischial angle extends posterior to the posterior

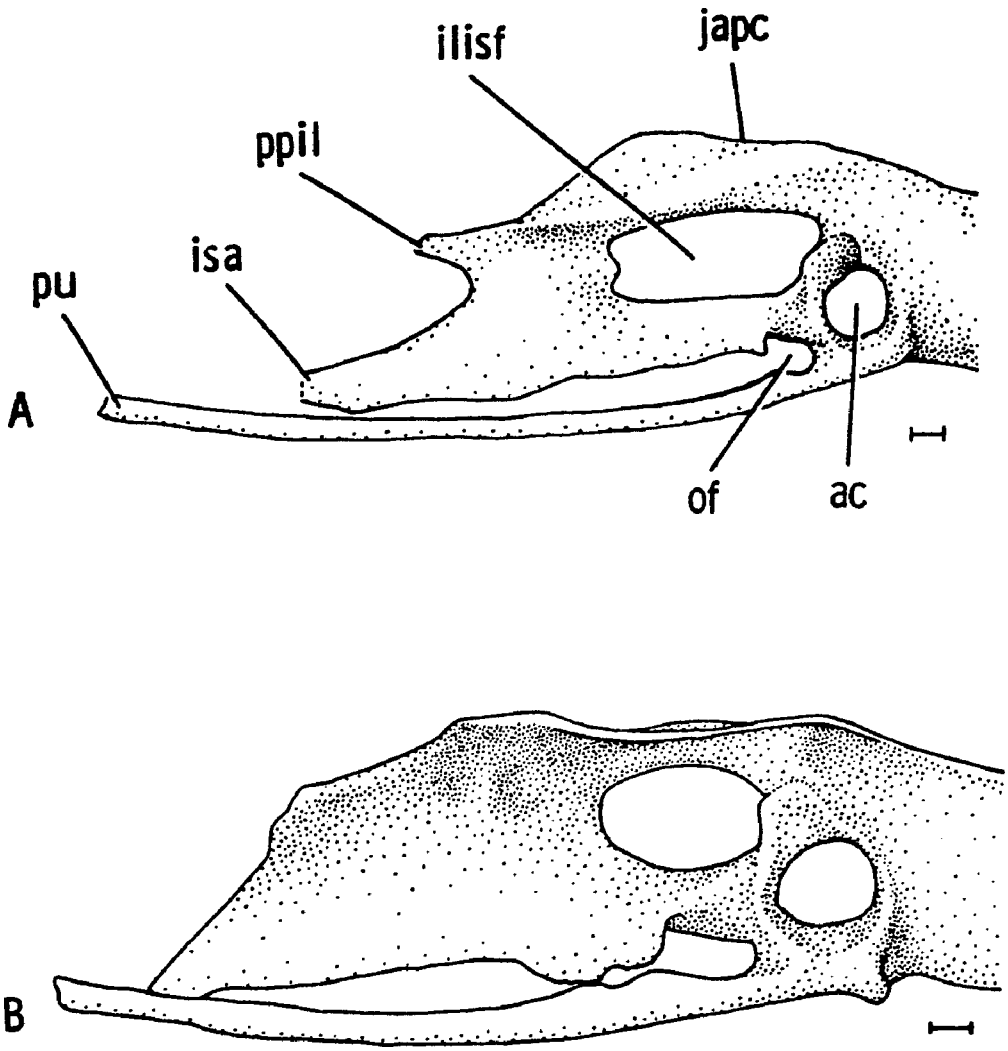


Fig. 29. Lateral view of the synsacra of two species. A. Thinornis novaeseelandiae (NZNM 1403); B. Metopidius indicus (UMMZ 214551). Abbreviations: ac, acetabulum; ilisf, ilioischiatic fenestra; isa, ischial angle; japc, junction of anterior and posterior crests; of, obturator foramen; ppil, posterior projection of ilium; pu, pubis. Scales represent 1 mm.

projection of the ilium, often as far as the end of the pubis. This is probably the primitive condition.

Coding: primitive: ischial angle extending posterior to posterior projection of ilium (A) (Fig. 29B); derived: ischial angle relatively short and about even with posterior projection of ilium (B) (Fig. 29A).

Character 59: fusion of the ischium and pubis (Fig. 29). In most Charadriiformes the ischium and pubis are not fused or are fused only near their posterior ends. This is probably the primitive condition. In some species, however, the ischium and pubis are fused immediately posterior to the obturator foramen.

Coding: primitive: ischium and pubis not fused immediately behind obturator foramen (A) (Fig. 29A, 29B); derived: ischium and pubis fused immediately posterior to obturator foramen (B) (not illustrated).

Character 60: shape of junction of anterior and posterior crests of the pelvis (Fig. 29). In the most widespread and presumably primitive condition for the Charadriiformes the junction of the anterior and posterior crests of the pelvis is smooth and rounded. In some species the crests form a distinct projection over the ilioischiatic fenestra.

Coding: primitive: junction of anterior and posterior crests of pelvis smooth and rounded (A) (Fig. 29B); derived: junction of anterior and posterior crests of pelvis forming a distinct projection over ilioischiatic fenestra (B) (Fig. 29A).

Hind Limb Characters

Character 61: relative positions of trochlea for digits II and IV of the tarsometatarsus (Fig. 30A, 30B, 30C). I found three patterns for the relative positions of the trochlea for digits II and IV: either they are equally and only slightly elevated compared to the trochlea for digit III, or they are both elevated with that for digit II slightly more so than that for digit IV, or they are both considerably elevated with that for digit II much more so than that for digit IV. The distribution of the states among the Gruiformes, Charadriiformes, and Columbiformes indicates that the condition in which the trochlea

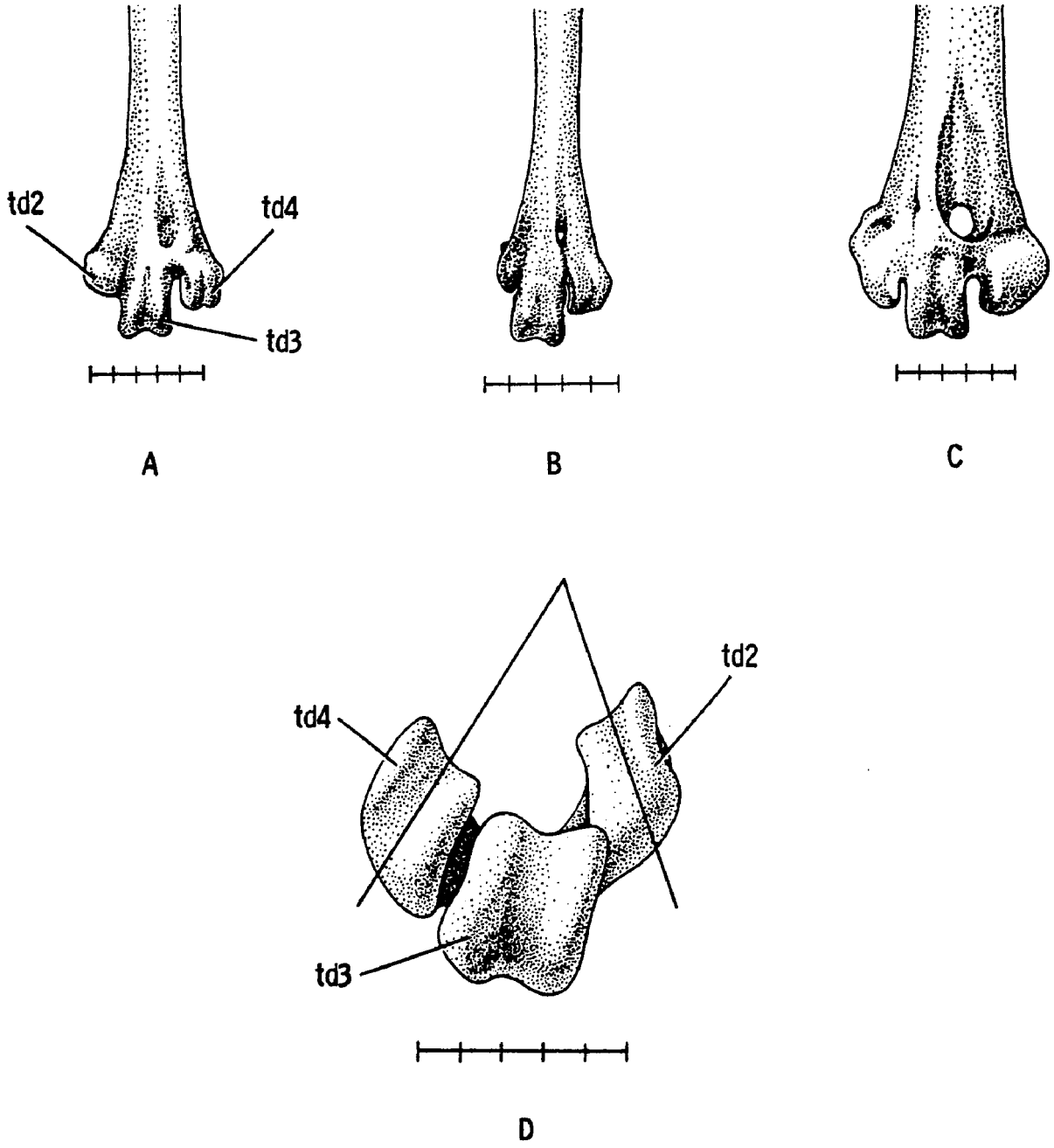


Fig. 30. View of the distal end of the tarsometatarsi of four species. Anterior view: A. Aphriza virgata (UMMZ 291182); B. Thinornis novaeseelandiae (NZNM 1403); C. Metopidius indicus (UMMZ 214551). Ventral view: D. Cladorhynchus leucocephala (UMMZ 214181). Abbreviations: td2, trochlea for digit II; td3, trochlea for digit III; td4, trochlea for digit IV. Each scale unit represents 1 mm.

for digit II is slightly elevated is probably the primitive state.

Coding: primitive: trochlea for digits II and IV elevated compared to that for digit III, trochlea for digit II only slightly more elevated than that for digit IV (A) (not illustrated); derived from primitive: trochlea for digits II and IV considerably elevated compared to that for digit III, trochlea for digit II more so than that for digit IV (B) (Fig. 30A, 30B); derived from primitive: trochlea for digits II and IV only slightly elevated compared to that for digit III (C) (Fig. 30C).

Character 62: hallux (not illustrated). Most Gruiformes, Charadriiformes, and Columbiformes have a well-developed hallux; this is probably the primitive state.

Coding: primitive: hallux present (A); derived: hallux absent (B).

Character 63: angle formed by trochleae for digits II and IV (Fig. 30D). The angles formed between the trochleae for digits II and IV fall into three groups: those larger than 35 degrees, those between 35 and 25 degrees, and those smaller than 25 degrees. The middle group appears to be the primitive state, based on its distribution within the Charadriiformes.

Coding: primitive: angle between 35 and 25 degrees (A) (not illustrated); derived from primitive: angle larger than 35 degrees (B) (Fig. 30D); derived from primitive: angle smaller than 25 degrees (C) (not illustrated).

Characters 64, 65, 66, 67, 68, 69, 70: hypotarsus (Fig. 31). The pattern of tendinal canals in the hypotarsus is complex and offers abundant comparative material for phylogenetic and functional studies. While the patterns of muscles and tendons in bird legs have received considerable attention, little has been published on the patterns of the passage of the tendons through and around the hypotarsus. Storer's (1963) use of the hypotarsus in inferring relationships among the grebes represents one of the few systematic uses of these characters.

The arrangement of the tendons in the hypotarsus of the Blue Grouse, Dendragapus obscurus (Hudson, Lanzillotti, and Edwards 1959), and for the Common Crow, Corvus brachyrhynchos (Hudson 1937), were used to estimate which tendon is associated with the tendinal canals

Fig. 31. View of the proximal end of the tarsometatarsi of four species. A. Thinornis novaeseelandiae (NZNM 1403); B. Cladorhynchus leucocephala (UMMZ 214181); C. Cepphus grylle (UMMZ 151779); D. Scolopax rusticola (UMMZ 156165); E. Hypothetical hypotarsus showing the six possible tendinal canals. Abbreviations: tc1-6, tendinal canals of hypotarsus No. 1-6. Each scale unit represents 1 mm.

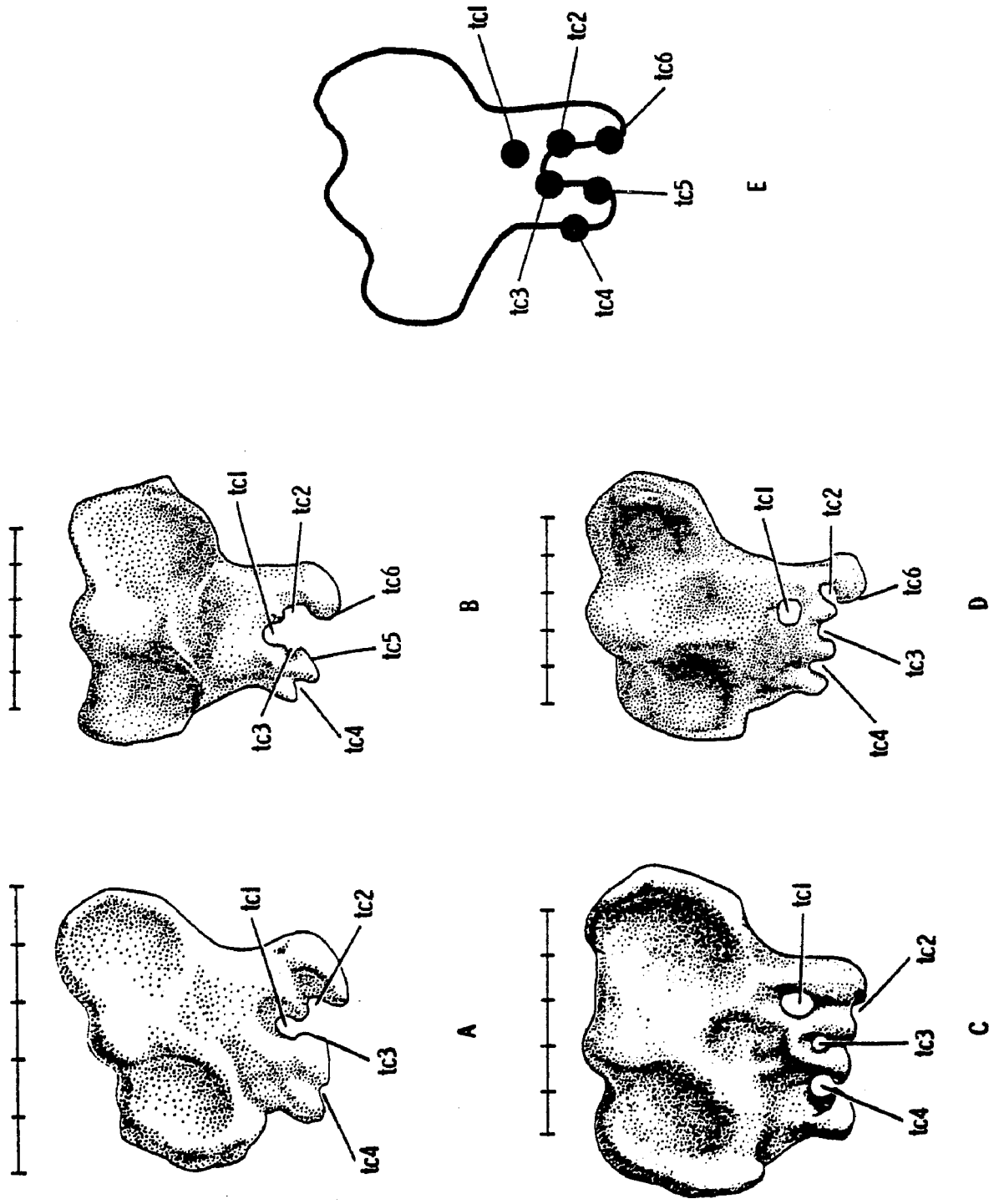


Fig. 31

of charadriiform hypotarsi. The hypothetical charadriiform hypotarsus illustrated in Fig. 31E shows the relative locations of six tendons, which could account for all the patterns found. The assumed homologies for each tendon are as follows: No. 1, tendon for M. flexor digitorum longus. George and Berger (1966) state that this tendon is the only one which traverses a bony canal in Totanus (= Tringa) and Larus; No. 2, tendon of M. flexor perforatus digiti IV and/or tendon for M. flexor perforans et perforatus digiti II; No. 3, tendon of M. flexor hallucis longus (In species with a very small or no hallux this tendon has been found to fuse with the tendon of M. flexor digitorum longus (George and Berger op. cit.).); No. 4, tendon for M. peronaeus longus; No. 5, tendon for M. flexor perforatus digiti IV; No. 6, tendon for M. flexor perforans et perforatus digiti III. There is a canal for a tendon lying between tendons 2 and 3 in Rhinoptilus chalcopterus, R. cinctus, and some specimens of Haematopus. This condition may represent a separation of the pathways of the tendons assumed to pass through No. 1.

Character 64: tendinal canal No. 1. In most charadriiform birds a bony canal is present for this tendon; the condition in which only a groove is present is probably derived.

Coding: primitive: tendinal canal No. 1 a bony canal (B) (Fig. 31C, 31D); derived: tendinal canal No. 1 a groove (A) (Fig. 31A, 31B).

Character 65: location of tendinal canal No. 1 (Fig. 31). The canal for tendon No. 1 is found either directly anterior to the canal for tendon No. 2, anterior to the space between the canals for tendons No. 2 and 3, or directly anterior to the canal for tendon No. 3. The distribution of the states for this character within the Charadriiformes indicates that the primitive condition is probably for the canal for tendon No. 1 to be directly anterior to the canal for tendon No. 2.

Coding: primitive: canal for tendon No. 1 directly anterior to canal for tendon No. 2 (B) (Fig. 31C, 31D); derived from primitive: canal for tendon No. 1 anterior to space between canals for tendons No. 2 and 3 (A) (not illustrated); derived from (A): canal for tendon No. 1 directly anterior to canal for tendon No. 3 (C) (Fig. 31A, 31B).

Character 66: tendinal canal for tendon No. 3 (Fig. 31). The

canal for this tendon is either a bony canal, a groove, or is undetectable on the surface of the bone. The state in which only a groove is present is probably the primitive state for the order.

Coding: primitive: canal for tendon No. 3 a groove (A) (Fig. 31A, 31B, 31D); derived from primitive: canal for tendon No. 3 a bony canal (B) (not illustrated); derived from primitive: canal for tendon No. 3 a bony canal in Alcidae (D) (Fig. 31C); derived from primitive: canal for tendon No. 3 not detectable on bone (C) (not illustrated).

Character 67: tendinal canal for tendon No. 4 (Fig. 31). The description of this character is the same as for the canal for tendon No. 3.

Coding: primitive: canal for tendon No. 4 a groove (A) (Fig. 31A, 31B, 31C, 31D); derived from primitive: canal for tendon No. 4 a bony canal (C) (not illustrated); derived from primitive: canal for tendon No. 4 not detectable on bone (B) (not illustrated).

Character 68: tendinal canal for tendon No. 6 (Fig. 31). A canal for this tendon is not detectable on the bones of most Charadriiformes; this is probably the primitive state.

Coding: primitive: no canal for tendon No. 6 detectable on bone (A) (Fig. 31A, 31C); derived from primitive: canal a groove on bone for tendon No. 6 (B) (Fig. 31B, 31D).

Character 69: tendinal canal for tendon No. 5 (Fig. 31). Like the canal for tendon No. 6, the canal for this tendon is usually not detectable on the bone. Grooves are found only in the Vanellinae and Recurvirostrinae.

Coding: primitive: no canal for tendon No. 5 detectable on bone (A) (Fig. 31A, 31C, 31D); derived from primitive: canal a groove for tendon No. 5 (B) (Fig. 31B).

Character 70: alignment of tendinal canals No. 2, 3, and 4 (Fig. 31). The derived state for this character is the condition found in the snipes and woodcocks, in which the canals for tendons No. 2, 3, and 4 lie on a straight line passing through the centers of canals No. 2 and 4.

Coding: primitive: canals for tendons No. 2, 3, and 4 not on a straight line (A) (Fig. 31A, 31B, 31C); derived: canals for tendons

No. 2, 3, and 4 on straight line passing through centers of canals No. 2 and 4 (B) (Fig. 31D).

Charadriinae Plumage Characters

Character pp1: eyestripe. An eyestripe is found in the Burhinidae, Pluvianus, the Glareolidae, and most of the small plovers. I chose the condition in which the eyestripe extends behind the head as the probable primitive state for the plovers.

Coding: primitive: eyestripe extending over eye around back of head (A); derived from primitive: eyestripe present but not extending around back of head (B); derived from (B): eyestripe absent but head not completely black (C); derived from (C): head completely black (D).

Character pp2: loral region. The most common condition among the Charadriinae is the presence of a pigmented loral region (Graul 1973), which is probably the primitive state for this group.

Coding: primitive: darkly pigmented loral region (A); derived from primitive: loral region unpigmented (B); derived from primitive: loral region washed with pale orange-brown like rest of face, unique to Peltohyas (C).

Character pp3: neck collar. The neck of some plovers is completely encircled by a white collar. The state in which a collar is absent was chosen as primitive because it is the state found in most Charadrii.

Coding: primitive: no white collar extending around back of neck (A); derived: white collar completely encircling neck (B).

Character pp4: Area at base of back of neck. In most plovers the back of the neck is the same color as the back; this is assumed to be the primitive state.

Coding: primitive: back of neck same color as back (A); derived from primitive: back of neck black, sometimes connected to a breast band but never an extension of facial pattern (B); derived from primitive: back of neck black and always an extension of facial pattern, sometimes connected to a breast band (C).

Characters pp5, pp6, pp7; breast banding. The wide variation in the markings on the breast plumage of the Charadriinae extends from a completely unpigmented white breast, through various patterns of breast

bands, to a solidly pigmented breast. Breast bands, when present, vary among the species in number, width, and coloration. In this study I used the banding pattern of the breast of the Killdeer (Charadrius vociferus) as a standard to define three breast areas: the area of the upper breast band (Character pp5), the area between the breast bands (Character pp6), and the area of the lower breast band (Character pp7). I recognized only two states for each character, pigmented or unpigmented. (A third state for Character pp7 was used for the finely barred breast of Phegornis.) Since the area of the upper breast band is pigmented and the other areas unpigmented in the juvenal, non-breeding, or breeding plumages of the majority of the Charadriinae, that condition was chosen as primitive. Admittedly, this is a rather crude coding scheme for these characters, but it is adequate as a first approximation.

Coding: Character pp5: primitive: area of upper breast band pigmented (A); derived: area of upper breast band unpigmented (B).

Character pp6: primitive: area between breast bands unpigmented (A); derived: area between breast bands pigmented (B).

Character pp7: primitive: area of lower breast band unpigmented (A); derived from primitive: area of lower breast band pigmented (B); derived from primitive: area of lower breast band finely barred (unique to Phegornis) (C).

Character pp8: belly color. The belly of most of the Charadrii is unpigmented; this is assumed to be the primitive state for the Charadriinae.

Coding: primitive: belly unpigmented (A); derived: belly pigmented (B).

Character pp9: color of under tail coverts. The under tail coverts of most of the Charadrii are unpigmented; this is assumed to be the primitive state in the Charadriinae.

Coding: primitive: under tail coverts unpigmented (A); derived: under tail coverts pigmented (B).

Character pp10: area above forehead. In most of the Charadriinae the color of the forehead and the color of the crown meet directly. In some species with a black forehead a white line separates the forehead from the crown. This latter condition is assumed to be derived

and to represent at least three different states. The condition in Charadrius dubius is thought to be unique because it is found with states of Characters pp3 and pp4 not found in any of the other species which have the white line. The white line is present in the plumage of C. melanops but is partially obscured by an extension of the black forehead mark onto the crown.

Coding: primitive: white line between black forehead and crown absent (A); derived from primitive: white line separating black forehead from crown (B); derived from primitive: like state B for C. dubius (C); derived from state B: white line present but partially obscured by extension of black forehead mark onto crown (D).

Character pp11: tail markings. The usual tail pattern of the Charadriinae is for the outer tail feathers to be white or only partially pigmented proximally, the amount of pigmentation gradually increasing on the inner feathers, with the central tail feathers usually pigmented to the tips. This is assumed to be the primitive condition.

Coding: primitive: outer tail feathers white or partially pigmented proximally, pigmentation increasing toward almost completely pigmented central tail feathers (A); derived from primitive: tail feathers white-tipped with a distinct, darkly pigmented area immediately proximal to the white tips (B); derived from (B): black band across end of tail, with or without white tips (C); derived from primitive: barred or variegated tail pattern (D).

Haematopus Color Characters

Character hp1: eye color. All Old World oystercatchers have red eyes, while all New World ones have yellow eyes. Red eyes were arbitrarily chosen as primitive.

Coding: primitive: red eyes (A); derived: yellow eyes (B).

Character hp2: back color. The plumage of the back of most oystercatchers is dark brown; this is assumed to be the primitive state.

Coding: primitive: back dark brown (A); derived: back black (B).

Character hp3: rump color. Since most of the close relatives (lapwings, avocets, and stilts) of the oystercatchers have a white rump, this state was chosen as primitive.

Coding: primitive: rump white (B); derived: rump same color as back (A).

Character hp4: belly color. Most of the Charadrii have white, unpigmented bellies; this is assumed to be the primitive state for the oystercatchers.

Coding: primitive: white belly (A); derived: dark pigmented belly (B).

Character hp5: color of the base of the quills. The base of the quills is white in most of the Charadrii; this is assumed to be the primitive state for the oystercatchers.

Coding: primitive: base of quills white (A); derived: base of quills pigmented (B).

Character hp6: eye-ring color. The eye-ring of most oystercatchers is red or orange; this is taken to be the primitive state.

Coding: primitive: eye-ring red or orange (A); derived: eye-ring yellow (B).

Character hp7: under wing coverts. The under wing coverts of most oystercatchers are the same color as the belly; this is assumed to be the primitive state.

Coding: primitive: under wing coverts same color as belly (A); derived: under wing coverts contrasting with belly (B).

Avocets and Stilts Color and Foot Characters

Character as1: foreneck color. The foreneck of most avocets and stilts is white; that is assumed to be the primitive state.

Coding: primitive: foreneck white (A); derived: foreneck reddish (B).

Character as2: wingbars. Most avocets and stilts lack wingbars, a state which is assumed to be primitive because of its presence in most oystercatchers and plovers.

Coding: primitive: no wingbars (A); derived: wingbars present (B).

Character as3: under wing coverts. The under wing coverts of most avocets and stilts and their close relatives the oystercatchers are white; this is assumed to be the primitive state.

Coding: primitive: under wing coverts white (A); derived from

primitive: primary under wing coverts black, secondary under wing coverts white (B); derived from (B): under wing coverts all black (C).

Character as4: foot webbing. Since the feet of most of the Charadriinae are unwebbed, webbed feet is assumed to be the derived state.

Coding: primitive: feet unwebbed (A); derived: feet webbed (B).

RESULTS OF THE COMPATIBILITY ANALYSES

I. The Charadriiformes

The compatibility analysis of the 70 characters and 227 EUs in this study yielded one largest clique of 23 characters:

Charadriiformes Clique: 1, 7, 9, 13, 14, 17, 19, 21, 22, 26, 33, 37, 39, 40, 42, 43, 46, 48, 49, 52, 53, 55, 70.

The tree defined by this clique (Fig. 32) shows that the Charadriiformes form three monophyletic lines which I shall call suborders: the Scolopaci (Jacanidae, Rostratulidae, Scolopacidae, Phalaropodidae, and Thinocoridae: nodes bb, cu, do, go, j1, j2, pe, s1, s2, sc, t1, and t2); the Charadrii (Stercorariidae, Laridae, Dromadidae, Glareolidae, Burhinidae, Chionididae, Charadriidae, Haematopodidae, Ibidorhyncha, and Recurvirostridae: nodes ch, co, ep, gt, hc, ja, mp, po, sb, tk, v1, v2, and wb); and the Alcidae (nodes a1 and a2).

Since the relationships among the Scolopaci and among the Charadrii are poorly resolved by this analysis, each suborder was analyzed separately to find secondarily compatible characters. Subsequently, analyses of smaller and smaller subgroups identified as monophyletic by a previous analysis were made until all locally compatible characters had been found and maximal resolution of relationships had been made. The Alcidae were not analyzed further.

II. The Suborders of the Charadriiformes

A. The Scolopaci

The compatibility analysis of the 54 characters which vary among the 87 EUs in this group yielded eight largest cliques of 25 characters each:

Scolopaci Clique A: 1, 3, 4, 6, 8, 9, 17, 18, 21, 22, 23, 24, 26, 28, 44, 45, 46, 47, 48, 52, 61, 62, 66, 68, 70

Scolopaci Clique B: 1, 3, 4, 6, 8, 9, 17, 18, 21, 22, 23, 24, 26, 28, 44, 45, 46, 47, 48, 52, 61, 62, 67, 68, 70

Fig. 32. Preliminary estimate of the phylogeny of the Charadriiformes. The tree defined by the 23 primary characters for the order. Abbreviations: a1, Endomychura; a2, Cepphus, Uria; bb, Limicola; ch, Dromas, Glareolidae (part); co, Cursorius; cu, Prosobonia, Bartramia, Numenius; do, Limnodromus; ep, Pluvianus; go, Limosa; gt, Stercorariidae (part), Laridae, Rynchops; hc, Hoploxypterus; j1, Jacanidae (part); j2, Jacanidae (part); ja, Stercorariidae (part); mp, Pluvianellus; pe, Actitis, Aphriza, Calidris, Eurynorhynchus, Micropalama, Tryngites, Philomachus; po, Peltohyas, Charadriinae (part), Haematopus, Ibidorhyncha, Recurvirostridae; t1, Tringa (part), Catoptrophorus, Heteroscelus; t2, Tringa (part); tk, Burhinidae; s1, Coenocorypha; s2, Lymnocryptes, Gallinago, Philohela, Scolopax; sc, Phalaropodidae, Thinocoridae, Rostratulidae, Xenus, Arenaria; v1, Vanellinae (part); v2, Vanellinae (part); wb, Anarhynchus.

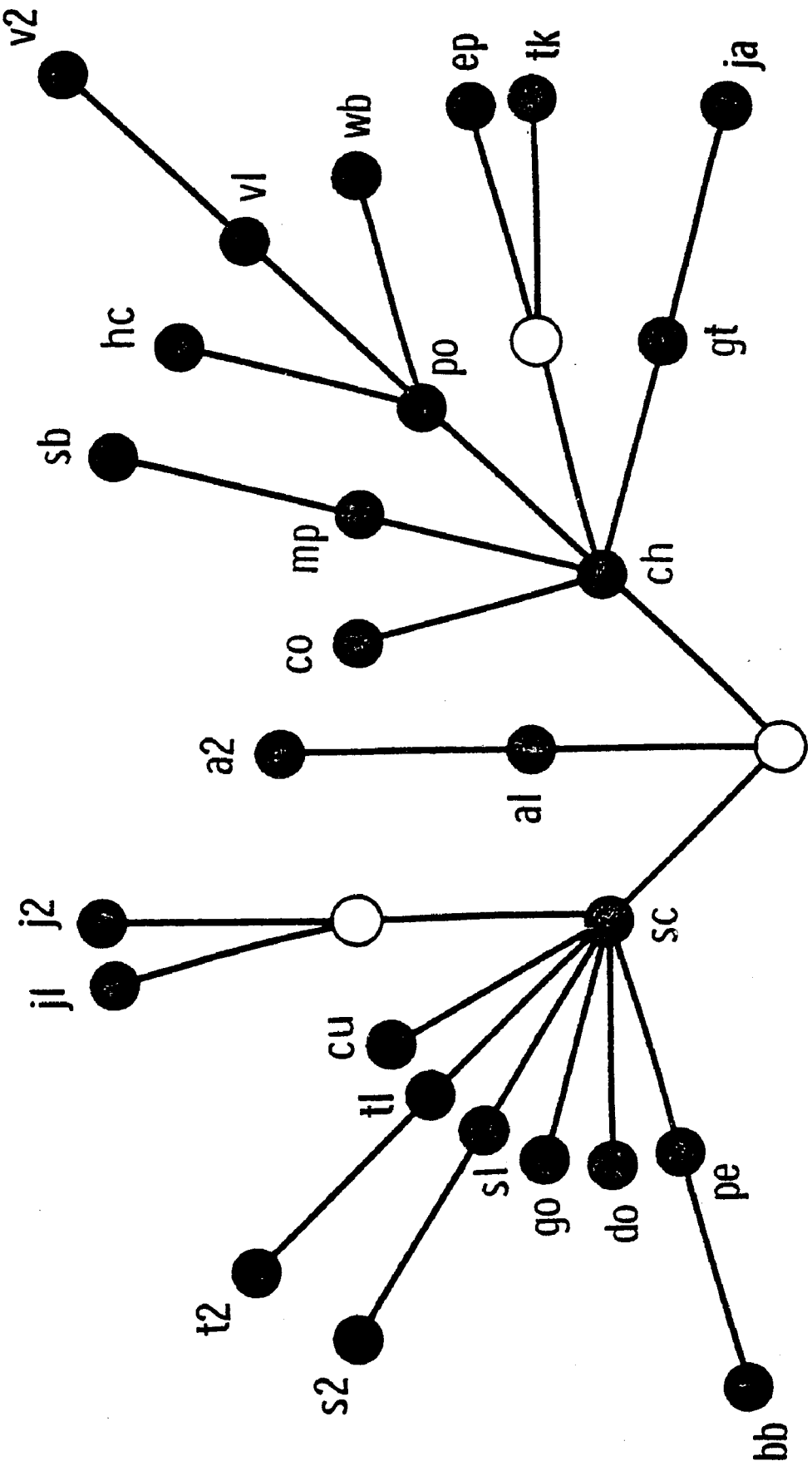

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Fig. 32

Scolopaci Clique C: 1, 3, 4, 8, 9, 17, 18, 19, 21, 22, 23, 24, 26, 28, 44, 45, 46, 47, 48, 52, 61, 62, 66, 68, 70

Scolopaci Clique D: 1, 3, 4, 8, 9, 17, 18, 19, 21, 22, 23, 24, 26, 28, 44, 45, 46, 47, 48, 52, 61, 62, 67, 68, 70

Scolopaci Clique E: 1, 3, 4, 6, 8, 9, 13, 17, 21, 22, 23, 24, 26, 28, 44, 45, 46, 47, 48, 52, 61, 62, 66, 68, 70

Scolopaci Clique F: 1, 3, 4, 6, 8, 9, 13, 17, 21, 22, 23, 24, 26, 28, 44, 45, 46, 47, 48, 52, 61, 62, 67, 68, 70

Scolopaci Clique G: 1, 3, 4, 8, 9, 13, 17, 19, 21, 22, 23, 24, 26, 28, 44, 45, 46, 47, 48, 52, 61, 62, 66, 68, 70

Scolopaci Clique H: 1, 3, 4, 8, 9, 13, 17, 19, 21, 22, 23, 24, 26, 28, 44, 45, 46, 47, 48, 52, 61, 62, 67, 68, 70.

While this seems like a bewildering set from which to pick a best estimate, the choice is straightforward. Twenty-two characters appear in all the cliques. If one compares pairs of cliques starting with Clique A, both members of a pair are identical except that the first member contains Character 66 while the second contains Character 67. These two characters assort the species of Gallinago and Lymnocryptes between nodes s2 and s3 on all the trees defined by these cliques. The choice of Character 66 versus 67 is discussed in a subsequent analysis. This leaves a choice among four pairs of cliques; only four remaining characters (6, 13, 18, and 19) do not appear in all the cliques. Of these, only Characters 13 and 19 were included in the largest clique found in the Charadriiformes analysis; thus they have already been found reliable in a more rigorous analysis. On this basis the tree defined by Clique D (Fig. 33B) was chosen as the best estimate of relationships among the Scolopaci. Fig. 33A shows the tree defined by Clique A, which includes Characters 6 and 18.

On Tree B two lines diverge from the ancestor of the suborder. The Jacanidae (nodes j1 and j2) share derived states of Characters 44, 45, 46, 47, 48, 52, and 61, while the Rostratulidae, Scolopacidae, Phalaropodidae, and Thinocoridae (nodes bb, cu, do, go, pe, ph, ro, s1, s2, s3, sa, ss, t1, t2, ts, tr, w1, w2, and xe) share derived states of Characters 24 and 61.

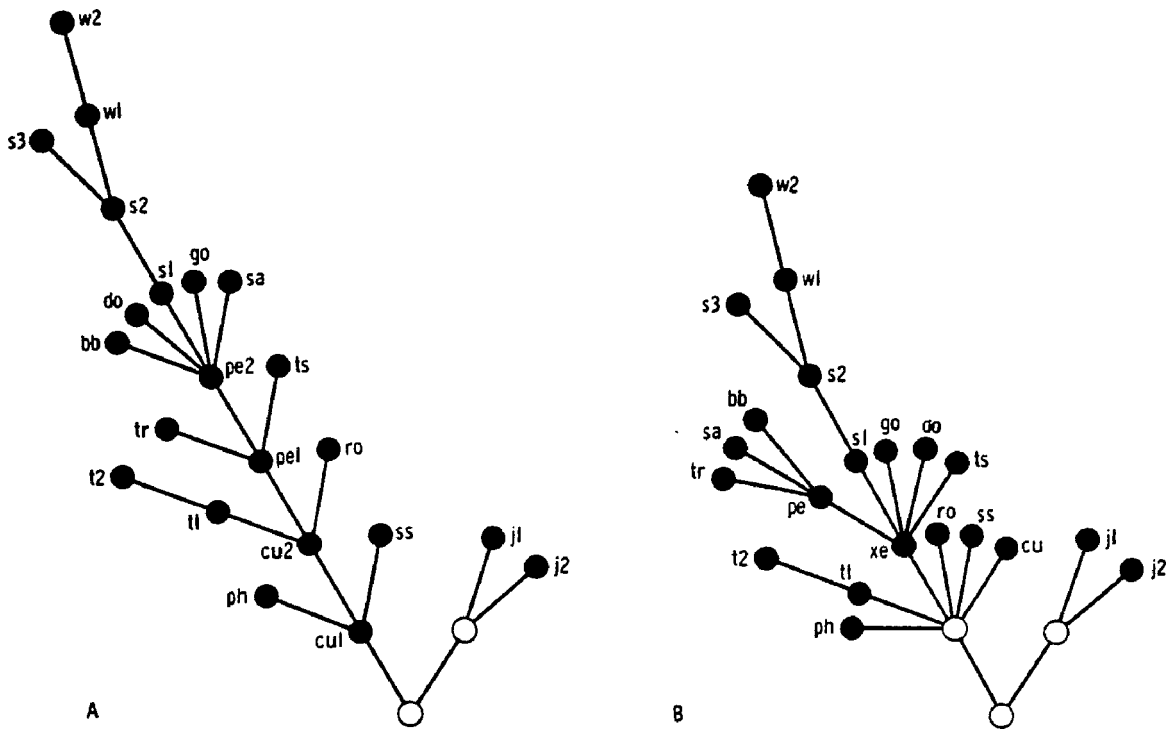

Fig. 33. Two estimates of the phylogeny of the Scolopaci. Abbreviations: bb, Limicola; cu, Prosobonia, Bartramia, Numenius; cul, Prosobonia, Bartramia, Numenius (part); cu2, Numenius (part); do, Limnodromus; go, Limosa; jl, Jacanidae (part); j2, Jacanidae (part); pe, Actitis, Aphriza, Calidris (part), Eurynorhynchus, Micropalama, Philomachus; pel, Actitis, Aphriza, Calidris (part), Philomachus; pe2, Xenus, Calidris (part), Eurynorhynchus, Micropalama; ph, Phalaropus; ro, Rostratula, Nycticryphes; sl, Coenocorypha; s2, Lymnocryptes (if Character 66 is true), Gallinago (part); s3, Lymnocryptes (if Character 67 is true), Gallinago (part); sa, Calidris alba; ss, Thinocoridae; tl, Tringa (part), Catoptrophorus, Heteroscelus; t2, Tringa stagnatilis; ts, Arenaria; tr, Tryngites; wl, Philohela; w2, Scolopax; xe, Xenus.

1. The Rostratulidae, Scolopacidae, Phalaropodidae, and Thinocoridae

The compatibility analysis of the 46 characters which vary among the 79 EUs in this assemblage yielded eight largest cliques of 20 characters each. These Cliques are identical to the cliques found in the Scolopaci analysis except that Characters 24, 44, 45, 46, 47, 48, 52, and 61 have been deleted (since they do not vary among the Scolopacoidea) and Characters 10, 41, and 56 added to each clique. As in the Scolopaci analysis only one pair of cliques includes Characters 13 and 19, and it is thus chosen as the best estimate of relationships in this group. Only the tree defined by Clique D (Fig. 34; compare with Fig. 33B) is illustrated. This tree shows that two lines diverge from the common ancestor of this group. The Thinocoridae (node ss) share derived states of Characters 4 and 8, while the Rostratulidae, Scolopacidae, and Phalaropodidae (nodes bb, cu, do, go, pe, ph, ro, s1, s2, t1a, t1b, t2, ts, tr, w1, w2, and xe) share a derived state of Character 10.

2. The Rostratulidae, Scolopacidae, and Phalaropodidae

The compatibility analysis of the 45 characters which vary among the 76 EUs in this assemblage yielded eight largest cliques of 19 characters each. These cliques are identical to the cliques found in the previous analysis except that Character 10 has been deleted from each clique.

On the tree defined by the pair of cliques which include Characters 13 and 19 (see Fig. 34) five phyletic lines radiate from the ancestor of this assemblage. The Rostratulidae (node ro) share derived states of Characters 8 and 35; the Phalaropodidae (node ph) share a derived state of Character 35; Tringa, Catoptrophorus, and Heteroscelus (nodes t1a, t1b, and t2) share derived states of Characters 8, 17, and 22; Prosobonia, Bartramia, and Numenius (node cu) share a derived state of Character 13; and the sandpipers, snipes, and woodcocks (nodes bb, do, go, pe, s1, s2, s3, sa, tr, ts, w1, w2, and xe) share a derived state of Character 4.

Since they contain too few species, the Rostratulidae and Phalaropodidae were not analyzed further. The other lines were examined

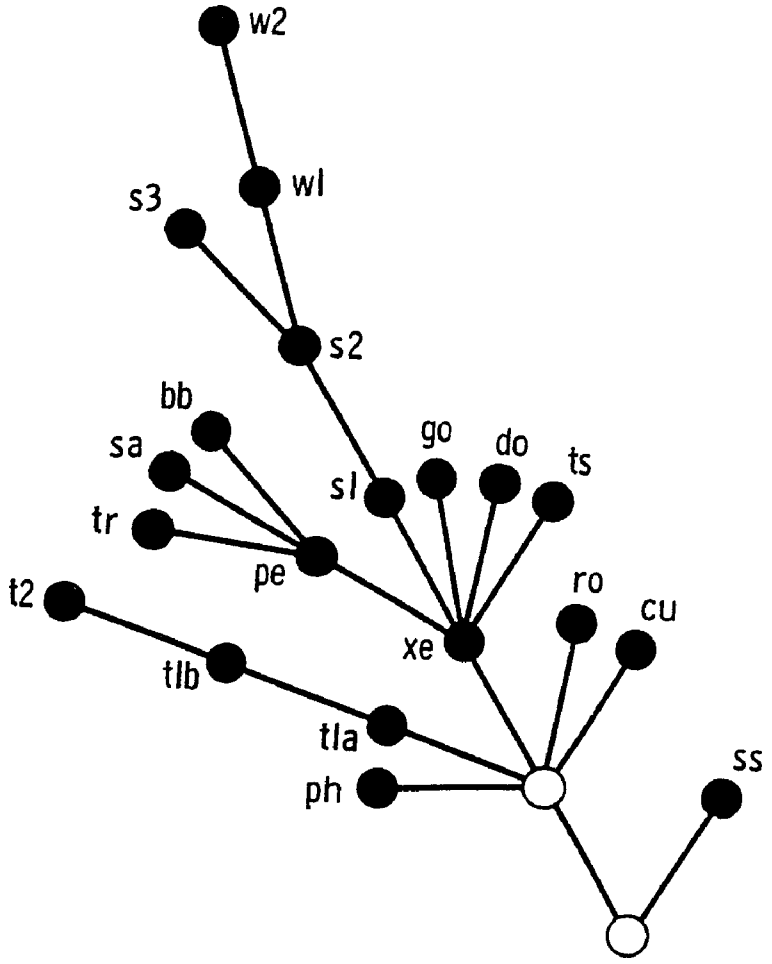

Fig. 34. An estimate of the phylogeny of the Rostratulidae, Scolopacidae, Phalaropodidae, and Thinocoridae. Abbreviations as in Fig. 33 plus tla, Tringa (part), Catoptrophorus; tlb, Tringa (part), Heteroscelus.

in greater detail.

a. The Sandpipers, Snipes, and Woodcocks

The compatibility analysis of the 38 characters which vary among the 49 EUs in this group yielded one largest clique of 22 characters:

Sandpipers, Snipes, and Woodcocks Clique: 1, 3, 5, 8, 9, 19, 20, 21, 22, 23, 28, 29, 51, 54, 56, 58, 60, 62, 64, 66, 68, 70.

This clique includes Character 66 but not 67, an alternative to 66 in the two previous analyses. The tree defined by this clique (Fig. 35) shows that this assemblage consists of two phyletic lines. The snipes and woodcocks (nodes s1, s2, s3, s4, w1, and w2) share derived states of Characters 3, 20, 21, and 22, while the sandpipers (nodes bb, do, er1, er2, go, sa, tr, ts, and xe) share a derived state of Character 5.

Compatibility analysis of the 24 characters which vary among the 14 EUs in the snipes and woodcocks yielded two largest cliques of 17 characters each:

Snipes and Woodcocks Clique A: 1, 5, 15, 20, 23, 25, 31, 35, 36, 50, 54, 56, 58, 59, 66, 68, 70

Snipes and Woodcocks Clique B: 1, 5, 15, 20, 23, 25, 35, 36, 50, 51, 54, 56, 58, 59, 66, 68, 70.

These two cliques differ in only one character. (Character 31 in Clique A is replaced by Character 51 in Clique B.) Since Character 51 was included in the more rigorous Sandpipers, Snipes, and Woodcocks analysis, it is probably more reliable than Character 31, and the tree defined by Clique B (Fig. 36B) is accepted as a better estimate of the relationships among the snipes and woodcocks than the tree defined by Clique A (Fig. 36A).

Tree B shows that the snipes and woodcocks consist of two phyletic lines. Coenocorypha (node s1) possesses a derived state of Character 50; the other species of snipes and woodcocks (nodes s2, s5, s6, w1, w2, and w3) share derived states of Characters 1, 5, 15, 59, and 70. Lymnocryptes (node s2) possesses a derived state of Character 36, while Gallinago and the woodcocks (nodes s5, s6, w1, w2, and w3) share derived states of Characters 25 and 54. The species

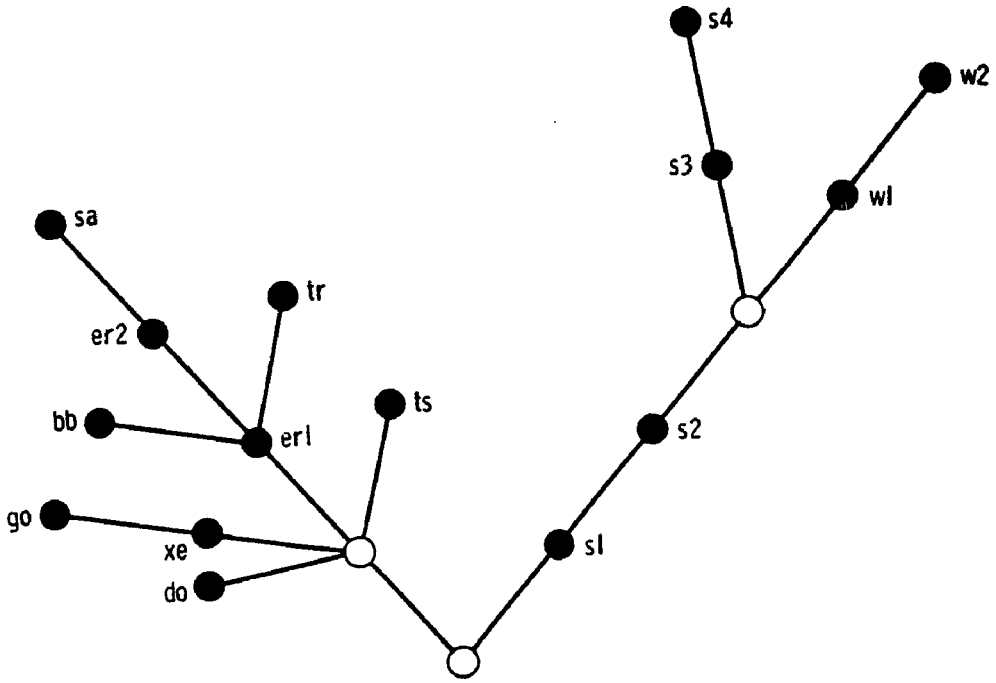

Fig. 35. An estimate of the phylogeny of the sandpipers, snipes, and woodcocks. Abbreviations: bb, Limicola; do, Limnodromus; erl, Actitis, Aphriza, Calidris (part); er2, Calidris (part), Eurynorhynchus, Micropalama, Philomachus; go, Limosa; sl, Coenocorypha; s2, Lymnocryptes; s3, Gallinago (part); s4, Gallinago (part); sa, Calidris alba; tr, Tryngites; ts, Arenaria; wl, Philohela; w2, Scolopax; xe, Xenus.

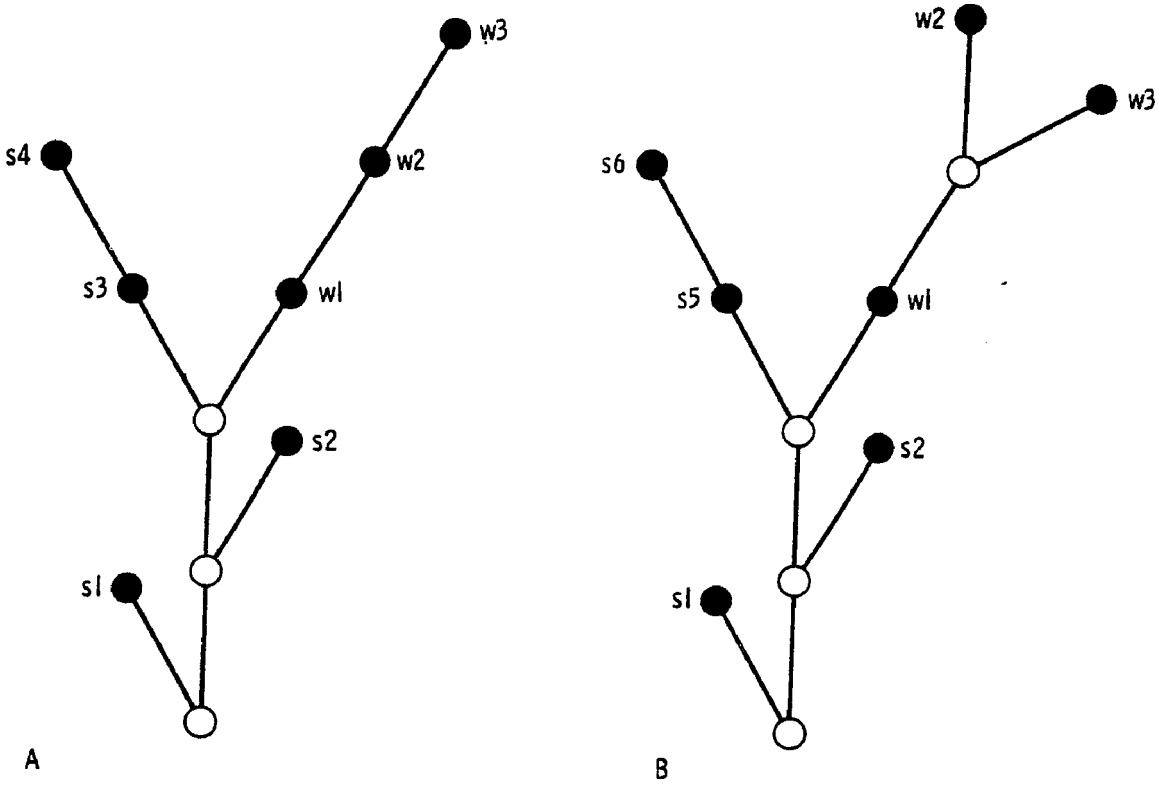

Fig. 36. Two estimates of the phylogeny of the snipes and woodcocks. Abbreviations: s1, Coenocorypha; s2, Lymnocryptes; s3, Gallinago macrodactyla, media, paraguaiae, undulata; s4, G. hardwickii, stenura, megala, nigripennis, gallinago; s5, G. hardwickii, megala, macrodactyla, media, gallinago, paraguaiae; s6, G. stenura, nigripennis, undulata; w1, Philohela; w2, Scolopax r. rusticola; w3, S. r. mira.

of Gallinago (nodes s5 and s6) share a derived state of Character 66, with stenura, nigripennis, and undulata (node s6) sharing a derived state of Character 51. The woodcocks (nodes w1, w2, and w3) share derived states of Characters 35, 56, and 68, with the forms of Scolopax (nodes w2 and w3) sharing derived states of Characters 20, 23, and 68. Scolopax r. rusticola (node w2) possesses a derived state of Character 51, while S. r. mira (node w3) possesses a derived state of Character 50.

Unfortunately, skeletons of the snipes and woodcocks were available for only about 60% of the species; many were in poor condition. Until more and better specimens are available it will be impossible to work out the relationships within the group in greater detail than is presented here.

The compatibility analysis of the 19 characters which vary among the 35 EUs in the sandpipers yielded three largest cliques of 13 characters each:

Sandpipers Clique A: 6, 8, 9, 12, 28, 31, 32, 35, 50, 57, 60, 62, 64

Sandpipers Clique B: 8, 9, 12, 19, 28, 31, 32, 35, 50, 57, 60, 62, 64

Sandpipers Clique C: 8, 9, 12, 19, 28, 29, 31, 32, 35, 57, 60, 62, 64.

These cliques are identical in 11 characters. Only Clique C includes all the characters found to be reliable in previous analyses, while the other two cliques reject characters previously accepted. Thus the tree for Clique C is believed to estimate best the evolutionary history of this group. Tree C (Fig. 37C) states that the sandpipers consist of five phyletic lines. The species of Arenaria (node ts) share a derived state of Character 8; Xenus and Limosa (nodes xe and go) share a derived state of Character 64; the species of Limosa (node go) share derived states of Characters 9, 12, and 60; the species of Limnodromus (node do) share a derived state of Character 9; Limicola (node bb) possesses a derived state of Character 9; and the species of Actitis, Aphriza, Calidris, Eurynorhynchus, Micropalama, Tryngites, and Philomachus (nodes p4, p6, p7, ru, sa, and tr) share a derived state of Character 19.

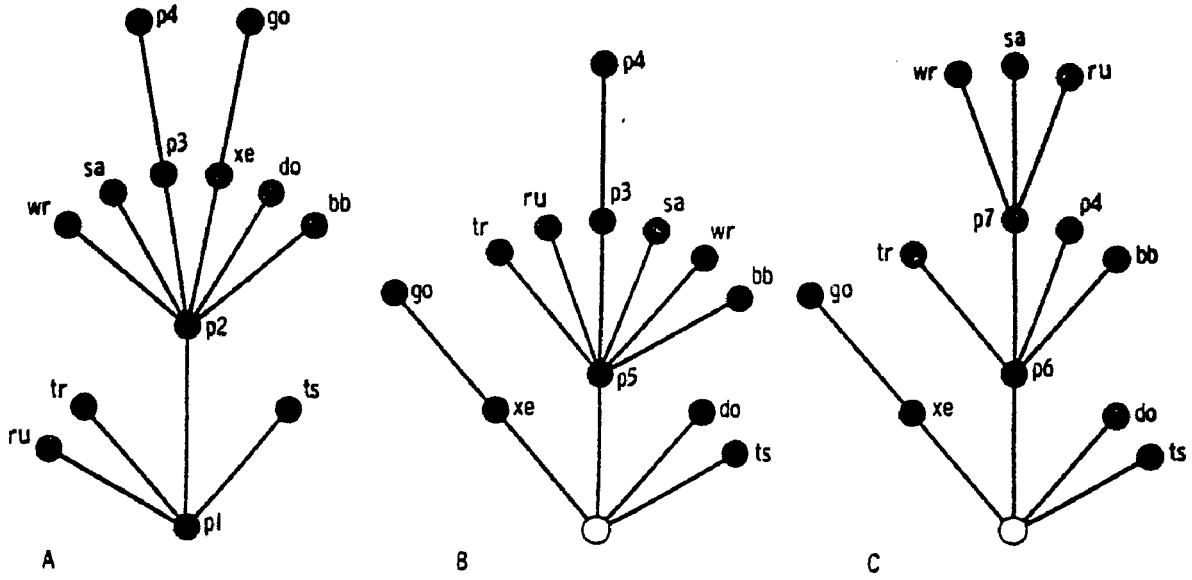

Fig. 37. Three estimates of the phylogeny of the sandpipers. Abbreviations: bb, Limicola; do, Limnodromus; go, Limosa; pl, Actitis, Aphriza, Calidris (part); p2, Calidris (part), Eurynorhynchus, Micropalama; p3, Calidris (part); p4, Calidris subminuta; p5, Actitis, Aphriza, Calidris (part), Eurynorhynchus, Micropalama; p6, Actitis, Aphriza, Calidris (part); p7, Calidris (part), Eurynorhynchus, Micropalama; ru, Philomachus; sa, Calidris alba; tr, Tryngites; ts, Arenaria; wr, Calidris fuscicollis; xe, Xenus.

The compatibility analysis of the 14 characters which vary among the 25 EUs of peeps and their allies yielded four largest cliques of nine characters each:

Peeps and Allies Clique A: 6, 25, 28, 31, 32, 35, 36, 57, 62

Peeps and Allies Clique B: 6, 25, 28, 30, 31, 32, 35, 57, 62

Peeps and Allies Clique C: 6, 28, 31, 32, 35, 36, 50, 57, 62

Peeps and Allies Clique D: 6, 28, 30, 31, 32, 35, 50, 57, 62.

All these cliques, however, reject Character 29, which was included in the best clique of the previous analysis. The Peeps analysis also yielded two cliques of eight characters each:

Peeps and Allies Clique E: 28, 31, 32, 35, 36, 57, 62, 63

Peeps and Allies Clique F: 28, 29, 30, 31, 32, 35, 57, 62.

Clique F is the largest clique which contains Character 29, thus agreeing with the previous analysis, and on the basis of previous analyses the tree it defines (Fig. 38F) is probably the best estimate of relationship which can be obtained from the characters used.

b. The Tattlers

Two largest cliques of six characters each were found in the compatibility analysis of the 13 characters which vary among the 12 EUs in this group:

Tattler Clique A: 26, 30, 36, 50, 63, 65

Tattler Clique B: 26, 30, 36, 41, 50, 63.

These two cliques differ by only one character. (Character 65 in Clique A is replaced by Character 41 in Clique B.) While Character 30 separates all the other tattlers from Tringa solitaria on the trees defined by these cliques (Fig. 39), its truth is in doubt, since it is based on Burton's (1974) discovery of the probable primitive state in his dissection of a single specimen of Tringa solitaria. All the other tattlers except some specimens of T. totanus have the derived state for this character. The usual state for T. solitaria thus may well be the derived state as in all the other tattlers. The skeletal characters

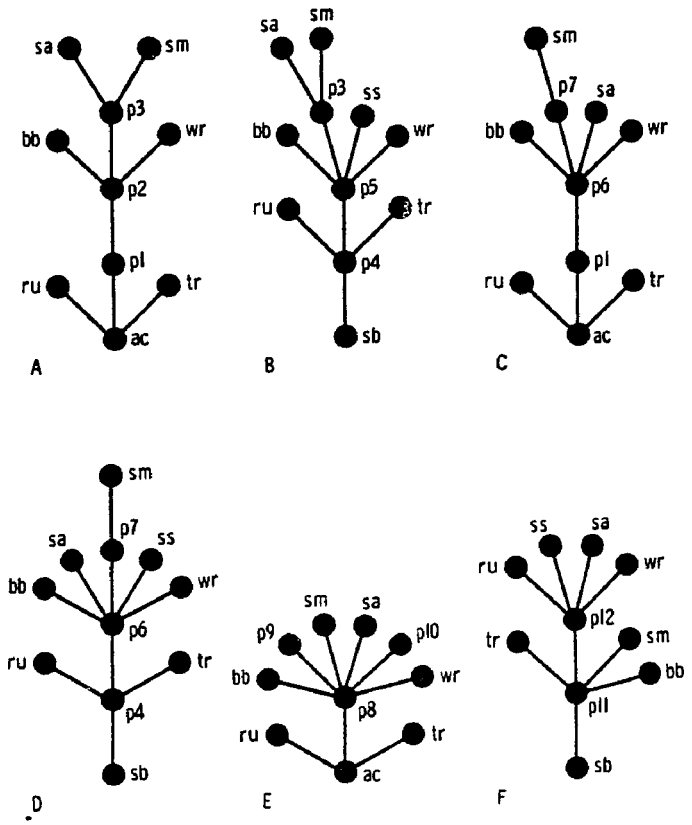

Fig. 38. Six estimates of the phylogeny of the peeps and allies. Abbreviations: ac, Actitis; bb, Limicola; p1, Aphriza, Calidris canutus, tenuirostris, bairdii, melanotos, acuminata; p2, C. pusilla, mauri, ruficollis, minuta, temminckii, maritima, ptilocnemis, ferruginea, Eurynorhynchus; p6, C. pusilla, mauri, ruficollis, minuta, maritima, ptilocnemis, alpina, ferruginea, Eurynorhynchus, Micropalama; p7, C. temminckii, minutilla; p8, C. pusilla, mauri, minuta, bairdii, melanotos, acuminata; p9, Aphriza, C. canutus, tenuirostris, temminckii, maritima, ptilocnemis, alpina, ferruginea, Micropalama; p10, C. ruficollis, minutilla, Eurynorhynchus; p11, Actitis, C. canutus, tenuirostris, ferruginea; p12, C. pusilla, mauri, ruficollis, minuta, temminckii, minutilla, bairdii, melanotos, acuminata, maritima, ptilocnemis, alpina, Eurynorhynchus; ru Philomachus; sa, C. alba; sb, Aphriza; sm, C. subminuta; ss, Micropalama; tr, Tryngites; wr, C. fuscicollis.

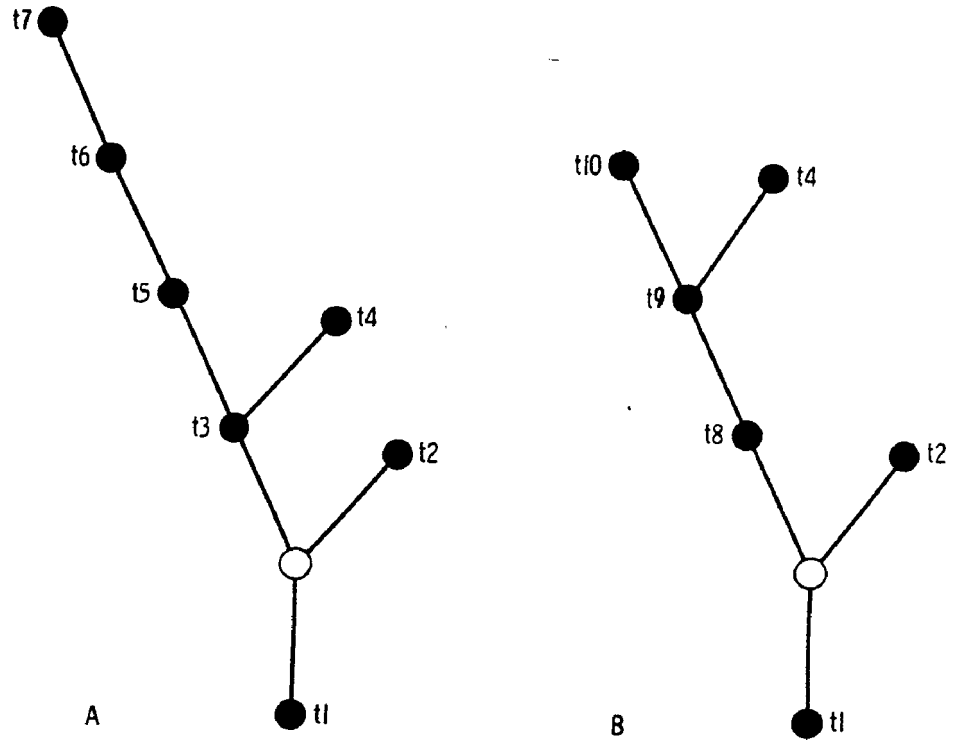

Fig. 39. Two estimates of the phylogeny of the tattlers. Abbreviations: t1, Tringa solitaria; t2, T. ochropus; t3, T. erythropus, melanoleuca, glareola, Catoptrophorus; t4, T. stagnatilis; t5, T. totanus, flavipes, nebularia; t6, Heteroscelus brevipes; t7, H. incanus; t8, T. erythropus, totanus, flavipes, melanoleuca, Catoptrophorus; t9, T. nebularia, glareola; t10, Heteroscelus.

used here are probably insufficient for estimating the relationships among the tattlers (Fig. 39).

c. The Curlews and Prosobonia

The compatibility analysis of the ten characters which vary among the ten species of this group yielded one largest clique of seven characters:

Curlews Clique: 12, 18, 29, 32, 51, 57, 60.

The tree defined by this clique (Fig. 40) states that the curlews and Prosobonia group consists of two phyletic lines. Prosobonia (node pr) possesses derived states of Characters 51 and 57; the species of Bartramia and Numenius (nodes c1, c2, and c3) share derived states of Characters 12 and 29. The species of Numenius, except for minutus, borealis, and tenuirostris on node c1, (nodes c2 and c3) share a derived state of Character 60; tahitiensis and madagascariensis (node c2) share a derived state of Character 32, while phaeopus, arquata, and americanus (node c3) share a derived state of Character 18.

3. The Jacanidae

The compatibility analysis of the seven characters which vary among the eight EUs in this group yielded one largest clique of five characters:

Jacana Clique: 31, 46, 51, 56, 59.

The tree defined by this clique (Fig. 40B) shows that the Jacanidae consist of two phyletic lines. Metopidius, Microparra, Actophilornis, and Irediparra (nodes j1 and j2) share a derived state of Character 46 (wing knobs); Hydrophasianus and Jacana (nodes j3, j4, and j5) share a derived state of Character 46 (wing spurs). Microparra, Actophilornis, and Irediparra (node j2) share a derived state of Character 59, while Jacana jacana and J. spinosa (nodes j4 and j5) share a derived state of Character 56. J. spinosa (node j5) possesses a derived state of Character 51.

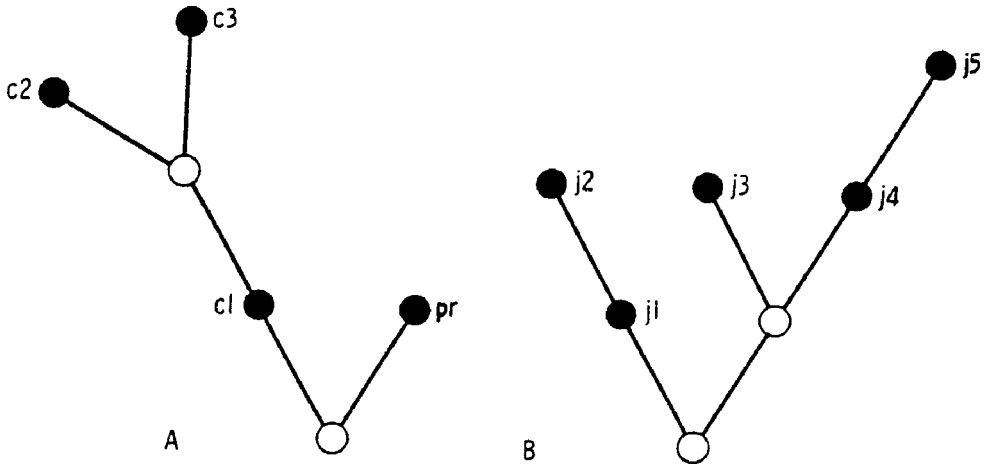

Fig. 40. An estimate of the phylogeny of the curlews and Prosobonia (A) and an estimate of the phylogeny of the Jacanidae (B). Abbreviations: c1, Bartramia, Numenius minutus, borealis, tenuirostris; c2, N. tahitiensis, madagascariensis; c3, N. phaeopus, arquata, americanus; j1, Metopidius; j2, Microparra, Actophilornis, Irediparra; j3, Hydrophasianus; j4, Jacana jacana; j5, J. spinosa; pr, Prosobonia.

B. The Charadrii

The compatibility analysis of the 56 characters which vary among the 137 EUs in this suborder yielded a largest clique of 22 characters:

Charadrii Clique: 1, 3, 6, 7, 10, 11, 12, 15, 33, 37, 39, 41, 45, 46, 49, 53, 54, 55, 58, 59, 66.

On the tree defined by this clique (Fig. 41) Dromas (node d) is not separated from the ancestor of the suborder. (An analysis to define better the relationship of Dromas to the rest of the suborder is discussed below.) This tree defines five phyletic lines in the Charadrii. The Stercorariidae and Laridae (nodes g, ja, and t) share derived states of Characters 37, 41, and 49; Pluvianus and the Burhinidae (nodes ep and tk) share derived states of Characters 1 and 7; the Glareolidae, except Pluvianus and Peltohyas, (nodes c1, c2, c3, and c4) share derived states of Characters 3 and 11; Pluvianellus and Chionis (nodes mp and sb) share derived states of Characters 21 and 46; the species of Chionis (node sb) share a derived state of Character 53, while the plovers and their allies (nodes bs, ch, hc, he, ib, kp, re, rn, v1, v2, and wb) share derived states of Characters 10 and 21.

This analysis indicates that neither Pluvianus nor Peltohyas is a member of the Glareolidae, that Peltohyas is a member of the Charadriidae, and that Pluvianellus is not a member of the Charadriidae but rather is close to Chionis. Since there are so few species in Pluvianellus and Chionis, no further analysis was done on the phyletic line leading to them. Analyses of the other lines are discussed below.

1. The Stercorariidae and Laridae

The skeletons of 32 of the approximately 90 species in this group, which includes 19 of the 20 genera recognized by Peters (1934), were examined in this study. The compatibility analysis of the 15 characters which vary among these species yielded two largest cliques of eight characters each:

Stercorariidae and Laridae Clique A: 32, 34, 54, 55, 57, 64, 65, 67

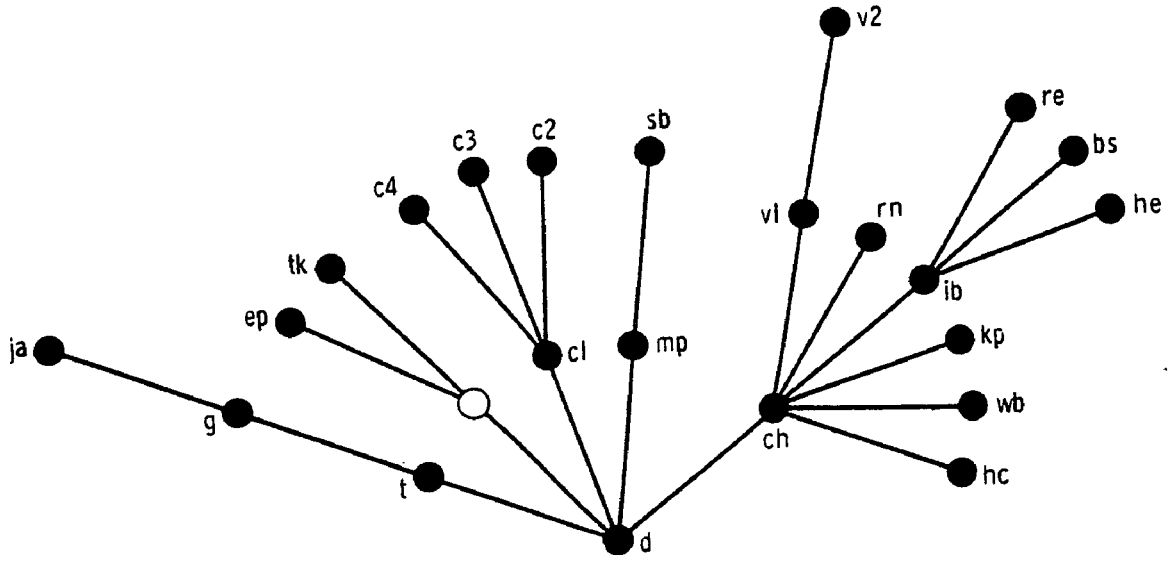

Fig. 41. An estimate of the phylogeny of the Charadrii. Abbreviations: bs, Cladorhynchus; cl, Rhinoptilus (part), Glareola; c2, Cursorius; c3, Rhinoptilus cinctus; c4, Stiltia; ch, Peltohyas, Charadriinae (part); d, Dromas; ep, Pluvianus; g, Stercorariidae (part), Larinae; hc, Hoploxypterus; he, Haematopus; ib, Ibidorhyncha, Himantopus; ja, Stercorariidae (part); kp, Charadrius pecuarius; mp, Pluvianellus; re, Recurvirostra; rn, Charadriinae (part); sb, Chionis; t, Sterninae; tk, Burhinidae; vl, Vanellinae (part); v2, Vanellinae (part); wb, Anarhynchus.

Stercorariidae and Laridae Clique B: 8, 32, 34, 54, 55, 57, 65, 67.

These cliques differ by only one character: Character 64 in Clique A is replaced by Character 8 in Clique B. On both trees (Fig. 42) the gulls and skuas (nodes gu, jl, and j2) share derived states of Characters 54 and 57; the skuas (nodes jl and j2) share a derived state of Character 67, while Stercorarius pomarinus and parasiticus (node j2) share a derived state of Character 55. Gygis (node gy) possesses a derived state of Character 34, while the species of Rynchops (node sk) share a derived state of Character 32. The two trees differ, however, in the arrangement by which these nodes are interrelated. On Tree A (Fig. 42A) the gulls, skuas, and skimmers (nodes gu, jl, j2, and sk) share a derived state of Character 64, while on Tree B (Fig. 42B) the terns and skimmers (nodes gy, sk, and te) share a derived state of Character 8. Unfortunately, the evidence is insufficient to choose between these two estimates. Although it is clear that the skuas and the gulls share a most recent common ancestor, the exact relationships among the gulls, terns, and skimmers remain unresolved.

2. Pluvianus and the Burhinidae

The compatibility analysis of the 16 characters which vary among the EUs in this group yielded two largest cliques of 12 characters each:

Pluvianus and Burhinidae Clique A: 24, 29, 30, 32, 33, 45, 46, 47, 51, 58, 60, 63

Pluvianus and Burhinidae Clique B: 2, 24, 29, 30, 32, 33, 45, 46, 58, 60, 63.

These two cliques differ by only one character: Character 47 in Clique A is replaced by Character 2 in Clique B. On both trees (Fig. 43) Pluvianus (node ep) possesses derived states of Characters 24, 29, 46, and 63, while the Burhinidae (nodes bl, bb, bm, bo, and bv or b2, bb, bm, and bo) share derived states of Characters 30, 33, 45, 58, and 63. On Tree A Burhinus vermiculatus, bistriatus, magnirostris, oedicnemus, and senegalensis (nodes bl, bb, bm, and bo) share a derived state of Character 47, while on Tree B B. vermiculatus, capensis, superciliaris,

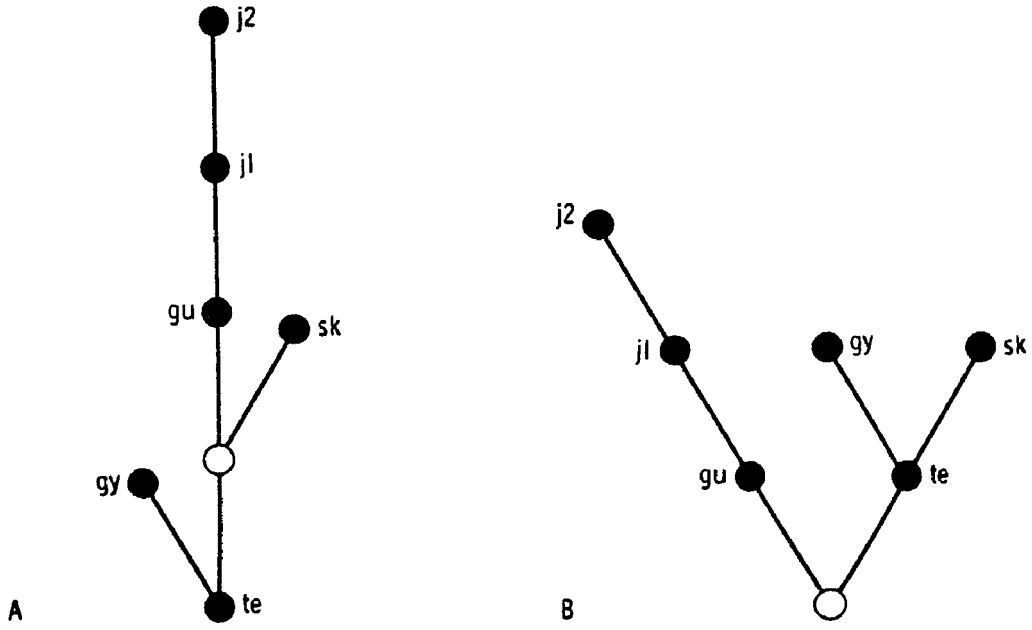

Fig. 42. Two estimates of the phylogeny of the Stercorariidae, Laridae, and Rynchopidae. Abbreviations: gu, Gabianus, Pagophila, Larus, Rhodostethia, Rissa, Creagrus, Xema; gy, Gygis; jl, Catharacta, Stercorarius longicaudus; j2, S. pomarinus, parasiticus; sk, Rynchops; te, Chlidonias, Phaetusa, Gelochelidon, Hydroprogne, Sterna, Thalasseus, Larosterna, Anous.

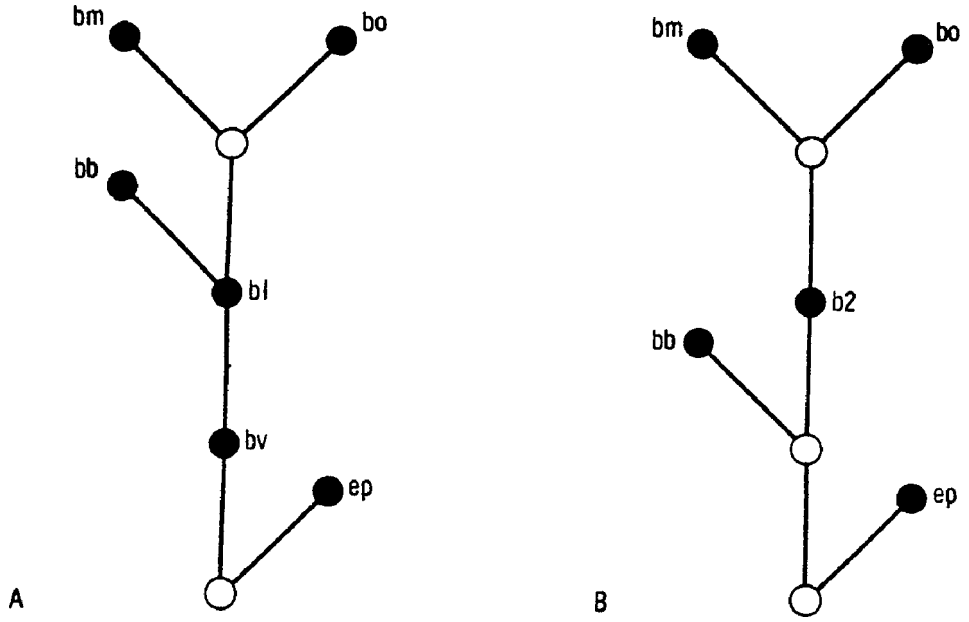

Fig. 43. Two estimates of the phylogeny of the Burhinidae and Pluvianus. Abbreviations: b1, Burhinus capensis, superciliaris, Esacus; b2, B. vermiculatus, capensis, superciliaris, Esacus; bb, B. bistriatus; bm, B. magnirostris; bo, B. oedicnemus, senegalensis; bv, B. vermiculatus; ep, Pluvianus.

magnirostris, oedicnemus, senegalensis, and Orthorhamphus (nodes b2, bm, and bo) share a derived state of Character 2. An enlarged character set is needed to work out further the relationships among the Burhinidae.

3. The Glareolidae

The compatibility analysis of the 17 characters which vary among the species in this family yielded one largest clique of 13 characters:

Glareolidae Clique: 18, 20, 24, 30, 32, 39, 44, 50, 51, 60, 62, 66, 67.

On the tree defined by this clique (Fig. 44) the species of Cursorius and Rhinoptilus (nodes c1, c2, r1, r2, and r3) share derived states of Characters 44 and 62; the species of Glareola and Stiltia (nodes g1, g2, and st) share a derived state of Character 30. Rhinoptilus chalcopterus and cinctus (nodes r2 and r3) share derived states of Characters 20, 24, and 51, while cinctus (node r3) possesses a derived state of Character 66. The species of Cursorius (nodes c1 and c2) share derived states of Characters 20 and 39, while C. cursor and rufus (node c2) share derived states of Characters 50 and 67. Stiltia (node st) possesses a derived state of Character 66; the species of Glareola (nodes g1 and g2) share derived states of Characters 32 and 60, while G. nuchalis, cinerea, and lactea (node g2) share a derived state of Character 18.

4. The Plovers and Their Allies

The compatibility analysis of the 35 characters which vary among the 78 EUs in this group yielded one largest clique of 21 characters:

Plovers and Allies Clique: 2, 6, 8, 12, 15, 20, 21, 25, 27, 29, 33, 38, 41, 46, 47, 50, 51, 59, 60, 64, 67.

The tree defined by this clique (Fig. 45) shows the small plovers, Charadriinae (nodes hc, kp, p1, p2, r1, r2, and wb) as the basal group of this line. The lapwings (nodes v1, v2, v3), oystercatchers (nodes h1, h2), the Ibisbill (node ib), and the avocets and stilts (nodes a1, a2, bs, and st) share a derived state of Character 29.

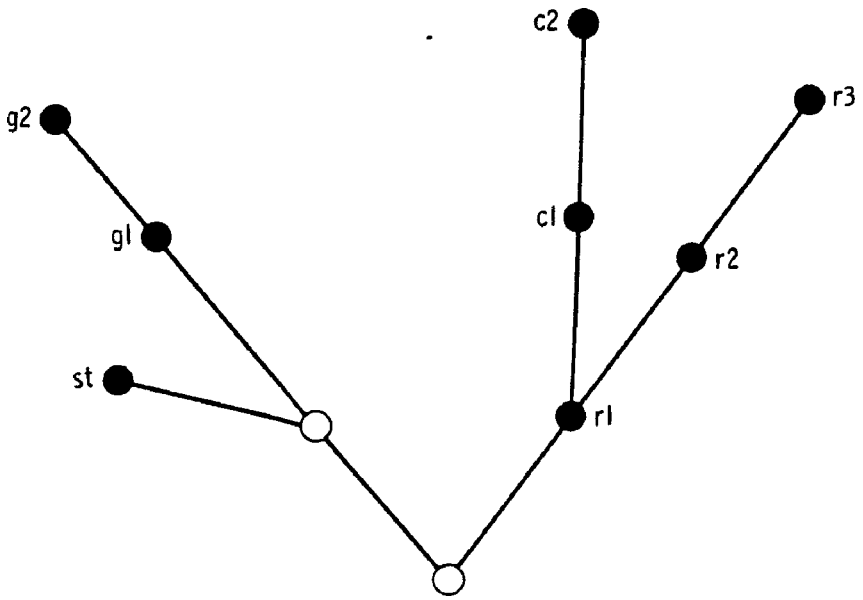

Fig. 44. An estimate of the phylogeny of the Glareolidae. Abbreviations: c1, Cursorius temminckii, coromandelicus; c2, C. cursor, rufus; g1, Glareola pratincola, maldivarum, nordmanni, ocularis; g2, G. nuchalis, cinerea, lactea; r1, Rhinoptilus africanus; r2, R. chalcopterus; r3, R. cinctus; st, Stiltia.

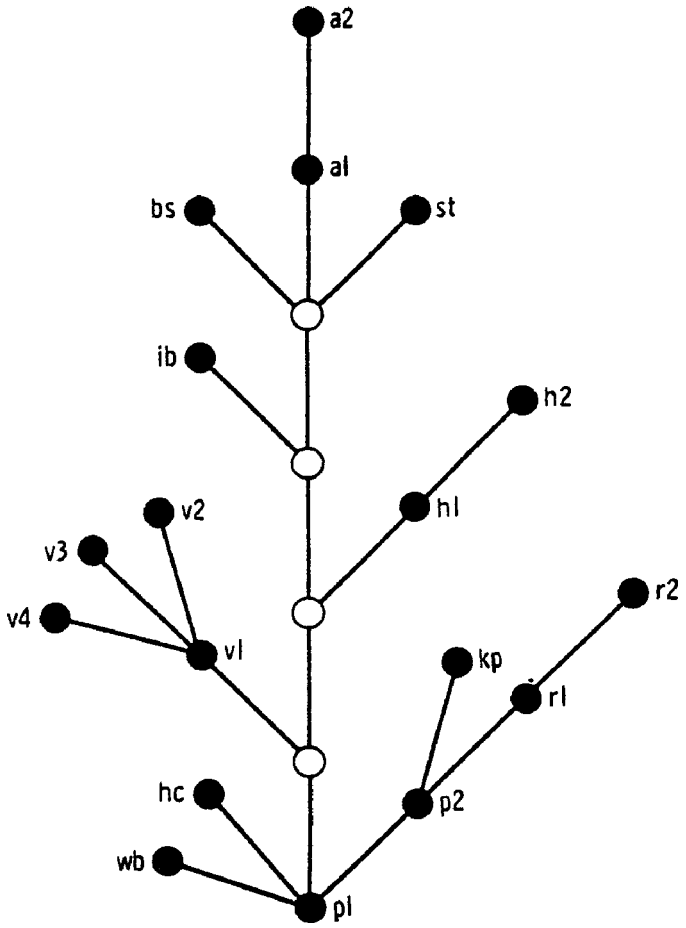

Fig. 45. An estimate of the phylogeny of the plovers and their allies. Abbreviations: a1, Recurvirostra (part); a2, R. avosetta; bs, Cladorhynchus; h1, Haematopus (part); h2, Haematopus (part); hc, Hoploxypterus; ib, Ibidorhyncha; kp, Charadrius pecuarius; p1, Peltohyas, Pluvialis, Charadrius (part), Phegornis; p2, Charadrius (part), Thinornis; r1, Charadrius (part); r2, C. placidus; st, Himantopus; v1, Vanellus (part); v2, Vanellus (part); v3, V. lugubris; v4, V. tricolor; wb, Anarhynchus.

a. The Charadriinae

The compatibility analysis of the 12 characters which vary among the species of the Charadriinae yielded one largest clique of seven characters:

Charadriinae Clique A: 21, 25, 30, 41, 46, 50, 59.

The tree defined by this clique is shown in Fig. 46A. Since four of the seven characters have derived states unique to one EU each, they are of no use in determining relationships. All the species of small plovers except Hoploxypterus, the species of Pluvialis, Charadrius bicinctus, mongolus, asiaticus, veredus, ruficollis, morinellus, modestus, and Phegornis on nodes hc and pl (nodes p2, p3, wb, kp, rl, and r2) share the derived state of Character 30 (site of origin of M. rectus capitis); C. pecuarius, ruficapillus, sanctaehelenae, tricollaris, melanops, cinctus, cucullatus, hiaticula, semipalmatus, melodus, dubius, alexandrinus dealbatus, a. tenuirostris, marginatus, vociferus, wilsonia, placidus, and Thinornis (nodes p3, kp, rl, and r2) share the derived state of Character 25 (presence of an origin of M. complexus on vertebra 4), while C. cucullatus, hiaticula, semipalmatus, melodus, dubius, alexandrinus dealbatus, a. tenuirostris, marginatus, vociferus, wilsonia, and placidus (nodes rl and r2) share the derived state of Character 41 (symphysis of furcula).

This result is unsatisfactory. The estimates of relationship are based on only three characters. Furthermore, two of these (25 and 30) are based on published data (Burton 1974) and were not directly observed in this study. (The states for some species were estimated here.) Finally, two species, Charadrius mongolus and leschenaultii, which are almost identical except in size and which are likely sister species, have been placed on different nodes.

To estimate better the relationships among the Charadriinae an additional set of 11 plumage characters (see Character Descriptions and Appendix IV) was devised, and a compatibility analysis was made on the combined set of the original 12 skeletal and the 11 new plumage characters. This analysis yielded two largest cliques of 11 characters each:

Fig. 46. Three estimates of the phylogeny of the Charadriinae. Abbreviations: ad, Peltohyas; eu, Charadrius asiaticus, veredus; hc, Hoploxypterus; kp, C. pecuarius; p1, Pluvialis, C. bicinctus, mongolus, asiaticus, veredus, ruficollis, morinellus, modestus, Phegornis; p2, Peltohyas, C. obscurus, venustus, falklandicus, alticola, collaris, leschenaultii, montanus; p3, C. ruficapillus, sanctaehelenae, tricollaris, melanops, cinctus, Thinornis; p4, C. obscurus, venustus, falklandicus, alticola, collaris, leschenaultii, montanus; p5, C. bicinctus, mongolus, modestus, Phegornis; p6, C. obscurus, ruficapillus, falklandicus, alticola, bicinctus, collaris, tricollaris, mongolus, leschenaultii, montanus, modestus, Phegornis; p7, C. sanctaehelenae, cinctus, Thinornis; p8, C. melanops; pd, Pluvialis dominicus; ps, P. squatarola, apricaria, C. ruficollis, morinellus; r1, C. cucullatus, hiaticula, semipalmatus, melodus, dubius, marginatus, alexandrinus dealbatus, a. tenuirostris, vociferus, wilsonia; r2, C. placidus; r3, C. alexandrinus dealbatus, a. tenuirostris, wilsonia; r4, C. cucullatus, hiaticula, semipalmatus, melodus, vociferus; r5, C. dubius; wb, Anarhynchus.

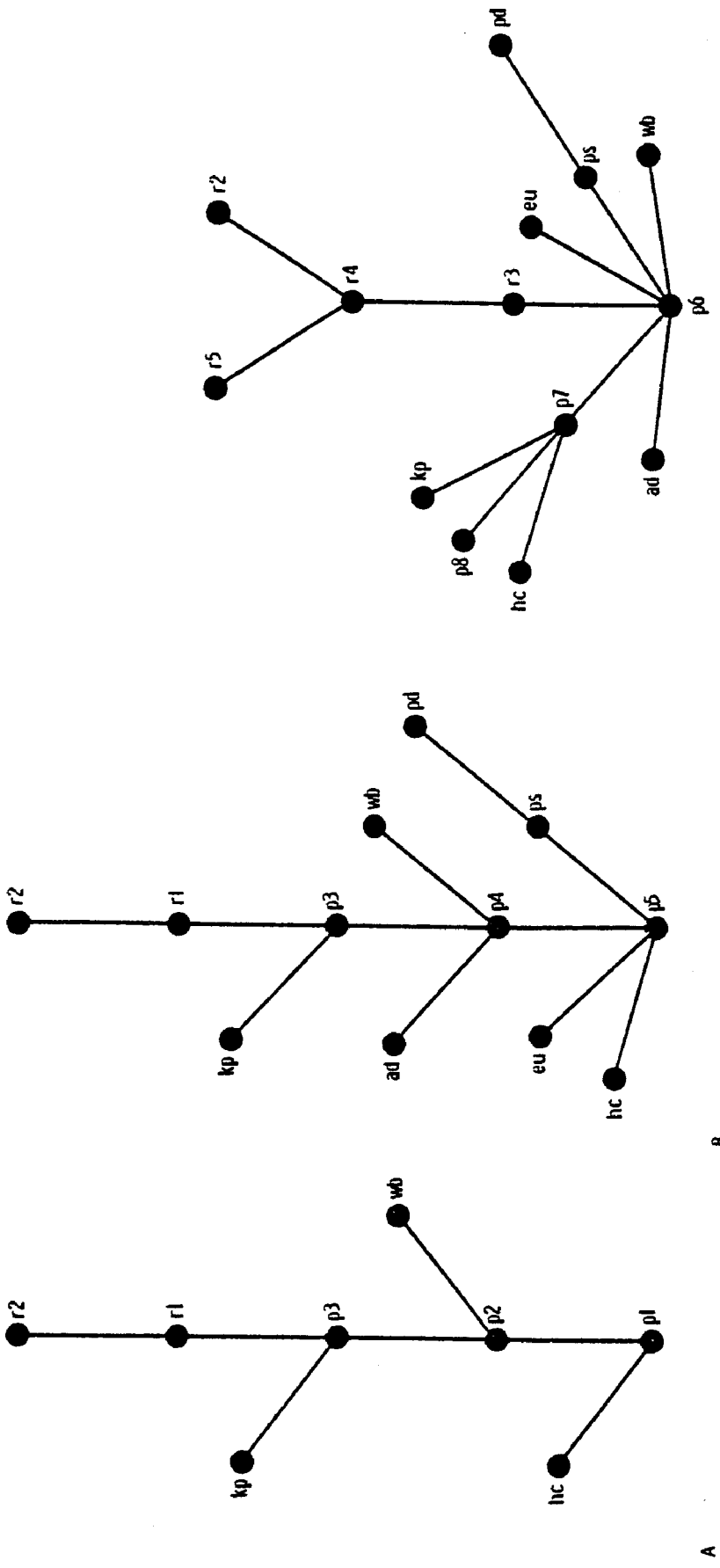
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Fig. 46

Charadriinae Clique B: 21, 25, 30, 41, 46, 50, 59, pp2, pp3, pp8, pp9

Charadriinae Clique C: 21, 41, 46, 50, 59, pp2, pp3, pp4, pp8, pp9, pp10.

Clique B includes Clique A plus four plumage characters; the tree which it defines (Fig. 46B) is the same as that defined by Clique A (Fig. 46A) with five additional steps placed on it. Clique C rejects skeletal Characters 25 and 30, which were questioned above, and includes two plumage characters not included in Clique B. The tree defined by Clique C (Fig. 46C) places C. mongolus and leschenaultii on the same node (p6). Clique C is probably better, since the two characters it accepts (Characters pp4 and pp10) are more complex than the two competing characters (25 and 30) accepted in Clique B.

On Tree C (Fig. 46C) the species of Pluvialis and Charadrius ruficollis and morinellus (nodes ps and pd) share the derived state of Character pp8 (belly pigmentation). C. marginatus, alexandrinus dealbatus, a. tenuirostris, wilsonia, cucullatus, hiaticula, semipalmatus, melodus, vociferus, placidus, and dubius (nodes cm, r2, r3, r4, and r5) share derived states of Character 41 (symphysis of furcula) and Character pp3 (white collar around back of neck), while cucullatus, hiaticula, semipalmatus, melodus, vociferus, placidus, and dubius (nodes r2, r4, and r5) share a derived state of Character pp4 (area behind neck). Hoploxypterus, C. pecuarius, sanctaehelenae, cinctus, melanops, and Thinornis (nodes hc, kp, p7, and p8) share derived states of Character pp4 and Character pp10 (area behind forehead).

b. The Vanellinae

The compatibility analysis of the 13 characters which vary among the 21 EUs in the Vanellinae yielded one largest clique of eight characters:

Vanellinae Clique: 25, 30, 35, 46, 57, 67, 68, 69.

The tree defined by this clique is shown in Fig. 47. Since five of the eight characters in the clique have derived states unique to one EU each, they are of no use in determining relationships. The species

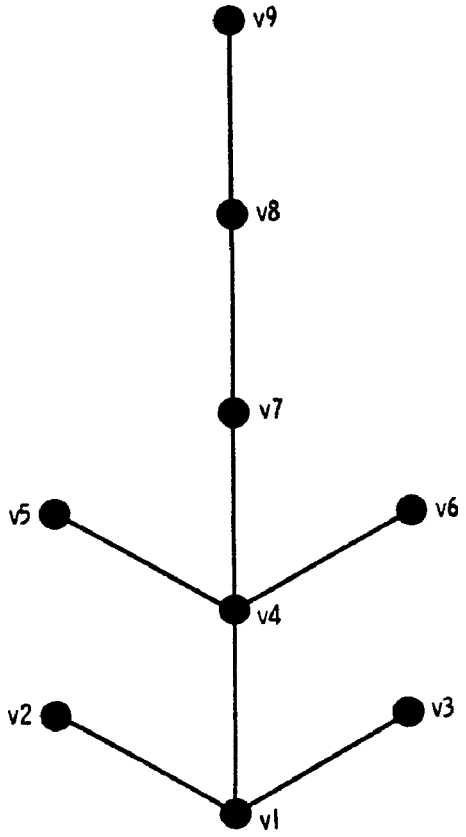

Fig. 47. An estimate of the phylogeny of Vanellus. Abbreviations: v1, Vanellus melanopterus, malabaricus; v2, tricolor; v3, lugubris; v4, gregarius, cinereus, coronatus, tectus; v5, leucurus; v6, vanellus; v7, chilensis, resplendens, albiceps, senegallus, spinosus, armatus, duvaucelii; v8, indicus, macropterus, miles; v9, crassirostris.

of Vanellus except for melanopterus, lugubris, malarbarica, and tricolor on nodes v1, v2, and v3 (nodes v4 through v9) share a derived state of Character 57; chilensis, resplendens, albiceps, senegallus, spinosus, armatus, duvaucelii, indicus, macropterus, miles, and crassirostris (nodes v7, v8, and v9) share a derived state of Character 46 (wing spurs), while indicus, macropterus, miles, and crassirostris share a derived state of Character 68.

c. Haematopus, Ibidorhyncha, Himantopus, Cladorhynchus, and Recurvirostra

The compatibility analysis of the 25 characters which vary among the species of Haematopus, Ibidorhyncha, Himantopus, Cladorhynchus, and Recurvirostra yielded one largest clique of 20 characters:

Haematopus, Ibidorhyncha, Himantopus, Cladorhynchus, and Recurvirostra Clique: 2, 4, 6, 8, 12, 15, 20, 27, 30, 32, 38, 47, 50, 51, 57, 60, 61, 63, 68, 69.

The tree defined by this clique (Fig. 48) is identical in its branching pattern to the branch on which these species occur in the Plovers and Allies analysis tree (Fig. 45). The species of Haematopus (nodes h1 and h2) share derived states of Characters 4, 12, 32, and 38. The species of Ibidorhyncha, Himantopus, Cladorhynchus, and Recurvirostra (nodes a1, a2, bs, ib, and st) share derived states of Characters 27 and 57, while those of Himantopus, Cladorhynchus, and Recurvirostra (nodes a1, a2, bs, and st) share derived states of Characters 8, 61, 63, 68, and 69.

The forms of Haematopus I examined varied in only three skeletal characters. To estimate better their relationships I devised an additional set of seven plumage and eye color characters (see Character Descriptions and Appendix V). The compatibility analysis of this enlarged set of characters yielded three largest cliques of seven characters each:

Haematopus Clique A: 18, 31, hp1, hp3, hp5, hp6, hp7

Haematopus Clique B: 18, 31, hp2, hp3, hp4, hp6, hp7

Haematopus Clique C: 18, 31, hp3, hp4, hp5, hp6, hp7.

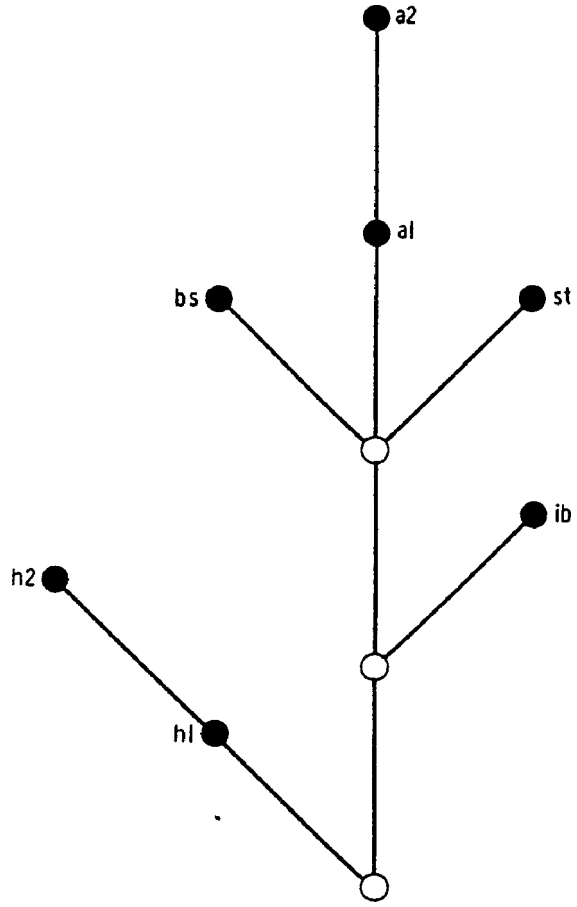

Fig. 48. An estimate of the phylogeny of Haematopus, Ibidorhyncha, Himantopus, Cladorhynchus, and Recurvirostra. Abbreviations: a1, Recurvirostra (part); a2, R. avosetta; bs, Cladorhynchus; h1, Haematopus (part); h2, Haematopus (part); ib, Ibidorhyncha; st, Himantopus.

Since the derived states of four of the characters (18, 31, hp6, and hp7) are unique to one EU each, they are of no use in determining relationships. Although the three cliques differ by only one character each, they make quite different estimates of the relationships among the forms. All the forms except ostralegus and finschi on node h1 (nodes h2 through h9) share the derived states of Characters hp3 (rump color) and hp5 (color of the base of the quills). On Tree A (Fig. 49A) bachmani, frazari, ater, palliatus, and leucopodus (nodes h3, h4, and h5) share the derived state of Character hp1 (eye color), on Tree B (Fig. 49B) leucopodus and moquini (nodes h5 and h7) share the derived state of Character hp2 (back color), and on Tree C (Fig. 49C) bachmani, moquini, fuliginosus, and ater (node h9) share the derived state of Character hp4 (belly color).

The reliability of these trees may be evaluated with outside evidence. The differences between dark brown and black feathers (the states of Character hp2) represent different concentrations of the same pigment and may occur on the same feather (Baker 1974). Such differences thus are probably poor indicators of relationship. The interbreeding of populations of Haematopus having white bellies with those having black bellies (the states of Character hp4) are known in New Zealand (Baker 1973) and in North America (Webster 1943) and suspected in South America (Jehl, Rumboll, and Winter 1973). Belly color is thus probably also a poor indicator of relationship. Since all the Old World Haematopus have red eyes while all those in the New World have yellow eyes (the states of Character hp1), there is zoogeographic evidence that eye color may be a true cladistic character. Only a thorough and detailed analysis of the differences among the breeding populations, such as that of Baker (1973), will unravel the true relationships among these birds.

The compatibility analysis of the nine characters which vary among the species of Himantopus, Cladorhynchus, and Recurvirostra yielded one largest clique of eight compatible characters:

Avocets and Stilts Clique: 6, 15, 35, 47, 51, 60, 62, 65.

The tree defined by this clique (Fig. 50) shows two phyletic lines. The species of Recurvirostra (nodes a1 and a2) share derived states

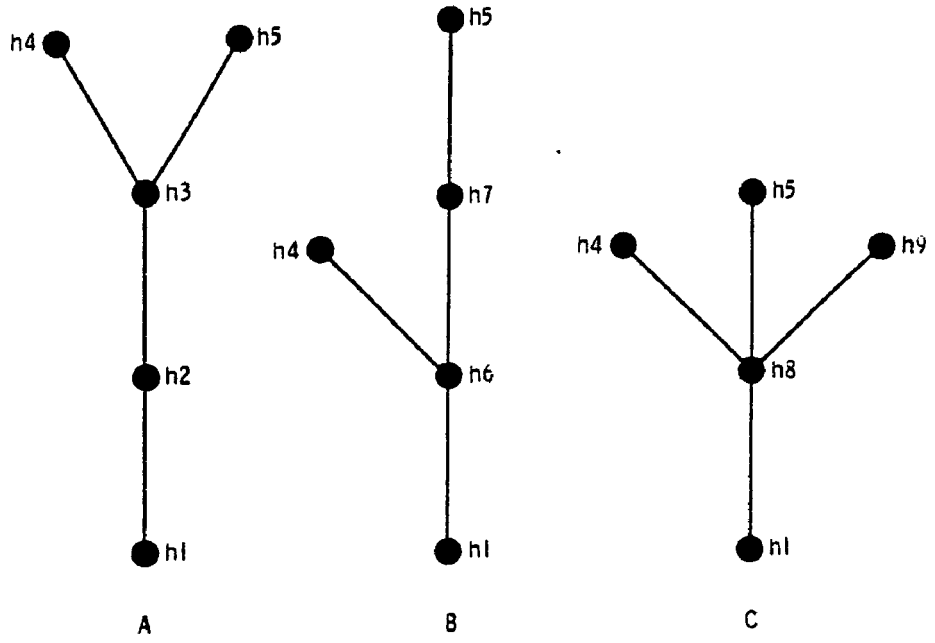

Fig. 49. Three estimates of the phylogeny of Haematopus. Abbreviations: h1, Haematopus ostralegus, finschi; h2, moquini, fuliginosus; h3, bachmani, frazari, ater; h4, palliatus; h5, leucopodus; h6, bachmani, frazari, fuliginosus, ater; h7, moquini; h8, frazari; h9, bachmani, moquini, fuliginosus, ater.

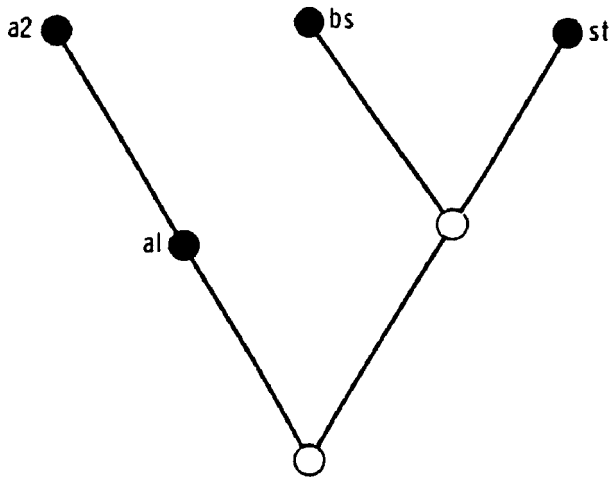

Fig. 50. An estimate of the phylogeny of the avocets and stilts. Abbreviations: a1, Recurvirostra americana, novaehollandiae, andina; a2, R. avosetta; bs, Cladorhynchus; st, Himantopus.

of Characters 6 and 47; R. avosetta (node a2) possesses a derived state of Character 51; Cladorhynchus and Himantopus (nodes bs and st) share a derived state of Character 62; Cladorhynchus (node bs) possesses a derived state of Character 15, while Himantopus (node st) possesses derived states of Characters 35, 60, and 65. This tree indicates that Cladorhynchus is closer to Himantopus than to Recurvirostra. An analysis discussed below, however, indicates that this may not be the case.

III. Analysis of the Charadrii Using Hypothetical Ancestors

My original analysis of the Charadrii produced a tree (Fig. 41) on which Dromas is not separated from the ancestor of the suborder. Furthermore, the other lines in the suborder radiate fanwise from the ancestor, a result which indicates little about the relationships among the various lines. I then investigated the possibility that some of the characters rejected in this analysis would prove compatible with the original clique if some of the lines were replaced by their hypothetical ancestors. Hypothetical ancestors were constructed for the Stercorariidae and Laridae, Glareolidae, Charadriinae, Vanellinae, Haematopus, and the avocets and stilts. The character states for the ancestors were estimated as follows: the ancestor was assigned the most primitive state found in the group for all characters included in the largest clique in the analysis of the group; for characters rejected in the analysis of the group the ancestor was assigned the state found in the majority of the EUs placed near the base of the group tree; if the ancestral state for the group could not be assigned by these two methods, the most primitive state found in the group was used. The hypothetical ancestors constructed thus were used along with the real EUs Dromas, Pluvianus, Pluvianellus, Chionis, Peltohyas, and Ibidorhyncha for a compatibility analysis. The compatibility analysis of the 42 characters which vary among the 13 real and hypothetical EUs in this group yielded one largest clique of 26 characters:

Charadrii Clique B: 1, 3, 7, 10, 11, 12, 16, 20, 21, 32, 33, 34, 37, 38, 41, 44, 45, 46, 49, 51, 53, 57, 58, 68, 69.

Characters 6, 15, 39, 54, 55, 59, and 66, which were included in the original Charadrii clique, were not included in this analysis because

they are constant throughout the EUs used in this analysis. Characters 16, 20, 23, 32, 34, 38, 44, 51, 57, 68, and 69, which were rejected in the original analysis, are included in the largest clique found in this analysis. The tree defined by Charadrii Clique B (Fig. 51) has five internodes not on the original Charadrii tree (Fig. 41); these are defined by Characters 20, 23, 44, 57, 68, and 69. The steps defined by Characters 20, 57, 68, and 69 are the same steps found in the Haematopus, Ibidorhyncha, Himantopus, Cladorhynchus, and Recurvirostra analysis. The steps defined by Characters 23 and 44, however, are unique to this analysis. All the Charadrii except the Stercorariidae and Laridae (nodes as, co, cp, ep, ha, ib, mp, pl, sb, tk, and va) share the derived state of Character 23 and thus form a sister group with the Stercorariidae and Laridae (node gt). The derived state for Character 25 has appeared several times in the Stercorariidae and Laridae. Dromas (node cp) is on a line defined by the derived state of Character 44 in this analysis. The derived state of this character occurs in both the Stercorariidae and Laridae and the Glareolidae.

IV. Analyses Incorporating Possible Reversals

When the character states of each character for each EU are plotted on the final composite estimate of evolutionary history of the Charadriiformes (Fig. 56) several different patterns of character state distribution are found. The primary characters for the study naturally show no instances of homoplasy on the tree, while all the other characters exhibit homoplasy. Some characters (such as Character 34, which shows about 14 transitions on the composite tree but only three transitions on the character state tree) show many transitions on the composite tree which are distributed apparently randomly. Other characters (such as Character 4, which shows about five transitions on the composite tree but only two on the character state tree) show only a few extra transitions on the composite tree. These latter characters are often found to be locally compatible for large portions of the composite tree. (Character 4, for instance, is a true cladistic character for the Scolopaci.) In a few cases, where the distribution of character states suggests that a reversal has taken

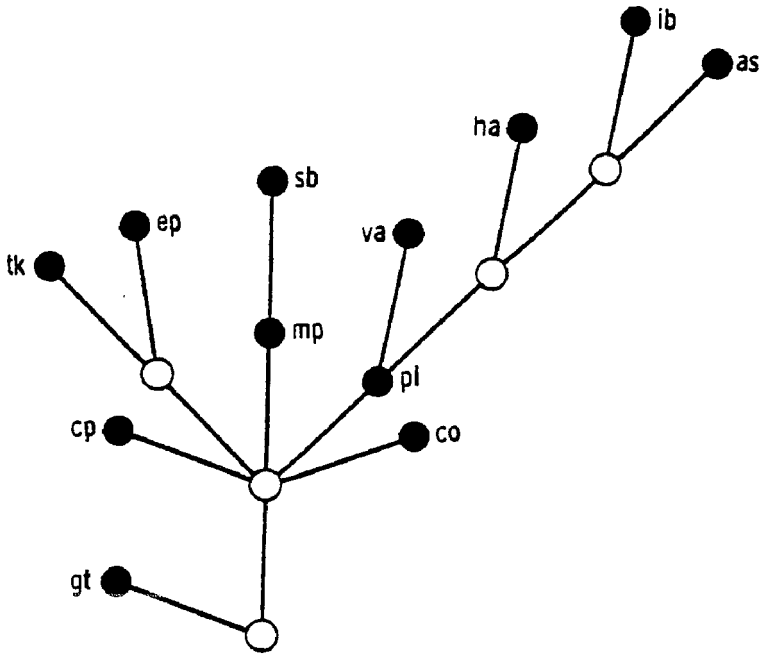

Fig. 51. An estimate of the phylogeny of the Charadrii using hypothetical ancestors. Abbreviations: as, hypothetical ancestor of the avocets and stilts; co, hypothetical ancestor of the Glareolidae; cp, Dromas; ep, Pluvianus; gt, hypothetical ancestor of the Stercorariidae and Laridae; ha, hypothetical ancestor of Haematopus; ib, Ibidorhyncha; mp, Pluvianellus; pl, hypothetical ancestor of the Charadriinae; sb, Chionis; tk, hypothetical ancestor of the Burhinidae; va, hypothetical ancestor of the Vanellinae.

place, a reanalysis using a modified character state tree might be in order. For instance, in the plovers and their allies (Fig. 45) species on nodes h1, h2, kp, p1, p2, r1, r2, v1, v2, v3, v4, and wb share the derived state of Character 4, while species on nodes a1, a2, bs, ib, and st share the primitive state of Character 4. Either the ancestors of the groups with the derived state had the primitive state, and the derived state arose at least three times during the history of the plovers and their allies, or the ancestor of the plovers and their allies had the derived state, and the primitive state was derived once from the derived state (reversal) during the history of the plovers and their allies. The latter hypothesis is a more parsimonious explanation of the character state distribution.

In a few cases a reanalysis of the compatibilities of the characters which vary among the EUs in the snipes and woodcocks, and the plovers and their allies, where possible reversals were identified, was made, using modified character state trees which incorporated the suspected reversals. Revision of the character state trees and reanalyses were not made to make further characters conform to the cladistic patterns already found, but rather to examine whether the reanalyses suggested changes in the original branching patterns. In fact, the results of these analyses suggested the realignment of only one EU and confirmed the branching patterns already determined.

A. The Snipes and Woodcocks

An examination of the distribution of the states of Characters 11, 15, 57, 59, and 63 among the Scolopaci or among the sandpipers, snipes, and woodcocks suggests that the instances of the presumed primitive states of these characters among the snipes and woodcocks represent probable reversals. Reanalysis gave two largest cliques which define the same trees as found in the original snipes and woodcocks analysis (Fig. 36). Characters 15, 59, and 63 with reversals are included in these cliques, but Characters 11 and 57 with reversals, the only two whose inclusion would change the branching patterns previously found, were rejected.

B. The Plovers and Their Allies

An examination of the distribution of the states of Characters 4, 61, 63, and 65 among the plovers and their allies suggests that the instances of the presumed primitive states of these characters among the plovers and their allies represent probable reversals. Reanalysis gave two largest cliques of 23 characters each:

Plovers and Allies Clique B: 2, 4, 6, 8, 12, 15, 20, 21, 25, 27, 29, 33, 38, 41, 46, 47, 50, 51, 59, 60, 64, 65, 67

Plovers and Allies Clique C: 2, 6, 8, 12, 15, 20, 21, 25, 29, 33, 38, 41, 46, 47, 50, 51, 59, 60, 61, 63, 64, 65, 67.

The cliques differ in only two characters: Characters 4 and 27 in Clique B are replaced by Characters 61 and 63 in Clique C. Clique B is identical to Clique A of the original analysis with the addition of Character 4. The trees defined by these cliques (Fig. 52A, 52B) differ in whether the Haematopodidae (nodes h1 and h2) and Ibidorhyncha (node ib) share a common ancestor not shared by other members of the group. Both trees differ from the original tree (Fig. 45) in that Cladorhynchus (node bs) and Recurvirostra (nodes a1 and a2) share a common ancestor not shared with Himantopus (node st).

A reanalysis of the compatibility of the characters which vary among the species of Haematopus, Ibidorhyncha, Himantopus, Cladorhynchus, and Recurvirostra, using the character state trees incorporating the probable reversals, yielded one largest clique of 19 characters:

Haematopus, Ibidorhyncha, Himantopus, Cladorhynchus, and Recurvirostra Revised Clique: 2, 4, 6, 8, 12, 15, 20, 27, 30, 32, 38, 47, 50, 51, 57, 60, 65, 68, 69.

This clique includes Characters 4 and 27 but rejects Characters 61 and 63. The tree defined by this clique (Fig. 53) shows the same branching patterns as Tree A (Fig. 52A) in the previous analysis. This clique differs from the one found in the original analysis in that it rejects Characters 61 and 63 if they are reversed and accepts Character 65 if it is reversed. Character 4 is included either way it is coded.

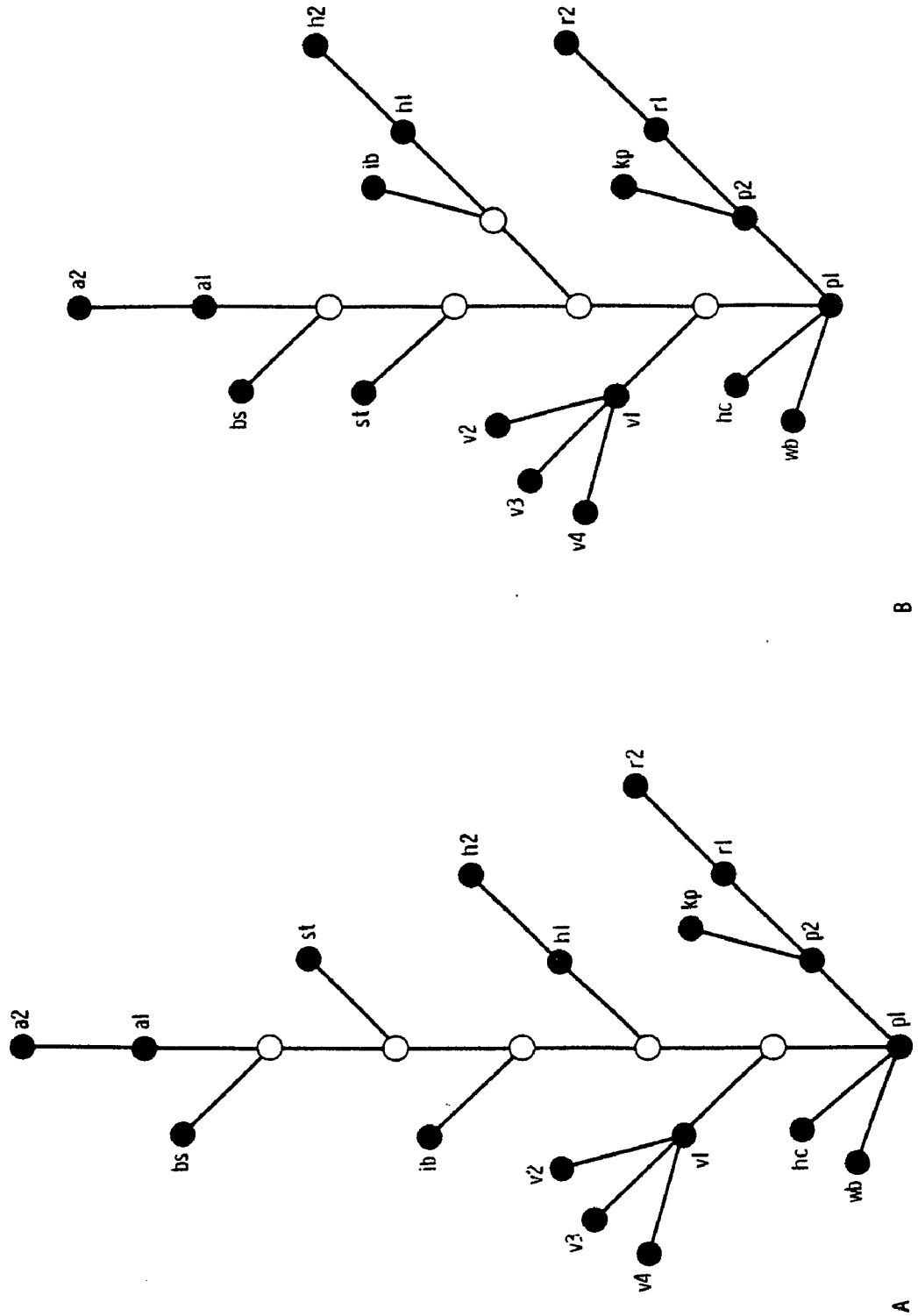

Fig. 52. Two estimates of the plovers and their allies incorporating possible character state reversals. Abbreviations as in Fig. 45.

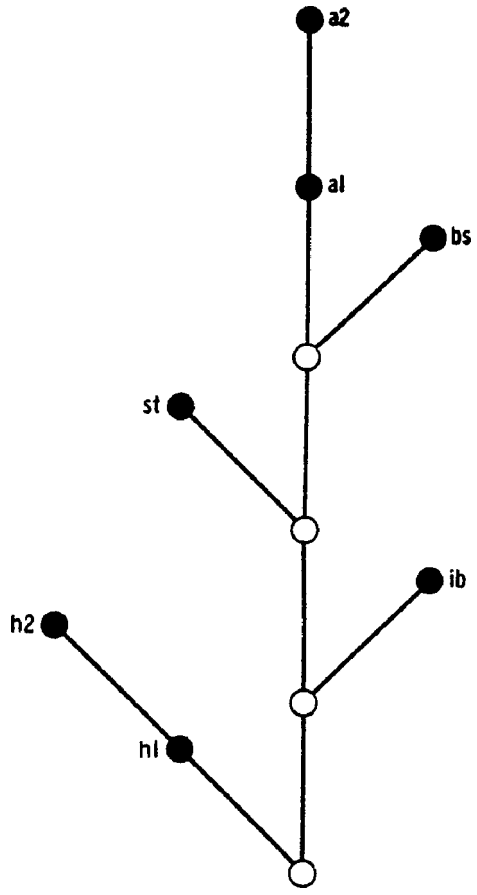

Fig. 53. An estimate of the phylogeny of Haematopus, Ibidorhyncha, Himantopus, Cladorhynchus, and Recurvirostra incorporating possible character state reversals. Abbreviations as in Fig. 48.

A reanalysis of the compatibility of the characters which vary among the species of avocets and stilts yielded two largest cliques of seven characters each:

Avocets and Stilts Clique B: 6, 15, 35, 47, 51, 60, 65

Avocets and Stilts Clique C: 6, 15, 35, 47, 51, 60, 62.

These two cliques differ in only one character: Character 65 in Clique B is replaced by Character 62 in Clique C. The trees defined by these cliques (Fig. 54A, 54B) differ in whether Cladorhynchus (node bs) shares a most recent ancestor with the avocets (nodes al and a2) or with the stilts (node st).

To investigate these relationships further I devised four additional characters for these species, three plumage characters and one concerning foot webbing (see Character Descriptions and Appendix VI). The compatibility analysis of the set of nine skeletal and four integument characters which vary among these species gave two largest cliques of ten characters each:

Avocets and Stilts Clique D: 6, 15, 35, 47, 51, 60, 62, 65, asl, as2

Avocets and Stilts Clique E: 6, 15, 35, 47, 51, 60, 65, asl, as2, as4.

These two cliques differ by only one character: Character 62 in Clique D is replaced by Character 95 in Clique B. Clique D contains Clique A obtained by the first analysis of skeletal characters alone. The trees defined by Cliques D and E (Fig. 55A, 55B) differ in whether Cladorhynchus (node bs) is closer to the avocets ("a" nodes) or to the stilts (node st). When this analysis was repeated using Character 65 with reversals Clique E was obtained.

Within the plovers and their allies only Cladorhynchus and Recurvirostra possess state A of Character 65 and the derived state of Character rp4 (webbed feet); both the primitive and derived states of Character 62 (hallux) occur in the Charadriinae and Vanellinae, but the character is rejected in all analyses of those subfamilies and appears to be very homoplastic. Since Character 62 is probably unreliable for determining relationships, the tree defined by Clique E

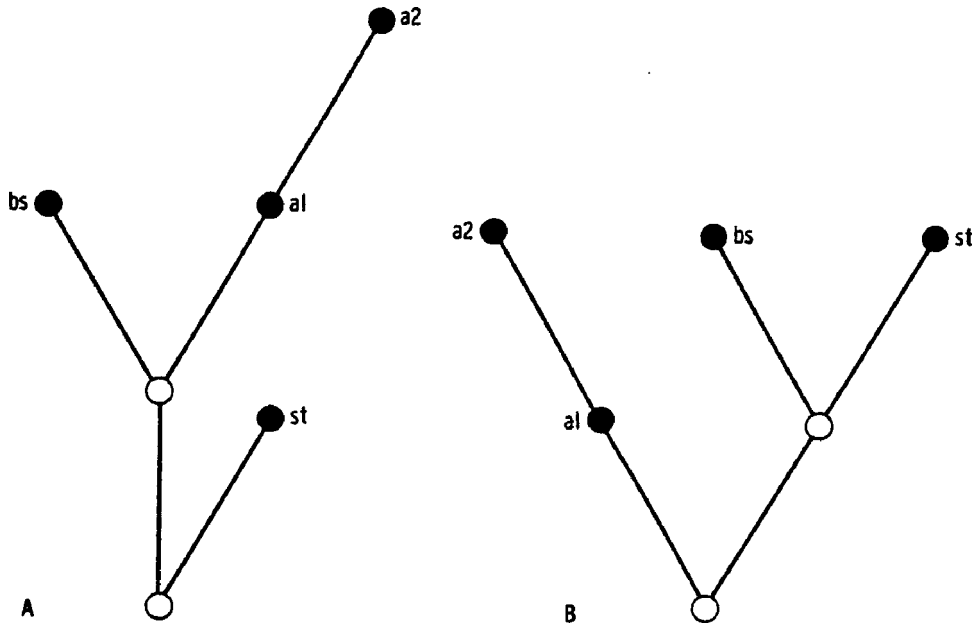

Fig. 54. Two estimates of the phylogeny of the avocets and stilts incorporating possible reversals. Abbreviations as in Fig. 50.

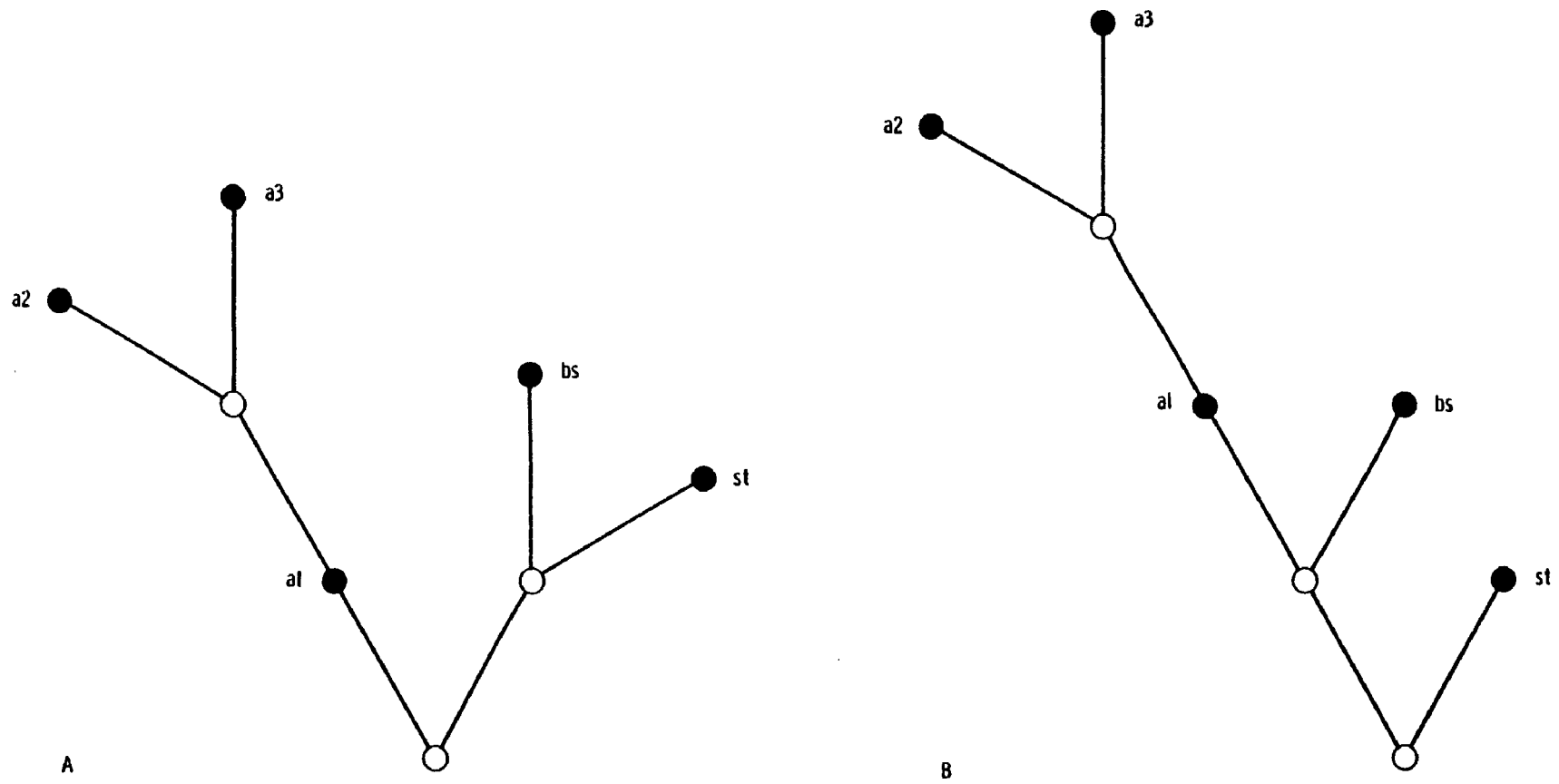

Fig. 55. Two estimates of the phylogeny of the avocets and stilts based on skeletal, plumage, and foot characters. A. without character state reversals; B. with possible character state reversals. Abbreviations: al, Recurvirostra andina; a2, R. americana, novaehollandiae; a3, R. avosetta; bs, Cladorhynchus; st, Himantopus.

(Fig. 55B) is accepted as the best estimate of relationships among the avocets and stilts.

V. Summary of the Cladistic Relationships Among the Charadriiformes

Fig. 56 shows my final estimate of the evolutionary history of the Charadriiformes. This tree, a composite of the analyses discussed above, was constructed by replacing each branch in the first charadriiform tree (Fig. 32) with the branch found in the analysis of that branch alone. This process was repeated until most of the cladistic detail found in the above analyses had been placed on the tree. For clarity some of the detail found in the analyses of smaller groups has been omitted (e.g., the Charadriinae are represented only by node 29). The groups which occur on each of the nodes in Fig. 56 are identified in Table 1. The character states which define each monophyletic group are identified in Table 2.

Fig. 56. Final estimate of the phylogeny of the Charadriiformes. See Table 1 for identification of the groups on each node.

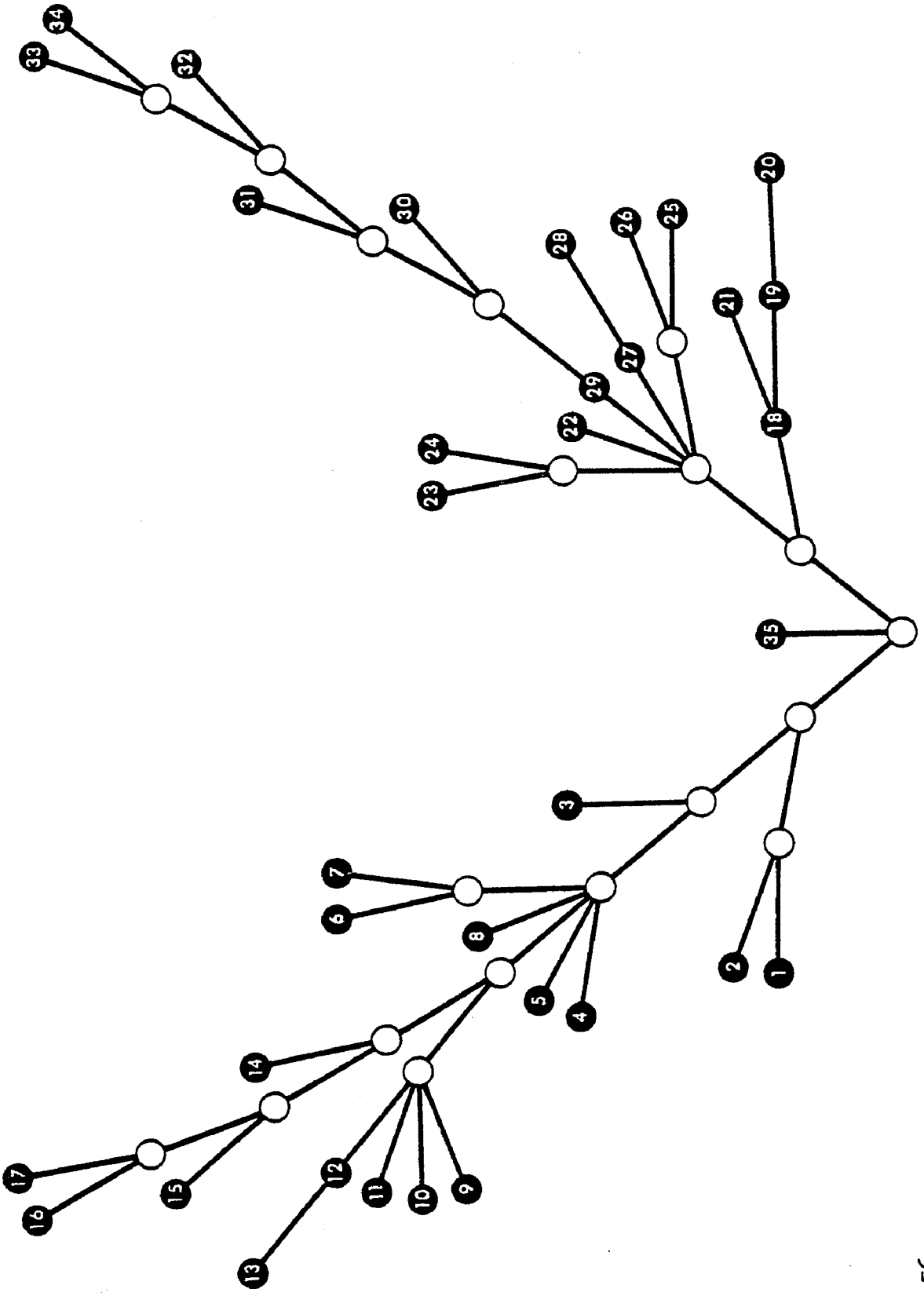
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Fig. 56

Table 1. Groups on Nodes in Fig. 56

Node	Group
1	Microparra, Actophilornis, Irediparra, Metopidius
2	Hydrophasianus, Jacana
3	Thinocoridae
4	Rostratulidae
5	Phalaropodidae
6	Prosobonia
7	Bartramia, Numenius
8	Tringa, Catoptrophorus, Heteroscelus
9	Actitis, Aphriza, Calidris, Eurynorhynchus, Micropalama, Tryngites, Philomachus, Limicola
10	Arenaria
11	Limnodromus
12	Xenus
13	Limosa
14	Coenocorypha
15	Lymnocryptes
16	Gallinago
17	Philohela, Scolopax
18	Sterninae
19	Larinae
20	Stercorariidae
21	Rynchops
22	Dromas
23	Burhinidae
24	Pluvianus
25	Cursoriinae
26	Glareolinae
27	Pluvianellus
28	Chionis

Table 1. Continued

Node	Group
29	Charadriinae, Peltohyas
30	Vanellinae
31	Haematopus
32	Ibidorhyncha
33	Himantopus
34	Cladorhynchus, Recurvirostra
35	Alcidae

Table 2. Character States Defining Monophyletic Groups in Fig. 56

Nodes	Character Number	Shared Derived Character State
1-17	14	maxillopalatine strut A absent
	39	coracoidal foramen absent
	42	ridge in capital groove of humerus
1-2	44	poorly-developed pneumatic possa II of humerus
	45	ectepicondylar prominence of humerus absent
	46	ancestral Jacanidae state of extensor process of metacarpus of carpometacarpus
	47	intermetacarpal tuberosity lying within groove formed at junction of metacarpals II and III
	48	ossified bridge over distal metacarpal symphysis of carpometacarpus
	52	lateral synsacral strut falling short of acetabulum
	61	trochlea for digits II and IV only slightly elevated compared to that for digit III
1	46	jacana wing knobs and blade-like radius
2	46	jacana wing spurs
3-17	24	origin of M. complexus on vertebra 3 absent
	61	trochlea for digits I and IV considerably elevated compared to that for digit III, trochlea for digit III more so than that for digit IV
3	4	angle between lateral nasal bar and jugal bar about 70 degrees or more
	8	short, stubby, finch-like bill tip
4-17	10	basipterygoid articulation of pterygoid and basipterygoid processes on basisphenoid rostrum
4	8	dorsal bar of upper jaw flattened with a distinctive ridge along top
5	8	distinct flange of bone on dorsal bar of upper jaw
6-7	13	flat sheet of bone at junction of jugal bar and ventral bar of upper jaw
6	51	posterior synsacral strut present
	57	posterior medial and medial edge of ilium forming smooth curve
7	12	maxillopalatines and palatines considerably but not completely fused
	29	origin of M. splenius capitis on vertebrae 2 and 3

Table 2. Continued

Nodes	Character Number	Shared Derived Character State
8	8	dorsal and ventral bars of upper jaw fused for about one-half length of bill
	17	maxillopalatine strut D present
	22	posterior process of mandible normal with corresponding bump on supraangular present
9-17	4	angle between lateral nasal bar and jugal bar about 70 degrees or more
9-13	5	zygomatic process shorter than suprameatic process
9	19	foramen magnum distinctly heart-shaped
10	8	bill tip a sharp, short cone
11	9	cross-section of dorsal bar of upper jaw T-shaped
12-13	64	tendinal canal No. 1 of hypotarsus a groove
13	9	cross-section of dorsal bar of upper jaw like inverted U
	12	maxillopalatines and palatines considerably but not completely fused
	60	junction of anterior and posterior crests of pelvis forming distinct projection over ilioischiatic fenestra
14-17	3	ectethmoid and frontal fused
	20	exorbital nasal gland
	21	prearticular process of mandible expanded and hollow and without flange
	22	posterior process of mandible shifted posteriad
14	50	synsacral strut extending from fourth vertebra
15-17	1	lacrimal-ectethmoid complex connected with postorbital process
	5	zygomatic process connected with lacrimal-ectethmoid complex
	15	maxillopalatine strut B absent
	59	ischium and pubis fused immediately posterior to obturator foramen
	70	tendinal canals of hypotarsus for tendons No. 2, 3, and 4 lying in straight line
15	36	medial sternal notch present
16-17	25	no origin of M. complexus on vertebra 4
	54	posterior end of renal depression deep and abrupt

Table 2. Continued

Nodes	Character Number	Shared Derived Character State
16	66	tendinal canal of hypotarsus for tendon No. 3 a bony canal
17	20	nasal gland neither supraorbital nor exorbital
	23	posterior mandibular fossa absent
	58	ischial angle relatively short and about even with posterior projection of ilium
18-34	43	anconal surface of deltoid crest of humerus concave
18-21	37	posterior lateral sternal process and xiphial area extending about equal distance posteriad
	41	distinct groove extending into furcular process
	49	proximal phalanx, digit III perforated
19-20	54	distinct strut at posterior end of renal depression
	57	posterior medial and medial edge of ilium forming smooth curve
20	67	no canal for tendon No. 4 on hypotarsus
21	32	12 neck vertebrae
22-34	23	posterior mandibular fossa absent
22	44	pneumatic fossa II of humerus poorly developed
23-24	1	lacrimal-ectethmoid complex abutting jugal bar
	7	holorhinal nostrils
23	30	origins of M. rectus capitis only on vertebrae 1-4
	33	burhinid cervical vertebral strut present
	45	no ectepicondylar prominence of humerus
	58	ischial angle relatively short and about even with posterior projection of ilium
	63	angle formed by trochleae for digits II and IV smaller than 25 degrees
24	24	no origin of M. complexus on vertebra 3
	29	origin of M. splenius capitis on vertebrae 2 and 3
	46	wing knob present
	63	angle formed by trochleae for digits II and IV larger than 35 degrees
25-26	3	ectethmoid and frontal fused
	11	medial condyle of quadrate raised and twisted so that it faces outward

Table 2. Continued

Nodes	Character Number	Shared Derived Character State
25	44	pneumatic fossa II of humerus poorly developed
	62	hallux absent
26	30	origins of M. rectus capitis only on vertebrae 1-4
27-28	21	no flange on prearticular process of mandible
	46	wing knobs present
28	53	four parapophyses on lumbar vertebrae
29-34	10	basipterygoid articulation of pterygoid and basipterygoid processes on basisphenoid rostrum
	21	flange on prearticular process of mandible fused to supraangular
30-34	29	origins of M. splenius capitis on vertebrae 2 and 3
30	33	Vanellinae cervical vertebral strut present
31-34	12	maxillopalatines and palatines considerably but not completely fused
	64	tendinal canal No. 1 of hypotarsus a groove
31	4	angle between lateral nasal bar and jugal bar about 70 degrees or more
	12	maxillopalatines and palatines completely fused
	32	12 neck vertebrae
	38	ventral manubrial spine of sternum not dividing coracoidal sulci
32-34	27	no origin of M. complexus on vertebra 6
	57	posterior medial and medial edge of ilium forming smooth curve
32	2	lacrimal and ectethmoid not in contact
	20	exorbital nasal gland
	30	origins of M. rectus capitis only on vertebrae 1-4
33-34	8	bill tip long, dorsal and ventral bars of upper jaw fused for about one-half length of bill
	61	trochlea for digits II and IV considerably elevated compared to that for digit III, trochlea for digit II more so than that for digit IV
	63	angle between trochleae for digits I and IV larger than 35 degrees
	68	tendinal canal No. 6 of hypotarsus present as a groove

Table 2. Continued

Nodes	Character Number	Shared Derived Character State
33-34	69	tendinal canal No. 5 of hypotarsus present as a groove
33	35	five costal processes on sternum
	60	junction of anterior and posterior crests of pelvis forming distinct projection over ilioischiatic fenestra
34	65	tendinal canal No. 1 of hypotarsus directly anterior to tendinal canal No. 2 (reversal)
	as4	webbed feet
35	40	brachial tuberosity of coracoid twisted so that it does not roof triosseal canal
	52	no lateral synsacral strut

DISCUSSION

The initial choice of the members of a study collection is critical to any study. To the extent that the membership of the study collection deviates from a true monophyletic assemblage, any estimate of evolutionary relationships within the group will be distorted. Usually some members of a monophyletic group are unavailable for inclusion in the study collection. If the missing members are closely related to some of the members in the collection and differ little from them, their absence will have little effect on the outcome of the analysis. If, however, the missing members represent distinct lineages not otherwise represented in the study collection, omitting them can seriously affect the outcome of any analysis. When such groups are omitted, distinctive elements of the diversity of the group, such as unique character states and unique combinations of character states, are neglected in the analysis.

Unfortunately most workers considered only a portion of the known diversity among the Charadriiformes when attempting to determine their relationships. Since few authors clearly stated their beginning assumptions of relationship, it is difficult to be sure what they were. The idea that the order consists of three distinct and presumably monophyletic groups: the shorebirds, the Lari, and the alcids, dates from Gadow's (1892) classification. That the Lari and the alcids are monophyletic assemblages seems well established and almost universally accepted. Agreement on the status of the shorebirds, however, is not universal. Previous workers either assumed that all shorebirds represent a monophyletic group (Jehl 1968b; Burton 1974), or they assumed that the Charadriidae and Scolopacidae together form a monophyletic group and then tried to place the remaining shorebirds with them or with the Lari (Shufeldt 1903; Lowe 1931c; Yudin 1965). Even Lowe (1916a), who thought that a "gull is only a highly specialized plover," placed shorebirds and the Lari in different suborders. The results of this study indicate that it is unlikely that the Charadriidae and Scolopacidae together form a monophyletic group within the order.

Jehl (1968b) noted the distinctiveness of the plovers and the sandpipers, but he argued only that they represent distinct families. Only Ahlquist (1974) found that the plovers are closer to the Lari than they are to the sandpipers; unfortunately his methodology and the spuriousness of some of his findings cast doubt on them all.

All of the known diverse elements of the Charadriiformes are included in this study. Skeletons of almost all species of shorebirds, all but one of Peters' (1934) genera of Lari, and species representing the major lines of the alcids (Storer 1945) were studied (see Appendix III). My analyses have not neglected any of the major diversity within the order. All the characters used in defining my groups are not discussed in detail below. Their persuasiveness lies in their inclusion in the cliques, in which all the characters support a consistent story.

I. The Charadriiformes

My division of the order into three phyletic lines (Fig. 56) differs from past results in dividing the shorebirds into two major groups, the scolopacine and charadriine shorebirds sensu lato, in placing the charadriine shorebirds on a line with the Lari, and in not placing the Lari and alcids on the same line.

In spite of Bock's (1958) extreme statement that "there is no longer any need for maintaining family status for the plovers...the most consistent classification is to include the plovers as a subfamily of an enlarged family of shorebirds," there is abundant evidence that the plovers and sandpipers are very different. Osteologically they differ in five of the primary characters found in this study, as well as in several others described herein and in Lowe (1915b, 1925, 1926, 1931c) and Zusi and Jehl (1970). Sibley and Ahlquist (1972) and Ahlquist (1974) discuss the differences in the elctrophoretic patterns of their egg white proteins. Jehl (1968b) points out the differences in the plumage patterns of their downy young. Burton (1974) found several consistent differences in feeding behavior and in jaw musculature and tongue structure. Although few species have yet been examined, the sperm morphology of the Scolopacidae is unique among non-passerine

birds, while sperm of the Charadriidae, Laridae, and Alcidae are almost identical and are also similar to that of other non-passerine orders (Retzius 1909, 1911; McFarlane 1963).

Gadow (1892) characterized his Charadriidae, which included both plovers and sandpipers, as cosmopolitan, schizorhinal, and having basipterygoid processes. Of the possible types of geographic distribution a cosmopolitan one is least informative for making inferences of relationship; all charadriiform birds except Pluvianus and the Burhinidae are schizorhinal; and, as shown in this study, the condition of the basipterygoid processes is probably not a true cladistic character at the ordinal level. Lowe's (1931c) table of 14 characters which distinguish the suborders of his order Telmatomorphae includes only one, the presence of basipterygoid processes, which is unique to his suborder Limicolae (Rostratulidae, Charadriidae, and Scolopacidae).

Showing that the Charadriidae and Scolopacidae represent two distinct phyletic lines, however, does not in itself demonstrate that they are not a monophyletic line sharing a common ancestor not shared by any other charadriiform. It is also necessary to support the contention, as has been done here, that each shares most recent common ancestors with other groups which are not shared with each other. As discussed above, few workers have included non-shorebirds in their considerations when exploring these possibilities. They presented evidence, however, that particular groups are closer to either the Scolopacidae or the Charadriidae. This evidence is discussed below.

A close relationship between the alcids and Lari has been postulated many times (Gadow 1892; Boetticher 1934; Storer 1960; Yudin 1965; Sibley and Ahlquist 1972; Ahlquist 1974). Hudson et al. (1969), however, argued that the two groups differed sufficiently in their wing and leg musculature to be placed in separate suborders. None of the characters used in this study indicate that the Lari and alcids form a monophyletic assemblage which excludes other charadriiforms. (Hudson et al. (1969) report that they share a patagial fan sesamoid not found in the Charadrii they examined.) They do, however, share the primitive states of many characters and in that sense are quite similar. Possibly my Charadrii and Alcae (Appendix VII) together represent a monophyletic line which does not include the Scolopaci, but I have no evidence for

this view.

There has been much speculation on whether the ancestral charadriiform bird was gull-like or more like a shorebird, perhaps resembling Dromas (Yudin 1965; Hudson et al. 1969). This speculation is an expression of the common belief that gulls are generalized and thus more or less primitive. However, if we had a specimen of the ancestral charadriiform, we would doubtlessly recognize many specializations in modern gulls. Regardless of what sort of bird the ancestor was, my results indicate that the modern Lari diverged from the line leading to the charadriine shorebirds, which is independent of the line which gave rise to the alcids. The alcids are thus best considered distinct from the Lari unless new evidence indicates otherwise.

II. The Suborders of the Charadriiformes

A. The Scolopaci

The Jacanidae, Rostratulidae, Thinocoridae, and Scolopacidae are a monophyletic group (Fig. 32) defined by absence of a maxillopalatine strut A (Fig. 15), absence of a coracoidal foramen (Fig. 23), and presence of a ridge in the capital groove of the humerus (Fig. 25).

The relationships of the Jacanidae, Rostratulidae, and Thinocoridae have been the subject of considerable debate. Forbes (1881) argued on the basis of pterylosis, development of the cecum, morphology of the patagial tendons, and osteology that jacanas are more like shorebirds than they are like rails, and indeed Gadow's (1892) and most later classifications included tham in the Charadriiformes. Lowe (1925), on the basis of the differences in morphology of the quadrato-tympanic articulation observed between Gruiformes and Charadriiformes, argued that jacanas are rails. He also declared that the color pattern of downy young is crane-like, even though jacana young are strongly patterned (Jehl 1968b) and crane young hardly at all (Walkinshaw 1973; pers. obs.); that the possession of basipterygoid processes places them with the more primitive Gruiformes, even though the processes are rare in the Gruiformes but are the usual condition in the Charadriiformes; and that jacanas have a ralline pelvis when compared with plovers, although comparison with the pelvis of a painted snipe or a

true snipe, shows the resemblance to rails to be superficial. In the same paper Lowe pointed out that the quadrato-tympanic articulation of the Scolopacidae is also somewhat gruiform, which he attributed to the close relationship of the Gruiformes and Charadriiformes. Later he decided (Lowe 1931b) that jacanas are not really rails but "apparently a more generalized or primitive group than the rest of the Gruiformes." This appears only to sidestep the issue of their true affinities. Except for Verheyen (1961), who based his classification on an idiosyncratic type of numerical taxonomy, and Stresemann (1969), who placed every distinctive group in a separate order, all recent workers place the Jacanidae in the Charadriiformes, as I do on the basis of my Prim network analysis (Fig. 1). Kitto and Wilson (1966) found the mobility of their S-malate dehydrogenase like that of other charadriiforms.

Many recent workers suggested that the jacanas are closest to the painted snipes. Yudin (1965) thought that Jacana represents an early radiation of the shorebirds which took place before the plovers and sandpipers diverged, apparently because he assumed that Pluvialis represents the primitive charadriiform type and found that Jacana and Pluvialis differ little in their jaw musculature. Ahlquist (1974) found that the IFPA patterns of the egg white proteins of the jacanas resemble those of the sandpipers.

My analyses indicate that the Jacanidae are a monophyletic group defined by a poorly-developed pneumatic fossa II of the humerus (Fig. 25), lack of an ectepicondylar prominence on the humerus (Fig. 25), a specialized condition of the extensor process of the metacarpus (see Character Descriptions for the hypothetical ancestral jacana state used here), an intermetacarpal tuberosity lying within the grooved formed by the junction of metacarpals II and III, an ossified bridge over the distal metacarpal symphysis of the carpometacarpus (Fig. 26), a lateral synsacral strut which falls short of the acetabulum (Fig. 28), and the trochlea for digits 2 and 4 only slightly elevated compared to digit 3 (Fig. 30). The remainder of the scolopacine shorebirds are a monophyletic group defined by an origin of M. complexus on vertebra 3 and the trochlea for digits 2 and 3 considerably elevated compared to that for digit 3, and with the trochlea for digit 2 more raised than that for digit 4 (Fig. 30). The jacanas may also be characterized by their

usually dark glossy plumage, often with a naked or wattled forehead, their long toes and claws, and their ecology. With increased knowledge of the social habits of the other members of the suborder (Pitelka, Holmes, and Maclean 1974) their polyandrous behavior no longer distinguishes them. There are two distinct groups of jacanas (Fig. 40B): one (Microparra, Actophilornis, Irediparra, and Metopidius) distinguished by a wing knob and blade-like radius and the other (Hydrophasianus and Jacana) distinguished by a wing spur. The two groups can also be separated by plumage characters; Hydrophasianus and Jacana both have light-colored wing stripes in all plumages except the neonatal; in addition, a black eye strip is present in young birds. None of the members of the other genera have either of these character states in any plumage.

The painted snipes (Rostratulidae) are usually thought to be closest to the jacanas (Beddard 1901; Jehl 1968b; Sibley and Ahlquist 1972; Ahlquist 1974) or to the Scolopacidae, perhaps near the true snipes (Yudin 1965; Ahlquist 1974). Lowe (1931b) thought that they are shorebirds but distinctive enough to be given family rank. In my analyses they cluster with the Scolopacidae (Fig. 9) because they possess basipterygoid processes; they are distinguished by their unique bill morphology (Fig. 10).

The Thinocoridae superficially resemble grouse or finches, probably reflecting adaptations for their (atypical for Charadriiformes) vegetarian diet. Since Gadow (1892) they have usually been accepted as modified Charadriiformes of uncertain relationship. Garrod (1877) thought them closest to the Glareolidae on the basis of palate structure and lack of basipterygoid processes. Lowe (1931b) first placed the Thinocoridae in a suborder with the Glareolidae, Chionididae, Dromadidae, and Laridae, but later (1931c) decided that they should be placed in a suborder of their own. Boetticher (1934) thought the Thinocoridae closest to Chionis because to him they both seemed to be "primitive collective types." On similar grounds, as well as because of similarities in jaw musculature, basic similarity of body structure, presence of a crop, and lack of toe webbing, Yudin (1965) also thought the Thinocoridae closest to Chionis. Jehl (1968b) decided that the downy plumage of seedsnipes offered no clue to their

relationships and followed Yudin in placing them near the Chionididae.

I find the seedsnipes likely to be a sister group to the Scolopacidae (Fig. 34), defined by the angle between the lateral nasal bar and the jugal bar of more than 70 degrees and by a short, stubby, finch-like bill tip (Fig. 10). I did not try to work out the relationships among them. Lowe (1931c) found the Thinocoridae like the sandpipers in downy plumage pattern, pterylosis, patagial fan, and several osteological characters. Since he also noted that several features of the skull seemed gruiform, he placed them in a separate suborder between shorebirds and his Grues. Ahlquist (1974) presented protein evidence that there is a "real connection among the seedsnipes, painted snipes, and sandpipers" but failed to define its exact form.

The data and analyses presented here strongly support the hypothesis that the Jacanidae, Rostratulidae, Thinocoridae, and Scolopacidae are a monophyletic group. The cladistic relationships found among these four groups are not as strongly supported and require further study. While it is clear that the jacanas and sandpipers represent the two major phyletic lines of scolopacine shorebirds, the problem is to determine the positions of the painted snipes and seedsnipes. The skeletons of the painted snipes and the jacanas seem similar in many ways, but this is not expressed in the Prim network (Fig. 1) or the compatibility analyses. Perhaps, as Ahlquist (1974) suggests, there is a "real distant relationship between the jacanas and the painted snipes." On the other hand, the painted snipes are similar to the true snipes in some skeletal features, but my results indicate that these represent convergence rather than recent common ancestry. The inclusion of the painted snipes in the Scolopacidae in my analyses may be the result of an inadequate character set.

The Thinocoridae may be even closer to the Scolopacidae than my analyses indicate. Besides the similarities of their downy young (discounted by Jehl 1968b), the pattern of the head and upper back plumage of juveniles and some adults is similar to that of sandpipers.

The sperm morphology of the Jacanidae, Rostratulidae, and Thinocoridae is unknown. In light of the distinctive sperm morphology of the Scolopacidae, such knowledge might be quite valuable in unraveling the relationships among these four families.

Within the Scolopacidae there are three well-defined groups: the tattlers (Tringa and allies), the peeps (Calidris amd allies), and the snipes and woodcocks (Gallinago and allies). However, there are numerous genera (Prosobonia, Bartramia, Numenius, Limosa, Xenus, Actitis, Aphriza, Arenaria, Limnodromus, Limicola, and Phalaropus), the relationships of which have long been debated. These genera exhibit combinations of the character states of the three main species groups and are intermediate in several ways. Part of the uncertainty about their relationships, however, stems from few past workers' having suitable specimens of all of the genera available for study at one time or by considering large enough character sets in arriving at their decisions. My analyses indicate that the Scolopacidae consists of five main groups (Fig. 34): the painted snipes (Rostratula and Nycticryphes), defined by their unique bill morphology (Fig. 10); the phalaropes (Phalaropus), defined by their unique bill morphology; the tattlers (Tringa, Catoptrophorus, and Heteroscelus), defined by a bill tip in which the dorsal and ventral bars are fused for about one-half the length of the bill (Fig. 10), the presence of maxillopalatine strut D (Fig. 15), and the posterior process of the mandible normal with a corresponding bump on the supraangular (Fig. 18); the curlews (Prosobonia, Bartramia, and Numenius), defined by the flat sheet of bone which extends from the prepalatine bar to the jugal bar (Fig. 14, 15); and a group which includes the remaining sandpipers, the peeps, and the snipes and woodcocks, defined by a large angle between the lateral nasal bar and the jugal bar. Lowe (1915b) listed several characters which defined his Eroliinae and Tringinae, but his distinctions fail when applied to the intermediate genera.

The species of tattlers share many similarities of adult and downy plumage patterns (Lowe 1915a; Jehl 1968b) and feeding behavior (Burton 1974). As mentioned previously, my character set is not adequate to determine the relationships among them (Fig. 37). The three species of phalaropes are often placed in a separate family, but both Lowe (1931c) and Jehl (1968b) argued that they should be included in the Scolopacidae. They have been described as tringine in their downy color patterns (Lowe 1915a, 1931c; Jehl 1968b), in lack of ossification of the nasal septum (Lowe 1931c), in bill morphology (Kozlova

1961), and in the characteristics of their egg white proteins (Ahlquist 1974). I found that the morphology of their upper mandible differs in some ways from that of tattlers, and the lack of ossification of the nasal septum is shared by some species of Calidris. Burton (1974) found them like Calidridinae but unlike the tattlers in lacking L. jugomandibulare externus. Clearly their relationships are not yet settled.

Prosobonia (I follow Zusi and Jehl (1970) in merging Aechmorhynchus and Prosobonia), found on only a few islands of the Tuamotu Archipelago, has been observed in life by few ornithologists. I studied the same skeleton examined by Zusi and Jehl (1970) as well as a series of four skins in The University of Michigan Museum of Zoology. Lowe (1927, 1931a) thought that Prosobonia (= Aechmorhynchus cancellatus) is a diminutive curlew and described many details of plumage and skull morphology which support his claim. Murphy (1924) quotes from the notes of Rollo H. Beck that in life Prosobonia "remind one of tiny Upland Plovers (Bartramia)." Zusi and Jehl (1970), however, found Prosobonia more closely related to the Tringini than to the Numenini. Although they report that the plumage of Prosobonia is like that of Tringa glareola, I find this true only to the degree that there similarities between the plumages of Tringa and Numenius; the plumage of Prosobonia appears to me to be more like that of Numenius phaeopus variegatus than of any other shorebird. Zusi and Jehl describe details of the skull in which Prosobonia is more tringine than calidridine but do not include Numenius, which is similar to Tringa in many ways, in their comparisons. They describe Prosobonia as more like the Tringini than the Numenini in two characters, the form of the lacrimal and the attachment of maxillopalatine strut C. I found the shape of the lacrimal to be so variable throughout the order, with many species showing intermediate conditions, that I could not divide the character into discrete character states; I thus doubt its usefulness. I also found the attachment of strut C to differ little if at all between tattlers and curlews: both conditions described by Zusi and Jehl are found in both groups. Finally, they describe four characters of the sternum (see their Table 3) in which Prosobonia is more like Actitis (assumed by them to be tringine) than it is like Numenius, especially in the combination of the

character states it possesses. There are, however, problems with these characters. If, as Zusi and Jehl grant, each character varies within a species or genus, its usefulness is suspect. Unfortunately only one skeleton of Prosobonia was available for study, and there is no certainty that it is typical. If the variability is ignored by assigning the most common state to the species they list in their Table 3, only three of their characters (the first three in the table) are mutually compatible; these define two groups, one which includes Prosobonia Actitis, and Calidris and another which includes Tringa and Philomachus. On the basis of the characters used in this study and others this must be a false result. Upon examination of an independent series of specimens of similar or larger size for each species, I found that the ventral manubrial spine is variable in both species of Actitis, with five of seven specimens of hypoleucos having the state opposite that reported by Zusi and Jehl. I found the sternocoracoidal process to be intermediate in many specimens. On one sternum of Catoptrophorus it slopes forward on one side and backward on the other; it slopes backward in four of seven specimens of hypoleucos and backward (or at least more like Philomachus in slope than like Calidris) in the seven specimens of Tryngites I examined. The sternum of Prosobonia is clearly four-notched, as hinted in Zusi and Jehl's Fig. 7, not two-notched as they coded it. If their characters are recoded according to my findings, the largest possible clique is two. It is clear that these sternal characters are by themselves of little value in determining the relationships among these species.

The flat sheet of bone which extends from the prepalatine bar to the jugal bar defines the Prosobonia-curlew line (Fig. 34). The analysis of this line shows that it gives rise to two lines (Fig. 40A): one which leads to Prosobonia, defined by considerable but not complete fusion of the maxillopalatines and palatines and origins of M. splenius capitis on vertebrae 2 and 3; the other leading to the curlews (Bartramia and Numenius), defined by a second synsacral strut lying posterior to the usual strut and the posterior medial and medial edge of the ilium forming a smooth curve. On the curlew line the analysis defines a basal group of curlews which includes the species with slight bills: Bartramia longicauda, Numenius minutus, borealis, and tenuirostris

(only the overlap in bill lengths of N. phaeopus and tenuirostris keeps this from being the group with the shortest bills); and a more derived group which includes the species with robust and generally long bills. That B. longicauda, N. minutus, and borealis are also similar in plumage color and markings and tarsal scutellation supports this grouping. A more detailed study is necessary to clarify the relationships among the curlews.

On the basis of his two-dimensional ovalbumin tryptic peptide maps Ahlquist (1974) decided that Numenius is close to the avocets and stilts. This would be an intriguing idea if it were not based on such flimsy evidence. Ahlquist's decision rests on his ability to identify homologies among the spots of the peptide maps of two or more species. He fails to discuss the effects that amino acid substitutions have upon the net charge and solubility of peptides and their ultimate positions on the maps. Depending on the magnitude of these effects the homologous peptides of two very closely related species might have quite different locations on the maps, while the non-homologous peptides of distantly related species might occur at the same locations. As Corbin (1967) states, "Ultimately, homologies must be based upon compositional and sequence studies and not upon the relative positions of the peptides within the chromatogram pattern."

Numenius appears to cluster near Recurvirostra and Himantopus in Ahlquist's analyses largely because their maps share a spot, Y, not identified on the maps of other species. I found unidentified spots on Ahlquist's maps for Nycticryphes and Anous which occur in the same relationship to spots 3 and 4 as they do on the maps of Numenius and Recurvirostra. If position is the indicator of homology, these spots also appear to be Y.

Corbin (1967) illustrates the variation among the maps of four domestic breeds of Columba livia; the differences between Ahlquist's maps of Tringa and Numenius appear to be of the same degree.

Ahlquist (1974) also cites similarities in the skulls and tarsal scutellation of curlews and avocets and stilts. I have already discussed above why the shape of the lacrimal is of little use for suggesting relationships; Ahlquist had merely to examine a skull of Bartramia to realize that the ectethmoids of all curlews do not resemble

those of avocets as much as they do those of tattlers. His account of the distribution of a forked vomer is of no use whatever in inferring relationships. The partially reticulate condition of the tarsi of some curlews may resemble that of avocets, but so do those of Arenaria. On the other hand, the tarsi of Bartramia, Numenius minutus, and borealis have rectangular plates on the anterior and posterior borders of the tarsi just as do most tattlers. There appears to be no plausible evidence of a close relationship between curlews and avocets and stilts.

The remaining line of the Scolopacidae in turn gives rise to two lines (Fig. 35): one defined by having the zygomatic process shorter than the suprameatic process, which includes the remainder of the sandpipers, and one defined by having the ectethmoid and frontal in contact or fused, no flange on the prearticular process of the mandible, the posterior process of the mandible shifted posteriad, and exorbital nasal glands, which includes the snipes and woodcocks. The line which includes the remainder of the sandpipers in turn consists of four phyletic lines: one defined by a groove for tendinal canal No. 1, which leads to Xenus and Limosa; one defined by a T-shaped cross-section of the dorsal bar of the upper jaw (Fig. 11), which leads to Limnodromus; one defined by a short, sharp, cone-shaped bill tip (Fig. 10), which leads to Arenaria; one defined by a heart-shaped foramen magnum (Fig. 16), which leads to Actitis, Aphriza, Calidris, Eurynorhynchus, Limicola, Micropalama, Tryngites, and Philomachus.

Lowe (1915a, b) described several characters of the downy plumage pattern and skeleton which separate the Calidridinae (his Eroliinae) from the Tringinae. These characters indicate that Micropalama and Philomachus are calidridine. Using the same characters he later (Lowe 1931c) also included Tryngites and Limicola in the Calidridinae. The close relationship among these species has been reaffirmed several times (Jehl 1968b; Burton 1971). Except for its bill tip, Eurynorhynchus is a typical calidridine (Anderson 1876; Burton 1971). Larson (1957) suggested that Eurynorhynchus and Limicola are closely related, but Burton (1971) found no evidence for this. Burton (1972b) found the feeding behavior of Micropalama to be typically calidridine, and Jehl (1973) suggested its closest relative to be Calidris ferruginea.

I agree with Jehl (1968a) that all available evidence indicates

that Aphriza is a calidridine sandpiper, probably close to the knots, as Lowe (1931c) also suggested. Jehl presented convincing evidence that its closest relative is Calidris tenuirostris; in addition I have observed that they are the only two calidridines with a pectinate claw on the middle toe.

Arenaria, along with Aphriza, has often been classified in a separate subfamily, the Arenariinae. Lowe (1931c) thought that both Arenaria and Aphriza are specialized calidridines. Jehl (1968b) found "no consistent pattern in this genus" but decided that the downy plumage pattern of Arenaria is tringine. The face of Arenaria chicks, however, is marked identically to that of Calidris. Except for the presence of white tips on some of the feathers, the downy plumage of Tryngites seems quite similar to that of Arenaria. Kozlova (1961) thought the skull of Arenaria similar to that of the Tringinae. Burton (1974) lists several features of the jaw musculature in which Arenaria is like Calidris but differs from Tringa. Ahlquist's (1974) protein evidence indicates that Arenaria is closer to Calidris than to Tringa. The juvenal plumage of Arenaria is similar to that of several species of Calidris. Arenaria thus appears to be calidridine in most of its features; I agree with Jehl (1968a), however, that there is no reason to consider it particularly close to Aphriza.

An unexpected result of my analyses was the inclusion of Actitis in the same group as Calidris. Traditionally Actitis has been placed in the Tringinae, sometimes merged with Tringa. Lowe (1931c) thought that Actitis is a well-defined genus because the downy color pattern is so distinct from that of Tringa. Dixon (1933) thought the behavior of Heteroscelus like that of Actitis, but the loud vocalizations and teetering habits he cites are found in many unrelated stream-side birds and may represent convergence (Orenstein 1975). Jehl (1968b) thought the downy plumage pattern to be typically tringine, but failed to note its similarity to the downy plumage of Himantopus. This may be just another case, of the several noted by Jehl, in which the secondary loss of pattern in the downy plumage obscures relationships. Yudin (1965) noted that hypoleucos was the only member of his Tringa which had Tensor patagii brevis-1 undissected at its lower end, as found also in Philomachus, Calidris, Limicola, Arenaria, Aphriza, and

Phalaropus. Burton (1974) reported that Actitis lacks L. jugomandibulare externus, a condition found in the Calidridinae but not in the Tringinae. Although there are similarities between the plumages of Actitis and those of Heteroscelus and Catoptrophorus, its relationship to the tattlers, if any, is poorly defined. The juvenal plumages of Actitis and Calidris temminckii are quite similar and reinforce the results of my analyses.

Xenus is usually classified in the Tringinae close to Actitis, whose bobbing behavior and stiff-winged flight it has been said to share (Ferguson-Lees 1959). The bobbing behavior, however, may again represent convergence in a stream-side adaptation. Ferguson-Lees is the only author I found to mention the flight of Xenus as resembling that of Actitis; such a resemblance has not been recalled by anyone with whom I've talked who is familiar with both genera in life. Jehl (1968b) thought the downy plumage pattern intermediate between those of Actitis and Tringa; it is certainly much like that of Actitis in the illustrations I've seen. Burton (1974) found that Xenus, like Actitis and the Calidridinae, lacks L. jugomandibulare externus, which is present in all Tringa. The plumages of Xenus show similarities to those of Limosa, Tringa, Actitis, and Calidris and may be of little use in inferring relationships.

Lowe (1931c) placed Limosa and the curlews in his subfamily Limosinae, which he admitted represented the "residue" of the Scolopacidae after he had decided the affinities of the rest of the species. To him they seemed specialized along calidridine rather than tringine lines. Earlier (Lowe 1927), on the basis of similarities of the downy plumage patterns and several features of the skull, he placed godwits and curlews together. Jehl (1968b) thought that the "affinity between Numenius and Limosa...is confirmed by the similarity of their chicks." If, as Jehl asserted, simple downy plumage patterns are secondary adaptations to the nesting habitat and of little value for inferring relationships, these similarities are of doubtful value. Burton (1974) found that the jaw muscles of Limosa suggested affinities with both Numenius and Limnodromus, with sharp differences from the Calidridinae. Ahlquist (1974) found the IFPA patterns of Limosa to be unlike those of Numenius and similar to those of Limnodromus. He thought it improbable

that Limosa and Numenius are closely related. On the basis of their ectoparasites Timmermann (1957a, b) claimed that Limosa and Limnodromus are closely related and belong in the Calidridinae. Pitelka (1948) pointed out the plumage similarities between Limosa and Limnodromus, which Jehl (1968b) believed are "an outstanding example of convergence." Jehl's assertion appears premature; I find many similarities not only between the adult plumages of Limosa and Limnodromus, but also between them and the Calidridinae. My analyses indicate that Limosa is closer to Limnodromus and Calidris than it is to Numenius or Tringa.

Limnodromus is similar to the snipes in skull morphology (Lowe 1931c), downy plumage (Lowe 1931c; Jehl 1968b), adult plumage, and feeding behavior (Burton 1972b), but many of these similarities are also shared between the snipes and Calidris. Burton (1974) found that L. jugomandibulare externus is absent in Limnodromus as in the Calidridinae and Scolopacinae. Yudin (1965) found that in the structure of Tensor patagii brevis-1 and that of M. biceps propatagialis Limnodromus is more like Calidris than it is like Limosa or the snipes. Burton (1974) thought that "perhaps Limnodromus is best regarded as a rather conservative genus within the Scolopacinae retaining features which indicate their close affinities to the Tringinae and perhaps especially to Limosa." I find Limnodromus to be closer to Limosa and Calidris than to the snipes (Fig. 35).

The Scolopacinae (snipes and woodcocks) are usually associated with the Calidridinae on the basis of similarities of their downy young (Lowe 1915a; Mathews and Iredale 1920; Jehl 1968b). Burton (1974) noted that they both lack L. jugomandibulare externus. Ahlquist (1974) placed them along with Limosa, Limnodromus, and Rostratula in a separate subfamily. I find them to be a sister group to the line of shorebirds (Fig. 35) which includes Calidris and its allies; their similarities to the rostratulids appear to represent convergence.

Coenocorypha, Lymnocryptes, Gallinago (including Chubbia), Philohela, and Scolopax are usually recognized as a monophyletic group, the Scolopacinae. There has been little speculation on the relationships among the species, partly because of the great similarity of the species of Gallinago and because anatomical and skeletal specimens for many of the unusual species are unavailable. Lowe (1915c) thought Coenocorypha

neither a typical woodcock nor a typical snipe, but rather a "generalized or primitive Scolopacine form." My analyses indicate that it is a sister group to the rest of the snipes and woodcocks (Fig. 36). Mathews and Iredale (1920) and Jehl (1968b) noted that the downy plumage of woodcocks is very different from that of snipes. Jehl went so far as to suggest that woodcocks and snipes arose from a tringine common ancestor and should be placed in separate subfamilies. He also suggested that the Calidridinae then arose from the same line that gave rise to the snipes. The facial patterns of the downy young of woodcocks and snipes are almost identical; to me woodcock young look like the young of snipe which have been bleached and the white feather tips removed. My analyses indicate that the woodcocks arose from the snipes (Fig. 36).

While the characters I have used to estimate relationships among the Scolopacidae are the largest set of mutually consistent characters which has ever been used for this purpose, much work remains to be done. On the basis of my results, other similarities of the skeleton, plumage characters, and my observations of various species in life, I suspect that the tattlers and curlews are more closely related to each other than is indicated by my present characters. Similarly, I think that Arenaria is a calidridine derivative and that the Calidridinae, Limnodromus, and the Scolopacinae are closely related. Limosa probably also belongs to this last group, but its similarities to the tattlers need further study. The majority of the evidence indicates that Actitis and Xenus are more calidridine than tringine. The phalaropes are probably closer to the tattlers than to any other groups of shorebirds, but the evidence for such a relationship is still weak.

That there are characters which support so many conflicting ideas of relationship among the Scolopacidae is evidence of considerable convergence among them. Many of the characters which define my groups are skull characters, and it is possible that the compatibilities I find are the result of functional convergence rather than an indication of phylogeny. The relationships I have found clearly need to be tested with further characters.

B. The Charadrii

My analyses yield a monophyletic line which includes the Stercorariidae, Laridae, Rynchopidae, Dromadidae, Burhinidae, Glareolidae, Chionididae, Charadriidae, Haematopodidae, and Recurvirostridae (Fig. 32), defined by a concave anconal surface of the deltoid crest (Fig. 25). Since most authors have not considered the Lari when studying the relationships among the shorebirds, little evidence has been published in support of this arrangement. Burton (1974, in litt.), in studies restricted to shorebirds, found that only the Dromadidae, Burhinidae, Pluvianus, Chionis, Pluvianellus, Peltohyas, the Charadriidae and Recurvirostridae possess the Ap. A^1 slip of M. adductor externus, while the Haematopodidae do not. He also found that N. pterygoideus passes through Part O of M. pterygoideus only in the Burhinidae, Pluvianus, Chionis, Pluvianellus, the Charadriidae, Haematopodidae, and Recurvirostridae. In a specimen of Larus argentatus N. pterygoideus passes between Parts O and M of M. pterygoideus (Orenstein pers. comm.) as it does in Dromas, Rhinoptilus, Cursorius, Stiltia, and Glareola (Burton in litt.). These two characters tend to confirm some of my findings of relationship; however, the condition in the remaining genera will have to be ascertained before more definite conclusions can be drawn.

The Charadrii consist of two major lines (Fig. 41): one leading to the skuas, gulls, terns, and skimmers which is defined by the posterior lateral sternal processes and the xiphial area extending about equally posteriad, extension of a groove into the furcular process (Fig. 24), and a perforated proximal phalanx, digit III; and another leading to the charadriine shorebirds sensu lato, defined by lack of a posterior mandibular fossa (Fig. 19).

The skuas, gulls, terns, and skimmers are generally agreed to be closely related, but there is little agreement on the relationships among them. Lowe (1916a), mainly on the basis of similarities he detected between the skulls of Stercorarius and Chionis, though the skuas more generalized and closer to the shorebirds than are the gulls. On the other hand, he thought the gulls to be only highly specialized plovers. On the basis of their simple but gull-like behavior Moynihan (1959) thought the skuas to be the most "primitive" group. He thought

the terns to be derived from a gull or gull-like form, which on the basis of their "purely hostile Low Oblique patterns" might be similar to the "primitive" hooded gulls. Similarly, he stated that while the terns are a natural group, the distinctive behavioral repertoire of the noddies, especially their complex silent Nodding and pre-copulatory Mutual Preening, indicates a "profound and ancient" separation between them and the other terns. Since the hostile behavior of skimmers is "relatively simple and quite different from the complex and elaborate hostility of most terns," he concluded that they represent an independent derivation from some primitive gull. Zusi (1962) found the skimmers to embody a mixture of gull-like and tern-like characteristics and arrived at no decision of relationship. Yudin (1965) found the jaw musculature of skuas less modified in comparison to Pluvialis than that of gulls, terns, or skimmers and thus thought them an early offshoot of this line. He regarded the terns and gulls as closer than the gulls and skuas and thought the terns a special offshoot of the gull line. He reported the propatagial mechanisms of skimmers generally like those of terns and thought them an early split in the tern line. Hudson et al. (1969) thought, on the basis of wing and leg musculature, that skuas and gulls are "clearly the most primitive of the Lari" but found no convincing evidence that either group is more primitive than the other. They found skimmers very different from the other three groups but slightly closer to terns; they doubted that the ancestors of skimmers were terns, however. In a phenetic study of skeletons Schnell (1970a, b) found that skuas clustered closer to gulls than to terns or skimmers, that the gap between skuas and gulls was greater than that between gulls and terns, and that skimmers always clustered with terns. He concluded that the relationships among skuas, gulls, and terns awaited a more detailed cladistic analysis and that terns and skimmers are cladistically closely related. Ahlquist (1974) found the IFPA patterns and peptide maps of skuas and gulls similar and those of skimmers more like gulls than like terns. He decided that it is "highly probable that Rynchops was derived from a larine ancestor." The IFPA patterns gave evidence that noddies may be an early offshoot of the main tern line. Sears, Moseley, and Mueller (1976) found that skimmers share behavioral patterns with gulls, terns, and skuas, none of which suggested a close

relationship. Their evidence led them to "believe that the divergence of the skimmers from their parental evolutionary line took place at least as early as the divergence of the gulls and terns and perhaps significantly earlier."

My results indicate that gulls and skuas are sister groups defined by a distinct strut at the posterior end of the renal depression and a smooth curve formed by the posterior medial and medial edge of the ilium. The relationship of terns and skimmers to each other and to gulls and skuas is not resolved by my characters (Fig. 42). My best estimate is the intersection of the two cliques found in the Stercorariidae and Laridae analysis (Fig. 56). This intersection is compatible with several possible estimates of the evolutionary history of this group (see Fig. 3).

The relationships of the Crab Plover, Dromas ardeola, which looks like a mixture of gull, thickknee, and avocet, have long been a puzzle. In early classifications it was placed near the storks or herons, but since the writings of Huxley (1867) and van der Hoeven (1868) it has been placed in the Charadriiformes. Van der Hoeven (1868) pointed out skeletal similarities with both thickknees and oystercatchers. Lowe (1916b) noted that its pterylosis differs sharply from that of plovers and sandpipers, that the morphology of the occipital and squamosal regions, as well as the squamosal articulation of the quadrate, are gull-like, that the lacrimal has a modified plover-like arrangement, that the palatal structures are like those of the thickknees, and that the humerus is plover-like. He decided that its affinity with these other groups was one of "a common ordinal or subordinal fellowship." Mainly on the basis of the lack of basipterygoid processes in the adult he later (Lowe 1931c) placed it with the Glareolidae and Chionididae in his suborder Lari-Limicolae. Boetticher (1934) thought Dromas belonged between the coursers and thickknees. Yudin (1965) also discussed the resemblance of the skull of Dromas to those of the Lari; he thought that "the similarity to terns shows a convergent character, to gulls consanguinity." He concluded that Dromas represents an early offshoot of a line which also gave rise to the Lari. Jehl (1968b) found the downy plumage of Dromas to give no clue to relationships and suggested that the "similarity of the adult in body form to burhinids and in

plumage pattern to the recurvirostrids might indicate they are distantly related to that major line."

Dromas was not distinguished from the ancestor of the suborder by any of the primary characters in the original analysis of my Charadrii (Fig. 41). While Dromas shares few derived character states with any of the other Charadrii, it shares many primitive character states with them and thus is phenetically similar to them. Depending on which of these similarities are most striking to the observer, they could be used to support almost any hypothesis of relationship within the suborder. My second analysis of the suborder, which used hypothetical ancestors for several groups, placed Dromas with the charadriine shorebirds (Fig. 51) on the basis of the lack of a posterior mandibular fossa; it is distinguished from them by a poorly-developed pneumatic fossa II of the humerus. Burton's (1974) report of the distribution of the Ap. A^1 slip of M. adductor externus supports the inclusion of Dromas in the Charadrii. (It is not known whether this slip occurs in the Lari.) The course of N. pterygoideus in Dromas, however, indicates that it is closer to the Lari than to the charadriine shorebirds (Burton in litt.). The leg scutellation of Dromas consists of large rectangular plates and is unlike that of any other shorebird of similar size, though it does resemble that of coursers and the larger gulls. Dromas also shares the presence of an ossified preethmoideum with the Glareolidae (omitting Pluvianus and Peltohyas) and some Lari. Its nesting behavior and the appearance and behavior of its chick seem most like those of the Lari. Dromas may prove closer to the latter than to any other group.

The inclusion of the Burhinidae in the Charadriiformes has long been debated, mostly because of their superficial resemblances to the Otididae and the uncertainties of the relationships of that family. On the basis of the morphology of the quadrato-tympanic articulation Lowe (1925) first placed the Burhinidae as a separate suborder in the Charadriiformes but later (1931c) decided that they are more gruiform. About half of his characters which purport to demonstrate the gruiform nature of the thickknees also apply to other Charadriiformes. He noted that the downy plumage pattern is similar to that of Haematopus but thought this only to "confirm the close relationships of the Gruae and Limicolae." Yudin (1965) thought their jaw

musculature to be like the primitive Charadriinae and Cursorius and their skeletons half like bustards and half like plovers; he excluded them from the Charadriiformes. Kitto and Wilson (1966) found the mobility of burhinid S-malate dehydrogenase like that of other Charadrii forms. Jehl (1968b) reaffirmed earlier observations that the downy plumage pattern is markedly different from that of bustards but like that of oystercatchers and other Charadriiformes. Stepanyan (1970) reviewed the non-morphological evidence in the literature and thought it indicated a close relationship between the Burhinidae and the Charadriiformes. As noted above, Burton (1974, in litt.) found the course of N. pterygoideus in the Burhinidae to be the same as in Pluvianus, Pluvianellus, Chionis, the Haematopodidae, Charadriidae, and Recurvirostridae. Ahlquist found the IFPA patterns of Burhinus to resemble those of Haematopus, Recurvirostra, and some sandpipers more than those of bustards. He thought that the Burhinidae may be the most primitive group in the Charadriiformes. In my Prim network analysis I found the skeletons of the Burhinidae and Otididae to be very different (Fig. 1).

Pluvianus has usually been placed in the Glareolidae; Seebohm (1886a) went so far as to lump it with Cursorius. Lowe (1931c) thought the color pattern of the chick almost exactly like that of adult Cursorius, which he took as "certain proof that Pluvianus is only a specialized courser." Burton (1974) found that its jaw musculature generally resembles that of the Glareolidae but that the course of N. pterygoideus is like that found in plovers. Yudin (1965) appears to be the first to recognize the distinctions between Pluvianus and the Glareolidae. He found it so different from the coursers and pratincoles, as well as from the "shorebirds proper," that additional investigations might show that it was not a charadriiform. My analyses indicate that Pluvianus is not a glareolid and that the Burhinidae and Pluvianus are more closely related to each other than either is to any other group (Fig. 41). Their group is defined by a lacrimal-ectethmoid complex which abuts the jugal bar and holorhinal nostrils (Fig. 7, 9), character states which are probably functionally related. In agreement with my findings, Yudin (1965) thought that Pluvianus differs from other Charadriiformes "by precisely the same structural features

as Burhinus." Other than the characters used in my analysis and the quite general trends noted by Yudin, I find little other evidence indicating a close relationship between Pluvianus and the Burhinidae; most of their similarities are those shared by other charadriine shorebirds. On the other hand, Pluvianus does not seem particularly close to either the glareolids or the plovers. The relationship with the Burhinidae found here is probably best considered tentative until new evidence of its relationships is found.

Lowe (1931c) placed the Glareolidae, along with Dromas and Chionis, in his suborder Lari-Limicolae, his special category for groups which possess a combination of shorebird-like and gull-like features. He thought the forearm skeleton of Glareola gull-like and the skull a combination of gull- and plover-like character states. Moynihan (1956) watched the hostile behavior patterns of a captive individual of Glareola maldivarum. He thought that they resembled certain hostile displays of gulls and terns and that they might provide evidence of close relationship between the Glareolidae and Laridae. Bock (1964), impressed with the great similarity of the external and skull morphology of plovers and glareolids, thought that their placement in separate families should be reviewed. Yudin (1965) thought the Glareolidae an early branch of the line which gave rise to the Lari even though he found the wing muscles and tendons of Cursorius extremely similar to those of plovers. Jehl (1968b) thought the downy plumage patterns of glareolids similar to those of plovers. Burton (in litt.) found that the course of N. pterygoideus in the glareolids is different from that in plovers. The IFPA patterns of the glareolids and plovers were found "not readily separable" by Ahlquist (1974), who thought them closely related. My analyses show the Glareolidae to be charadriine shorebirds (Fig. 41) but do not indicate to which group they are closest. They are defined by the contact or fusion of the ectethmoid and frontal and a raised, outward-twisted medial condyle of the quadrate. Pluvianus and Peltohyas were found not to be members of the Glareolidae.

Among the Charadrii only the coursers, pratincoles, Dromas, and the Lari have the path of N. pterygoideus between Parts M and O of M. pterygoideus (Burton 1974, in litt.; Orenstein pers. comm.), which

appears to be the primitive condition for the order. Many specimens of pratincoles (including Stiltia) have a partially perforated proximal phalanx, digit III, of the wing, a character state which defines the Lari. In the pratincoles the perforations appear in a thin, delicate sheet of bone, are rough-edged, and have the appearance of damaged or not yet fully ossified areas; in the Lari the perforations are always sharp-edged, and there is no indication of ossification across them. Digit III is well-ossified in Dromas. The glareolids (but not Pluvianus or Peltohyas) share with Dromas and some of the Lari possession of an ossified preethmoideum. A similar-appearing structure is also found in some of the Jacanidae and Thinocoridae and may have been overlooked in other groups because it can easily be lost in the preparation of skeletons. The glareolids also share similarities of tarsal scutellation with Dromas and the Lari. Present evidence does not strongly indicate to which group the glareolids are most closely related.

Even omitting Pluvianus and Peltohyas, there is considerable diversity within the Glareolidae. The pratincoles (Glareola) feed like swallows (Hirundinidae), are mostly plain, usually brownish- or grayish-colored, and have short legs; Stiltia looks like a pratincole with long legs. The long-legged coursers fall into two groups: Cursorius, which as adults are plain, usually rufous-colored, with black-and-white head markings, and Rhinoptilus, each species of which has a unique complex plumage. Boetticher (1934) thought that the pratincoles and coursers are distinct enough from each other to be placed in separate families. Both Jehl (1968b) and Maclean (1973) found the downy plumage patterns of little help in defining relationships within the family. The juvenal plumage of Cursorius, however, is quite similar to that of Rhinoptilus. The debate on the relationships of Stiltia has been summarized by Maclean (1973), who thought that literature accounts indicated its behavior to be like that of coursers and little like that of pratincoles. Yudin (1965), on the basis of few specimens, thought Rhinoptilus "like a courser exteriorly, approximating a pratincole internally."

My analysis of the family shows that it probably consists of two phyletic lines (Fig. 44): the pratincoles (including Stiltia), defined by origins of M. rectus capitis only on vertebrae 1-3; and the coursers, defined by a poorly-developed pneumatic fossa II of the humerus (Fig.

25) and lack of a hallux. Within the coursers Cursorius arises on a line defined by supraorbital nasal gland grooves which form foramina in the skull roof (Fig. 17) and the lack of a coracoidal foramen. The primary characters for the family do not distinguish Rhinoptilus africanus from the ancestor of the coursers; the other two species of Rhinoptilus studied occur on a line derived from this ancestor. These results do not indicate that Rhinoptilus is an unnatural taxon, as has been suggested by Jehl (1968b) on the basis of the downy plumage patterns.

Pluvianellus has been placed with the plovers ever since its discovery toward the end of the nineteenth century. Until Jehl's (1975) detailed study of its biology, no one who considered its relationships had seen the species in life. Boetticher (1934) thought it united characteristics of the plovers and lapwings but failed to describe the characteristics he had in mind. Even casual examination of skins of the species is sufficient to show that it is unlike any known plover in bill and foot structure. Burton (1974) found the course of N. pterygoideus like that in plovers, a characteristic it shares with Chionis (Burton in litt.). Jehl found that it differs from plovers in its body form, bill and leg morphology, foraging, territorial, courtship, and distraction behavior, the relatively small size of its eggs, the semi-precocial nature of its chicks, its natal down, possession of a crop, and its dove-like drinking behavior. He thought it like oystercatchers in its territorial and piping behavior and in the feeding of its young, and like Chionis in general body form, bowing, threat, bill-wiping, and pre-copulatory behavior, its small clutch size, the feeding of the young, and its possession of a crop. Its behavior as described by Jehl is reminiscent of that of pigeons (Columbidae), but he and I have independently decided by comparison of skeletons that there is no similarity between them and Pluvianellus. Jehl recommended that until further studies are made Pluvianellus be placed in a separate family.

My analyses indicate that Pluvianellus and Chionis are members of a monophyletic line (Fig. 41) defined by lack of a flange on the prearticular process (Fig. 18) and possession of a knob on the extensor process of the metacarpus. The many similarities Jehl found between

Pluvianellus and Chionis support this relationship.

Like their probable close relative, Pluvianellus, the species of Chionis have proved enigmatic to students of the Charadriiformes. Shufeldt (1893) reviewed the literature on Chionis up to that time, in which various authors had argued that Chionis was closest to oystercatchers, glareolids, plovers, gulls, seedsnipes, and Dromas. Shufeldt's opinion on its relationships was itself a puzzle, since he advocated both that it was "one of the links among the plovers and gulls" and that its "nearest allies" were Haematopus and Glareola. Lowe (1916a, b, 1926) found Chionis to have a mixture of gull- and plover-like characteristics and thus placed it in his Lari-Limicolae (1931c) with Dromas and the Glareolidae. Boetticher (1934) thought Chionis closest to the Thinocoridae. On the basis of their similarities in jaw musculature, possession of a crop, and lack of toe webbing, Yudin (1965) thought Chionis and the seedsnipes close to each other, an opinion followed by Jehl (1968b). Burton (1974) found that Chionis possesses an Ap. A^1 slip of M. adductor externus and that M. pterygoideus passes through Part O of M. pterygoideus (Burton in litt.), states known only in the charadriine shorebirds sensu lato. Ahlquist (1974) found the IFPA patterns and peptide maps of Chionis like those of the Lari, not especially like those of plovers, and little like those of seedsnipes. He thought that Chionis probably lies near the base of the Lari stem, perhaps near the skuas.

My characters indicate that the similarities of the Chionididae to the Thinocoridae and the Lari are restricted to the sharing of primitive states. The best evidence available indicates that they are closest to Pluvianellus.

The remaining line of the charadriine shorebirds includes the species usually included in the Charadriidae (except Pluvianellus), Haematopodidae, Recurvirostridae, and Peltohyas (Fig. 41) and is defined by possession of a basipterygoid articulation of the pterygoid and basipterygoid processes on the basisphenoid rostrum (Fig. 12) and by fusion of the flange of the prearticular process of the mandible to the supraangular (Fig. 18). The close relationship among the plovers, lapwings, oystercatchers, Ibisbill, avocets, and stilts was recognized by Lowe (1931c), who placed them in his Charadriidae. Jehl (1968b)

thought them closely related on the basis of similarities of the downy plumage patterns, but also on the same basis thought that the Burhinidae belong to this group. Burton (1974) found an entirely cartilaginous entoglossum only in the plovers, lapwings, oystercatchers, Ibisbill, avocets, and stilts. While Ahlquist (1974) found the IFPA patterns of Haematopus closest to those of plovers, he thought that his peptide maps indicated that the avocets and stilts are close to Numenius. The inadequacies of his data have been discussed above. My evidence strongly indicates that the oystercatchers, Ibisbill, avocets, and stilts are modified plovers.

Early workers recognized Peltohyas as a plover, but Mathews (1913) placed it in the Glareolidae using characters which Bock (1964) found unconvincing. Indeed, Mathews and Iredale (1921) admitted that the placement of Peltohyas in the Glareolidae might prove inaccurate. Unfortunately, Lowe (1931c), examining what must have been an imperfect or atypical skull, found that Peltohyas lacked basipterygoid processes and also placed it in the Glareolidae. Bock (1964) and Yudin (1965) have presented evidence that Peltohyas is a plover and not a glareolid. On the basis of a photograph and written description of a chick, Jehl (1968b) argued that the color pattern and feather structure of the downy plumage place Peltohyas in the Glareolidae. On the basis of sharing a condition of the insertion of M. pseudotemporalis superficialis otherwise unique to the plovers, as well as other features of the jaw musculature, Burton (1974) argued that Peltohyas is a plover. In a review of the biology of Peltohyas Maclean (1973) found the evidence relating it to coursers unconvincing and pointed out that it is like plovers and not coursers in clutch size and egg-covering behavior. The osteological evidence used in this study suggests that Peltohyas is a plover.

The biology of Phegornis, which is found only at high elevations in the Andes, is little known. Although it does not closely resemble any other species, its plumage pattern (except for its finely barred breast) is plover-like. Its long, thin bill represents an extreme among plovers. On superficial grounds Seebohm (1888) placed Phegornis and Prosobonia in the same genus. Lowe (1931c) correctly recognized it as a plover, but Bock (1958), who had no skeleton to examine, was

misled by Lowe's poor illustration of Phegornis and thought its relationships not yet well established. Zusi and Jehl (1970) presented strong evidence that it is a plover, and Burton (1974) found its jaw musculature typical of plovers. Other than its long bill, I find its skeleton that of a typical plover.

Little attention has been given to the relationships of Hoploxypterus. Seebohm (1888) placed it among the lapwings on the basis of the amount of white on the central tail feathers, Sharpe (1896) placed it and several other Charadriinae among the lapwings on the basis of leg scutellation, while Ridgway (1919) took no stand on whether it is a lapwing but placed it immediately after them in his text; his key places it with the Charadriinae. Peters (1934) placed it in the Vanellinae, an arrangement Bock (1958) thought "natural." Bock thought the plumage pattern of Hoploxypterus "unique" with features of the breast and head pattern like those of some African lapwings. The plumage pattern of Hoploxypterus is typical of Charadrius and almost identical to that of C. melanops. The difference in color of the scapulars (black in Hoploxypterus and red in C. melanops) is no more than that which appears between the sexes in some species (e.g., the breast band of the breeding plumage of some races of C. wilsonia). Zusi and Jehl (1970) were the first to report that all presumed lapwings except Hoploxypterus have a unique strut on some of the cervical vertebrae. More recently Burton (1974) found that all presumed lapwings except Hoploxypterus have a large Ap. A^1 slip of M. adductor externus and a double origin of M. splenius capitis. He thought this to represent convergence with Charadrius. My analyses place Hoploxypterus with the Charadriinae (Fig. 45). I suspect that if Hoploxypterus did not have a wing spur, it would never have been thought a lapwing.

Lowe (1922, 1933a, b) thought that the color of the back plumage and the morphology of the skull, especially that associated with the development of the supraorbital grooves, held the key to determining the relationships among the plovers. His characters, however, are highly correlated with environmental conditions, even though he argued otherwise. The development of the supraorbital grooves is related to the size of the nasal gland, which is contained in them and which is known to be functionally related to environmental salinity in many

charadriiforms (Staaland 1967). Bock (1958) argued that Lowe's characters have little value for making phylogenetic inference.

Although Bock doubted that it is possible to determine the relationships among the Charadriinae from a study of museum skins, he proposed a series of five groups of closely related species on the basis of head and breast patterns and back color. Bock's characterizations of his groups and his methods for arriving at them are vague. He placed Charadrius pecuarius and hiaticula in the same group on the false assumption that their head patterns are the same. I find that his groups do not reflect plumage similarities well and disagree with his dendrogram of relationships.

My analyses only partially resolve the relationships among the Charadriinae. The best tree which I have been able to construct (Fig. 46) has many of the species clustered on the basal node from which are derived only three lines leading to more than one species. (A fourth line leads to C. asiaticus and veredus, thought by some to be conspecific.) One line, defined by the presence of a distinct ridge across the bottom of the groove in the symphysis of the furcula (Fig. 24) and a white collar around the back of the neck in the adult, leads to C. marginatus, alexandrinus (excluding ruficapillus), wilsonia, cucullatus, hiaticula, semipalmatus, vociferus, placidus, and dubius. On the basis of its plumage pattern, peronii probably also belongs in this group. A second line, defined by possession of a black collar around the back of the neck which is an extension of the facial pattern and a white line behind a black forehead (from which the forehead pattern of melanops probably arose), leads to C. pecuarius, sanctaehelenae, novaeseelandiae, cinctus, melanops, and Hoploxypterus. On the basis of its plumage pattern, thoracicus undoubtedly is a member of this group. Of all the plovers, this group appears to have been most successful in colonizing islands. The third line, defined by possession of a pigmented lower belly, leads to Pluvialis, C. morinellus, and ruficollis. Although the members of this group share several similarities of plumage pattern, more evidence is needed to confirm a close relationship among them. Bock (1958) thought C. obscurus close to Pluvialis on the basis of plumage pattern and a supposed breeding record of Pluvialis in New Zealand. I find the plumage of obscurus

typical of Charadrius and never spotted as is that of Pluvialis. Since Robson's (1884) report of Pluvialis breeding in New Zealand does not include a description of the bird he claimed to have observed, it is probably unreliable. Among the basal species, ruficapillus, falklandicus, alticola, bicinctus, and collaris have many similarities in plumage pattern and coloration and may prove to be a natural group when further characters are examined.

My analyses indicate that the lapwings (Vanellinae), oystercatchers, Ibisbill, avocets, and stilts are all derived from an ancestor close to the Charadriinae (Fig. 45) and that they have split off sequentially from one phyletic line, which is defined by origins of M. splenius capitis on vertebrae 2 and 3. This character state may be related to the generally larger size of the birds which arise from this line, but some of the basal group of plovers are larger than some of the lapwings, and there seems to be no correlation of this character state with size in other groups in the order in which it is found. This branch gives rise to two lines: one leading to the lapwings, defined by a distinctive strut on the cervical vertebrae (Fig. 20), the other leading to the oystercatchers, Ibisbill, avocets, and stilts, defined by considerable but not complete fusion of the maxillopalatines and palatines and the presence of tendinal canal No. 1 of the hypotarsus only as a groove (Fig. 31). The lapwings are usually considered to be a group of plovers, distinct in their black-and-white wing and tail patterns, their generally larger size, and the occurrence in some of wing spurs and facial wattles. Jehl (1968b) thought the downy young patterns of Vanellus and Charadrius so similar as to confirm common ancestry.

The lapwings are puzzling in that few trends in structure or plumage are discernible among them. Since Peters (1934) placed the 23 species into 18 genera, few workers have tried to clarify the relationships among them. White (1952) placed the African species into four genera on the basis of whether they had facial wattles, wing spurs, or both. Boetticher (1954) added the condition of the hallux to White's character set and also proposed four genera. Neither of these recommendations have been widely used, probably because the species they placed together seem so different in other respects. Bock (1958) was unable to find any clearly separable species groups and recommended

that all the species be placed in Vanellus. Recently Wolters (1974) asserted that the species are too heterogeneous to be placed in the same genus, declaring that while the plumage patterns and facial wattles are good characters for phylogenetic inference, the hallux and wing spurs are not good characters. He proposed an unlikely phylogeny for the group (which included Hoploxypterus) but gave no details on the characters used or how they were analyzed. While it is premature to assume that my analyses (see Fig. 47) have led to the true relationships among the lapwings, they have shown that the presence of a wing spur appears to be a true cladistic character.

The oystercatcher-Ibisbill-avocet-stilt line gives rise to two further lines: one leading to the oystercatchers, defined by an angle of 70° or more between the lateral nasal bar and jugal bar, complete fusion of the maxillopalatines and palatines, 12 neck vertebrae, and no ridge between the coracoidal sulci of the sternum; and one leading to the Ibisbill, avocets, and stilts, defined by an origin of M. complexus on vertebra 6 and formation of a smooth curve by the posterior medial and medial edge of the ilium. The evidence for a close relationship between the oystercatchers and the plovers has been discussed above. On the basis of size and similarities of adult plumage, Jehl (1968b) thought that oystercatchers might be close to the lapwings. The skeletons of the oystercatchers have given few clues to the relationships among them (see Fig. 49).

The Ibisbill-avocet-stilt line in turn gives rise to two lines: one leading to the Ibisbill, defined by a lack of contact between the lacrimal and ectethmoid, exorbital nasal glands (Fig. 17), and origins of M. rectus capitis on only vertebrae 1-4; the other line leading to the avocets and stilts, defined by a long bill tip with the dorsal and ventral bars of the upper jaw fused for about half the bill length (Fig. 10), trochlea for digits II and IV considerably elevated compared to that for digit II, the trochlea for digit II more elevated than that for digit IV (Fig. 30), the angle between trochleae II and IV larger than 35 degrees (Fig. 30D), and tendinal canals No. 5 and 6 detectable as grooves.

Little attention has been given to the relationships of Ibidorhyncha. The evidence for its membership in this group has been discussed

above. Boetticher (1934) thought it closest to the oystercatchers. Jehl (1968b) thought that it should be placed in a monotypic family until further study indicated its relationships. Hamilton (1975) thought that the fragmentary literature accounts of its habits do not indicate any particularly close relationship with the avocets and stilts.

The avocets and stilts have generally been accepted as closely related. Seebohm (1886b) placed all of them in one genus, but Sharpe (1896) placed them in the three currently recognized. Hamilton (1975) found the behavior of the North American representatives similar in many respects and reaffirmed their close relationship. Cladorhynchus appears to be a mixture of avocet and stilt. My analyses of the relationships among the avocets and stilts (Fig. 50, 55) arrived at no clear decision on which group Cladorhynchus is closer to. Since the hallux has proven of little value in making phylogenetic inferences among the plovers and the rest of their allies, I doubt that it is a true cladistic character for the avocets and stilts. A multivariate analysis of skeletal elements (Strauch unpublished) shows that Cladorhynchus is more like avocets than stilts in body size and proportions. Its habit of nesting in large colonies (McGilp and Morgan 1931) is also more typical of avocets. On the basis of the available evidence I favor aligning it with the avocets.

The relationships among the charadriine shorebirds are not yet well resolved. Five phyletic lines: the Burhinidae and Pluvianus; Dromas; the Glareolidae; Chionis and Pluvianellus; and the plovers and their allies, have been identified, but the relationships among them are unspecified by my character set. Dromas and the Glareolidae may still prove closer to the Lari than to the charadriine shorebirds, and the relationship between the Burhinidae and Pluvianus needs further examination. On the other hand, Chionis and Pluvianellus appear to be closely related, while the oystercatchers, Ibisbill, avocets, and stilts are found to be closely related to the plovers and lapwings.

The estimates of the phylogenetic relationships among the Charadriiformes which I have made are more detailed and more objective than have been made previously. A classification based on these results is presented in Appendix VII. The results presented here can

now be extended and refined by including characters of other organ systems, such as musculature and plumage patterns, in further character compatibility analyses.

APPENDIX I. Characters Used for Outgroup Prim Network Analysis

Outgroup Character Number	Character Description	Character States
1	Basipterygoid articulation of pterygoid and basitemporal process on basispenoid rostrum	0 present 1 absent
2	Supraoccipital foramen	0 present 1 absent
3	Lacrimal-ectethmoid complex	0 complex not near jugal 1 complex touching or almost touching jugal
4	Anterior process on lacrimal	0 absent 1 present but poorly developed 2 well developed
5	Prearticular process of mandible	0 absent 1 present but poorly developed 2 well developed
6	Posterior process on mandible	0 absent 1 poorly developed 2 well developed
7	Number of caudal vertebra omitting pygostyle	range 4 to 9
8	Number of neck vertebrae omitting axis and atlas	range 10 to 20
9	Number of costal processes on sternum	range 2 to 9
10	Medial sternal notch	0 present 1 absent
11	Lateral sternal notch	0 present 1 absent
12	Ridge in capital groove of humerus	0 absent 1 present
13	Phalanx 1, digit III	0 not perforated 1 perforated
14	Coracoid fenestra	0 present 1 absent

APPENDIX I. Continued

Outgroup Character Number	Character Description	Character States
15	Tarsometatarsus trochlea	0 trochlea for digits 2 and 4 raised, that for digit 2 more so
		1 trochlea for digits 2 and 4 about equally raised
		2 trochlea for digits 2 and 4 little or not raised relative to that for digit 3
16	Hallux	0 present
		1 absent
17	Claw of digit III	0 pectate
		1 not pectate
18	Plumage iridescence	0 none of plumage iridescent
		1 some of plumage iridescent
19	Cervical vertebrae strut	0 absent
		1 present
20	Deltoid crest of humerus	0 anconal surface concave
		1 anconal surface convex
21	Maxillopalatine strut A	0 absent
		1 present
22	Maxillopalatine strut B	0 absent
		1 present
23	Maxillopalatine strut C	0 absent
		1 present
24	Medial and posterior condyles of quadrate	0 connected with high ridge
		1 connected with low ridge
		2 groove between condyles
25	Posterior and lateral condyles of quadrate	0 connected with high ridge
		1 connected with low ridge
		2 groove between condyles

APPENDIX I. Continued

Outgroup Character Number	Character Description	Character States
26	Lacrimal-ectethmoid	0 fused or touching 1 not in contact
27	Ectethmoid-frontal	0 fused or touching 1 not in contact
28	Ossified alinasal	0 absent 1 present
29	Nostrils	0 holorhinal 1 schizorhinal
30	Supraorbital process on lacrimal	0 absent 1 present
31	Grooves for nasal glands	0 inter- or preorbital 1 exorbital 2 supraorbital
32	Retroarticular process of mandible	0 absent 1 poorly developed 2 well developed
33	Rear fossa of mandible	0 absent 1 present as small hole 2 large and well developed
34	Hypapophysis of atlas	0 two well-developed lateral spines 1 intermediate or indeterminate 2 one well-developed medial spine
35	Renal depression of synsacrum	0 posterior end flat and indistinct 1 distinct, forming slight depression 2 distinct, forming distinct depression 3 distinct, forming hollowed-out area
36	Depression on posterior of ilium	0 absent 1 slight depression 2 deep depression

APPENDIX I. Continued

Outgroup Character Number	Character Description	Character States
37	Interapophyseal foramina of synsacrum	0 absent 1 one or two per side 2 three or more per side
38	Brace from sacral-caudal vertebrae to acetabulum	0 absent 1 present but falls short of acetabulum 2 brace to acetabulum
39	Lateral process of sternum	0 much longer than xiphial area 1 slightly longer than xiphial area 2 about same length as xiphial area 3 slightly shorter than xiphial area 4 much shorter than xiphial area
40	Ventral manubrial spine of sternum	0 absent 1 present and below coracoidal sulces 2 present and above coracoidal sulces 3 present and splits coracoidal sulces
41	Dorsal manubrial spine of sternum	0 absent 1 well developed 2 well developed and splits coracoidal sulces
42	Pneumatic fossa II of humerus	0 absent 1 poorly developed 2 well developed
43	Deltoid crest of humerus	0 smooth and rounded 1 acute angle on top
44	Ectepicondylar prominence of humerus	0 absent 1 present
45	Junction of coracoid and scapular	0 acromion of scapular higher than procoracoid 1 acromion and procoracoid even

APPENDIX I. Continued

Outgroup Character Number	Character Description	Character States
46	Brachial tuberosity of coracoid	0 poorly developed and not roofing over triosseal canal 1 well developed and roofing over triosseal canal

APPENDIX II. Basic Data Matrix for Prim Network Analysis

Species	Characters 1234	567-8	9012	3456	7890	1234	5678	9012	3456	7890	1234	56
Gaviidae												
Gavia adamsi	1110	20612	9100	0000	1101	0002	1110	0022	1100	0000	0000	00
Gavia stellata	1110	20612	8100	0000	1001	0002	1100	0022	2200	1041	0100	10
Podicipedidae												
Podilymbus podiceps	1110	22717	5100	0100	0001	0000	2000	0010	1200	0000	0000	00
Podiceps auritus	1110	20817	6100	0100	1001	0000	1100	0010	1100	0000	0000	00
Aechmophorus occidentalis	1110	21820	6100	0100	1001	0002	2100	0010	1200	0000	0000	00
Turnicidae												
Turnix nigricollis	0110	00613	2000	0111	1001	0000	0001	1011	1110	0140	2000	11
Gruidae												
Grus canadensis	1010	21616	8110	0000	1010	0102	0100	1110	2230	1211	0000	00
Aramidae												
Aramus guarauna	1100	21614	6110	0000	1110	0101	0100	1110	1230	1221	0000	00
Rallidae												
Rallus longirostris	1100	21712	5100	0000	1001	0102	0100	0112	1130	0201	0000	00
Rallina fasciata	1100	21712	5100	0000	1001	0101	0100	0112	1130	1211	0000	00
Aramides ypecaha	1100	21713	6100	0000	1000	0101	0100	0112	1030	0201	0000	00
Porzana carolina	1100	21812	5100	0000	1001	0101	0100	0112	1030	0201	0000	00
Amaurornis phoenicurus	1100	21712	6100	0000	1001	0101	0100	0112	2230	0201	0000	00
Gallinula chloropus	1100	21812	6100	0000	1001	0101	0100	0112	0130	0201	0000	00
Fulica americana	1100	21813	7100	0000	1001	0101	0100	0112	1230	0201	0000	00
Heliornithidae												
Heliornis fulica	1100	21713	6100	0020	1101	0100	0100	1111	1130	0211	0000	00
Eurypygidae												
Eurypyga helias	1100	10715	5000	0120	1000	0101	1110	1101	2232	2231	0000	00
Otididae												
Tetrax tetrax	1111	00412	6000	0121	1001	0001	0010	0001	0022	2130	0000	00
Chlamydotis undulata	1111	00415	5000	0121	1001	0001	0000	0001	1122	0140	0000	00

APPENDIX II. Continued

Species	Characters											
			1			2			3			4
	1234	567-8	9012	3456	7890	1234	5678	9012	3456	7890	1234	56
Otididae												
Eupodotis australis	1111	00714	4000	0121	1011	0000	0010	0001	0122	0240	0000	00
Lissotis melanogaster	1111	00516	5000	0121	1001	0111	0000	0001	1122	1140	0100	00
Jacanidae												
Metopidius indicus	0100	01513	5101	0120	1101	0001	0000	1012	2121	0133	0200	11
Jacana spinosa	0100	01613	6101	0120	1101	0002	1000	1011	2120	2223	0100	11
Rostratulidae												
Rostratula benghalensis	0000	10711	5101	0100	1001	0000	1010	1012	2111	2233	0201	11
Nycticryphes semicollaris	0001	00712	5101	0100	1001	0002	1010	1012	2110	0243	0201	11
Haematopodidae												
Haematopus ostralegus	0102	12710	6000	0021	1000	0102	0010	1022	1210	2232	0201	11
Charadriidae												
Vanellus vanellus	0002	11811	6000	0000	1110	1102	0010	1022	0111	2232	0201	11
Vanellus spinosus	0102	12712	6000	0001	1110	1112	0010	1022	0100	2232	0201	11
Charadrius semipalmatus	0002	22812	6000	0011	1000	1001	0010	1022	0111	2232	0201	11
Scolopacidae												
Prosobonia cancellatus	0100	02812	5101	0100	1001	0012	1010	1012	2110	2233	0201	11
Bartramia longicauda	0102	02813	6001	0120	1001	0012	0000	1022	2111	2233	0201	11
Tringa flavipes	0002	00812	6001	0100	1001	0012	0010	1022	2110	2233	0201	11
Actitis hypoleucos	0002	00812	6101	0100	1001	0012	1000	1022	2110	2233	0201	11
Arenaria interpres	0001	02812	5001	0110	1001	0012	1000	1022	1011	2233	0201	11
Calidris bairdii	0001	02912	6001	0120	1001	0012	1010	1022	2100	2232	0201	11
Recurvirostridae												
Ibidorhyncha struthersii	0002	21812	6000	0021	1000	0101	0110	1012	1100	2233	0201	11
Himantopus himantopus	0002	11712	6000	0001	1000	1102	1010	1022	2211	2232	0201	11
Recurvirostra americana	0002	11812	6000	0000	1000	1102	1010	1022	2111	2222	0201	11
Phalaropodidae												
Phalaropus tricolor	0102	02812	6001	0100	1001	0012	0010	1022	2111	2233	0201	11

APPENDIX II. Continued

Species	Characters											
			1			2			3		4	
	1234	567-8	9012	3456	7890	1234	5678	9012	3456	7890	1234	56
Dromadidae												
Dromas ardeola	1102	10812	6000	0000	0000	0102	1000	1022	1111	1242	0101	11
Burhinidae												
Burhinus oedicnemus	1110	11711	5100	0021	1010	0102	0110	0021	1211	2222	0100	11
Glareolidae												
Pluvianus aegyptius	1111	11812	4000	0021	1100	1102	1010	0002	0110	2242	0201	11
Rhinoptilus africanus	1112	00712	5001	0111	0000	1001	0000	1022	0111	2232	0101	11
Stiltia isabella	1102	00712	5001	1000	1000	0102	0000	1021	1011	2233	0201	11
Glareola pratincola	1102	00712	5001	1010	0000	1102	0000	1021	1111	2232	0201	11
Thinocoridae												
Attagis gayi	1101	02812	6101	0120	1001	0102	0000	1022	1111	2133	0201	11
Thinocorus orbignyianus	1101	00912	6101	0100	1001	0002	0000	1022	2111	2233	0201	11
Chionididae												
Chionis alba	1100	00812	6000	0010	1000	1102	0110	1022	1210	2133	0201	11
Stercorariidae												
Stercorarius parasiticus	1101	10812	6100	1020	1000	1101	1000	1020	1022	2212	0101	11
Laridae												
Larus delawarensis	1100	20812	6000	1000	1000	0002	1000	1020	2111	2212	0201	11
Rhodostethia rosea	1102	10812	7000	1010	1000	0102	2000	1020	2110	2222	0201	11
Rissa tridactyla	1101	20812	6000	1020	1000	0002	1000	1020	2111	2212	0201	11
Xema sabini	1101	20812	6000	1000	1000	0002	1000	1020	2111	2212	0201	11
Chlidonias nigra	1102	20812	6000	1010	1000	0102	1000	1020	1111	2232	0201	11
Sterna hirundo	1102	10812	6000	1000	1000	0002	1000	1020	2101	2222	0201	11
Thalasseus sandvicensis	1102	10812	6000	1020	0000	0002	1000	1020	2111	2222	0201	11
Alcidae												
Uria aalge	1100	11912	7100	0001	1001	0102	1000	1022	2010	2032	0200	10
Cepphus grylle	1101	10912	6100	0001	1001	0002	1000	1022	1022	2043	0200	10
Endomychura hypoleucus	1000	10912	7100	0001	1001	0101	1000	1022	2000	1033	0201	10

APPENDIX II. Continued

Species	Characters											
			1			2			3		4	
	1234	567-8	9012	3456	7890	1234	5678	9012	3456	7890	1234	56
Pteroclidae												
Pterocles lichtensteinii	0110	11512	5000	0120	1001	0001	0001	1001	0020	1040	0010	01
Pterocles bicinctus	0110	00611	5000	0120	1001	0001	0001	1001	0110	1040	0010	01
Columbidae												
Treron delalandii	0110	00611	4000	0120	1001	0001	0001	1001	0112	0141	1010	01
Columba cayennensis	0110	00611	4000	0120	1001	0001	0001	1001	0111	0141	1010	01
Columbigallina talpacotl	0110	00610	3000	0120	1001	0001	0001	1001	0111	0241	1010	01

APPENDIX III. Character states of the species examined

Species	Character Number 1 12345 67890	2 12345 67890	3 12345 67890	4 12345 67890	5 12345 67890	6 12345 67890	7 12345 67890
Metopidius indicus	AABAB AABAB	BAAAA BAAAB	AAAAA ABAAA	ECAAB ACABA	BBABA HBBAA	ABACA AABAB	CAABB AAAAA
Microparra capensis	AABAB AABAB	BAAAA BAAAB	AAAAA ABAAA	ECAAB ACABA	ABABA HBBAD	ABACA AABBB	CAABB AAAAA
Actophilornis africana	AABAB AABAB	BAAAA BAAAB	AAAAA ABAAA	ECAAB ACABA	BBABA HBBAA	ABACA AABBB	CAABB AAAAA
Actophilornis albinucha	AABAB AABAB	BAAAA BAAAB	AAAAA ABAAA	ECAAB ACABA	BBABA HBBAB	ABACA AABBB	CAABB AAAAA
Irediparra gallinacea	AABAB AABAB	BAAAA BAAAB	AAAAA ABAAA	ECAAB ACABA	BBABA HBBAA	ABACA AABBB	CAABB AAAAA
Hydrophasianus chirurgus	AABAB AABAB	BAAAA BAAAB	AAAAA ABAAA	GCAAB ACABA	ABABA EBBAD	ABACA AABAB	CAABB AAAAA
Jacana jacana	AABAB AABAB	BAAAA BAAAB	AAAAA ABAAA	ECAAB ACABA	ABABA EBBAA	ABACA BABAB	CAABB AAAAA
Jacana spinosa	AABAB AABAB	BAAAA BAAAB	AAAAA ABAAA	ECAAB ACABA	BBABA EBBAB	BBACA BABAB	CAABB AAAAA
Thinocorus orbignyianus	AABCA AADAA	BAAAA BAAAB	AAABA AAAAA	BAAAA ACABA	ABAAB AAAAA	AAAAA ABABA	BAABB AAAAA
Thinocorus rumicivorus	AABCA AADAA	BAAAA BAAAB	AAABA AAAAB	BAAAA ACABA	ABAAB AAAAA	AAAAA ABABA	BAABB AAAAA
Attagis gayi	AABCA AADAA	BAAAA BAAAB	AAABA AAAAA	BAAAA ACABA	ABAAB AAAAB	AAAAA ABABA	BACBB AAAAA
Rostratula benghalensis	AABAB AACAB	BAAAA BABAB	AAABA ABAAB	AAAAB ACABA	ABAAB AAAAA	AAACA AABAA	BAABB AAAAA
Nycticryphes semicollaris	AABAB AACAB	BAAAA BABAB	AAABA ABAAB	AAAAB ACABA	ABAAB AAAAA	AAACA AABAA	BAABB AAAAA
Phalaropus tricolor	AABAA AAFAB	BAAAA BAAAC	AAABA AAAAB	BAAAA BCABA	ABAAB AAAAA	AAAAA ABABA	BAABA AAAAA
Phalaropus lobatus	AABAA AAFAB	BAAAA BAAAC	AAABA ABAAB	BAAAA BCABA	ABAAB AAAAA	AAAAA ABABA	BAABB AAAAA
Phalaropus fulicarius	AABAA AAFAB	BAAAA BAAAC	AAABA ABAAB	BAAAA BCABA	ABAAB AAAAA	AAAAA ABABA	BAABB AAAAA

APPENDIX III. Continued

Species	Character Number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Tringa														
solitaria	AABAA	AAAAB	BAAAB	BBBAC	ABABA	ABABA	AAAAA	ACABA	ABAAB	AAAAA	AAAAA	AAAAA	BAABB	AAAAA
glareola	AABAA	AAAAB	BAAAB	BBBAC	ABABA	AAABB	AAAAA	BCABA	BBAAB	AAAAA	AAAAA	AAAAA	BAABB	AAAAA
erythropus	AABAB	AAAAB	BAAAB	BBBAC	ABABA	ABAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	AAAAB	BAAAB	AAAAA
totanus	AABAA	AAAAB	BAAAB	BBBAC	ABABA	ABABB	AAAAA	BCABA	ABAAB	AAAAA	AAAAA	AAAAB	BAABA	AAAAA
flavipes	AABAA	AAAAB	BAAAB	BBBAC	ABABA	ABABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	AAAAB	BAAAA	AAAAA
melanoleuca	AABAB	AAAAB	BAAAB	BBBAC	ABABA	ABABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	AAAAB	BAAAB	AAAAA
ocrophus	AABAA	AAAAB	BAAAB	BBBAC	ABABA	AAABB	BAAAA	ACABA	ABAAB	AAAAD	AAAAA	AAAAB	BAABB	AAAAA
nebularia	AABAA	AAAAB	BAAAB	BBBAC	ABABA	ABABB	AAAAA	BCABA	BBAAB	AAAAA	AAAAA	AAAAB	BAAAA	AAAAA
stagnatilis	AABAA	AAAAB	BAAAB	BBBAC	ABABA	BBABB	BAAAA	BCABA	BBAAB	AAAAA	AAAAA	AAAAB	BAAAB	AAAAA
Catoptrophorus														
semipalmatus	AABAA	AAAAB	BAAAB	BBBAC	ABABA	AAABB	AAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABAAB	BAABB	AAAAA
Heteroscelus														
brevipes	AABAA	AAAAB	BAAAB	BBBAC	ABABA	AAABB	AAAAA	BCABA	BBAAB	AAAAA	AAAAA	AAAAA	BACBA	AAAAA
incanus	AABAA	AAAAB	BAAAB	BBBAC	ABABA	AAABB	AAAAA	BCABA	BBAAB	AAAAA	AAAAA	AAAAA	BACAC	AAAAA
Prosobonia														
cancellatus	AABAA	AABAB	BABAA	BAAAC	AAABA	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	BAAAA	AAABA	BAABB	AAAAA
Bartramia														
longicauda	AABAA	AABAB	BBBAA	BAAAB	AAABA	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA
Numenius														
minutus	AABAA	AABAB	BBBAA	BAAAC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA
borealis	AABAA	AABAB	BBBAA	BAAAC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAAAB	AAAAA
tenuirostris	AABAA	AABAB	BBBAA	BAAAC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAB	AAAAA	ABABA	BAABB	AAAAA
tahitiensis	AABAA	AABAB	BBBAA	BAAAC	AAABA	AAABB	BBAAA	BCABA	ABAAB	AAAAA	AAAAA	ABAAB	BAABB	AAAAA
madagascariensis	AABAA	AABAB	BBBAA	BAAAC	AAABA	AAABB	BBAAA	BCABA	ABAAB	AAAAA	AAAAA	ABAAB	BAABB	AAAAA
phaeopus	AABAA	AABAB	BBBAA	BABAC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABB	BAABB	AAAAA
arquata	AABAA	AABAB	BBBAA	BABAC	AAABA	AAABA	BAAAA	BCABA	ABAAB	AAAAB	AAAAA	ABAAB	BAABB	AAAAA
americanus	AABAA	AABAB	BBBAA	BABAC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAB	AAAAA	ABABB	BAABB	AAAAA

APPENDIX III. Continued

Species	Character Number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Actitis														
hypoleucos	AABBA	AABAB	BAAAA	BABBC	AAABA	AAAAB	BAAAA	ACABA	ABAAB	AAAAA	AAAAA	ABABA	BAABA	AAAAA
macularia	AABBA	AABAB	BAAAA	BABBC	AAABA	AAAAB	BAAAA	ACABA	ABAAB	AAAAA	AAAAA	ABABA	BAABA	AAAAA
Aphriza														
virgata	AABBA	AABAB	BAAAA	BABBC	AAABA	AAAAA	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BABBA	AAAAA
Calidris														
canutus	AABBA	AABAB	BAAAA	BABBC	AAABA	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BABBB	AAAAA
tenuirostris	AABBA	AABAB	BAAAA	BABBC	AAABA	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BABBA	AAAAA
alba	AABBA	BABAB	BAAAA	BABBC	AAABB	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BBABA	AAAAA
pusilla	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA
mauri	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABA	AAAAA
ruficollis	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BACBB	AAAAA
minuta	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA
temminckii	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAD	AAAAA	ABABA	BABBA	AAAAA
subminuta	AABBA	BABAB	BAAAA	BABBC	AAABB	AAAAB	AAAAA	BCABA	ABAAB	AAAAD	AAAAA	ABABA	BAABA	AAAAA
minutilla	AABBA	BABAB	BAAAA	BABBC	AAABB	AAABB	BAAAA	BCABA	ABAAB	AAAAD	AAAAA	ABABA	BACBB	AAAAA
fuscicollis	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABB	BAAAD	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BABBA	AAAAA
bairdii	AABBA	AABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABA	AAAAA
melanotos	AABBA	AABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA
acuminata	AABBA	AABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA
maritima	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BABBB	AAAAA
ptilocnemis	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BABBB	AAAAA
alpina	AABBA	BABAB	BAAAA	BABBC	AAABB	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BABBA	AAAAA
ferruginea	AABBA	BABAB	BAAAA	BABBC	AAABA	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BABBA	AAAAA
Eurynorhynchus														
pygmeus	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BACBA	AAAAA
Limicola														
falcinellus	AABBA	BABBB	BAAAA	BABBC	AAABA	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA

APPENDIX III. Continued

Species	Character Number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Micropalama														
himantopus	AABBA	BABAB	BAAAA	BABBC	AAABA	AAABC	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BABBA	AAAAA
Tryngites														
subruficollis	AABBA	AABAB	BAAAA	BABBC	AAABA	AABAB	BAAAA	ACABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA
Philomachus														
pugnax	AABBA	AABAB	BAAAA	BABBC	AAABA	AAABB	BCAAA	ACABA	ABAAB	AAAAA	AAAAA	AAABA	BAABB	AAAAA
Arenaria														
interpres	AABBA	AAEAB	BAAAA	BABAC	AAABB	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABA	AAAAA
melanocephala	AABBA	AAEAB	BAAAA	BABAC	AAABB	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABA	AAAAA
Limnodromus														
griseus	AABBA	BABDB	BAAAA	BABAC	AAABB	AAAAA	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA
scolopaceus	AABBA	BABDB	BAAAA	BABAC	AAABB	AAAAA	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAABB	AAAAA
Xenus														
cinereus	AABBA	BABAB	BAAAA	BABAC	AAABA	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	ABABA	BAAAA	AAAAA
Limosa														
limosa	AABBA	BABCB	BBAAA	BABAC	AAABA	AAAAA	BAAAA	ACABA	ABAAB	AAAAA	AAAAA	ABABB	BABAB	AAAAA
haemastica	AABBA	BABCB	BBAAA	BABAC	AAABA	AAAAA	BAAAA	ACABA	ABAAB	AAAAA	AAAAA	ABABB	BABAB	AAAAA
lapponica	AABBA	BABCB	BBAAA	BABAC	AAABA	AAAAA	BAAAA	ACABA	ABAAB	AAAAA	AAAAA	ABABB	BABAB	AAAAA
fedoa	AABBA	BABCB	BBAAA	BABAC	AAABA	AAAAA	BAAAA	ACABA	ABAAB	AAAAA	AAAAA	ABABB	BABAB	AAAAA
Coenocorypha														
aucklandica	AAABB	BABAB	BCAAB	BABAB	ECABA	AAAAB	BBAAA	ACABA	ABAAB	AAAAD	AAAAA	AAAAA	BACBB	AAAAA
Lymnocryptes														
minima	CAABC	BABAB	BCAAA	BABAB	ECABA	AAAAB	BAAAA	BCABA	ABAAB	AAAAA	AAAAA	AAABA	BAABB	ACAAB
Gallinago														
hardwickii	CAABC	BABAB	ACAAA	BABAB	ECABB	AAAAB	CAAAA	ACABA	ABAAB	AAAAA	AAACA	AAABA	BACBB	BCAAB
stenura	CAABC	BABAB	ACAAA	BABAB	ECABB	AAAAB	CAAAA	ACABA	ABAAB	AAAAA	BAACA	AAABA	BACBB	BAAAB
megala	CAABC	BABAB	ACAAA	BABAB	ECABB	AAAAB	CAAAA	ACABA	ABAAB	AAAAA	AAACA	AAABA	BACBB	BAAAB
nigripennis	CAABC	BABAB	ACAAA	BABAB	ECABB	AAAAB	CAAAA	ACABA	ABAAB	AAAAA	BAACA	AAABA	BACBB	BAAAB
macrodactyla	CAABC	BABAB	ACAAA	BABAB	ECABB	AAAAB	BAAAA	ACABA	ABAAB	AAAAA	AAACA	AAABA	BACBB	BAAAB

APPENDIX III. Continued

Species	Character Number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Gallinago														
media	CAABC	BABAB	ACAAA	BABAB	ECABB	AAAAB	BAAAA	ACABA	ABAAB	AAAAA	AAACA	AAABA	BACBB	BAAAB
gallinago	CAABC	BABAB	BCAAA	BABAB	ECABB	AAAAB	CAAAA	ACABA	ABAAB	AAAAA	AAACA	AAABA	BACBB	BAAAB
paraguaiae	CAABC	BABAB	ACAAA	BABAB	ECABB	AAAAB	BAAAA	ACABA	ABAAB	AAAAA	AAACA	AAABA	BACBB	BAAAB
undulata	CAABC	BABAB	ACAAA	BABAB	ECABB	AAAAB	BBAAA	ACABA	ABAAB	AAAAA	BAACA	AAABA	BACBA	BAAAB
Philohela														
minor	CAABC	BABAB	ACAAA	BABAA	ECBBB	AAAAB	BAAAA	ACABA	ABAAB	AAAAA	AAACA	AABBA	BACBB	AAAAB
Scolopax														
r. rusticola	CAABC	BABAB	BCAAA	BABAA	ECBBB	AAAAB	AAAAD	ACABA	ABAAB	AAAAA	CAACA	BBBBA	BACBA	AABAB
r. mira	CAABC	BABAB	BCAAA	BABAA	ECBBB	AAAAB	AAAAD	ACABA	ABAAB	AAAAB	AAACA	BBBBA	BACBB	AABAB
Catharacta														
skua	AABAB	AABAA	AAABB	AAAAC	AABAA	AAAAC	AAAAA	BAAAA	BABBB	AAABA	CAABA	AAAAA	AACAB	ABAAA
Stercorarius														
pomarinus	AABAB	AABAA	AAABB	AAAAC	AABAA	AAAAA	BAAAA	BAAAA	BABBB	AAABD	AAABB	AAAAA	AACAB	ABAAA
parasiticus	AABAB	AABAA	AAABB	AAAAC	AABAA	AAAAA	BAAAA	BAAAA	BABBB	AAABA	AAABB	AAAAA	AACAB	ABAAA
longicaudus	AABAB	AABAA	AAABB	AAAAC	AABAA	AAAAA	AAAAA	BAAAA	BABBB	AAABA	AAABA	AAAAA	AACAB	ABAAA
Gabianus														
scoresbii	AABAB	AABAA	AAABB	AAAAC	AAAAA	AAAAA	BAAAA	BAAAA	BABAB	AAABD	AAABA	AAAAA	AACAB	AAAAA
Pagophila														
alba	AABAB	AABAA	AAABB	AAAAC	AAAAA	AAAAA	BAAAA	BAAAA	BABAB	AAABD	AAABA	AAAAA	AACAB	AAAAA
Larus														
heermanni	AABAB	AABAA	AAABB	AAAAC	AAAAA	AAAAA	BAAAA	BAAAA	BABAB	AAABA	AAABA	AAAAA	AACAB	AAAAA
delawarensis	AABAB	AABAA	AAABB	AAAAC	AAAAA	AAABA	BAAAA	BAAAA	BABAB	AAABA	AAABA	AAAAA	AACAB	AAAAA
argentatus	AABAB	AABAA	AAABB	AAAAC	AAAAA	AAAAA	BAAAA	BAAAA	BABAB	AAABA	AAABA	AAAAA	AACAB	AAAAA
serranus	AABAB	AABAA	AAABB	AAAAC	AAAAA	AAAAA	BAAAA	BAAAA	BABAB	AAABA	AAABA	AAAAA	AACAB	AAAAA
novaehollandiae	AABAB	AABAA	AAABB	AAAAC	AAAAA	AAAAA	BAAAA	BAAAA	BABAB	AAABA	CAABA	AAAAA	AACAB	AAAAA
philadelphia	AABAB	AABAA	AAABB	AAAAC	AAAAA	AAAAA	BAAAA	BAAAA	BABAB	AAABD	AAABA	AAAAA	AACAB	AAAAA
minutus	AABAB	AABAA	AAABB	AAAAC	AAAAA	AAAAA	BAAAA	BAAAA	BABAB	AAABD	AAABA	AAAAA	AACAB	AAAAA

APPENDIX III. Continued

Species	Character number 1 2 3 4 5 6 7 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890
Rhodostethia rosea	AABAB AABAA AAABB AAAAC AAAAA AAAAA BAAAA BAAAA BABAB AAABD BAABA AAAAA AACAB AAAAA
Rissa tridactyla	AABAB AABAA AAABB AAAAC AAAAA AAAAA BAAAA BAAAA BABAB AAABD AAABA AAAAA AACAB AAAAA
Creagrus furcatus	AABAB AABAA AAABB AAAAC AAAAA AAAAA BAAAA BAAAA BABAB AAABA AAABA AAAAA AACAB AAAAA
Xema sabini	AABAB AABAA AAABB BAAAC AAAAA AAAAA BAAAA BAAAA BABAB AAABD AAABA AAAAA AACAB AAAAA
Chlidonias nigra	AABAB AAAAA AAABB AAAAC AABAA AAAAA BAAAA BAAAA BABAB AAABA AAAAA ABAAA AACBB AAAAA
Phaetusa simplex	AABAB AAAAA AAABB AAAAC AABAA AAAAA BAAAA BAAAA BABAB AAABA AAAAA ABAAA AACBB AAAAA
Gelochelidon nilotica	AABAB AAAAA AAABB AAAAC AAABA AAAAA BAAAA BAAAA BABAB AAABD AAAAA ABAAA AACBB AAAAA
Hydroprogne caspia	AABAB AAAAA AAABB AAAAC AABAA AAAAA BAAAA BAAAA BABAB AAABA AAAAA ABAAA AACBB AAAAA
Sterna hirundo	AABAB AAAAA AAABB AAAAC AAAAA AAAAA BAAAA BAAAA BABAB AAABD AAAAA ABAAA AACBB AAAAA
vittata	AABAB AAAAA AAABB BAAAC AAAAA AAAAA AAAAA BAAAA BABAB AAABD AAAAA ABAAA AACBB AAAAA
trudeaui	AABAB AAAAA AAABB AAAAC AABAA AAAAA BAAAA BAAAA BABAB AAABA BAAAA ABAAA AACBB AAAAA
Thalasseus bergii	AABAB AAAAA AAABB AAAAC AABAA AAAAA BAAAA BAAAA BABAB AAABB AAAAA ABAAA AACBB AAAAA
sandvicensis	AABAB AAAAA AAABB AAAAC AAABB AAAAA BAAAA BAAAA BABAB AAABA AAAAA ABAAA AACBB AAAAA
Larosterna inca	AABAB AAAAA AAABB BAAAC AABAA AAAAA BAAAA BAAAA BABAB AAABD AAAAA ABAAA AACBB AAAAA
Anous stolidus	AABAB AAAAA AAABB AAAAC AABAA AAAAA BAAAA BAAAA BABBB AAABA AAAAA ABAAA AACBB AAAAA
tenuirostris	AABAB AAAAA AAABB AAAAC AAAAA AAAAA BAAAA BAAAA BABAB AAABD AAAAA ABAAA AACBB AAAAA

APPENDIX III. Continued

Species	Character Number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Gygis														
alba	AABAB	AAAAA	AAABB	BAAAC	AABAA	AAAAA	BAABA	BAAAA	BABAB	AAABD	AAAAA	ABAAA	AACBB	AAAAA
Rynchops														
nigra	AABAB	AAAAA	AAABB	AAAAC	AAABA	AAABB	BBAAA	BAAAA	BABBB	AAABB	AAAAA	ABAAA	AACAB	AAAAA
flavirostris	AABAB	AAAAA	AAABB	AAAAC	AAABA	AAABB	ABAAA	BAAAA	BABAB	AAABA	AAAAA	ABAAA	AACAB	AAAAA
Dromas														
ardeola	AABAB	AAAAA	AAABB	BAAAC	AABBA	AAAAB	BAAAA	BCAAA	AABBB	AAAAB	AAAAA	ABAAA	AAAAA	AAAAA
Stiltia														
isabella	AAAAB	AABAA	CAABB	BAAAC	AABAA	AAAAB	AAAAB	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BAAAA	CAAAA
Glareola														
pratincola	AAAAB	AABAA	CAABB	BAAAC	AABAA	AAAAB	ABAAB	BCAAA	AABAB	AAAAA	AAAAA	ABAAB	BAABB	AAAAA
maldivarum	AAAAB	AABAA	CAABB	BAAAC	AABAA	AAAAB	ABAAA	BCAAA	AABAB	AAAAA	AAAAA	ABAAB	BAABB	AAAAA
nordmanni	AAAAB	AABAA	CAABB	BAAAC	AABAA	AAAAB	ABAAB	BCAAA	AABAB	AAAAA	AAAAA	ABAAB	BAAAB	AAAAA
ocularis	AAAAB	AABAA	CAABB	BAAAC	AABAA	AAAAB	ABAAB	BCAAA	AABAB	AAAAA	AAAAA	ABAAB	BAABB	AAAAA
nuchalis	AAAAB	AABAA	CAABB	BABAC	AABAA	AAAAB	DBAAB	BCAAA	AABAB	AAAAA	AAAAA	ABAAB	BAABB	AAAAA
cinerea	AAAAB	AABAA	CAABB	BABAC	AABAA	AAAAB	ABAAB	BCAAA	AABAB	AAAAA	AAAAA	ABAAB	BAAAB	AAAAA
lactea	AAAAB	AABAA	CAABB	BABAC	AABAA	AAAAB	ABAAA	BCAAA	AABAB	AAAAA	AAAAA	ABAAB	BAABB	AAAAA
Rhinoptilus														
africanus	AAAAB	AABAA	CAABB	BAAAC	AABAA	AAAAA	AAAAB	BCAAA	AABBB	AAAAA	AAAAA	ABAAA	BBAAB	AAAAA
cinctus	AAAAB	AABAA	CAABB	BAAAB	AABBA	AAAAA	AAAAB	BCAAA	AABBB	AAAAA	BAAAA	ABAAA	BBABB	BAAAA
chalcopterus	AAAAB	AABAA	CAABB	BAAAB	AABBA	AAAAA	AAAAB	BCAAA	AABBB	AAAAA	BAAAA	ABAAA	BBAAB	AAAAA
Cursorius														
coromandelicus	AAAAB	AABAA	CAABB	BAAAD	AABAA	AAAAA	DAAAA	BCACA	AABBB	AAAAA	AAAAA	ABAAA	BBABC	AAAAA
temminckii	AAAAB	AABAA	CAABB	BAAAD	AABAA	AAAAA	DAAAA	BCACA	AABBB	AAAAA	AAAAA	ABAAA	BBABC	AAAAA
cursor	AAAAB	AABAA	CAABB	BAAAD	AABAA	AAAAA	DAAAB	BCACA	AABBB	AAAAB	AAAAA	ABAAA	BBABC	ACAAA
rufus	AAAAB	AABAA	CAABB	BAAAD	AABAA	AAAAA	DAAAB	BCACA	AABBB	AAAAB	AAAAA	ABAAA	BBABC	ACAAA
Burhinus														
oedicnemus	BBBAB	ABBAA	AAABB	BAAAC	AABAA	ABAAB	ABCAB	BCBAA	AABAA	ABAAB	AAAAA	ABBAB	ABCAA	AAAAA
senegalensis	BBBAB	ABBAA	AAABB	BAAAC	AABAA	ABAAB	ABCAB	BCBAA	AABAA	ABAAB	AAAAA	ABBAB	ABCBA	AAAAA

APPENDIX III. Continued

Species	Character number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Burhinus														
vermiculatus	BBBAB	ABBAA	AAABB	BAAAC	AABAA	ABAAB	AACAB	BCBAA	AABAA	AAAAB	AAAAA	ABBAA	ABCBA	AAAAA
capensis	BBBAB	ABBAA	AAABB	BAAAC	AABAA	ABAAB	AACAB	BCBAA	AABAA	ABAAB	AAAAA	ABBAA	ABCAA	AAAAA
bistriatus	BABAB	ABBAA	AAABB	BAAAC	AABAA	ABAAB	AACAB	BCBAA	AABAA	ABAAB	CAAAA	ABBAA	ABCBA	AAAAA
superciliaris	BBBAB	ABBAA	AAABB	BAAAC	AABAA	ABAAB	AACAB	BCBAA	AABAA	ABAAB	AAAAA	ABBAA	ABCAA	AAAAA
magnirostris	BBBAB	ABBAA	AAABB	BAAAC	AABAA	ABAAB	AACAC	BCBAA	AABAA	ABAAB	BAAAA	ABBAB	ABCBA	AAAAA
Esacus														
magnirostris	BBBAB	ABBAA	AAABB	BAAAC	AABAA	ABAAB	AACAA	BCBAA	AABAA	ABAAB	AAAAA	ABBAA	ABCAB	AAAAA
Pluvianus														
aegyptius	BABAB	ABBAA	AAABB	BAAAC	AABBA	ABABA	AAAAC	BCBAA	AABAB	BAAAB	AAAAA	ABAAA	ABBBA	AAAAA
Pluvianellus														
socialis	ABBBB	AABAA	AAABB	BABAC	CABBA	AAAAA	BAAAA	BCAAA	AABAB	IAAAA	BAAAA	ABAAA	AAABC	AAAAA
Chionis														
alba	ABBBB	AABAA	AAABB	BAAAC	CABBA	AAAAA	BAAAA	BCAAA	AABAB	IAAAB	BABAA	ABAAA	AAAAC	AAAAA
Peltohyas														
australis	AABBB	AABAB	AAABB	BAAAC	BABBA	AAAAB	BAABB	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Charadrius														
obscurus	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAB	CBABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
mongolus	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAA	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
leschenaultii	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAB	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
montanus	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAB	BBABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
collaris	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAB	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
venustus	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAB	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
ruficapillus	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
bicinctus	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAA	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
falklandicus	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAB	BBABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
alticola	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAB	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Anarhynchus														
frontalis	AABBB	AABAB	AAABB	BABAC	DABBA	AAAAB	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA

APPENDIX III. Continued

Species	Character Number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Charadrius														
modestus	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAA	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BABBC	AAAAA
tricollaris	AABBB	AABAB	AAABB	AABAC	BABBB	AAAAA	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Phegornis														
mitchellii	AABBB	AABAB	AAABB	AABAC	BABBA	AAAAA	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Charadrius														
asiaticus	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAA	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
veredus	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAA	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
ruficollis	AABBB	AABAB	AAABB	AABAC	BABBA	AAAAA	AAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
morinellus	AABBB	AABAB	AAABB	AABAC	BABBA	AAAAA	ABABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Pluvialis														
squatarola	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAA	AAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BABBC	AAAAA
apricaria	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAA	AAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
dominica	AABBB	AABAB	AAABB	BABAC	BABBA	AAAAA	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Charadrius														
pecuarius	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	ABABA	BCAAA	AABAB	AAAAA	AAAAA	ABABA	BBBBC	AAAAA
sanctaehelenae	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	ABABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Thinornis														
novaeseelandiae	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Charadrius														
cinctus	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BABBC	AAAAA
melanops	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	AAABA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Hoploxypterus														
cayanus	AABBB	AABAB	AAABB	AABAC	BABBA	AAAAA	BAABA	BCAAA	AABAB	FAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Charadrius														
marginatus	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BBABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
alexandrinus														
dealbatus	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BBABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
tenuirostris	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BAABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA

APPENDIX III. Continued

Species	Character Number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Charadrius														
wilsonia	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	AAABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
cucullatus	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BAABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
hiaticula	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BAABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
semipalmatus	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BAABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
melodus	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	ABABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
vociferus	AABBB	AABAB	AAABB	AABAC	BABBB	AAAAB	BAABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
placidus	AABBB	AABAB	AAABB	BABAC	BABBB	AAAAB	BAABA	BCAAA	CABAB	AAAAD	AAAAA	ABAAA	BBBBC	AAAAA
dubius	AABBB	AABAB	AAABB	AABAC	BABBB	AAAAB	BBABA	BCAAA	CABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
Vanellus														
malabaricus	AABBB	AABAB	AAABB	AABAC	BABBA	AAABA	AABBA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
melanopterus	AABBB	AABAB	AAABB	AABAC	BABBA	AAABA	AABBA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
lugubris	AABBB	AABAB	AAABB	AABAC	BABBA	AAABA	AABBA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	ACAAA
tricolor	AABBB	AABAB	AAABB	BAAAC	BABBC	AAABA	BBBBA	BCAAA	AABAB	AAAAA	AAAAA	ABAAA	BBBBC	AAAAA
gregarius	AABBB	AABAB	AAABB	AABAC	BABBA	AAABA	AABBA	BCAAA	AABAB	AAAAA	AAAAA	AAAAA	BABBC	AAAAA
leucurus	AABBB	AABAB	AAABB	AABAC	BABBA	AAABA	ABBBB	BCAAA	AABAB	AAAAA	AAAAA	AAAAA	BABBC	AAAAA
coronatus	AABBB	AABAB	AAABB	AAAAC	BABBA	AAABA	AABBA	BCAAA	AABAB	AAAAA	AAAAA	AAAAA	BBBBC	AAAAA
cinereus	AABBB	AABAB	AAABB	AAAAC	BABBA	AAABA	AABBA	BCAAA	AABAB	AAAAA	AAAAA	AAAAA	BABBC	AAAAA
tectus	AABBB	AABAB	AAABB	AAAAC	BABBA	AAABA	BABBA	BCAAA	AABAB	AAAAA	AAAAA	AAAAA	BBBBC	AAAAA
vanellus	AABBB	AABAB	AAABB	BABAC	BABBA	AAABB	BBBBA	BCAAA	AABAB	AAAAA	AAAAA	AAAAA	BABBC	AAAAA
chilensis	AABBB	AABAB	AAABB	BABAC	BABBA	AAABA	BBBBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BABBC	AAAAA
resplendens	AABBB	AABAB	AAABB	BABAC	BABBA	AAABA	BBBBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BBBBC	AAAAA
albiceps	AABBB	AABAB	AAABB	AAAAC	BABBA	AAABA	ABBBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BBBBC	AAAAA
senegallus	AABBB	AABAB	AAABB	AABAC	BABBA	AAABA	AABBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BABBC	AAAAA
spinosus	AABBB	AABAB	AAABB	BAAAC	BABBA	AAABA	AABBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BBBBC	AAAAA
armatus	AABBB	AABAB	AAABB	AAAAC	BABBA	AAABA	AABBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BBBBC	AAAAA
duvaucelii	AABBB	AABAB	AAABB	AABAC	BABBA	AAABA	BABBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BBBBC	AAAAA
miles	AABBB	AABAB	AAABB	BAAAC	BABBA	AAABA	BABBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BABBC	AABAA
macropterus	AABBB	AABAB	AAABB	AAAAC	BABBA	AAABA	AABBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BABBC	AABAA

APPENDIX III. Continued

Species	Character Number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Vanellus														
indicus	AABBB	AABAB	AAABB	AABAC	BABBA	AAABA	AABBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BABBC	AABAA
crassirostris	AABBB	AABAB	AAABB	BABAC	BABBA	AAABA	BABBA	BCAAA	AABAB	CAAAA	AAAAA	AAAAA	BABBC	AABBA
Haematopus														
ostralegus	AABBB	AABAB	ACABB	BAAAC	BABBA	AAABA	ABABA	BCBAA	AABAB	AAAAB	AAAAA	ABAAA	ABAAC	AAAAA
finschi	AABBB	AABAB	ACABB	BAAAC	BABBA	AAABA	ABABA	BCBAA	AABAB	AAAAB	AAAAA	ABAAA	ABAAC	AAAAA
moquini	AABBB	AABAB	ACABB	BAAAC	BABBA	AAABA	ABABA	BCBAA	AABAB	AAAAB	AAAAA	ABAAA	ABAAC	AAAAA
fuliginosus	AABBB	AABAB	ACABB	BAAAC	BABBA	AAABA	ABABA	BCBAA	AABAB	AAAAA	AAAAA	ABAAA	ABAAC	AAAAA
palliatus	AABBB	AABAB	ACABB	BAAAC	BABBA	AAABA	DBABA	BCBAA	AABAB	AAAAB	AAAAA	ABAAA	ABAAC	AAAAA
frazari	AABBB	AABAB	ACABB	BAAAC	BABBA	AAABA	ABABA	BCBAA	AABAB	AAAAB	AAAAA	ABAAA	ABAAC	AAAAA
bachmani	AABBB	AABAB	ACABB	BAAAC	BABBA	AAABA	ABABA	BCBAA	AABAB	AAAAB	AAAAA	ABAAA	ABAAC	AAAAA
ater	AABBB	AABAB	ACABB	BAAAC	BABBA	AAABA	ABABA	BCBAA	AABAB	AAAAB	AAAAA	ABAAA	ABAAC	AAAAA
leucopodus	AABBB	AABAB	ACABB	BABAC	BABBA	AAABA	ABABA	BCBAA	AABAB	AAAAA	AAAAA	ABAAA	ABAAC	AAAAA
Ibidorhyncha														
struthersii	ABBAB	AABAB	ABABB	BABAB	BABBA	ABABB	BAABB	BCAAA	AABAB	AAAAA	AAAAA	AAAAA	ABAAC	AAAAA
Himantopus														
h. himantopus	AABAB	AAAAB	ABABB	BABAC	BABBA	ABABA	AAABB	BCAAA	AABAB	AAAAA	AAAAA	AAAAB	BBBAC	AABBA
h. mexicanus	AABAB	AAAAB	ABABB	BABAC	BABBA	ABABA	AAABB	BCAAA	AABAB	AAAAA	AAAAA	AAAAB	BBBAC	AABBA
h. melanurus	AABAB	AAAAB	ABABB	BABAC	BABBA	ABABA	AAABB	BCAAA	AABAB	AAAAA	AAAAA	AAAAB	BBBAC	AABBA
Cladorhynchus														
leucocephala	AABAB	AAAAB	ABABA	BABAC	BABBA	ABABA	AAABA	BCAAA	AABAB	AAAAA	AAAAA	AAAAA	BBBAA	AABBA
Recurvirostra														
novaehollandiae	AABAB	BAAAB	ABABB	BABAC	BABBA	ABABA	BAABA	BCAAA	AABAB	ABAAA	AAAAA	AAAAA	BABAA	AABBA
americana	AABAB	BAAAB	ABABB	BABAC	BABBA	ABABA	AAABA	BCAAA	AABAB	ABAAA	AAAAA	AAAAA	BABAA	AABBA
andina	AABAB	BAAAB	ABABB	BABAC	BABBA	ABABA	AAABA	BCAAA	AABAB	ABAAA	AAAAA	AAAAA	BABAA	AABBA
avosetta	AABAB	BAAAB	ABABB	BABAC	BABBA	ABABA	AAABA	BCAAA	AABAB	ABAAA	CAAAA	AAAAA	BABAA	AABBA
Endomychura														
hypoleuca	AABAB	AABAA	AAABB	BABAC	AAAAA	AAAAA	CAAAA	ACAAB	AAAAA	AAAAC	ACAAA	ACAAB	BBCBB	AAAAA

APPENDIX III. Continued

Species	Character number 1 12345	67890	2 12345	67890	3 12345	67890	4 12345	67890	5 12345	67890	6 12345	67890	7 12345	67890
Uria aalge	AABAB	AABAA	AAABB	BAAAC	AAAAA	AAAAA	CAAAD	ACBAB	CAAAA	DAAAC	ACAAA	ACAAB	BBCAB	AAAAA
Cepphus grylle	AABAB	AABAA	AAABB	BAAAC	AAAAA	AAAAA	CAAAA	ACAAB	CAAAA	DAAAC	ACAAA	ACAAB	BBCBB	DAAAA

APPENDIX IV. Small Plovers Plumage Characters

Species	pp1	pp2	pp3	pp4	pp5	pp6	pp7	pp8	pp9	pp10	pp11
Peltohyas australis	C	C	B	A	B	B	B	A	A	A	A
Charadrius obscurus	B	A	B	A	A	B	B	A	A	A	A
Charadrius mongolus	B	A	B	A	B	A	A	A	A	A	A
Charadrius leschenaultii	B	A	B	A	A	A	A	A	A	A	A
Charadrius montanus	B	A	B	A	B	A	A	A	A	A	A
Charadrius collaris	B	A	B	A	A	A	A	A	A	A	A
Charadrius venustus	B	A	B	A	A	A	A	A	A	A	A
Charadrius ruficapillus	B	A	B	A	B	A	A	A	A	A	A
Charadrius bicinctus	B	A	B	A	A	A	B	A	A	A	A
Charadrius falklandicus	B	A	B	A	A	A	B	A	A	A	A
Charadrius alticola	B	A	B	A	A	A	B	A	A	A	A
Anarhynchus frontalis	B	A	B	A	A	A	A	A	A	A	A
Charadrius modestus	A	A	B	A	A	B	B	A	A	A	A
Charadrius tricollaris	A	A	B	A	A	A	B	A	A	A	B
Phegornis mitchelli	A	A	B	A	A	A	C	A	A	A	A
Charadrius asiaticus	B	B	B	A	A	B	A	A	A	A	A
Charadrius veredus	B	B	B	A	A	B	A	A	A	A	A
Charadrius ruficollis	B	A	B	A	A	B	B	B	A	A	B
Charadrius morinellus	A	A	B	A	A	A	B	B	A	A	B
Pluvialis squatarola	B	A	B	A	A	B	B	B	A	A	D
Pluvialis apricaria	B	A	B	A	A	B	B	B	A	A	D
Pluvialis dominica	B	A	B	A	A	B	B	B	B	A	D
Charadrius pecuarius	A	A	B	C	B	A	A	A	A	B	A
Charadrius sanctaehelenae	A	A	B	C	B	A	A	A	A	B	A
Thinornis novaeseelandiae	A	A	B	C	A	A	A	A	A	B	A
Charadrius cinctus	D	A	B	C	A	B	A	A	A	D	A
Charadrius melanops	A	A	B	C	A	A	A	A	A	D	B
Hoploxypterus cayanus	A	A	B	C	A	A	A	A	A	B	C
Charadrius marginatus	B	A	A	A	B	A	A	A	A	A	A
Charadrius alexandrinus dealbatus	B	A	A	A	B	A	A	A	A	A	A
Charadrius alexandrinus tenuirostris	B	A	A	A	B	A	A	A	A	A	A
Charadrius wilsonia	B	A	A	A	A	A	A	A	A	A	A
Charadrius cucullatus	D	A	A	B	A	A	A	A	A	A	B
Charadrius hiaticula	B	A	A	B	A	A	A	A	A	A	B
Charadrius semipalmatus	B	A	A	B	A	A	A	A	A	A	B
Charadrius melodus	B	A	A	B	A	A	A	A	A	A	B
Charadrius vociferus	B	A	A	B	A	A	B	A	A	A	B
Charadrius placidus	B	A	A	B	A	A	A	A	A	A	B
Charadrius dubius	B	A	A	B	A	A	A	A	A	C	B

APPENDIX V. Oystercatchers Plumage Characters

Forms	Characters						
	hp1	hp2	hp3	hp4	hp5	hp6	hp7
Haematopus							
ostralegus	A	A	B	A	A	A	A
finschi	A	A	B	A	A	A	A
moquini	A	B	A	B	B	A	A
fuliginosus	A	A	A	B	B	A	A
palliatus	B	A	A	A	B	A	A
frazari	B	A	A	A	B	A	A
bachmani	B	A	A	B	B	A	A
ater	B	A	A	B	B	A	A
leucopodus	B	B	A	A	B	B	B

APPENDIX VI. Avocets and Stilts Plumage and Foot Characters

Species	Characters			
	hp1	hp2	hp3	hp4
Himantopus				
h. himantopus	A	A	C	A
h. mexicanus	A	A	C	A
h. melanurus	A	A	C	A
Cladorhynchus				
leucocephala	A	A	B	B
Recurvirostra				
novaehollandiae	B	B	A	B
americana	B	B	B	B
andina	A	A	B	B
avosetta	A	B	A	B

APPENDIX VII. A Classification of the Charadriiformes

Cracraft (1972) presented arguments (following Hennig 1966) for using objective cladistic methods for classifying groups rather than the subjective methods of the "evolutionary taxonomists." If followed, however, Hennig's rules for classifying cladistically would lead to an absurd number of categories. Simpson (1966) recommended that classifications be based on monophyly (his examples indicate that he would also use paraphyly) and the amount of divergence between groups. He stressed that a classification should be based on an estimate of phylogeny but that many classifications can be equally consistent with the same phylogeny. Since there appears to be no evolutionarily meaningful, objective method for determining the amount of divergence between groups, classifications will always be somewhat subjective and tradition-oriented, or, as Simpson states, "art." Phylogenetic relationships are best shown on a tree diagram. While they are always distorted in a linear list of categories based on the Linnean hierarchical system, linear lists are useful and necessary for many purposes, however, and as closely as possible should reflect the evolutionary history of the groups being classified.

The classification recommended here (Table 3) consists of monophyletic and paraphyletic groups based on my final estimates of the evolutionary history of the Charadriiformes (Fig. 56). Because my groups have been chosen to emphasize relationships among diverse organisms rather than to emphasize differences among them, I propose the merger of many currently recognized genera. I have avoided monotypic genera whenever the closest relatives of the species involved are well-established.

I recommend dividing the order into three monophyletic suborders: the Scolopaci, the Charadrii, and the Alcae. The Scolopaci should be divided into two monophyletic superfamilies, the Jacanoidea and the Scolopacoidea. The only family in the Jacanoidea, the Jacanidae, consists of two well-marked species groups for which, on the basis of the evidence discussed previously, I recommend recognizing two genera. I propose dividing the Scolopacoidea into three families: the Thinocoridae and the Rostratulidae, which are monophyletic, and the Scolopacidae, which is paraphyletic. I would not include the rostratulids

Table 3. A Classification of the Charadriiformes

Order Charadriiformes

- Suborder Scolopaci
  - Superfamily Jacanoidea
    - Family Jacanidae
      - Genus *Actophilornis* (includes *Microparra*, *Irediparra*, and *Metopidius*)
      - *Jacana* (includes *Hydrophasianus*)
  - Superfamily Scolopacoidea
    - Family Thinocoridae
      - Genus *Attagis*
      - *Thinocorus*
    - Family Rostratulidae
      - Genus *Rostratula* (includes *Nycticryphes*)
    - Family Scolopacidae
      - Subfamily Phalaropodinae
        - Genus *Phalaropus* (includes *Steganopus* and *Lobipes*)
      - Subfamily Tringinae
        - Genus *Prosobonia*
        - *Numenius* (includes *Bartramia*)
        - *Tringa* (includes *Catoptrophorus*, *Pseudototanus*, and *Heteroscelus*)
      - Subfamily Calidridinae
        - Genus *Actitis*
        - *Calidris* (includes *Aphriza*, *Eurynorhynchus*, *Limicola*, *Micropalama*, *Tryngites*, and *Philomachus*)
        - *Arenaria*
        - *Limnodromus*
        - *Xenus*
        - *Limosa*
      - Subfamily Scolopacinae
        - Genus *Coenocorypha*
        - *Gallinago* (includes *Lymnocryptes* and *Chubbia*)
        - *Scolopax* (includes *Philohela*)

- Suborder Charadrii
  - Superfamily Laroidea
    - Family Laridae
      - Subfamily Sterninae
        - Genus *Sterna* (includes *Chlidonias*, *Phaetusa*, *Gelochelidon*, *Hydroprogne*, *Thalasseus*, and *Larosterna*)
        - *Anous* (includes *Procelsterna* and *Gygis*)
      - Subfamily Larinae
        - Genus *Larus* (includes *Gabianus*, *Pagophila*, *Rhodostethia*, *Rissa*, *Creagrus*, and *Xema*)
      - Subfamily Stercorariinae
        - Genus *Stercorarius* (includes *Catharacta*)
      - Subfamily Rynchopinae
        - Genus *Rynchops*

Table 3. Continued

Superfamily Charadrioidea
- Family Dromadidae
  - Genus Dromas
- Family Burhinidae
  - Genus Burhinus (includes Esacus and Orthorhamphus)
- Family Pluvianidae
  - Genus Pluvianus
- Family Glareolidae
  - Subfamily Cursoriinae
    - Genus Rhinoptilus
      Cursorius
  - Subfamily Glareolinae
    - Genus Glareola (includes Stiltia)
- Family Chionididae
  - Subfamily Pluvianellinae
    - Genus Pluvianellus
  - Subfamily Chionidinae
    - Genus Chionis
- Family Charadriidae
  - Subfamily Charadriinae
    - Genus Peltohyas
      Charadrius (includes Pluvialis, Pluviorhynchus, Elseyornis, Eupoda, Oreopholus, Eudromias, Zonibyx, Thinornis, Anarhynchus, Phegornis, and Hoploxypterus)
  - Subfamily Vanellinae
    - Genus Vanellus
  - Subfamily Haematopodinae
    - Genus Haematopus
  - Subfamily Ibidorhynchinae
    - Genus Ibidorhyncha
  - Subfamily Recurvirostrinae
    - Genus Recurvirostra (includes Cladorhynchus and Himantopus)

Suborder Alcae
- Family Alcidae

in the Scolopacidae because the evidence for placing them there is not yet sufficiently convincing. Since I think there is no purpose in retaining two genera for such closely related species, I recommend merging Nycticryphes with Rostratula. My evidence indicates that the phalaropes should be placed in the Scolopacidae. In the Scolopacidae I recommend four subfamilies: the Phalaropodinae, the Tringinae, the Calidridinae, and the Scolopacinae. I propose that many of the genera presently recognized in the family be merged. Bartramia is clearly a short-billed curlew and should be placed in Numenius. Likewise, I recommend that Catoptrophorus, Pseudototanus, and Heteroscelus be placed in Tringa; Aphriza, Eurynorhynchus, Limicola, Tryngites, and Philomachus in Calidris; Chubbia and Lymnocryptes in Gallinago; and Philohela in in Scolopax.

I would recognize two monophyletic superfamilies in the Charadrii, the Laroidea and the Charadrioidea. The diversity among the Laroidea does not seem to be any greater than that among the species usually placed in the Scolopacidae; thus I prefer to recognize only one family, the Laridae, which I divide into four subfamilies: the Sterninae, the Larinae, the Stercorariinae, and the Rynchopinae. Since there is evidence (Moynihan 1959; Ahlquist 1974; Olson pers. comm.) that the noddies may represent a distinct phyletic line separate from the other terns, I recommend recognition of two genera of terns, Sterna and Anous. The gulls are so similar to each other that I recommend placing them in one genus, Larus. I recommend merging Catharacta with Stercorarius, since I think there is no good reason to have two genera for only four closely related species.

My analyses indicate that there are five phyletic lines in the Charadrioidea, but I prefer to divide it into six familes: the Dromadidae, the Burhinidae, the Pluvianidae, the Glareolidae, the Chionididae, and the Charadriidae. Pluvianus is placed in a separate family because its close relationship to the Burhinidae is not well-established. Although Jehl (in litt.) recommends placing Pluvianellus and Chionis in separate families, I prefer to emphasize their close relationship by placing them in the same family. I see no merit in maintaining more than one genus for the Burhinidae. I am somewhat uncertain how many genera to recognize in the Glareolidae. Clearly the family

consists of two well-marked lines, the pratincoles and the coursers, which I recognize as subfamilies. Stiltia should undoubtedly be merged with Glareola. On the basis of differences in plumage patterns (which they admit are correlated with habitat differences, however) Kemp and Maclean (1973) thought that as many as four genera of coursers might be recognized. Since the three species currently placed in Rhinoptilus appear to be a monophyletic group, no purpose would be served by recognizing three genera for them, in spite of the differences in their downy and adult plumages. Cursorius and Rhinoptilus are quite close; I maintain their separation only because they are clearly distinctive in several ways and each includes more than one species.

I recommend placing the plovers, lapwings, oystercatchers, Ibisbill, avocets, and stilts into one diverse family in which I recognize five subfamilies: the Charadriinae, the Vanellinae, the Haematopodinae, the Ibidorhynchinae, and the Recurvirostrinae. Although Peters (1934) recognized 14 genera (12 of them monotypic) for the Charadriinae, almost all of these have been placed in Charadrius by other workers. I place all the plovers except Peltohyas, which seems distinct in many ways from all other plovers, in Charadrius. If further study indicates that the species usually placed in Pluvialis, Eudromias, and Oreopholus are more closely related to each other than they are to any other plovers, it would probably be useful to recognize them as a separate genus (Pluvialis). I follow Bock (1958) in placing all the Vanellinae in Vanellus. I recommend merging Cladorhynchus with Recurvirostra. The allopatric populations of Himantopus are of doubtful rank; following the guide lines of Mayr (1969), I prefer to regard them as members of one species, and thus Himantopus would be monophyletic. Since I prefer to avoid monotypic genera whenever their closest relatives are well-established, I propose that Himantopus also be merged with Recurvirostra.

Since I have not studied the relationships among the alcids, I have no recommendations on their classification at this time.

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