

PHYLOGENETIC RELATIONSHIPS AMONG CHARADRIIFORMES: REANALYSIS OF PREVIOUS DATA

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ABSTRACT.—Data on waders and allies (Charadriiformes) previously published by Strauch are reanalyzed using cladistic techniques, rather than compatibility analysis as in the original paper. The resulting trees are compared to those of Strauch, to a previous cladistic reanalysis, and to trees based on DNA-DNA hybridization data. In contrast to all previous results, the current analysis shows scolopacine and charadriine waders to be a monophyletic group, each of them being monophyletic. The alcids form a very basal group. The thick-knees (Burhinidae) form a sister group to all waders and larids (gulls and terns). *Chionis* and *Dromas* are sister taxa to glareolids and waders. The data contain several uncertainties in character codings and polarizations, which in turn may affect the outcome in various ways. Received 30 November 1993, accepted 11 February 1994.

THE PHYLOGENETIC RELATIONSHIPS among the waders, gulls, and allies (Charadriiformes: Aves) have been subject to much research and controversy over the years (see reviews by Strauch 1978, Sibley and Ahlquist 1990). Basically, this group consists of waders (Charadriinae in the broad sense), gulls and terns (Larinae), and auks and puffins (Alcinae). A major disagreement among systematists has involved the relative position of these taxa. It has long since been recognized that the waders are not monophyletic, but probably consist of two groups (Charadriinae and Scolopacinae). Several radically different views of relationships exist for each group. Two major works are by Strauch (1978) employing character-compatibility analysis on 70 skeletal characters of 227 taxa, and Sibley and Ahlquist (1990) based on DNA-DNA hybridization on 69 taxa.

Strauch (1978) identified three major groups, which he called Scolopaci, Charadrii (including larines), and Alcidae, but was not able to resolve their relationships and presented them as a trichotomy (Fig. 1A). Within the Scolopaci he placed the jacanas (Jacanidae and related taxa) as a sister taxon to the rest of the clade, and the seedsnipes (Thinocoridae) as a sister taxon to the scolopacine waders. For the Charadrii he placed the larids as a sister taxon to the rest of the clade, which consisted of an unresolved polytomy of glareolids and coursers (Glareolidae), thick-knees (Burhinidae), the crab plover (*Dromas*), and the charadriine waders including avocets and allies (Fig. 1A).

Sibley and Ahlquist (1990) distinguished two

major groups, parvorders Charadriida (including gulls, charadriine waders, glareolids and alcids) and Scolopacida (including jacanas and scolopacine waders). In Scolopacida the jacanas and allies form a sister group to the rest, while the thinocorids and the scolopacids are sisters (Fig. 2). In the Charadriida they recognized two major groups, one consisting of *Chionis*, Burhinidae, and the charadriine waders, and the other of the glareolids (including *Dromas*), the alcines, and the larines. *Chionis* was placed as a sister taxon to the rest of the charadriines, with Burhinidae as the sister to the charadriine waders (Fig. 2). The glareolids were set as a sister taxon to alcides and larides, which are sister taxa.

Strauch (1978) used compatibility analysis, a method that subsequently has been abandoned due to a number of problems including an uneconomical analysis of the data (Farris 1981, 1983). This was pointed out by Mickevich and Parenti (1980) in a review of Strauch (1978), and they also criticized Strauch's character analysis. The result of Mickevich and Parenti (1980) is presented in Figure 1B. Likewise, the DNA-DNA hybridization method and distance methods used by Sibley and Ahlquist (1990) have been subject to criticism with regard to methods of technical analysis and data processing (e.g. Farris 1981, Cracraft 1987, Houde 1987, Sarich et al. 1989, Springer and Krajewski 1989, Mindell 1992). Therefore, the issue of the relationships among the Charadriiformes is far from resolved. In this paper I will make use of the data matrix presented by Strauch (1978). Ultimately, the tree(s) obtained in a phylogenetic analysis

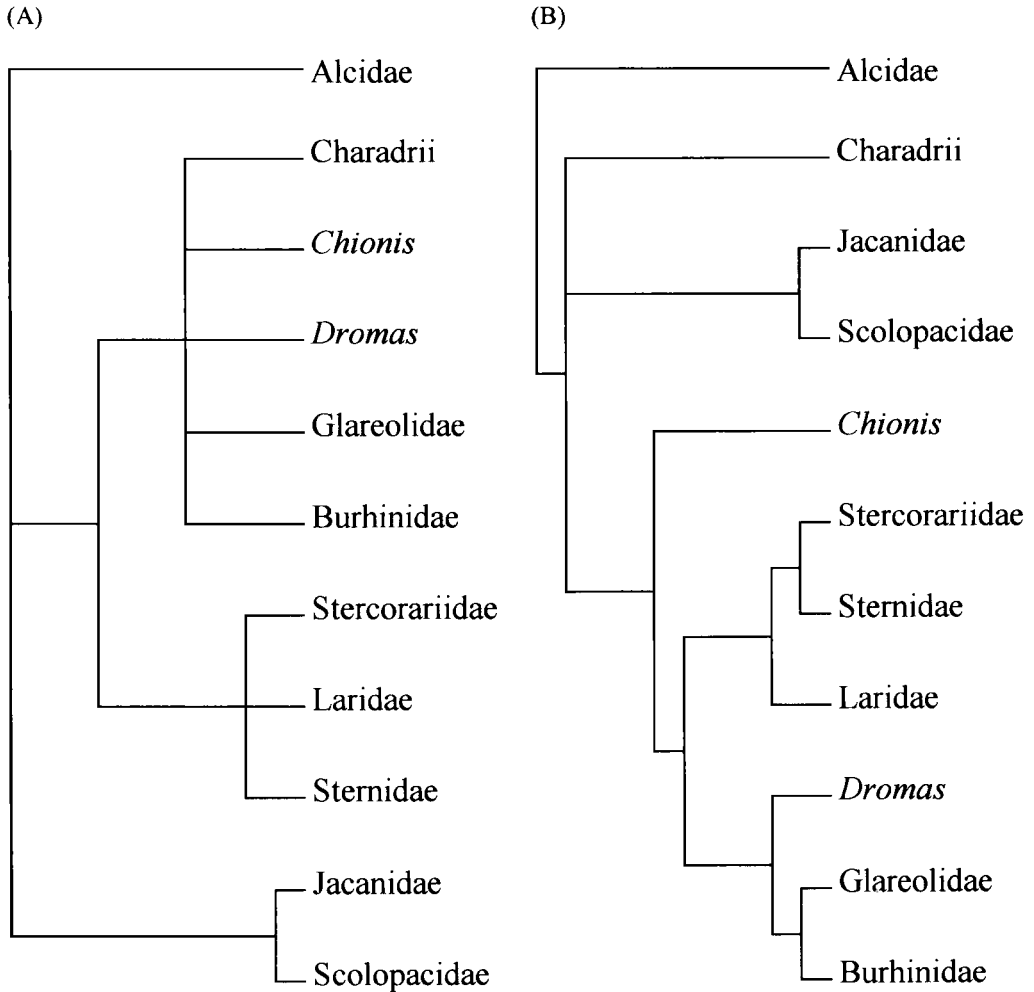


Fig. 1. Hypotheses of relationships among Charadriiformes by: (A) Strauch (1978); and (B) Mickevich and Parenti (1980).

depends on the data available. A special problem arises when we have characters with several states, a problem that has received much attention during recent years (e.g. Lipscomb 1990, 1992, Hauser and Presch 1991, Mickevich and Lipscomb 1991, Wilkinson 1992). The treatment of these characters will affect the reconstruction of the most-parsimonious tree. An additional problem is whether information on outgroup states is uncertain or simply missing (Nixon and Davis 1991, Platnick et al. 1991). Given these uncertainties, both of which are evident in the data set of Strauch (1978; see Mickevich and Parenti 1980), is it possible to extract useful phylogenetic information, or do

the uncertainties lead to a large number of equally parsimonious trees and a poor resolution?

METHODS

Strauch (1978) presented a detailed morphological analysis of 70 skeletal characters in 227 charadriiform taxa. Because there are many more taxa than characters, there is bound to be poor resolution in the resulting tree. Therefore, in the reanalysis I reduced substantially the number of taxa to a set of 18 taxa that correspond to the major groups above. Inclusion of more taxa invariably resulted in more equally parsimonious trees, resulting from uncertainties *within* these groups. Thus, the exclusion of a number of re-

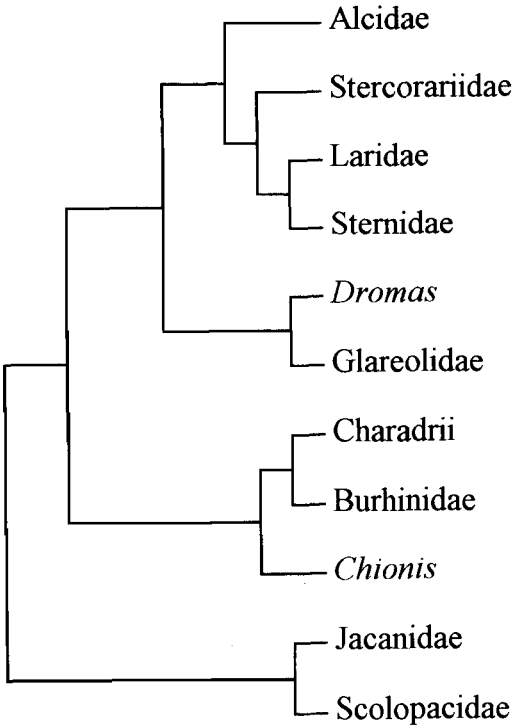


Fig. 2. Hypothesis of relationships among Charadriiformes by Sibley and Ahlquist (1990).

dundant taxa is not likely to seriously affect the major pattern. The groupings of taxa that I used are shown in Table 1. In the case of character conflicts within these groupings a “?” was entered.

A major problem is the polarity of the character states, as pointed out by Mickevich and Parenti (1980). Strauch (1978) did not make use of a rigorous method, such as outgroup comparison, but in many cases (41) based designation of primitive states on which character state was the most common in the ingroup. Thus, I coded these characters “?” in the ancestor in this analysis, rather than delete the character as done by Mickevich and Parenti (1980). In 25 cases I used the states shared by related outgroup taxa (Otididae, Gruidae, and Columbiformes) as the primitive state. Several characters are multistate characters. In three of these, ordering was possible (see Appendix), while in others several different states may have arisen from the same ancestral state. Hence, I treated the latter as unordered. Four characters (31, 32, 46, and 50 in Strauch 1978) were discarded because of problems with character-state coding and extensive variation within taxa.

The data matrices were analyzed using Hennig86 (ver. 1.5, Farris 1988), heuristic searching and branch swapping on initially found trees (command *m**; *bb**),

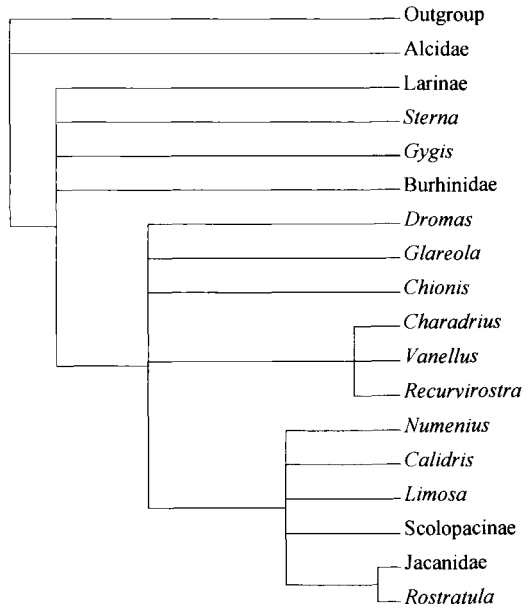


Fig. 3. Nelson consensus tree of relationships among Charadriiformes based on 32 equally parsimonious trees found in initial search.

and successive approximations weighting (Farris 1969, Carpenter 1988; by *xsteps w*; command). Successive weighting is an *a posteriori* weighting method that gives differential weight to characters in relation to their fit to the original tree(s). Strongly homoplasious characters are given low (or zero) weight since their informational content is low, while characters having few extra steps are given higher weight (Farris 1969, Carpenter 1988). The procedure is iterative and starts with a set of trees, based on equal weights of the characters, and adds different weights depending on their fit on the original tree. The procedure stops when weights becomes stable. In practice extra steps are added to the “best” characters, which results in trees that can be superficially much longer than the original tree. This method has been shown to be useful in cases where multiple equally parsimonious trees are found (Carpenter 1988).

The resulting trees were diagnosed using Clados (version 1.2, Nixon 1992). Several measures of support of tree structure are available (see Källersjö et al. 1992). I counted the increase in tree length as a result of collapsing a certain node (i.e. how many steps away one has to go to get the consensus tree of all intermediate trees to show the node as unresolved; Bremer support, Källersjö et al. 1992).

RESULTS AND DISCUSSION

The initial search found 32 equally parsimonious trees with a length of 123 steps and a

TABLE 1. Character-state matrix for phylogenetic analysis of Charadriiformes.

Taxon*	Character																											
	1	1	2	2	3	3	4	4	5	5	6	6	7	1	1	2	2	3	3	4	4	5	5	6	6	7		
1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	
Ancestor	?	0	0	0	0	?	?	?	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Jacaniidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rostratula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Numenius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calidris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scolopacinae	2	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sterna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gygis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dromas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glareola	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Burhinidae	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chionis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadrius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vanellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Recurvirostra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alcidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

* Key to taxa analyzed and genera included (if more than one): Jacaniidae (*Jacana*, *Metopidius*, *Microparra*, *Actilophilornis*, *Irediparra*, *Hydrophasianus*, *Thinocorus*, and *Attagis*); *Rostratula* (*Rostratula* and *Nycticryphes*); *Calidris* (*Calidris* and *Philomachus*); Scolopacinae (*Gallinago*, *Lymnocyrtus*, *Philophela*, *Scolopax*, and *Coenocorypha*); Larinae (*Larus*, *Stercorarius*, *Catharacta*, *Gabianus*, *Pagophila*, *Rhodostelia*, *Rissa*, *Creagrus*, and *Xema*); Burhinidae (*Esacus*, *Burhinus*, and *Pluvianus*); *Chionis* (*Chionis* and *Pluvianellus*); *Recurvirostra* (*Recurvirostra*, *Cladorhynchus*, *Himantopus*, and *Ibidorhyncha*); Alcidae (*Endomychura*, *Uria*, and *Cephus*).

consistency index (CI, Kluge and Farris 1969) of 0.56 and a retention index (RI, Farris 1989) of 0.64. The consensus tree from these 32 trees is shown in Figure 3. After successive weighting, one most-parsimonious tree was found with a length of 448 steps (including extra steps due to the successive approximations weighting procedure; CI = 0.86, RI = 0.89).

The auks and allies (Alcidae) were the sister group to the rest of the clade (Fig. 4). There was support for the monophyly of the charadriiform birds excluding alcids. The thick-knees (Burhinidae) are the sister group to the rest of the Charadriiformes; *Gygis* is a sister taxon to the gulls and terns. This larid group is a sister group to waders and glareolids. *Dromas* and *Chionis* form a clade, but one defined on the basis of a homoplasious character (Fig. 3). The glareolids are a sister taxon to the rest of the waders, which are found to be monophyletic. Although the waders are monophyletic they form two distinct sister taxa, each with considerable support (Fig. 3). The jacanas and allies are a sister taxon to the scolopacine waders. Within the scolopacines, the snipes and allies are very distinct morphologically with a number of synapomorphies and character-state changes shared by other taxa as well (Fig. 3).

My results differ from previous accounts in several ways. First, in contrast to Strauch (1978), Sibley and Ahlquist (1990) and others, the scolopacine and charadriine waders were found to be monophyletic (Fig. 4), although forming distinct sister groups. Second, the alcids were basal to all other Charadriiformes, rather than with the larids. This is similar to Strauch (1978), who placed the alcids in an unresolved basal trichotomy with larids-charadriine waders and the scolopacines. Second, the glareolids were found to be basal to the waders rather than to be associated with the larids, as suggested by Strauch (1978), Mickevich and Parenti (1980), and Sibley and Ahlquist (1990). Third, the position of *Dromas* and *Chionis* has been discussed considerably over the years. Strauch (1978) placed these within a group consisting of the thick-knees, glareolids and charadriine waders.

In their reanalysis, Mickevich and Parenti (1980) found *Chionis* to be a sister taxon to a clade consisting of the larids, and included *Dromas* with the glareolids and the thick-knees on the other. Sibley and Ahlquist (1990) placed the two species far from each other (Fig. 2). *Chionis* was placed together with the thick-knees and the charadriine waders, while *Dromas* was placed together with the glareolids as a sister clade to



Fig. 4. Phylogenetic hypothesis of relationships among Charadriiformes based on 66 skeletal characters adopted from Strauch (1978). Figures at nodes represent support as indicated by increase in number of steps to produce an unresolved node. Numbers refers to characters listed in Appendix.

the larids and alcids. In my analysis, *Chionis* and *Dromas* were found to be a sister group to the scolopacine and charadriine waders. Strauch (1978) placed the thick-knees with the glareolides and the Charadriine waders in an unresolved polytomy, while Mickevich and Parenti (1980) placed Burhinidae together with Glareolidae in the larid clade. Sibley and Ahlquist (1990) placed the thick-knees as the sister group to charadriine waders, which resembles the groupings of Strauch (1978), but is different from the results of my analysis and those of Mickevich and Parenti (1980).

To assess the support of my results in relation to alternative interpretations, I moved branches to make trees similar to the ones presented by Strauch (1978), Mickevich and Parenti (1980), and Sibley and Ahlquist (1990), but based on the current character-state distribution. Total similarity could not be achieved due to some differences in taxa used in the different analyses. The rationale is that if a different tree topology, such as that of Sibley and Ahlquist (1990), required only a few additional steps, then support for the current tree is weaker than if

the other tree is many steps away. The redrawing of the current tree to the Strauch (1978) tree has a cost of 10 extra steps, while the tree by Mickevich and Parenti (1980) is only 6 steps away. The construction of the Sibley and Ahlquist (1990) tree from the current tree increases the length with 14 steps. Thus, there is considerable support for the overall pattern found in this analysis in relation to the other trees.

My results and the contrast with other studies highlight the importance of detailed and careful character analysis. I have followed Strauch's original codings and treated unknown outgroup states as missing. Mickevich and Parenti (1980) simply deleted questionable characters, and favored a different tree (this can also be due to differences in algorithms). My approach to coding of the multistate characters could be questioned; an ordered series may be appropriate in some cases, and not in other. Treating the characters as unordered is as specific with regard to assumptions of evolution as an ordered case (contra Hauser and Presch 1991). In the unordered case, all states are assumed to be

able to change into any other by one step. This may or may not be true, and may distort the recovery of the "true" tree. More complicated transformation series are possible, but their biological validity are currently unknown. I have made certain hypotheses about character evolution when treating multistate characters as ordered or unordered. These are amenable to testing, but meanwhile the trees found should be viewed as the best phylogenetic hypothesis given the characters and the assumptions of character evolution. The results from my analysis also show that a high resolution is possible even though there are numerous uncertainties in the data. These uncertainties may not affect resolution power, but could influence the accuracy of the topology.

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APPENDIX

The 66 characters used in analysis adopted from Strauch (1978). Detailed morphological analyses of characters given in Strauch (1978). Original character numbers retained for comparison. Characters 31, 32, 46, and 50 were not used in this analysis. Data included on number of steps, consistency index (*CI*), and retention index (*RI*) for each character after the successive-weighting procedure.

1. Position of lacrimal-ectethmoid complex: (0) complex not abutting bar nor connected with post-orbital process; (1) complex abutting jugal bar; (2) connected with postorbital process. Unordered. Steps = 2, *CI* = 1.0, *RI* = 1.0. 2. Fusion of lacrimal and ectethmoid: (0) touching or fusing; (1) not in contact. Steps = 1, *CI* = 1.0, *RI* = 1.0. 3. Fusion of ectethmoid and frontals: (0) not in contact; (1) fused. Steps = 2, *CI* = 0.5, *RI* = 0.0. 4. Angle between jugal bar and lateral nasal bar: (0) $\leq 60^\circ$; (1) $> 60^\circ$. Steps = 5, *CI* = 0.2, *RI* = 0.2. 5. Length of zygomatic process relative to that of suprameatic process: (0) zygomatic process longer; (1) shorter; (2) connected with lacrimal-ectethmoid complex. Unordered. Steps = 2, *CI* = 1.0, *RI* = 1.0. 6. Anterior development of orbital septum: (0) not extending anterior to junction of jugal bar and nasal bar; (1) extending anterior. Steps = 1, *CI* = 1.0, *RI* = 1.0. 7. Nostril type: (0) nostril schizorhinal; (1) nostril holorhinal. Steps = 1, *CI* = 1.0, *RI* = 1.0. 8. Form of tip of bill: (0) short with dorsal and ventral bars of upper jaw fused only near tip of bill; (1) long with dorsal and ventral bars of upper jaw fused to about one-half length of bill; (2) short with stubby, finchlike tip; (3) like state 0, but with distinct flange of bone on both sides of dorsal bar of upper jaw covering nostril for about one-half length of bill; (4) like state 1, but dorsal bar flattened with distinctive ridge along top; (5) like state 0, but tip a sharp, short cone. Unordered. Steps = 4, *CI* = 0.4, *RI* = 0.0. 9. Shape of cross section of dorsal bar of upper jaw; (0) simple and unreinforced, but if reinforced cross section is oval, teardropshaped, or haystackshaped; (1) otherwise. Steps = 1, *CI* = 1.0, *RI* = 1.0. 10. Basipterygoid articulation of pterygoid and basipterygoid processes on basiphenoid rostrum in adults: (0) absent; (1) present. Steps = 1, *CI* = 1.0, *RI* = 1.0. 11. Medial condyle of quadrate: (0) distinct groove on anterolateral face of medial condyle of quadrate; (1) no groove; (2) medial condyle raised and twisted facing outwards, with little or no grooving on anterolateral face. Unordered. Steps = 3, *CI* = 0.66, *RI* = 0.75. 12. Degree of fusion of maxillopalatine complex: (0) little or no fusion; (1) considerable fusion; (2) total fusion. Steps = 2, *CI* = 0.5, *RI* = 0.66. 13. Configuration of junction of jugal bar, prepalatine bar, and ventral bar of upper jaw: (0) no sheet of bone where bars meet; (1) sheet present. Steps = 1, *CI* = 1.0, *RI* = 1.0. 14-17. Maxillopalatine strut A, B, C, D respectively: (0) present; (1) absent. Steps = 0-2, *CI* = 0.5-1.0, *RI* = 0.00-0.83. 18. Supraoccipital foramina: (0) absent; (1) present. Steps = 2, *CI*

= 0.50, *RI* = 0.85. 19. Shape of foramen magnum: (0) not distinctly heartshaped; (1) distinctly heartshaped. Steps = 1, *CI* = 1.0, *RI* = 1.0. 20. Position of nasal glands: (0) supraorbital nasal gland; (1) exorbital nasal gland; (2) neither supraorbital nor exorbital gland. Unordered. Steps = 2, *CI* = 0.5, *RI* = 0.5. 21. Prearticular process of mandible: (0) flange on prearticular process but not fused to supraangular; (1) flange fused to supraangular; (2) no flange; (3) prearticular process expand and hollow. Unordered. Steps = 3, *CI* = 0.0, *RI* = 0.0. 22. Posterior process of mandible: (0) in normal position; (1) process normal with corresponding bump on supraangular; (2) process shifted posteriorly on mandible. Unordered. Steps = 1, *CI* = 1.0, *RI* = 1.0. 23. Posterior mandible fossa: (0) present; (1) absent. Steps = 3, *CI* = 0.33, *RI* = 0.71. 24-28. Origin of *Musculus complexus* on vertebra 3, 4, 5, 6, 7, respectively: (0) present; (1) absent. Steps = 0-3, *CI* = 0.33-1.0, *RI* = 0.0-1.0. 29. Sites of origin of *M. spenius capitis*: (0) only on vertebra 2; (1) both on vertebra 2 and 3. Steps = 2, *CI* = 0.5, *RI* = 0.5. 30. Sites of origin of *M. rectus capitis*: (0) Origin on vertebrae 1-5; (1) 1-3; (2) 1-4. Unordered. Steps = 6, *CI* = 0.16, *RI* = 0.16. 33. Cervical vertebral strut: (0) absent; (1) present. Steps = 1, *CI* = 1.0, *RI* = 1.0. 34. Type of dorsal vertebrae: (0) heterocoelous; (1) opisthocoelous. Steps = 2, *CI* = 0.50, *RI* = 0.66. 35. Number of sternal costal processes: (0) 4; (1) 5; (2) 6; (3) 7. Ordered in increasing number of processes. Steps = 2, *CI* = 0.5, *RI* = 0.0. 36. Medial sternal notch: (0) absent; (1) present. Steps = 3, *CI* = 0.33, *RI* = 0.60. 37. Relative lengths of posterior lateral sternal process and xiphial area: (0) posterior lateral sternal process not extending to xiphial area; (1) extending farther. Steps = 1, *CI* = 1.0, *RI* = 1.0. 38. Ventral manubrial spine of sternum: (0) distinct ridge from ventral manubrial spine to sternal plate; (1) absent. Steps = 1, *CI* = 1.0, *RI* = 1.0. 39. Coracoidal foramen: (0) present; (1) absent. Steps = 1, *CI* = 1.0, *RI* = 1.0. 40. Brachial tuberosity of coracoid: (0) roofing triosseal canal; (1) twisted, not roofing. Steps = 1, *CI* = 1.0, *RI* = 1.0. 41. Symphysis of furcula: (0) no or only shallow groove on outward-facing surface; (1) distinct groove; (2) distinct ridge at bottom of groove. Unordered. Steps = 1, *CI* = 1.0, *RI* = 1.0. 42. Ridge in capital groove of humerus: (0) absent; (1) present. Steps = 1, *CI* = 1.0, *RI* = 1.0. 43. Shape of deltoid crest of the humerus: (0) anconal surface convex; (1) anconal surface concave. Steps = 2, *CI* = 0.50, *RI* = 0.85. 44. Pneumatic fossa II of humerus: (0) well-developed; (1) poorly developed. Steps = 2, *CI* = 0.5, *RI* = 0.0. 45. Ectepicondylar prominence of humerus: (0) well-developed; (1) absent. Steps = 2, *CI* = 0.5, *RI* = 0.5. 47. Position of intermetacarpal tuberosity on metacarpal II of carpometacarpal: (0) intermetacarpal tuberosity outside groove where metacarpal II and III join; (1) inside. Steps = 1, *CI* = 1.0, *RI* = 1.0. 48. Distal metacarpal symphysis of metacarpus: (0) ossified bridge over distal metacarpal symphysis of carpometacarpus absent; (1) bridge present. Steps = 2, *CI* = 0.5, *RI* = 0.0. 49. Proximal phalanx, digit III: (0) not

- perforated; (1) perforated. Steps = 1, $CI = 1.0$, $RI = 1.0$. **51.** Second synsacral strut: (0) absent; (1) present. Steps = 2, $CI = 0.5$, $RI = 0.0$. **52.** Position of lateral synsacral strut: (0) extending from fused sacral-caudal vertebrae to acetabulum; (1) strut falling short of acetabulum; (2) absent. Ordered in relation to length of lateral synsacral strut. Steps = 2, $CI = 1.0$, $RI = 1.0$. **53.** Number of lumbar vertebral parapophyses: (0) 3; (1) 4. Steps = 0. **54.** Condition of posterior end of renal depression: (0) flat with little or no discontinuity; (1) distinct strut at end of depression or end of depression deep and abrupt. Steps = 5, $CI = 0.4$, $RI = 0.0$. **55.** Foramina on ventral surface of ilium: (0) absent; (1) present. Steps = 0. **56.** Interapophyseal foramina of synsacrum: (0) 3 or more; (1) less than 3. Steps = 1, $CI = 1.0$, $RI = 1.0$. **57.** Shape of posterior medial edge of ilium: (0) forming abrupt right angle; (1) forming a smooth curve; (2) medial edge straight to ischial angle. Unordered. Steps = 4, $CI = 0.5$, $RI = 0.33$. **58.** Extent of ischium: (0) ischial angle extending posterior to posterior projection of ilium; (1) ischial angle relatively short and about even with posterior projection of ilium. Steps = 2, $CI = 0.5$, $RI = 0.5$. **59.** Fusion of ischium and pubis: (0) not fused immediately behind obturator foramen; (1) fused immediately posterior to obturator foramen. Steps = 1, $CI = 1.0$, $RI = 1.0$. **60.** Shape of junction of anterior and posterior crests of pelvis: (0) junction smooth and rounded; (1) junction forming a distinct projection over ilioschiatic fenestra. Steps = 4, $CI = 0.25$, $RI = 0.25$. **61.** Relative positions of trochlea for digits II and IV of tarsometatarsus: (0) trochlea for digits II and IV elevated compared to that for digit III, trochlea for digit II slightly more elevated than for digit IV; (1) trochlea considerably elevated, digit II more so than digit IV; (2) digits II and IV only slightly elevated compared to digit III. Unordered. Steps = 3, $CI = 0.66$, $RI = 0.83$. **62.** Hallux: (0) present; (1) absent. Steps = 3, $CI = 0.33$, $RI = 0.0$. **63.** Angle formed by trochlae for digits II and IV: (0) angle larger than 35°; (1) from 35° to 25°; (2) smaller than 25°. Ordered in relation to width of angle. Steps = 3, $CI = 0.66$, $RI = 0.85$. **64.** Hypotarsus: (0) tendinal canal no. 1 a bony canal; (1) tendinal canal no. 1 a groove. Steps = 4, $CI = 0.25$, $RI = 0.0$. **65.** Hypotarsus: (0) canal for tendon no. 1 directly anterior to canal for tendon no. 2; (1) canal anterior to space between canals for tendons no. 2 and 3, or directly anterior to canal for tendon no. 3. Steps = 3, $CI = 0.33$, $RI = 0.6$. **66.** Hypotarsus canal for tendon no. 3: (0) a groove; (1) a bony canal; (2) not detectable. Unordered. Steps = 0. **67.** Hypotarsus canal for tendon no. 4: (0) a groove; (1) a bony canal; (2) not detectable. Unordered. Steps = 0. **68.** Hypotarsus canal for tendon no. 6: (0) absent; (1) a groove. Steps = 1, $CI = 1.0$, $RI = 1.0$. **69.** Hypotarsus canal for tendon no. 5: (0) absent; (1) a groove. Steps = 1, $CI = 1.0$, $RI = 1.0$. **70.** Hypotarsus canals for tendons no. 2, 3, and 4: (0) not on a straight line; (1) on straight line passing through centers of canals no. 2 and 4. Steps = 1, $CI = 1.0$, $RI = 1.0$.