A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae)

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A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae)

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CONTENTS

The order Gruiformes, for which even familial composition remains controversial, is perhaps the least well understood avian order from a phylogenetic perspective. The history of the systematics of the order is presented, and the ecological and biogeographic characteristics of its members are summarized. Using cladistic techniques, phylogenetic relationships among fossil and modern genera of the Gruiformes were estimated based on 381 primarily osteological characters; relationships among modern species of Grues (Psophiidae, Aramidae, Gruidae, Heliornithidae and Rallidae) were assessed based on these characters augmented by 189 characters of the definitive integument. A strict consensus tree for 20 000 shortest trees compiled for the matrix of gruiform genera (length=967, CI=0.517) revealed a number of nodes common to the solution set, many of which were robust to bootstrapping and had substantial support (Bremer) indices. Robust nodes included those supporting: a sister relationship between the Pedionomidae and Turnicidae; monophyly of the Gruiformes exclusive of the Pedionomidae and Turnicidae; a sister relationship between the Cariamidae and Phorusrhacoidea; a sister relationship between a clade comprising *Eurypyga* and *Messelornis* and one comprising *Rhynochetos* and *Aptornis*; monophyly of the Grues (Psophiidae, Aramidae, Gruidae, Heliornithidae and Rallidae); monophyly of a clade (Gruoidea) comprising (in order of increasingly close relationship) *Psophia*, *Aramus*, *Balearica* and other Gruidae, with monophyly of each member in this series confirmed; a sister relationship between the Heliornithidae and Rallidae; and monophyly of the Rallidae exclusive of *Himantornis*. Autapomorphic divergence was comparatively high for *Pedionomus*, *Eurypyga*, *Psophia*, *Himantornis* and *Fulica*; extreme autapomorphy, much of which is unique for the order, characterized the extinct, flightless *Aptornis*.

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In the species-level analysis of modern Grues, special efforts were made to limit the analytical impacts of homoplasy related to flightlessness in a number of rallid lineages. A strict consensus tree of 20 000 shortest trees compiled (length = 1232, CI = 0.463) confirmed the interfamilial relationships resolved in the ordinal analysis and established a number of other, variably supported groups within the Rallidae. Groupings within the Rallidae included: monophyly of Rallidae exclusive of *Himantornis* and a clade comprising *Porphyrio* (including *Notornis*) and *Porphyrula*; a poorly resolved, basal group of genera including *Gymnocrex*, *Habroptila*, *Eulabeornis*, *Aramides*, *Canirallus* and *Mentocrex*; an intermediate grade comprising *Anurolimnas*, *Amaurolimnas*, and *Rougetius*; monophyly of two major subdivisions of remaining rallids, one comprising *Rallina* (paraphyletic), *Rallicula*, and *Sarothrura*, and the other comprising the apparently paraphyletic 'long-billed' rails (e.g. *Pardirallus*, *Cyanolimnas*, *Rallus*, *Gallirallus* and *Cabalus*) and a variably resolved clade comprising 'crakes' (e.g. *Atlantisia*, *Laterallus* and *Porzana*), waterhens (*Amaurornis*), moorhens (*Gallinula* and allied genera) and coots (*Fulica*). Relationships among 'crakes' remain poorly resolved; *Laterallus* may be paraphyletic, and *Porzana* is evidently polyphyletic and poses substantial challenges for reconciliation with current taxonomy. Relationships among the species of waterhens, moorhens and coots, however, were comparatively well resolved, and exhaustive, fine-scale analyses of several genera (*Grus*, *Porphyrio*, *Aramides*, *Rallus*, *Laterallus* and *Fulica*) and species complexes (*Porphyrio porphyrio*-group, *Gallirallus philippensis*-group and *Fulica americana*-group) revealed additional topological likelihoods. Many nodes shared by a majority of the shortest trees under equal weighting were common to all shortest trees found following one or two iterations of successive weighting of characters. Provisional placements of selected subfossil rallids (e.g. *Diaphorapteryx*, *Aphanapteryx* and *Capellirallus*) were based on separate heuristic searches using the strict consensus tree for modern rallids as a backbone constraint.

These analyses were considered with respect to assessments of robustness, homoplasy related to flightlessness, challenges and importance of fossils in cladistic analysis, previously published studies and biogeography, and an annotated phylogenetic classification of the Gruiformes is proposed.

Keywords: Aves; Gruiformes; Rallidae; rails; morphology; phylogenetics

1. INTRODUCTION

The higher-order systematics of the class Aves remain controversial (Stresemann 1959; Cracraft 1981*a*; Olson 1974*a*, 1981*a*, 1985; Sibley & Ahlquist 1990), but the order Gruiformes, for which even familial composition remains controversial, is perhaps the least well understood avian order from a phylogenetic perspective. The diversity of taxa included in the Gruiformes is indicated by the relatively high number of monotypic families recognized, the allocation of its members among ten orders by Stresemann (1927–1934) and Wolters (1975), and a recurrent view of the group as a possibly artificial assemblage (Lowe 1931; Verheyen 1957*a–c*, 1958; Olson 1985; Houde *et al.* 1997).

Early classifications of the order typically segregated several comparatively familiar and evidently closely related taxa, notably the cranes (Gruidae) and the speciose rails (Rallidae), with most also including the limpkin (Aramidae: *Aramus guarauna*) as a close relative of the cranes. Systematists varied considerably, however, in their taxonomic treatments of several geographically limited, comparatively depauperate, modern families considered by at least some ornithologists to be gruiform (Beddard 1898; Wetmore 1930, 1951, 1960*a*; Peters 1934; Stresemann 1927–1934; Mayr & Amadon 1951; Storer 1971; Morony *et al.* 1975): buttonquails (Turnicidae), plains-wanderer (Pedionomidae), bustards (Otididae), mesites (Mesitornithidae), sunbittern (Eurypygidae), kagu (Rhynochetidae), seriemas (Cariamidae), trumpeters (Psophiidae) and finfoots (Heliornithidae). Accordance of familial rank to each of these groups is in part a reflection of their uncertain higher-order relationships, as interordinal groups have been advanced only rarely by ornithological systematists. Recent investigations have resulted in poorly resolved or weakly supported phylogenetic reconstructions for modern taxa (Sibley & Ahlquist 1990; Harshman 1994*a*; Houde *et al.* 1997; Trewick 1997). The referrals of several fossil groups to the Gruiformes—e.g. 'terror cranes' (Phorusrhacidae and allies; Sinclair & Farr 1932), 'adzebills' (Aptornithidae; Livezey 1994), and 'Messel rails' (Messelornithidae; Hesse 1988*a*,*b*)—further complicated the troubled systematics of the order.

(a) *Order Gruiformes and family Rallidae*

The Gruiformes are considered to comprise 10–12 modern families, depending on authority, with only the Pedionomidae and Turnicidae having been subject to alternative ordinal assignments in recent years (Olson & Steadman 1981; Sibley & Ahlquist 1990; del Hoyo *et al.* 1996; Houde *et al.* 1997). The Rallidae greatly exceed other gruiform families in number of species, geographical distribution and taxonomic complexity, with recent authorites adopting substantially different subfamilial and generic classifications and recognizing different numbers of species in several problematic taxonomic groups (Olson 1973*a*, 1977; Ripley 1977; Taylor 1996). In addition, several other fossil groups—notably the Bathornithidae and Idiornithidae—have been included among the Gruiformes, but none is well represented and these classifications remain tentative (Brodkorb 1967; Cracraft 1968*a*, 1971; Olson 1985).

(i) *Geographical distributions and ecological patterns*

A number of gruiform families have restricted geographical distributions, with the Pedionomidae limited to Australia, Mesitornithidae to Madagascar, Rhynochetidae to New Caledonia, Aptornithidae to New Zealand and modern members of four families (Cariamidae, Eurypygidae, Psophiidae and Aramidae) endemic to the Neotropics (Turbott 1990; Baker-Gabb 1996; Bryan 1996; Evans *et al*. 1996; Gonzaga 1996; Hunt 1996; Sherman 1996; Thomas 1996). The Turnicidae and Otididae occur throughout much of Africa, Australia, India and southern Eurasia (Johnsgard 1991; Collar 1996; Debus 1996); the Gruidae are distributed in all major continental regions except South America and Greenland (Johnsgard 1983; Archibald & Meine 1996), with extinct insular endemics from the West Indies and Mediterranean known from subfossil remains (Fischer & Stephan 1971*a*; Northcote 1982, 1984). The three monotypic genera of Heliornithidae occupy parallel, widely separated, equatorial regions: *Heliornis* in the northern Neotropics, *Podica* in central and southern Africa, and *Heliopais* in India and southeast Asia (Bertram 1996). The Rallidae inhabit all major continental regions (exclusive of the Holarctic), as well as a multitude of oceanic islands from the equator to the subantarctic (Ripley 1977; Taylor 1996), and have one of the widest geographical distributions among families of terrestrial vertebrates (Olson 1973*a*). Although many genera are restricted to small geographical areas, several others are widespread and pose challenges for the delimitation of species (e.g. *Porphyrio*, *Rallus* and allies, *Gallinula*, *Laterallus* and *Porzana*).

The plains-wanderer, buttonquails, bustards, seriemas and mesites favour dry, typically open habitats (Johnsgard 1991; Starck 1991; Gonzaga 1996; Evans *et al.* 1996), whereas the kagu and trumpeters inhabit tropical woodlands (Hunt 1996; Sherman 1996). Limpkins and cranes are long-legged, wading birds that favour swamps and marshes (Johnsgard 1983; Archibald & Meine 1996; Bryan 1996), the sungrebe inhabits humid riverine forests (Thomas 1996), and finfoots are highly specialized for swimming and inhabit densely vegetated, freshwater ponds and streams (Bertram 1996). Variation in body size of Gruiformes exceeds two orders of magnitude (Dunning 1992), with most families being assignable to one of four broad groups on the basis of mean body mass: small (<100 g), Pedionomidae, Turnicidae and Mesitornithidae; moderately small (100–1000 g), Eurypygidae, Rhynochetidae and Heliornithidae; moderately large (1000–1500 g), Cariamidae, Psophiidae and Aramidae; and large (>1500 g), Gruidae. The Otididae include species in all but the smallest size category, whereas the Rallidae encompass all four size-groups (Cramp & Simmons 1980; Johnsgard 1991; Dunning 1992; Marchant & Higgins 1993; Taylor 1996). Pronounced sexual dichromatism is limited to the Pedionomidae, Turnicidae, Otididae, one genus of Mesitornithidae, most Heliornithidae and some Rallidae; most Gruiformes are monogamous, with polygamy restricted to the Psophiidae and those families showing sexual dichromatism (Pitman 1962; Appert 1968, 1985; Alvarez del Toro 1971; Sherman 1995*a*,*b*, 1996; Taylor 1996). Clutch size averages six or fewer for most gruiform families, with only the Psophiidae and some Rallidae typically laying larger clutches, and young of all but *Heliornis* are precocial (Geibel 1861; Schaub 1914; Krienke 1943; Rand 1951; Percy 1963; Starck 1991). Among Gruiformes, migration is characteristic only of some Otididae, most Gruidae and some Rallidae (Archibald & Meine 1996; Collar 1996; Taylor 1996), although variable seasonal movements are undertaken by the Pedionomidae and some Turnicidae (Baker-Gabb 1996; Debus 1996).

The Rallidae exceed all other gruiform families in included variation in body mass and most ecological parameters, including habitat, migratory habit, diet and reproduction. Members of the family inhabit a range of ecological environments, including freshwater and saltwater marshes, mangroves, sparsely vegetated atolls, cool–temperate woodlands, tropical forests and grasslands. Rallids range in mean body mass from finch-sized crakes (*Porzana* and *Micropygia*; 25 g) and fowl-sized wood rails (*Aramides*; 150–750 g) to comparatively ponderous swamphens (*Porphyrio*; 750–2500 g) and coots (*Fulica*; 500–2500 g); several subfossil species also attained substantial body sizes (e.g. *Diaphorapteryx hawkinsi*, *Nesotrochis debooyi*, and *Fulica chathamensis*). All Rallidae have powerful pelvic limbs and can swim, although members of the family exhibit a variety of specializations for life in dry uplands, wading in shallow water or aquatic locomotion. Many species of Rallidae are sedentary, others are migratory; some of the latter are renowned for remarkable incidents of long-distance vagrancy. The capacity for long-distance migration of many continental rails contrasts with the reluctance of most species to take flight when pursued and the relative frequency of permanent flightlessness among insular members of the family (Olson 1973*a*,*b*, 1977; Ripley 1977; Taylor 1996). Although the Mesitornithidae and Rhynochetidae are only weakly flighted (Evans *et al.* 1996; Hunt 1996), true flightlessness among non-rallid Gruiformes is limited to a subfossil crane (Fischer & Stephan 1971*a*), the fossil Phorusrhacidae and allies (Sinclair & Farr 1932), and the subfossil Aptornithidae (Livezey 1994, 1995*d*). The majority of rallids are omnivores (Taylor 1996), with foraging facilitated by especially sensitive olfaction (Bang 1968, 1971). Most Rallidae are monogamous (exceptions include occasional polygyny by *Crex*, serial polandry in *Porzana marginalis* and variably complex polygamy in *Porphyrio* and *Tribonyx*), construct terrestrial or slightly elevated, cup-shaped, variably concealed nests, have clutch sizes averaging 1–10 eggs (for single females) and have precocious young characterized by brown to black natal plumages (Ripley 1977; Wintle & Taylor 1993; Taylor 1996).

(ii) *Taxonomic history of non-rallid gruiforms*

Arrangements of gruiform birds in the classical works by Linnaeus (1758), Illiger (1811), Merrem (1813), Vieillot (1816), Cuvier (1817), Temminck (1820), Gray (1840, 1871), and Nitzsch (1840), each included groupings recognized to the present, as well as others no longer considered tenable; notable among the latter were placements of bustards with ratites (Paleognathae), cranes with herons (Ciconiiformes: Ardeidae), buttonquails with gallinaceous birds (Galliformes), and coots (Rallidae: *Fulica*) with grebes (Podicipediformes: Podicipedidae). Although a consensus was reached by the late 19th century concerning the majority of families to be included in the Gruiformes, substantial controversy attended the ordinal placements of the plains-wanderer (*Pedionomus torquatus*), buttonquails and bustards (Parker 1864, 1868; Huxley 1867, 1868; Gadow 1889, 1891, 1892, 1893; Newton 1893; Ogilvie-Grant 1893; Sharpe 1891, 1894, 1896; Seebohm 1895; Shufeldt 1903; Pycraft 1910; Beddard 1911; Lowe

1923; Hopkins 1942; Verheyen 1958; Hendrickson 1969; Johnsgard 1991). Disagreement persists concerning the ordinal positions of the plains-wanderer and buttonquails, the former being allied by some with the Charadriiformes (Bock & McEvey 1969; Olson & Steadman 1981; Marchant & Higgins 1993; Baker-Gabb 1996; del Hoyo *et al*. 1996; Houde *et al*. 1997) and the latter often considered of indeterminate relationships (Cracraft 1981*a*; Olson 1985; Sibley & Ahlquist 1985, 1990; Sibley *et al*. 1988, 1993; Debus 1996). Relationships among higher-order groups of 'gruiform' birds depicted by Sibley & Ahlquist (1990) and Sibley *et al*. (1993) differed from each other in a number of details, implied significant departures from traditional classifications and have been criticized on the grounds of phenetic methodology and poor representation of taxa (Cracraft 1987; Houde 1987; Lanyon 1992; Mindell 1992; Harshman 1994*a*). Furthermore, Sibley *et al*. (1993) were unable to identify the most likely sister group of the Rallidae among the gruiform and charadriiform taxa sampled. Houde *et al*. (1997) presented a number of reconstructions based on sequence data, the common elements of which differed markedly from those by Sibley & Ahlquist (1990). Significant differences among phylogenetic reconstructions of the Charadriiformes (Strauch 1978; Sibley & Ahlquist 1990; Björklund 1994; Chu 1994, 1995) have done little to clarify the positions of taxa averred to have both gruiform and charadriiform affinities.

Among the families for which assignment to the Gruiformes had received substantial support, relationships among the included families remained a vexing issue (Shufeldt 1894; Mitchell 1901*a*; Sibley & Ahlquist 1972). In that most gruiform families comprise only one or two genera, and four (including the Pedionomidae) are monotypic, reconstruction of the interfamilial relationships represents the most critical aspect of the systematics of the order. Several authorities recognized an especially close affinity among the rails, limpkin, cranes and (less frequently) trumpeters; the remaining families were often grouped as well, in part by default (Eyton 1867; Sclater 1868; Garrod 1873*a–c*; Sharpe 1891, 1894; Gadow 1892, 1893; Shufeldt 1894, 1904; Newton 1895; Beddard 1902; Lowe 1926; Glenny 1945, 1947, 1955, 1967; Tipton 1962; Sibley & Ahlquist 1972; Cracraft 1981*a*; Sibley *et al*. 1993; Sibley 1994; Houde *et al*. 1995, 1997). Also, several authorities (Forbes 1881; Gadow 1889; Beddard 1898; Mitchell 1901*b*; Chandler 1916; Lowe 1925, 1926, 1931) suggested that the Gruiformes were most closely related to the shorebirds (Charadriiformes), perhaps the jacanas (Jacanidae) in particular; the former hypothesis subsequently has gained general acceptance and further empirical support (Ridgway & Friedmann 1941; Howard 1950; Olson 1985; Cracraft 1988*a*; Sibley *et al*. 1988, 1993; Sibley & Ahlquist 1990; Sibley & Monroe 1990; McKitrick 1991).

Bustards remain poorly understood phylogenetically; currently recognized, narrowly delimited genera within the Otididae reflect, in large part, reactions by 19th-century taxonomists to interspecifically divergent plumage patterns of males critical to courtship displays (Clancey & Snow 1978; Johnsgard 1991). Study of the internal anatomy of the Otididae, however, revealed a number of diagnostic characters (Newton 1862; Murie 1868, 1869; Garrod 1873*a*,*b*, 1874*a–c*), and despite a comparative paucity of anatomical specimens for several genera (Wood *et al*. 1982; Wood & Schnell 1986), recognition of the family as a natural group has been virtually unanimous since the earliest taxonomic syntheses (e.g. Huxley 1867; Garrod 1874*a*; Morony *et al*. 1975; Collar 1996).

With few exceptions (Sundevall 1872; Gadow 1893), the Mesitornithidae have been included by systematists among the Gruiformes (Bartlett 1877; Milne-Edwards 1878*a*,*b*; Forbes 1882; Brasil 1914; Lowe 1924; Lavauden 1931, 1932; Rand 1936; Langrand 1990). However, a narrower placement of this small, distinctive, Madagascan group within the order continues to be debated (Sibley & Ahlquist 1990; Evans *et al*. 1996; Houde *et al*. 1997).

The intraordinal relationships of the seriemas also have remained the subject of speculation, in which affinities with bustards, cranes or trumpeters were advocated most frequently (Huxley 1867; Goodchild 1886; Fürbringer 1888; Beddard 1889; Gadow 1893; Cracraft 1973*a*; Gonzaga 1996; Houde *et al*. 1997). The giant phorusrhacids and allies generally are considered to be closely related to the Cariamidae (Andrews 1899; Sinclair & Farr 1932; Cracraft 1968*a*, 1971, 1973*a*; Mourer-Chauviré 1981, 1982, 1983; Peters 1987, 1991; Unwin 1993); the superficially similar Diatrymidae and Gastornithidae, formerly included in the Gruiformes, have been referred to other avian orders (Andors 1992; Martin 1992).

The neotropical sunbittern (*Eurypyga helias*) and New Caledonian kagu (*Rhynochetos jubatus*) have been included among the Gruiformes by most investigators, and many systematists considered the two genera to be especially closely related (Bartlett 1862; Parker 1864, 1869; Murie 1871*a*,*b*; Fürbringer 1888; Beddard 1891, 1911; Gadow 1893; Newton 1894; Mitchell 1915; Riggs 1948; Steinbacher 1968; Cracraft 1982; Hunt 1996; Thomas 1996; Houde *et al*. 1997), although alternative proposals have been advanced (Bartlett 1861). Inferences concerning the Eurypygidae and Rhynochetidae have been complicated further by proposed relationships between the kagu and the unique subfossil *Aptornis* of New Zealand (Cracraft 1982; Olson 1975*a*, 1985; Livezey 1994) and between the sungrebe and the fossil Messelornithidae of Europe (Hesse 1988*a*,*b*, 1990, 1992; Mourer-Chaurviré 1995); relationships have also been suggested between *Aptornis* and the Rallidae (Fürbringer 1888; Oliver 1945, 1955; Houde *et al*. 1997) or the Anseriformes (Hesse 1990; Weber & Hesse 1995).

The trumpeters have been allied most frequently with either the cranes and allies (Huxley 1867; Sharpe 1894; Clay 1950, 1953; Morony *et al*. 1975; Sibley & Ahlquist 1990; Houde *et al*. 1997) or the Cariamidae (Stejneger 1885; Beddard 1890*a*; Gadow 1893; Cracraft 1968*a*, 1982). The monotypic Aramidae have been considered closely related to the Gruidae and (to a lesser extent) the Rallidae by most systematists (Garrod 1876; Stejneger 1885; Sharpe 1891, 1894; Beddard 1902; Mitchell 1915; Shufeldt 1894, 1915*a*,*b*, 1916; Chandler 1916; Sibley 1960; Tipton 1962; Hendrickson 1969; Bryan 1996; Houde *et al*. 1995, 1997).

Phylogenetic relationships within the Gruidae have been studied more intensively than those of any other gruiform family (Walkinshaw 1973; Archibald 1976; Wood 1979; Johnsgard 1983). Most authorities segregated the crowned cranes (*Balearica*) from other Gruidae (Walkinshaw 1964, 1973; Brodkorb 1967; Ingold *et al.* 1987*a*; Feduccia & Voorhies 1992; Love & Deininger 1992; Archibald & Meine 1996; Houde *et al.* 1997), with two or three weakly differentiated genera of the remaining gruids being the conventional arrangement (Ingold *et al.* 1987*b*, 1989; Krajewski 1989*a*,*b*, 1990; Krajewski & Fetzner 1994; Krajewski & King 1996). Krajewski (1989*a*), Krajewski & Fetzner (1994) and Krajewski & King (1996) also estimated interspecific relationships within *Grus*, and molecular analyses of subgroups of *Grus* were conducted by Dessauer *et al.* (1992), Krajweski & Wood (1995), Love & Deininger (1992) and Wood & Krajewski (1996).

The finfoots (Heliornithidae) have remained a source of confusion with respect to the composition of the family (Sibley & Ahlquist 1990), relationships among the three included genera (Brooke 1984) and the position of the family within the Gruiformes (Beddard 1890*b*, 1893; Bertram 1996). Recently, Sibley & Ahlquist (1990) inferred that the Aramidae and Heliornithidae were sister groups, although Sibley (1994) later expressed doubts about this inference. Houde (1994) and Houde *et al.* (1995, 1997) confirmed the monophyly of the heliornithids but concluded that the group was less closely related to the Aramidae than are the Gruidae.

(iii) *Taxonomic history of rallids*

The Rallidae comprise the largest family in the Gruiformes and include approximately 135 modern species (tally varying with authority) and a number of fossil and subfossil species (Peters 1934; Brodkorb 1967; Olson 1973*a*,*b*, 1974*b*, 1975*a*–*c*, 1977, 1981*b*; Ripley 1977; Bock & Farrand 1980; Taylor 1996). Unlike most fossil Gruiformes (Lydekker 1891; Lambrecht 1933; Brodkorb 1967; Cracraft 1969, 1971, 1973*a*; Fischer & Stephan 1971*a*; Olson 1977), a number of subfossil rails are well represented by skeletal elements. Most of these extinct rallids were flightless and extirpated during historic times (Rothschild 1907*a*,*b*; Greenway 1967; Olson 1977; Halliday 1978; Fuller 1987) and formerly endemic to oceanic islands representing most major biogeographic regions: North Pacific, notably the Hawaiian Islands (Dole 1869, 1879; Rothschild 1900; Henshaw 1902; Fisher 1903, 1906; Perkins 1903, 1913; Bryan 1915; Bryan & Greenway 1944; Olson & James 1982*a*,*b*, 1991; Olson 1996); South Pacific, especially the New Zealand region (Hutton 1872, 1873, 1874; Travers 1872; Buller 1873*a*,*b*, 1888, 1892, 1905; Haast 1874; Forbes 1891, 1892*a*,*b*, 1893; Andrews 1896*a*–*c*; Fleming 1939*a*,*b*; Falla 1954; Fleming 1960; Medway 1967; McDowall 1969; Scarlett 1970; Olson 1975*a*,*b*; Steadman 1985, 1986, 1988*a*,*b*, 1989, 1992, 1995; Steadman & Olson 1985; Steadman *et al.* 1990; Balouet & Olson 1989; Atkinson & Millener 1991; Bell 1991; Millener 1991); North Atlantic, especially the West Indies (Wetmore 1918, 1922, 1937, 1938, 1956, 1960*b*; Fischer & Stephan 1971*b*; Olson 1978; Pieper 1985); South Atlantic (Stresemann 1953; Ashmole 1963*a*,*b*; Wetmore 1963; Beintema 1972; Olson 1973*b*, 1975*c*); and the Indian Ocean, especially Madagascar and the Mascarenes (Strickland & Melville 1848; Milne-Edwards 1868, 1869, 1874, 1875; Günther & Newton 1879; Newton & Gadow 1893; Newton 1896; Meade-Waldo 1908; Piveteau 1945; Cowles 1987).

Unfortunately, low population levels or declines in some continental and other insular Rallidae are indicated, and a number of species are considered rare or threatened with extinction (Meyer & Wiglesworth 1898; Hull 1909; Bassett-Hull 1910; Iredale 1910; Mathews 1928, 1936; Hindwood 1940; Hagen 1952; Elliott 1953, 1957; Holdgate 1965; McKean & Hindwood 1965; Elliott 1969, 1970; Penny & Diamond 1971; Stokes 1979; Bishop 1983; Ralph & van Riper 1985; Collar 1993; Collar & Stuart 1985; Fjeldså 1985; Ripley & Beehler 1985; Collar & Andrew 1988; Blaber 1990; Balouet 1991; Stinson *et al.* 1991). Consequently, many species of Rallidae are poorly represented in anatomical collections (Wood *et al.* 1982; Wood & Schnell 1986), and the vagaries of preservation have rendered some extinct rails better known osteologically than a number of extant confamilials. Threatened rallids include one species rediscovered after being presumed extinct (Mantell 1850; Parker 1885*a*,*b*; Park 1888*a*,*b*, 1890; Benham 1898*a*; Henry 1899; Forbes 1923; Mills *et al.* 1984, 1988; Beauchamp & Worthy 1988) and another only recently described (Yamashina & Mano 1981; Thiede 1982; Brazil 1985, 1991; Vuilleumier *et al.* 1992). Flightless rallids endemic to oceanic islands remain especially vulnerable to extirpation (Williamson 1981; Marshall 1988; Pimm *et al.* 1995). Although humans are implicated in most declines (Olson 1988, 1989, 1991*a*; Atkinson & Millener 1991; Baker 1991), reductions in the ranges of at least two flightless rallids during recent millennia have been inferred by some to be related, at least in part, to climatic change (Baird 1984, 1985, 1986, 1991, 1992; Mills *et al.* 1984, 1988; Beauchamp & Worthy 1988).

Rails have been the subject of substantial anatomical study, much of which has contributed to current perceptions of relationships, including examinations of the integument (Benham 1898*a*; Boyd & Alley 1948; Wetherbee & Meanley 1965; Dickerman 1968; Liversidge 1968; Dickerman & Haverschmidt 1971; Fjeldså 1975, 1981), vascular system (Glenny 1955), alimentary canal (Benham 1898*b*, 1899; McCann 1964), musculature (Lowe 1928*a*; Rosser 1980; Rosser *et al.* 1982; McGowan 1986; Kuroda 1993), and skeleton (Geibel 1855; Owen 1882; Shufeldt 1888, 1919; Lowe 1928*a*; Sigmund 1959; Macke 1969; Kuroda 1993). Difficulties in delimiting natural subgroups within the Rallidae have been acknowledged repeatedly (Sharpe 1893; Ridgway & Friedmann 1941; Olson 1973*a*). Nonetheless, taxonomic reviews have been undertaken on modern Rallidae at a number of taxonomic scales, including assessments of familial characters (Sclater 1868; Olson 1973*a*; Ripley 1977; Taylor 1996), intergeneric affinities and allocation (Sclater 1868; Hutton 1874; Voous 1961, 1962; Benson & Winterbottom 1968; Benson & Wagstaffe 1972; Olson 1973*a*,*d*, 1975*d*; Ripley 1977; Dowsett & Dowsett-Lemaire 1980; Trewick 1997), intrageneric relationships and diagnoses (Hutton 1873; Rothschild 1893; Mackworth-Praed 1937; Brodkorb & Dawson 1964; Gill 1964; Keith *et al.* 1970; Olson 1970, 1973*a*,*d*; Ripley 1977; Storer 1981; Keith 1986; Fjeldså 1990; Beauchamp 1989), and species limits and nomenclature (Coomans de Ruiter 1928; Conover 1934; Greenway 1952; Parkes & Amadon 1959; Olson 1986*a*; Ripley 1977; Scarlett 1979; Millener 1980, 1981;

Fjeldså 1982, 1983*a*–*c*; Diamond 1991; Elliott *et al.* 1991). With the exceptions of Olson (1973*a*), Ripley (1977) and Taylor (1996), however, taxonomic studies of the Rallidae have been limited to comparatively narrow subdivisions of the family.

Most recent classifications of the Rallidae (Olson 1973*a*, 1977; Ripley 1977; Sibley & Monroe 1991; Taylor 1996) share a number of elements, including familial monophyly, a basal position of the Nkulengu rail (*Himantornis haematopus*), a close relationship among the typical rails (e.g. *Rallus* and *Gallirallus*), and a close relationship among the swamphens (*Porphyrio*), moorhens (e.g. *Gallinula*) and coots (*Fulica*). Most modern taxa of Rallidae, however, continue to pose challenges for phylogenetic inference and classification, including the positions of several comparatively speciose genera (*Sarothrura*, *Porzana* and *Laterallus*) and the validity and relationships of a number of small, often monotypic genera (e.g. *Anurolimnas*, *Habroptila* and *Micropygia*). In addition, the relationships of most strictly subfossil genera of rallids (e.g. *Diaphorapteryx*, *Aphanapteryx*, *Nesotrochis* and *Capellirallus*) remain little studied. Explicit attempts to reconstruct phylogenetic relationships within the Rallidae have been based on a diversity of evidence, and include the intuitive assessment by Olson (1973*a*), phenetic estimates based on DNA hybridization by Sibley & Ahlquist (1990) and Sibley *et al.* (1993), and limited reconstructions by Houde *et al.* (1997) and Trewick (1997) based on sequence data. These analyses, however, have produced substantially divergent, only weakly supported groupings, and the phylogenetic relationships of many genera of Rallidae have not been examined from any methodological perspective.

(b) *Scope and objectives of this study*

This paper describes a phylogenetic analysis of the Gruiformes, including a species-level assessment of the Rallidae. This study was undertaken to provide an historical framework for a companion study of the evolution of flightlessness in rails (B. C. Livezey, unpublished data), a context necessary for evolutionary interpretations (Eldredge & Cracraft 1980; Felsenstein 1985*a*; Lauder 1990; Funk & Brooks 1990; Brooks & McLennan 1991; Harvey & Pagel 1991; Larson & Losos 1996). This investigation included all modern and selected fossil genera of Gruiformes and all modern and adequately represented fossil species of Rallidae as members of the ingroup; outgroup comparisons involved representatives of all families of Charadriiformes and, for characters posing particular challenges for polarities, reference to representatives of several other avian orders (especially Galliformes, Ciconiiformes and Falconiformes).

2. MATERIALS AND METHODS

(a) *Taxonomy and included taxa*

(i) *Taxonomy*

For preliminary organization of modern genera and species, I principally followed the traditional, generically conservative classification of Morony *et al.* (1975), the classification used in the global inventories of skeletal and anatomical specimens (Wood *et al.* 1982; Wood & Schnell 1986). The species-level delimitations by Ripley (1977) and Taylor (1996) were modified as needed to permit coding of characters consistently across terminal taxa; i.e. partitioning of several species complexes into two or more terminal taxa was necessary to include variation in characters important for phylogenetic reconstructions at higher levels. Modern species-groups subjected to such partitioning included *Porphyrio porphyrio*, *Aramides cajanea*, *Nesoclopeus poecilopterus*, *Gallirallus philippensis*, *Rallina tricolor*, *Sarothrura affinis*, *Laterallus jamaicensis*, *Amaurornis olivaceus*, *Gallinula chloropus* and *Fulica americana* (table 1). Taxonomy of subfossil rails principally followed Olson (1977), with subdivisions of the extinct *Fulica* of New Zealand after Millener (1980). These finer subdivisions of terminal taxa permitted the examination of possible paraphyly or polyphyly of groups traditionally recognized as single species, and is consistent with current concepts of species from the 'evolutionary' (emphasizing diagnosability) and 'phylogenetic' (emphasizing evolutionary independence) schools (Cracraft 1983, 1984, 1985, 1988*b*; McKitrick & Zink 1988; Ridley 1989; Frost & Hillis 1990; Kluge 1990; Nixon & Wheeler 1990; Frost & Kluge 1994; Zink & McKitrick 1995) and retains information regarding phylogenetically ambiguous, named lineages (Archibald 1994). In addition, character assessments based on these narrower taxonomic divisions provided a basis for an informed merging of terminals for analysis (table 1).

(ii) *Included taxa*

Non-rallid Gruiformes. All modern genera of Gruiformes were included in surveys of characters. Uniformity of states, unwieldy generic taxonomy and poor representation of several taxa in osteological collections subsequently prompted the merging of bustards (Otididae) into a single terminal taxon for analysis. Character codings and preliminary analyses of Psophiidae, Aramidae, Gruidae and Heliornithidae—families indicated as most closely related to the Rallidae in ordinal-level assessments herein—also were extended to species level (for modern taxa). Fossil gruiforms exclusive of the Rallidae included in the analysis were representatives of the Phorusrhacidae and allies (*Pelecyornis*, *Titanus*, *Andalgalornis*, *Mesembriornis*, *Phororhacos*, *Psilopterus* and *Procariama*), Messelornithidae (*Messelornis*) and Aptornithidae (*Aptornis otidiformis* and *A. defossor*). Fossil groups initially surveyed for characters but excluded because of fundamental deficiencies in available specimens were the Bathornithidae (Cracraft 1968*a*, 1971), Idiornithidae (Cracraft 1973*a*; Mourer-Chauviré 1981; Olson 1985), the extinct kagu *Rhynochetus orarius* (Balouet & Olson 1989), and the fossil cranes *Geranoides* (Wetmore 1933; Cracraft 1969) and *Eogrus* (Wetmore 1934).

Rallidae. All modern species of Rallidae (and diagnosable subgroups thereof) were surveyed for character analyses; a number of species complexes were merged, at least in part, to facilitate subsequent analyses (table 1). Adequately represented subfossil rallids were also studied (see Olson (1977), for review), including *Porphyrio kukwiedei* (Balouet & Olson 1989), *P.* (*m.*) *mantelli* (Owen 1848*a*; Trewick 1996), *Aphanocrex podarces* (Wetmore 1963; Olson 1973*b*), *Nesotrochis debooyi* (Wetmore 1918, 1922, 1937), *N. steganinos* (Olson 1974*b*), *Hovacrex roberti* (Andrews 1897), two undescribed, qualitatively identical species of *Rallus* from Bermuda differing principally in size (Olson

Table 1. *Gruidae and groups of separately coded, diagnosably distinct allospecies of Rallidae merged for selected phylogenetic analyses of Rallidae and closely related families*

(See Appendix C for subspecies included in listed allospecific taxa.)

species merged	group name
Psophia crepitans, *leucoptera*, and *viridis*	*Psophia* spp.
Balearica pavonina and *regulorum*	*Balearica* spp.
Anthropoides paradisea and *virgo*	*Anthropoides* spp.
Grus sensu stricto (i.e. excluding *carunculatus*, *leucogeranus*)	*Grus* spp.
Porphyrio exclusive of *pulverulentus*, *mantelli*, *hochstetteri*, and *kukwiedei*	*Porphyrio porphyrio*-group
Aramides cajanea, *albiventris*, *mexicana*, and *plumbeicollis*	*Aramides cajanea*-group
Tricholimnas sylvestris and *conditicius*	*Tricholimnas sylvestris*-group
Nesoclopeus poecilopterus, *woodfordi*, and *immaculatus*	*Nesoclopeus poecilopterus*-group
Rallus aquaticus and *indicus*	*Rallus aquaticus*-group
Rallus antarcticus and *semiplumbeus*	*Rallus antarcticus*-group
Rallus longirostris complex and *R. elegans* complex	*Rallus longirostris*-group
Rallus, small and large unnamed species from Bermuda	*Rallus* Bermuda-group
Gallirallus philippensis, *christophori*, *sethsmithi*, *goodsoni*, *ecaudatus*, and *assimilis*	*Gallirallus philippensis*-group
Gallirallus pectoralis, *muelleri*, and *mirificus*	*Gallirallus pectoralis*-group
Gallirallus australis and *greyi*	*Gallirallus australis*-group
Gallirallus torquatus, *sulcirostris*, and *celebensis*	*Gallirallus torquatus*-group
Rallina tricolor and *victa*	*Rallina tricolor*-group
Sarothrura affinis and *antonii*	*Sarothrura affinis*-group
Coturnicops noveboracensis and *exquisitus*	*Coturnicops noveboracensis*-group
Laterallus jamaicensis, *tuerosi*, and *murivagans*	*Laterallus jamaicensis*-group
Porzana ziegleri, *menehune*, *keplerorum*, *ralphorum*, and *severnsi*	*Porzana* Hawaiian-group
Porzana erythrops and *columbiana*	*Porzana erythrops*-group
Amaurornis olivaceus, *moluccanus*, and *ruficrissus*	*Amaurornis olivaceus*-group
Gallinula chloropus, *pyrrhorrhoa*, *cachinnans*, *galeata*, and *sandvicensis*	*Gallinula chloropus*-group
Porphyriornis nesiotis and *comeri*	*Porphyriornis nesiotis*-group
Fulica americana, *caribaea*, *alai*, and *ardesiaca*	*Fulica americana*-group
Fulica chathamensis and *prisca*	*Fulica chathamensis*-group

1977, p. 353), *Aphanapteryx bonasia* (Milne-Edwards 1868, 1869), *A. legauti* (Milne-Edwards 1874; Günther & Newton 1879), *Diaphorapteryx hawkinsi* (Forbes 1892*a*,*b*), *Capellirallus karamu* (Falla 1954; Scarlett 1970; Olson 1975*a*), *Atlantisia elpenor* (Olson 1973*b*), *Porzana astrictocarpus* (Olson 1973*b*), five *Porzana* from Hawaii (*P. ziegleri*, *P. menehune*, *P. keplerorum*, *P. ralphorum* and *P. severnsi*; Olson & James 1991), an undescribed species of *Porzana* from Bermuda (Olson 1977, p. 353; referred to here as 'Bermuda *Porzana*'), *Tribonyx hodgenorum* (Olson 1975*a*), *Fulica chathamensis* (Andrews 1896*c*; Olson 1975*a;* Millener 1980, 1981), *F. prisca* (Olson 1975*a;* Millener 1980, 1981) and *F. newtonii* (Milne-Edwards 1867). Several other subfossil rallids of potential interest were excluded, primarily because of poor quality or inaccessibility of material: *Porphyrio paepae* (Steadman 1988*a*), *Nesotrochis picapicensis* (Fischer & Stephan 1971*b*), *Gallirallus ripleyi* (Steadman 1986), *Gallirallus minor* (Hamilton 1893; Olson 1975*a*), an undescribed rail from the Brazilian island of Fernando de Noronha (Olson 1977, p. 357), *Porzana rua* (Steadman 1986) and *Tribonyx repertus* (Olson 1975*b*). Also, several modern rallid genera lacking most or all osteological elements (e.g. *Pareudiastes pacificus* and *Edithornis silvestris*) were excluded from the primarily osteological, genus-level analysis of the Gruiformes.

Charadriiformes and secondary outgroups. Representatives of all taxonomic families of Charadriiformes were examined to determine the states of osteological and selected integumentary characters that appeared to be informative for genera of Gruiformes; this also permitted the incorporation of variation in these characters among Charadriiformes. Certain exemplar taxa within each charadriiform family were consulted more routinely than others because of the skeletal material available (e.g. *Jacana*, *Rostratula*, *Dromas*, *Haematopus*, *Ibidorhyncha*, *Himatopus*, *Burhinus*, *Pluvianus*, *Glareola*, *Charadrius*, *Tringa*, *Thinocorus*, *Chionis*, *Stercorarius*, *Larus*, *Rynchops* and *Uria*), although comparisons were enlarged to include additional representatives (e.g. *Cursorius*, *Cladorhynchus*, *Calidris* and *Sterna*) where variation or problematic determinations were encountered. The states of charadriiform outgroups were compiled at familial level and combined into several merged taxa for purposes of analysis in which variation in states were indicated explicitly as polymorphism (see below). A deeper root for the analysis, which ameliorated the analytical effects of uncertain basal polarities of some characters based on the Charadriiformes and permitted a preliminary assessment of the hypothesis that two charadriiform families (Jacanidae and Rostratulidae) may be especially closely related to the Gruiformes (Lowe 1925, 1931; Verheyen 1957*c*), was based on a survey of problematic osteological characters among several secondary outgroups (Galliformes: Cracidae; Ciconiiformes: Ardeidae and Threskiornithidae; Falconiformes: Falconidae; Pelecaniformes: Sulidae).

(b) *Specimens and related data*

(i) *Skin specimens*

Study skins (including typical 'round' specimens, flat skins or mounts) of all modern species of Rallidae (and for many, qualitatively diagnosable partitions thereof) were examined, most taxa being assessed on the basis of series of specimens. The sole exception pertained to the extinct *Porzana monasa* (two unique skin specimens collected during 1827–1828 by Kittlitz, held at the Academy of Sciences, Zoological Institute, St Petersburg, Russia); fortunately, the latter species is characterized by a simple plumage pattern and essential integumentary character states can be taken from the literature. Direct study of specimens included the sole surviving specimen of *Porphyrio alba* (Merseyside Museum, Liverpool, UK), unique specimen of *Gallirallus* (*Stictolimnas*) *sharpei* (Rijksmuseum van Natuurlijke Historie; Olson 1986*a*), the unique holotype of *G. rovianae* (American Museum of Natural History; Diamond 1991), a recently acquired flat skin of the newly discovered *G. okinawae* (Museum of Zoology, University of Michigan, USA) and the unique specimen of *Tricholimnas conditicius* (Museum of Comparative Zoology, Harvard University, MA; Walters 1987; Olson 1992). Although adequate survey of natal plumages necessitated widespread use of collections worldwide through loans and visitation (see Acknowledgements), the study of integumentary characters of the Psophiidae, Aramidae, Gruidae, Heliornithidae and Rallidae was based principally on visits to the American Museum of Natural History, US National Museum of Natural History and the Natural History Museum (UK).

(ii) *Osteological specimens*

Modern taxa. Prepared skeletons of all modern genera of Gruiformes and most modern species of the Rallidae and closest relatives (Psophiidae, Aramidae, Gruidae and Heliornithidae) were studied, although complete skeletons were unavailable for a number of taxa (Wood & Schnell 1986), notably *Heliopais personata*, *Gymnocrex rosenbergii*, *G. plumbeiventris*, *Rougetius rougetii*, *Cyanolimnas cerverai*, *Tricholimnas lafresnayanus*, *Aramidopsis plateni*, *Rallus semiplumbeus*, *R. wetmorei*, *Micropygia schomburgkii*, *Coturnicops notata*, *Porzana* (*Neocrex*) *erythrops*, *Pareudiastes pacificus*, *Edithornis silvestris* and several species in *Rallina*, *Rallicula*, *Sarothrura*, *Laterallus*, *Porzana* and *Amaurornis*. The absence of skeletal specimens for a number of modern taxa exacerbated problems stemming from unavailable skeletal elements and integumentary material for subfossil taxa. In several cases, prepared skeletal specimens (Wood & Schnell 1986) were augmented by the partial removal of elements from study skins (*Gymnocrex plumbeiventris*, *Eulabeornis castaneoventris*, *Rougetius rougetii*, *Habropteryx insignis*, *Nesoclopeus poecilopterus*, *Porzana erythrops*, *Micropygia schomburgkii*, *Rallina rubra*, *Amaurornis akool*, *A. isabellinus* and *A. ineptus*) and partial dissection of fluid-preserved specimens (*Gymnocrex plumbeiventris*, *Cyanolimnas cerverai*, *Nesoclopeus poecilopterus*, *Gallirallus okinawae*, *Amaurornis ineptus* and *Pareudiastes pacificus*).

Fossil and subfossil taxa. In addition to lacking known character states for integumentary features, taxa known only from fossil or subfossil remains also generally provide only incomplete suites of osteological characters. In some cases, even the modest material available for study permitted robust placements of some fossil gruiforms (e.g. *Messelornis*), especially where data for several included taxa were 'pooled' to provide a single, composite set of states for a higher taxon (e.g. Phorusrhacoidea). However, even the best-represented subfossil rails—e.g. *Diaphorapteryx hawkinsi*, *Cabalus modestus* and *Fulica chathamensis*—lack some of the most fragile skeletal elements. Most subfossil rallids lack considerably more elements, but material was sufficient for analysis (e.g. *Nesotrochis debooyi*, *Aphanapteryx bonasia*, *Capellirallus karamu* and *Atlantisia elpenor*). However, regardless of abundance of material, fossil and subfossil rails present special problems associated with uncertain association, wear and breakage.

(iii) *Ancillary data*

In addition to anatomical references cited in the taxonomic histories, supplementary information on the anatomy of included taxa was taken from the following sources (by taxon): Charadriiformes (Jehl 1968; Fry 1983; Johnson 1984; Mickevich & Parenti 1980); Otididae (Neithammer 1940; Morgan-Davies 1965); Mesitornithidae (Glenny & Friedmann 1954; Appert 1968, 1985; Turner 1981; Schuurman 1996); Cariamidae (Heinroth 1924; Miranda-Ribeiro 1937; Olson 1973*c*); Rhynochetidae (Burckhardt 1900, 1901*a*; Schaub 1914; Balouet & Olson 1989); Aptornithidae (Owen 1846, 1848*a*,*b*, 1851, 1866, 1871, 1872, 1875, 1879); Psophiidae (Burckhardt 1901*b*); Aramidae (Tipton 1962); Gruidae (Roberts 1880; Berger 1956*a*; Cracraft 1969; Fischer & Stephan 1971*a*); Heliornithidae (Pitman 1962; Blake 1977); and Rallidae (Owen 1848*a*,*b*, 1871, 1879; Gould 1850; Sclater 1861; Buller 1885; Shufeldt 1915*b*; Forbes 1901, 1923; Hartert 1910; Mathews 1911; Mathews & Iredale 1914; Lowe 1934; Chapin 1939; Stresemann 1941; Piveteau 1945; Sharland 1945, 1973; Baker 1951; Ripley 1954, 1957*a*,*b*; Behn & Millie 1959; Moreau 1966; Falla 1967; Bang 1968; Heinroth & Heinroth 1968; Liversidge 1968; Ali & Ripley 1969; Goodwin 1974; Haverschmidt 1974; McFarlane 1975; Blake 1977; Mees 1977, 1982; Wagstaffe 1978; Sick 1979; Fisher 1981; Fullagar *et al.* 1982; Rosser *et al.* 1982; Fjeldså 1982, 1983*b*,*c*; Clancey 1985; Robertson & Beauchamp 1985; Frith & Frith 1990; Franklin & Barnes 1998).

Additional anatomical references were consulted during exploration of characters, including studies of the integument (Gadow 1888; Mitchell 1899; Pycraft 1899; Lönnberg 1904; Heidrich 1908; Schüz 1927; Boetticher 1929; Steiner 1956; Stresemann 1963; Stresemann & Stresemann 1966; Lucas & Stettenheim 1972; Johnston 1988), skeleton (Fürbringer 1902; Lebedinsky 1919; Boas 1929, 1934; Edinger 1929; Lemmrich 1931; Technau 1936; Curtis & Miller 1938; Edington & Miller 1941; Hofer 1945, 1949; Goebloed 1958; Bock 1960, 1962; Cracraft 1968*b*; Burton 1970; Butendieck 1980; Butendieck & Wissdorf 1982; Zusi 1984, 1993; Warheit *et al.* 1989), ontogeny (de Beer 1937; Fell 1939; Jollie 1957), musculature (Garrod 1873*b*, 1874*a*, 1875; Hudson 1937; Hofer 1950; Fisher & Goodman 1955; Berger 1956*b*; George & Berger 1966; McKitrick 1991), vascular anatomy (Garrod 1873*c*), excretory and digestive organs (Gadow 1879*a*,*b*, 1889; Holmes & Phillips 1985) and trachea (Rüppell 1933; Berndt 1938; King 1989, 1993; McLelland 1989).

(c) ***Anatomical nomenclature***

The nomenclature advocated by the International Committee on Avian Anatomical Nomenclature (ICAAN) was used in the description of anatomical characters (Baumel & Raikow 1993; Baumel & Witmer 1993; Clark

1993*a*,*b*; Vanden Berge & Zweers 1993). Critical features lacking approved names were named provisionally, annotated as 'new term' and briefly described parenthetically (Appendix A).

(d) *Definition of characters*

(i) *General concepts and approach*

Characters were defined for analysis as anatomical features, which show variation that was partitionable into two or more discrete states and deemed homologous across included taxa (see below). In some characters, states pertained to relative size or extent and represented points along a continuum, and discrete states were delimited according to emergent groups (Felsenstein 1988; Warheit 1992; Thiele 1993). This process of abstraction, however, was not always practical, and resulted in the exclusion of several characters showing virtually continuous variation among taxa without evident groupings, including some which had been employed for diagnosis by other workers (e.g. Steadman 1986). Autapomorphies, derived characters unique to a single terminal taxon and therefore not informative with respect to reconstruction of phylogeny, were included in the analysis because such character changes contribute to estimates of total divergence (Omland 1997) and include many features traditionally considered of taxonomic importance (e.g. Olson 1973*a*; Ripley 1977). Also, most morphological autapomorphies in this study were diagnosably unique to the terminal taxa in question (i.e. were unique, derived states for binary characters having consistency indices of one), and therefore such changes were neutral with respect to topological inferences and are not germane to analytical concerns attending long terminal branch-lengths (e.g. as in low-consistency sequence data; Swofford *et al.* 1996).

In total, 361 osteological characters were defined for outgroups, gruiform genera and species of the Psophiidae, Aramidae, Gruidae, Heliornithidae and Rallidae; one myological character, 12 characters of natal plumages, one character of the glandula uropygialis and five characters of the definitive integument also were codable for all genera examined, bringing the total tally for the ordinal analyses to 381 (83 of which were parsimony-uninformative). Problems of comparability of characters imposed limitations on the taxonomic scale sampled for most characters of the integument. Consequently, an additional 189 integumentary characters—notably colour patterns of definitive plumages and soft parts—were coded only for the species Rallidae and their closest relatives as inferred by the foregoing ordinal study (Psophiidae, Aramidae, Gruidae and Heliornithidae). The total number of characters coded for species-level assessments in the latter five families to 570 characters (Appendix B), of which 158 were invariant (variation restricted to more-basal nodes) and another 96 were parsimony-uniformative (unique autapomorphies).

(ii) *Homology and related issues*

Concepts of homology have been a source of perennial debate (Boyden 1943; Patterson 1982; Roth 1984, 1988, 1991; Wagner 1989*a*,*b*, 1994; de Pinna 1991; Haszprunar 1992; Goodwin 1994; Hall 1994, 1995; Lauder 1994, 1995; McKitrick 1994; Nelson 1994; Panchen 1994). In theoretical terms, homologies may be thought of as traits having common genetic and ontogenetic foundations and that therefore represent historically individuated entities imparting phylogenetic information (McKitrick 1994). Homologous characters are considered to have common evolutionary and developmental bases, and variation within such phenotypically identifiable features (here termed states) are deemed elements of a single, historical, transformation series across lineages and a common developmental trajectory within individuals (i.e. a semaphorant; Wiley 1981). In practice, however, morphological homologies generally are hypothesized on the basis of comparative anatomy, and traditional criteria of recognition derive from those of Remane (1956), namely: (i) similarity of position; (ii) specialized similarity of structure; and (iii) continuity of intermediate forms (Wiley 1981). In a phylogenetic context, hypotheses of homology are subjected to secondary confirmation, in which assessments of homology *a priori* are compared against their congruence with specific phylogenetic reconstructions.

Controversy and prejudice persist concerning the use of characters considered 'adaptive' or 'functional' for reconstruction of phylogeny (Cracraft 1981*b*; Baum & Larson 1991; Wake 1994), stemming either from the supposition that a hypothesis of utility implies an increased likelihood of homoplasy or that functional analyses must precede definition of characters. As speculations of selective advantage can be contrived for any feature and the need for functional evaluations in definition of characters has not been established, judgements of function or adaptive advantage were not employed here.

(iii) *Intraspecific variation, modal states and polymorphism*

Variation in character states within terminal taxa poses analytical challenges (Nixon & Davis 1991; Kesner 1994), and the implications of such variation differ depending on the taxonomic ranks of the terminal taxa in question (Wiens 1998). Although the quantification of frequencies of states within terminal taxa appears to provide the most power for phylogenetic reconstruction in the presence of such variation (Wiens 1995, 1998; Wiens & Servedio 1997), limitations of original character coding and subsequent analytical concerns precluded such refinements in this study. For characters used in the analyses of the higher-order (largely generic) terminal gruiform taxa, codings of polymorphism (Maddison & Maddison 1992) were limited to those cases where no distinct modality in observed states was evident; otherwise the terminal taxa were assigned the modal condition. Variation of this kind, as well as other complications of character definition (e.g. sexual dimorphism), are noted in the character descriptions (Appendix A); particular attention is directed to variation in scleral rings, wherein conspicuous intergeneric variation in pattern was accompanied by substantial intraspecific variation and (rarely) bilateral asymmetry. Intraspecific variation in the comparatively conservative, primarily osteological characters among the Rallidae and close allies generally was neglible, however, and where observed in terminal taxa was indicated by codes for polymorphism. In the supplementary characters of the integument of the Rallidae and allies, codings were made at species level or, where feasible, for named subspecific groups which partitioned observed variation (Kluge & Farris 1969; de Queiroz 1987; Nixon & Davis 1991). Analytical logistics, however, precluded unlimited subdivision of terminal taxa, and also necessitated further merging of separately coded taxa (with polymorphism codes for characters varying among merged taxa) for some analyses (Wiens 1998).

(e) *Phylogenetic analyses*

(i) *General principles and methodology*

Criterion of parsimony. Construction of trees by cladistic methodology and under the criterion of parsimony was employed here and is standard in phylogenetic analysis (Hennig 1966; Wiley 1981; Wiley *et al.* 1991), contrary to remaining detractors (Sneath 1995). Application of cladistic methods to characters of avian morphology include previous assessments of the phylogenetic relationships of Anseriformes (Livezey 1986, 1989*a*,*b*, 1991, 1995*a*–*c*, 1996*a*–*c*, 1997*a*,*b*; Livezey & Martin 1988) and reconstructions by other workers (e.g. Siegel-Causey 1988; Prum 1992; Chu 1995; Lee *et al.* 1997).

Binary and multistate characters. Definition of characters and included states remains the most problematic and analytically influential aspect of phylogenetic analysis (Pogue & Mickevich 1990; Pleijel 1995; Wilkinson 1995*a*,*b*). Binary characters (i.e. those comprising only two states) were defined where practical, but some characters assumed more than two evidently homologous, alternative conditions; although such multistate characters increase the number of possible transitions among states and can pose analytical challenges (Lipscomb 1992; Barriel & Tassy 1993), the latter characters were coded accordingly. A subset of these multistate characters represented logical gradations in magnitude or ordinal counts; these were treated as ordered characters, i.e. transitions between pairs of states within a character were assigned different numbers of steps (Hauser & Presch 1991; Slowinski 1993).

Undetermined or 'missing' states for characters can increase dramatically the number of shortest trees and the computations required to recover them (Nixon & Davis 1991; Platnick *et al.* 1991; Wilkinson 1995*a*–*c*). Two classes of conditions resulted in 'missing-datum' codes, for which the most parsimonious states were hypothesized *a posteriori* through analyses: states not determined because of inadequate material, or states not comparable because of fundamental, obscuring modification or evolutionary loss of the element concerned (Maddison 1993). Cases of non-comparability are indicated explicitly in the character descriptions, and were most frequent in flightless, highly autapomorphic *Aptornis* (Appendix A).

Weighting. Differential weighting of characters remains a point of controversy (Hillis 1991; Huelsenbeck *et al.* 1994; Hillis *et al.* 1996; Kluge 1997). Homoplasy, the recurrent acquisition or loss of characters coded as homologous, is an important, virtually universal problem in phylogenetic reconstruction and typically is inferred *a posteriori* based on the performance of characters on the recovered trees (Sanderson & Donoghue 1989, 1996; Sluys 1989; Sanderson 1991; Wake 1991; Doyle 1996). However, several characters associated with flightlessness in the Rallidae (characters 139, 162, 170, 209, 522 and 536) occur as well in flightless members of a number of other avian orders (Cracraft 1974*b*; Livezey & Humphrey 1986; Millener 1988; Livezey 1989*c*, 1990, 1992*a*,*b*, 1993*a*–*c*, 1994, 1995*d*) and permit the segregation of such characters *a priori* for purposes of phylogenetic inference. Furthermore, the insular distributions of flightless rallids lend credence to the idea that such characters were derived independently, evidently through heterochrony (e.g. Olson 1973*a*, 1977; Cracraft 1974*a*; Livezey 1995*b*). Accordingly, alternative analyses were performed in which these morphological correlates of avian flightlessness were deleted (i.e. assigned zero weight) to assess the impact of these apparently convergent conditions on phylogenetic inferences.

Where unweighted analyses of the Gruidae, Heliornithidae and Rallidae failed to resolve groups of particular interest, successive weighting was employed for comparative purposes (Farris 1969; Carpenter 1988). In all successive weighting exercises, characters were reweighted conservatively on the basis of rescaled consistency indices using base weights of one.

(ii) *Construction of matrices*

Genus-level matrices of Gruiformes and species-level matrices for the Rallidae and sister families (determined on the basis of the genus-level, ordinal assessments) were constructed in MACCLADE (Maddison & Maddison 1992) and imported into other software for analysis. For the genus-level, ordinal data, several groups of rallid genera united in polytomies were merged; these included several genera merged with *Porzana* by most recent authorities (e.g. *Aenigmatolimnas* and *Poliolimnas*). Initial appraisals of character states, however, prompted the recognition of several subgeneric groups of rallids for analysis at genus level: *Notornis* as distinct from *Porphyrio*; *Aphanapteryx bonasia* separately from '*A.*' *leguati*; '*Rallus*' *madagascariensis* from other *Rallus*; and *Hypotaenidia* proper (*philippensis*, *pectoralis*, *striatus*, *wakensis*, *owstoni*) as distinct from *Rallus*, *Gallirallus australis*-group and '*Gallirallus*' *torquatus*-group; and the large, flightless genera *Tricholimnas*, *Nesoclopeus*, *Aramidopsis* and *Habropteryx* from *Rallus* and *Gallirallus*. On the basis of these generic appraisals, however, several of these generic partitions were waived for the species-level analyses of the Rallidae (e.g. *Notornis* synonymized with *Porphyrio*, and *Hypotaenidia* with *Gallirallus*). Also, for the latter analyses, diagnosable subspecies or members of 'superspecies' of Psophiidae, Gruidae and Rallidae were merged (table 1) and included variation indicated as polymorphism (Maddison & Maddison 1992), thereby avoiding insurmountable computational hurdles through limited generalizations having little or no impact on higher-order inferences (Kluge 1989; Nixon & Carpenter 1996).

(iii) *Basal polarities and rooting*

Trees were rooted through comparison with outgroups (Watrous & Wheeler 1981; Maddison *et al.* 1984; Farris 1982; Nixon & Carpenter 1993; Weston 1994). Alternative methods of determining polarities, most notably the ontogenetic criterion (Bonde 1984; Alberch 1985; de Queiroz 1985; Kluge 1985; Kluge & Strauss 1985; Mabee 1989, 1993; Wake 1989; Wake & Roth 1989; Wheeler 1990; Williams *et al.* 1990; Bryant 1991; Horder 1994; de Pinna 1994; Patterson 1996), remain controversial and assessments based on ontogeny would be complicated in a number of characters evidently affected by paedomorphosis in flightless rallids (Olson 1973*a*, 1977; Cracraft 1974*a*; Livezey 1995*d*). In the genus-level analysis of the Gruiformes, primary outgroups were representatives of all families of Charadiiformes; qualitative identity or near-identity of states prompted merging of the charadriiform families into four working outgroups for analysis: Jacanidae and Rostratulidae; Laridae, Stercorariidae, and Rynchopidae; Alcidae; and other charadriiform families. Problematic polarities and variation among outgroup taxa in several characters led to the inclusion of a hypothetical ancestor as a final root for the tree (ancestor 1); this abstraction summarized distribution of states in secondary outgroups and has proven useful in similar applications (Livezey 1986, 1991, 1995*a–c*, 1996*a–c*, 1997*a*). A parallel approach was used to root the species-level analysis of the Rallidae; members of the families determined to be most closely related to the Rallidae based on the foregoing ordinal analysis, together with reference to other Gruiformes where basal polarities remained ambiguous, were used to compile a hypothetical ancestor for rooting trees (ancestor 2).

(iv) *Derivation of trees*

Phylogenetic signal. Skewness of sample distributions of tree-lengths (g_1) serve as general indices to the congruence of characters and generally are considered to be indicative of phylogenetic structure (Hillis 1991; Huelsenbeck 1991*a*; Novacek 1991; Hillis & Huelsenbeck 1992; Källersjö *et al.* 1992). Estimates of g_1 for data matrices were based on distributions of lengths for 10^6 randomly generated trees for the matrices in question. In addition, standard summary statistics indicative of such character congruence—consistency index excluding uninformative characters (CI), homoplasy index excluding uniformative characters (HI) and retention index (RI)—were compiled (Farris 1989; Sanderson & Donoghue 1989; Klassen *et al.* 1991). Methods predicated on null distributions and randomizations (Brooks *et al.* 1986; Archie 1989*a*,*b*, 1990; Faith 1991; Maddison & Slatkin 1991; Meier *et al.* 1991; Faith & Cranston 1991; Archie & Felsenstein 1993; Alroy 1994) were not used because of logistic demands that these methods impose for matrices of large dimension and ongoing controversy regarding their utility (Bryant 1992; Carpenter 1992; Trueman 1993; Faith & Ballard 1994; Farris *et al.* 1994; Faith & Trueman 1996; Swofford *et al.* 1996*b*).

Topological searches. Searches for shortest trees were performed with the widely used software PAUP, version 3.1 (Swofford 1993), although some searches were performed using test versions of the software (PAUP*). Large numbers of taxa included in each analysis limited the searches of primary data matrices to heuristic algorithms; initial searches comprised 100 replicates in which sequence of addition of taxa were randomized, using the option MULPARS, and employing TBR branch swapping. The samples of shortest trees retained in the initial searches then were subjected to heuristic searches with MAXTREES fixed at 20 000. These suites of searches were intended to minimize the likelihood of entrapment in local optima (Maddison 1991; Page 1993). Nonetheless, analytical circumstances conducive to inaccuracy may have prevented the discovery of shortest trees, e.g. those leading to long-branch attraction (Felsenstein 1978; Kim 1996) and the impracticality of retaining all equally parsimonious trees. Branch-and-bound searches were used to compile complete sets of shortest trees for selected subgroups of taxa in the species-level analyses; these solution sets were summarized using majority-rule consensus trees in which percentages pertaining to other compatible nodes also are given.

Fossil taxa can be important in phylogenetic reconstructions, primarily by providing character states for a greater diversity of taxa (Patterson 1981; Forey 1982, 1992; Fortey & Jefferies 1982; Schoch 1986; Donoghue *et al.* 1989; Huelsenbeck 1991*b*; Bryant & Russell 1992; Smith 1994). However, fossils can represent enormous computional burdens stemming from missing data (e.g. all characters of the integument). Also, inclusion of additional arrays of poorly known taxa in phylogenetic analyses is at best neutral with respect to accuracy of reconstructions (Wiens & Reeder 1995), and the associated enlargement of solution sets and reduced resolutions can obscure accurate reconstructions (Huelsenbeck 1991*b*; Shaffer *et al.* 1997). Moreover, most subfossil rallids are recently extirpated, flightless members of modern genera and impart no unique information for the delimitation of major groups. Accordingly, fossil taxa were placed subsequently through separate heuristic searches (MAXTREES=1000) in which the strict consensus tree of the shortest topologies for modern taxa was used as a backbone constraint (Swofford 1993).

Constraints on parsimony, including Dollo parsimony in which selected characters are not permitted to undergo reversals (Farris 1977; Bull & Charnov 1985; Sanderson 1993), were not employed in searches for shortest overall topologies. Strict and majority-rule consensus trees were used to summarize common elements among equally short trees, as opposed to their use as explicit phylogenetic hypotheses or for combining disparate sources of data (Adams 1972; Barrett *et al.* 1991; Wilkinson 1994; Wilkinson & Benton 1996). Such summaries of equally parsimonious trees under varying analytical assumptions were favoured over proposed criteria for choosing among topologies of equal length (Carpenter 1988; Le Quesne 1989; Goloboff 1991*a*,*b*; Mickevich & Lipscomb 1991; Rodrigo 1992; Sharkey 1993; Wilkinson & Benton 1996).

Topological support. In addition to simple counts of hypothesized character changes, empirical support for selected nodes was estimated using bootstrapping of characters (Felsenstein 1985*b*; Sanderson 1989, 1995; Hillis & Bull 1993; Penny *et al.* 1994; Hillis 1995). Logistic considerations limited bootstrapping exercises to 100 replicates with MAXTREES limited to 250. Outcomes of bootstrapping were summarized by majority-rule consensus trees indicating the percentages of 100 bootstrapped replicates in which each node was conserved. Related to the notion of character removal as a means of assessing support for nodes (Davis 1993), bootstrapping is predicated on repeated subsampling of characters, and here was used as an index to support as opposed to a formal statistical test with attendant distributional assumptions. For ease of analysis, bootstrapping was employed on entire data matrices; inclusion of uninformative characters (autapomorphies) in bootstrapping is considered either inconsequential (Harshman 1994*b*) or conservative (Carpenter 1996) with respect to resultant estimates of support.

An alternative measure of support or robustness of nodes employed was the support index of Bremer (1988, 1994). Support indices represent the number of additional steps required to violate a given node in the shortest tree(s), and were calculated only for nodes of particular interest common to the solution set(s). Support indices were estimated using inverse constraints in separate heuristic searches based on ten random-addition replicates, retaining up to 100 trees per replicate, and MAXTREES set at 1000. Jack-knifing, the differential exclusion of taxa from analysis to test the stability of inferred trees (Lanyon 1985, 1993; Sillén-Tullberg 1993; Siddall 1995), was not used in this study, as this procedure alters the phylogenetic problem at hand, as opposed to subsampling the information bearing on the relationships among the same set of taxa.

(v) *Phylogenetic classification*

Inferred phylogenetic relationships were summarized in a classification, after the recommendations of Wiley (1981), including the provision for sequencing paraphyletic taxa at the same rank to avoid the unwieldy proliferation of classificatory levels and unconventional, higher-order taxa (e.g. Livezey 1997*c*), and concessions regarding poorly resolved groups (Appendix C). Nomenclatural rules for taxonomy and associated citations follow the rules of the International Commission on Zoological Nomenclature (1985), and specific and family-group taxa and citations of authorship were based on key published sources (Peters 1934; Wolters 1975; Olson 1977; Ripley 1977; Bock 1994; Taylor 1996), while considering pertinent nomenclatural debates (Greenway 1952; Olson 1986*b*, 1987, 1991*b*, 1992; Walters 1987, 1988, 1989; Weber & Krell 1995; International Commission on Zoological Nomenclature 1997).

3. PHYLOGENETIC RECONSTRUCTIONS

(a) *Genera of Gruiformes*

(i) *Phylogenetic signal*

A sample of 10^6 randomly generated trees for the complete data matrix showed substantial negative skewness of total lengths ($g_1 = -0.4368$); the skewness of 10^6 tree lengths for the matrix excluding four characters notoriously related to flightlessness was similar ($g_1 = -0.4374$). Skewness statistics of this magnitude significantly exceed that expected for a sample drawn from a normally distributed population ($p < 0.001$), a finding indicative of significant phylogenetic signal.

(ii) *Topologies of shortest trees*

A strict consensus tree for a sample of 20 000 shortest recovered topologies (figure 1) revealed that most nodes supporting relationships among gruiform families and groupings within families other than the Rallidae were common to all trees (length = 967; CI (excluding uniformative characters) = 0.517; RI = 0.845; RC = 0.472); the CI substantially exceeds expectations for data sets of comparable size and taxonomic scale (Sanderson & Donoghue 1989; Klassen *et al.* 1991). Based on the outgroup families, there is weak evidence for the paraphyly of the Charadriiformes in that the Jacanidae and Rostratulidae were inferred to comprise the sister group of the Gruiformes (figure 1); this should not be considered a firm inference in that no concerted effort was made to reconstruct relationships among charadriiform families.

Within the Gruiformes, the most-basal bifurcation places a two-family clade—the plains-wanderer (Pedionomidae) and buttonquails (Turnicidae)—as the sister group of other members of the order. The latter were inferred to be monophyletic and comprise seven major groups (figure 1), and are (in order of increasingly close relationship): bustards (Otididae); mesites (Mesitornithidae); seriemas and fossil allies (Cariamidae and Phorusrhacoidea); sunbitterns (Eurypygidae), kagus (Rhynochetidae) and their respective extinct sister groups (Messelornithidae and Aptornithidae); trumpeters, limpkins and cranes (Psophiidae, Aramidae and Gruidae); finfoots (Heliornithidae); and rails (Rallidae). Although treated in more detail beyond, the last inference—substantiation of the monophyly of the Psophiidae, Aramidae, Gruidae, Heliornithidae and Rallidae—justified narrowing the species-level assessments of integumentary characters to these families as a means of reconstructing species-level relationships within the Rallidae (figure 1).

Within the cranes and allies, the trumpeters were inferred to be the sister group of the limpkins and cranes (figure 1); within the cranes, a basal grade comprising the crowned cranes (*Balearica*) and wattled crane (*Bugeranus*) subtends the monophyletic, typical cranes (*Anthropoides*, *Leucogeranus* and *Grus*). Within the finfoots, *Heliopais* is inferred to be the sister group of *Heliornis* and *Podica* (figure 1). For the Rallidae, the characters coded for the entire order supported unequivocally only a few nodes in addition to that corroborating familial monophyly. These additional nodes indicated the monophyly of all members exclusive of *Himantornis* and monophyly of several subgroups of rails exclusive of *Himantornis*. The latter inferences included sister relationships between several couplets of genera: *Porphyrio* with *Porphyrula*; *Rallus* with *Gallirallus*, and *Rallicula* with *Sarothrura*. The ordinal-level analysis also indicated that a poorly resolved set of rallid genera—*Gymnocrex*, *Porphyrio*, *Porphyrula*, *Eulabeornis*, *Aramides*, *Canirallus* (with sister group *Mentocrex*), *Habroptila* and *Anurolimnas*—were paraphyletic to the Rallidae exclusive of *Himantornis* (figure 1).

Within the last group of comparatively derived Rallidae, two other groupings were common to all shortest trees in the ordinal analysis (figure 1): a cluster of six taxa of flightless rails (*Aphanapteryx bonasia*, *A. legauti*, *Capellirallus*, *Cabalus*, *Nesotrochis* and *Diaphorapteryx*) united, in large part, on the basis of characters associated with the loss of flight; and a group of seven taxa which are comparatively specialized for aquatic habitats (*Amaurornis*, *Gallicrex*, *Gallinula* and allies, and *Fulica*). Exclusion of four osteological characters generally associated with avian flightlessness had no impact on the shortest topologies relating non-rallid genera (length = 927; CI = 0.524; RI = 0.850; RC = 0.481), but affected the strict consensus tree for the Rallidae as follows: collapsed the branch separating *Habroptila* and *Anurolimnas* in the basal grade described above; enlarged the group of 'typical' rails to comprise *Rallus* (including '*R.*' *madagascariensis*), *Gallirallus*

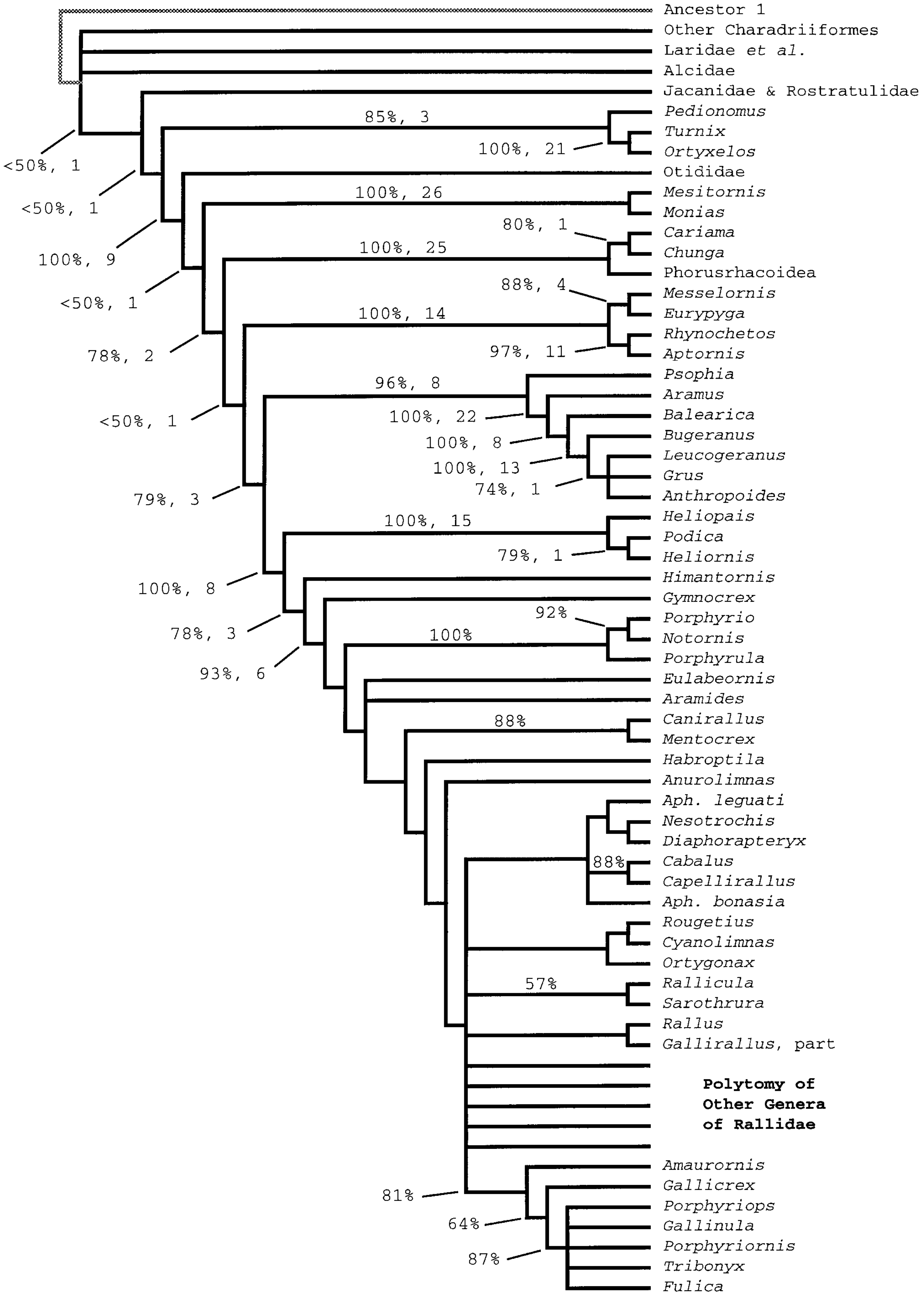

Figure 1. Strict consensus tree for sample of the 20 000 shortest trees for genera of Gruiformes and representative Charadriiformes, based on 381 primarily osteological characters (Appendix A). Nodes robust to bootstrapping are annotated by percentages of bootstrapped replicates in which the node was conserved; those for non-rallid genera are followed by support (Bremer) indices.

Table 2. *Branch-length ranges and diagnostic apomorphies* (*i.e. those having* CI = 1.0) *for selected robust nodes and terminal branches in phylogenetic tree of genera of Gruiformes* (*figure 1*)

(See Appendices A and B for character descriptions, and Appendix C for delimitation of taxonomic groups.)

taxonomic group(s)	branch-length range	diagnostic apomorphies
Turnices	8–11	57b
Turnicidae	22–28	51b, 56b, 66b, 83b, 193b, 203b, 228b, 233b, 314b, 319b
Gruiformes exclusive of Turnices	16–33	126b, 220b, 295b
Otididae	25–39	45b, 128b, 142b, 161b, 186b, 239b, 247b, 255b, 302b, 330b, 368b
Gruiformes exclusive of Turnices and Otidides	9–11	195b
Mesitornithidae	29–41	20b, 143b, 144b, 149b, 164b, 166b, 177b, 212b, 229b, 243b, 326b, 376b
Cariamae	28–40	5b, 15b, 22b, 29b, 30b, 36b, 42b, 54b, 63b, 91b, 213b, 227b, 245b, 299b, 340b
Phorusrhacoidea	22	46c, 175b, 181b, 219b, 266b, 323b
Eurypygae	20–35	35b, 38b, 50b, 105b, 217b, 232b, 240b, 250b, 271b, 297b, 376c
Eurypygoidea	7–22	176b
Rhynochetoidea	18–21	88b, 99b, 279b, 310b, 329b
Aptornithidae	61–68	6b, 12b, 13b, 14b, 26b, 40b, 48b, 55b, 61b, 75b, 78b, 81b, 85b, 100b, 112b, 118b, 119b, 122b, 131b, 136b, 150b, 166c, 180b, 197b, 199b, 225b, 231b, 235b, 256b, 281b, 303b, 317b, 335b, 339b, 344b, 349b

(including the *torquatus*-group); placed *Rallina* as the sister group of *Rallicula* and *Sarothrura*; and undermined the support for the six-taxon group of flightless rails defined above, including them in a large polytomy comprising the majority of rallid genera.

Autapomorphic divergence of genera of Gruiformes showed substantial variation (table 2). Whereas most genera were inferred to manifest only a few terminal character changes, several genera (*Pedionomus*, *Eurypyga* and *Himantornis*) showed a minimum of 7–15 terminal apomorphies (approximately 1–2% of total tree length). Two other genera (*Psophia* and *Fulica*) showed a minimum of 15–24 apomorphies (2–4% of total tree length); slightly higher minimal tallies of apomorphies characterized the Otididae and Phorusrhacoidea (25 and 22 apomorphies, respectively). Truly remarkable is the apomorphy shown by the flightless *Aptornis*, which was inferred to possess a minimum of 61 mostly unique autapomorphies (approximately 6% of total tree length), three times that of the branch subtending the four-family clade including *Aptornis* (table 2).

(iii) *Assessments of support*

Two measures of support—percentage of bootstrapped replicates conserved and magnitude of support (Bremer) indices—revealed concordant ranges in empirical support for the groupings shared by the 20 000 minimal-length trees summarized (figure 1), including diagnostic synapomorphies for well-supported nodes and terminal taxa shared by the set of shortest trees (table 2). Placement of the Jacanidae and Rostratulidae as sister group of the Gruiformes is only weakly supported (figure 1). Inclusion of the Pedionomidae and Turnicidae as one of two basalmost branches in the Gruiformes also received only marginal support; membership of this two-family clade among the Gruiformes is favoured by but a single step, and the node narrowly failed to be conserved in a majority of bootstrapped replicates (figure 1). Support for the Pedionomidae as the sister group of the Turnicidae is only moderate, whereas evidence of the monophyly of the Turnicidae is strong (figure 1).

Support for the monophyly of gruiform families exclusive of the Pedionomidae and Turnicidae is also strong (figure 1). However, the first four primary nodes paraphyletic to the cranes, rails and allies received only weak support, specifically those corresponding to the divergences of the following groups (figure 1): Otididae; Mesitornithidae; Cariamidae and fossil allies; and Eurypygidae, Rhynochetidae and (sub)fossil allies. Support for monophyly of each of these four clades, however, is great; the Otididae are united by 25 apomorphies (table 2), and the other three clades were conserved in 100% of bootstrapped replicates and had support indices of 26, 25 and 14, respectively (figure 1). Support for the monophyly of the Cariamidae (*Cariama* and *Chunga*) was only modest, whereas that of the two pairs of monogeneric families in the last of the four aforementioned clades—Eurypygidae and Messelornithidae, Rhynochetidae and Aptornithidae—was substantial (figure 1).

The node supporting the five-family 'crown-group' of the Gruiformes (Psophiidae, Aramidae, Gruidae, Heliornithidae and Rallidae) showed moderate robustness, as did a number of nodes within this assemblage (figure 1). Support for all nodes within the grade comprising the Psophiidae, Aramidae and Gruidae was strong; comparable evidence supported the sister relationship between the Heliornithidae and Rallidae (figure 1). The node supporting monophyly of the Rallidae was substantial but of lesser magnitude, whereas that uniting rallids exclusive of plesiomorphic *Himantornis* was strongly supported; few nodes within the Rallidae were strongly supported in the generic analyses (figure 1).

(b) ***Species of Grues***

(i) *Phylogenetic signal*

An expanded assessment of the Grues (trumpeters, limpkin, cranes, finfoots and rails), including characters of the integument and more finely partitioned terminal taxa, revealed substantial additional phylogenetic detail and minimal topological conflicts with the foregoing generic assessment. The skewness statistic (g_1) for a sample of 10^6 randomly generated trees for the complete data matrix (all characters, modern and fossil taxa) was -1.0904, a figure signficantly lower than that expected for a normal distribution ($p<0.001$) and indicative of substantial phylogenetic signal. The g_1 statistic for a similar sample of random trees for the matrix with subfossil taxa deleted was -1.1280 ($p<0.001$). Skewness statistics (g_1) for 10^6 randomly generated trees for all-taxon and modern-taxon matrices in which six flightlessness-related characters were excluded were similar (-1.0977 and -1.1277, respectively).

(ii) *Topologies of shortest trees*

All characters included. Heuristic searches of the complete matrix for the Grues resulted in an indeterminately large number of minimal-length trees (length = 1232; CI (excluding uniformative characters) = 0.463; RI = 0.828; RC = 0.421); the CI substantially exceeds minimal expectations for data sets of comparable size and taxonomic scale (Sanderson & Donoghue 1989; Klassen *et al.* 1991). A strict consensus tree of 20 000 minimal-length trees revealed a number of groups common to all members of the solution set. For reasons detailed below, however, this tree is not figured, and treatment of the all-character analysis is limited to the following textual summary. Inferences included relationships among genera of Psophiidae, Aramidae and Gruidae as given in the ordinal analysis (figure 1); the Heliornithidae and Rallidae as sister groups; monophyly of the Rallidae; and *Himantornis* as the sister group of other Rallidae. Within other Rallidae, the following groups were placed as a basal grade paraphyletic to other, comparatively derived members (listed in order of increasingly close relationship): swamphens (*Porphyrio* and *Porphyrula*); a polytomy involving *Aramides*, *Eulabeornis*, *Canirallus* (with sister group *Mentocrex*), *Gymnocrex* and *Habroptila* (including the last two genera as sister groups); and the chestnut-headed rail (*Anurolimnas*).

The remaining rallids included a number of distinct clades or lineages, including Rouget's rail (*Rougetius rougetii*); a clade comprising flufftails (*Sarothrura*) and close relatives (*Rallicula* and *Rallina*); a clade comprising the 'typical' or long-billed rails (e.g. *Pardirallus*, *Dryolimnas*, *Rallus* and *Gallirallus*); waterhens or bush hens (*Amaurornis*); chestnut crake (*Amaurolimnas*); crakes of the genus *Laterallus*; and a clade comprising moorhens (e.g. *Gallinula*, *Tribonyx* and *Porphyriornis*), coots (*Fulica*) and allies (*Gallicrex* and *Porphyriops*). However, crakes of the genus *Porzana* and allied taxa (e.g. *Neocrex* and *Poliolimnas*) were not confirmed as monophyletic; some members could not be placed unequivocally with respect to any of the aforementioned clades or any congener, whereas other members were placed in weakly supported groups involving other genera (e.g. *Coturnicops*, *Micropygia*, *Crex* and the moorhen–coot clade).

Furthermore, the all-character analysis resulted in a number of groupings which were suspect with respect to several characters associated with flightlessness, and these not only delimited phylogenetically dubious arrangements but also acted (indirectly) to disrupt other groups not including flightless members. Findings which were particularly suspicious from this perspective include the placement of *Gallirallus dieffenbachii* with other flightless rails as opposed to *G. philippensis* (with which it commonly is considered conspecific); inference of *Atlantisia rogersi* as the sister group of *Cabalus modestus*; and a failure to partition *Pardirallus*, *Cyanolimnas* and *Ortygonax* from other 'long-billed' rails (e.g. *Rallus*).

Flightlessness-related novelties excluded. Based on the segregation of characters known to be related to flightlessness *a priori* in other avian orders (characters 139, 162, 170, 209, 522 and 536), detailed descriptions of findings were based on analyses in which six of these characters were excluded. The set of minimal-length trees recovered had similar summary statistics (length = 1178; CI (excluding uniformative characters) = 0.476; RI = 0.835; RC = 0.437) and shared many of the groups recovered using the complete data matrix, but achieved somewhat greater resolution of several rallid groups while disbanding several tenuously supported clusters of taxa sharing characters associated with flightlessness (figures 2–4).

Topological arrangements among families were consistent among all shortest trees compiled (figure 2) and with the relationships inferred in the genus-level analysis of the order (figure 1). In addition, resolution of genera within the Gruidae was improved slightly. Two equally short topologies for the three genera of Heliornithidae were found, resulting in a trichotomy in the consensus tree. *Heliopais* and *Podica* were inferred to be sister groups in 68% of the sample of shortest trees, however, a topology common to a sample of 20 000 solutions following a single iteration of successive weighting of characters. A majority-rule consensus tree for the cranes and closest relatives based on the complete set of 12 shortest trees determined from a branch-and-bound search indicated that *Psophia leucoptera* and *P. viridis* are sister species (figure 5). Within *Grus* proper, a three-species group comprising *G. vipio*, *G. rubicunda* and *G. antigone* was common to all shortest trees. Also, among the set of shortest trees the following arrangements were most frequent (occurring in six out of 12 trees): *G. canadensis* as the sister group of other *Grus*; *G. rubicunda* and *G. antigone* as sister species; and a four-species clade in which *G. grus* and *G. nigricollis* are paraphyletic to the sister species *G. japonensis* and *G. americana* (figure 5). A strict consensus of the two shortest trees following two iterations of successive weighting produced the same groupings with the following exceptions: *Anthropoides* was placed as the sister group of gruids exclusive of *Balearica*; and *Grus canadensis* was included with *G. monacha* and *G. grus* as the sister group of the clade comprising *G. vipio*, *G. rubicunda*, and *G. antigone*.

Higher-order groups within the Rallidae (figures 2–4) were consistent with most of those indicated in the genus-level assessment of the order (figure 1), including the placement of *Himantornis* as sister group to the other Rallidae and inclusion of *Porphyrio*, *Porphyrula*, *Gymnocrex*, *Eulabeornis*, *Aramides*, *Canirallus* (with sister group *Mentocrex*), *Anurolimnas* and *Habroptila* as the basal-most branches of the Rallidae exclusive of *Himantornis*. The enlarged suite of characters and finer division of taxa, however, led to several differences in arrangements

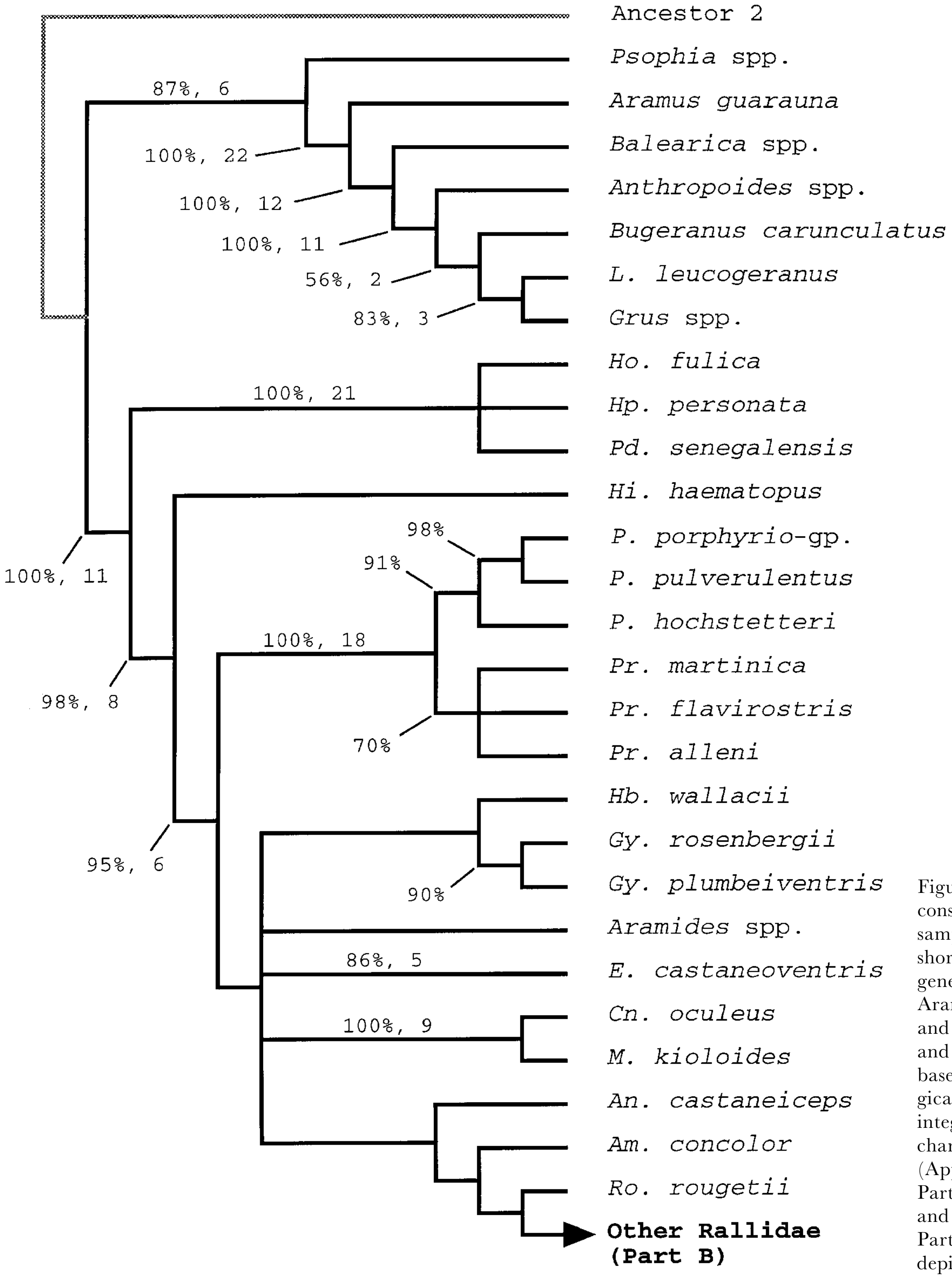

Figure 2. Strict consensus tree for sample of the 20 000 shortest trees for genera of Psophiidae, Aramidae, Gruidae and Heliornithidae, and species of Rallidae, based on 570 osteological, myological and integumentary characters (Appendix A). Part A, sister families and basal Rallidae. Part B of the tree is depicted in figure 3.

among these basal branches, including (figure 2) placement of the swamphens (*Porphyrio* and *Porphyrula*) as basal to the divergence of *Gymnocrex*; *Habroptila* as sister genus to *Gymnocrex*; failure to resolve the position of *Canirallus* and *Mentocrex* relative to *Aramides* and *Eulabeornis*; the weakly supported paraphyly of *Anurolimnas*, *Amaurolimnas* and *Rougetius* to remaining rallids; and a basal dichotomy among the remaining members in which the flufftails (*Sarothrura*) and allied genera (*Rallicula* and *Rallina*) comprise the sister group of other confamilials. A strict consensus tree for a sample of 20 000 shortest trees following a single iteration of successive weighting of characters indicated a number of additional groupings: the clade comprising *Habroptila* and *Gymnocrex* as the sister group of *Aramides*, and together these three genera as the sister group of rallids exclusive of *Himantornis*, *Porphyrio* and *Porphyrula*; and *Eulabeornis* as the sister group of *Canirallus* and *Mentocrex*.

Branch-and-bound searches of more finely subdivided taxa suggested variably supported consenses regarding relationships within the *P. porphyrio*-group. With the exception of confirming the respective monophyly and

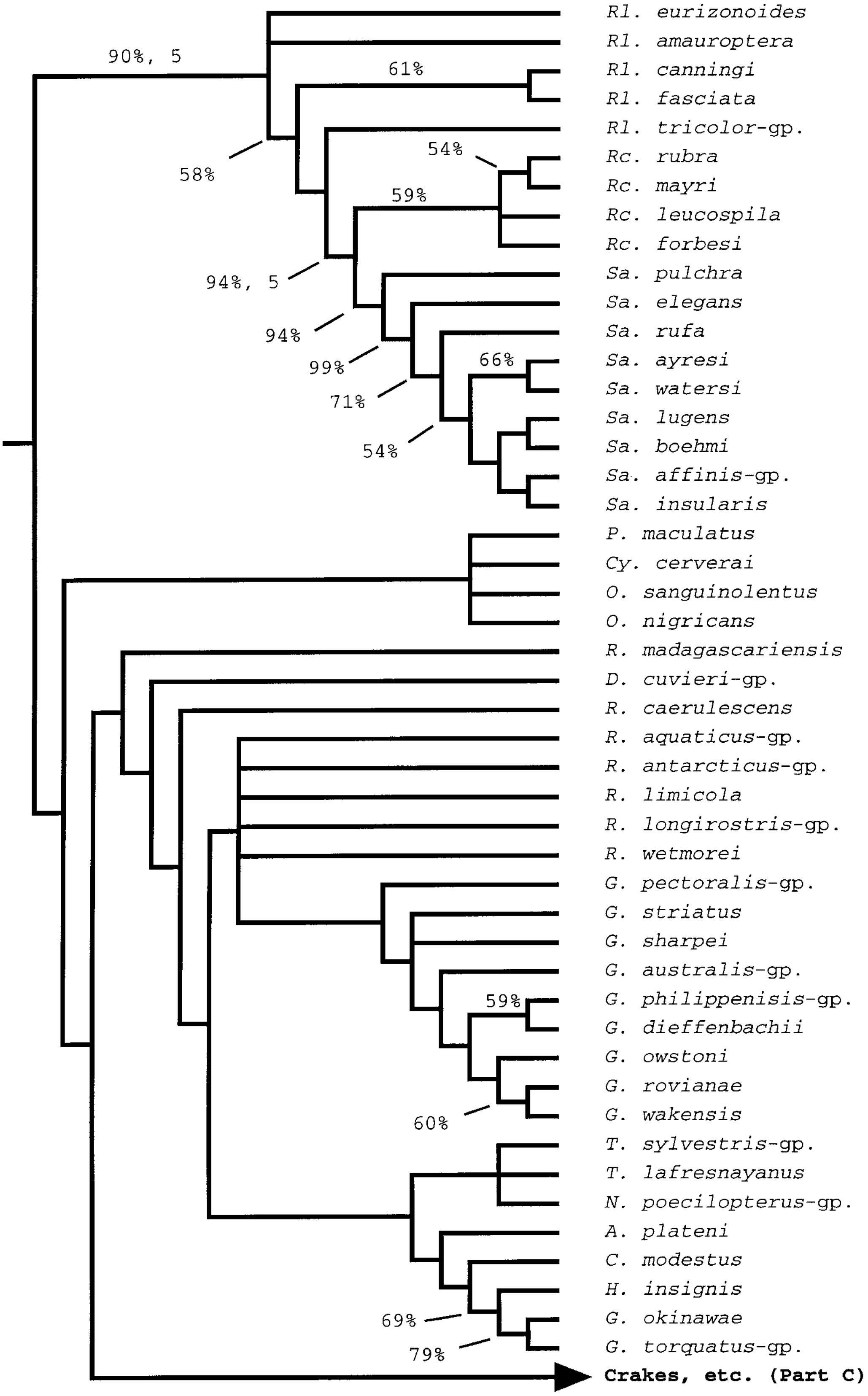

Figure 3. Strict consensus tree for sample of the 20 000 shortest trees for genera of Psophiidae, Aramidae, Gruidae and Heliornithidae, and species of Rallidae, based on 570 osteological, myological, and integumentary characters (Appendix A). Part B, long-billed (typical) rails, flufftails and allies. Part C of the tree is depicted in figure 4.

increasingly close relationship of the genera *Porphyrula* and *Porphyrio* in 100% of the 1304 shortest trees, however, only three nodes were shared by at least 50% of the solution set (figure 6). A sister relationship between *Porphyrula martinica* and paedomorphic *P. flavirostris* was favoured marginally in the unweighted analysis (figure 6), whereas a sister relationship between *Porphyrula martinica* and *P. alleni* was favoured by successive weighting of

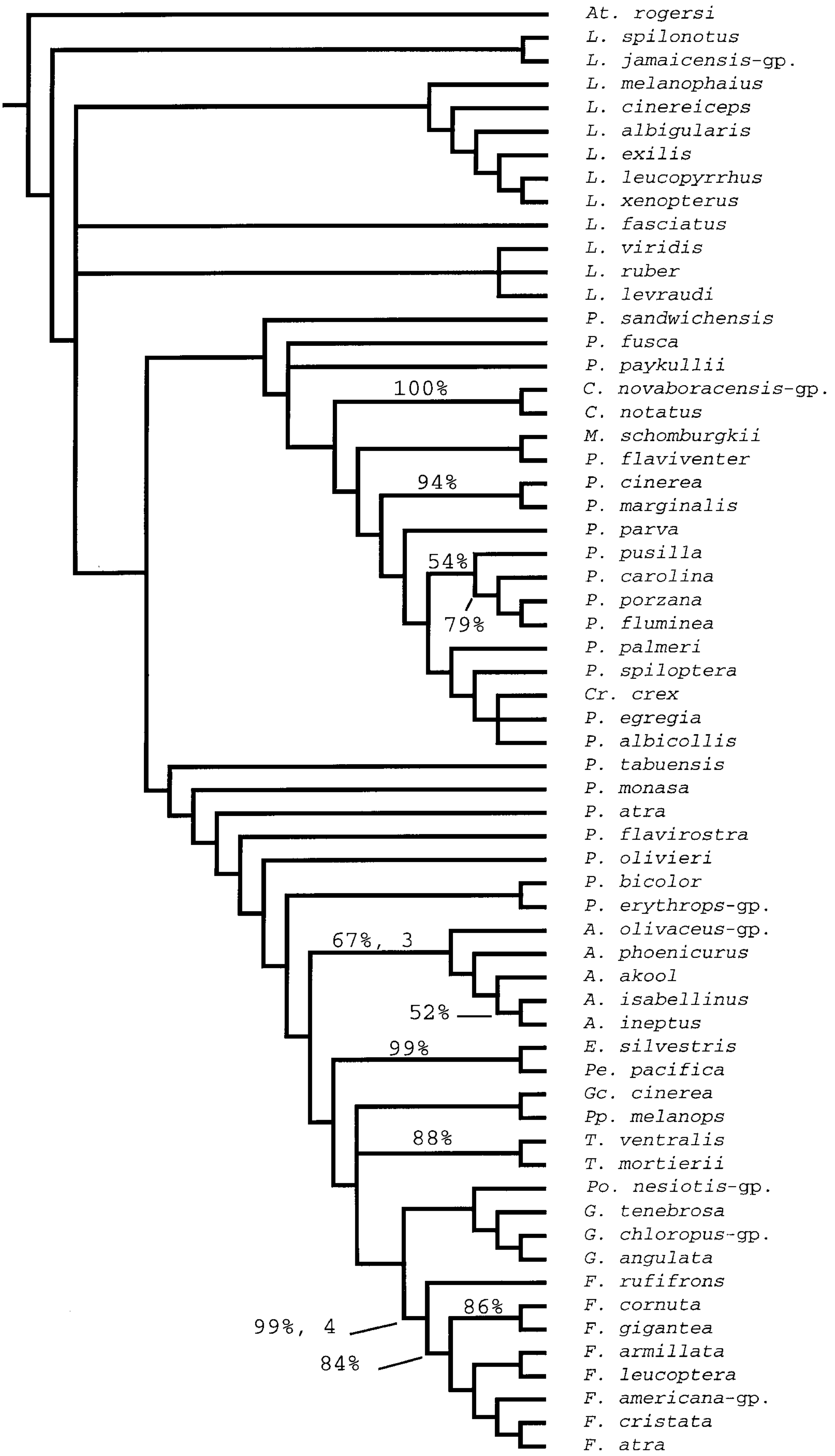

Figure 4. Strict consensus tree for sample of the 20 000 shortest trees for genera of Psophiidae, Aramidae, Gruidae and Heliornithidae, and species of Rallidae, based on 570 osteological, myological, and integumentary characters (Appendix A). Part C, crakes, moorhens and coots.

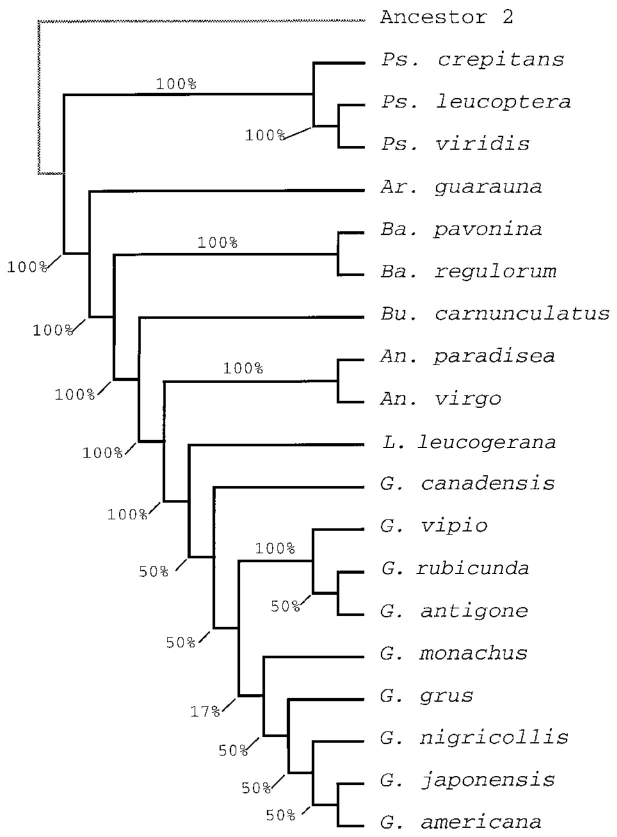

Figure 5. Majority-rule consensus tree for the 12 shortest trees recovered in a branch-and-bound analysis for species of Psophiidae, Aramidae and Gruidae. Trees were rooted using hypothetical ancestor 2 (see text); percentages are given for nodes conserved in the majority of the solution set and nodes compatible with the majority-rule nodes. See table 1 and Appendix C for details concerning delimitation of terminal taxa.

characters. A majority of shortest trees in the unweighted analysis indicated two species-pairs in *Porphyrio*: *P.* (*p.*) *bellus* and *P.* (*p.*) *indicus*; and *P.* (*p.*) *melanotus* and *P.* (*p.*) *melanopterus*. Topologies consistent with these nodes which were shared by the largest proportions of the solution set suggest additional topological details, and indicate that the conventional segregation of *P. pulverulentus* at species level renders polyphyletic the remaining forms in the complex (figure 6). Conservative successive weighting of characters failed to resolve any additional groups within *Porphyrio*.

Within *Aramides*, a number of nodes were supported by a majority of the 56 shortest trees found using branch-and-bound analyses: monophyly of the genus; a sister relationship between *A. saracura* and *A. calopterus*; monophyly of the genus exclusive of the preceeding species pair; a basal grade in the second subgroup consisting of *A. wolfi*, *A. ypecaha* and remaining taxa, respectively; and monophyly of the subgroup comprising *A.* (*c.*) *plumbeicollis*, *A.* (*c.*) *mexicana* and *A.* (*c.*) *albiventris* (figure 7). The interposition of *A. mangle* and *A. axillaris* between the latter three-species clade and *A.* (*c.*) *cajanea*, a taxon with which the three taxa traditionally are considered conspecific, represents the most common topology consistent with the majority-rule nodes, but this pertained only to a minority of the shortest trees (figure 7). A strict consensus of the two shortest trees following successive weighting of characters revealed similar groupings.

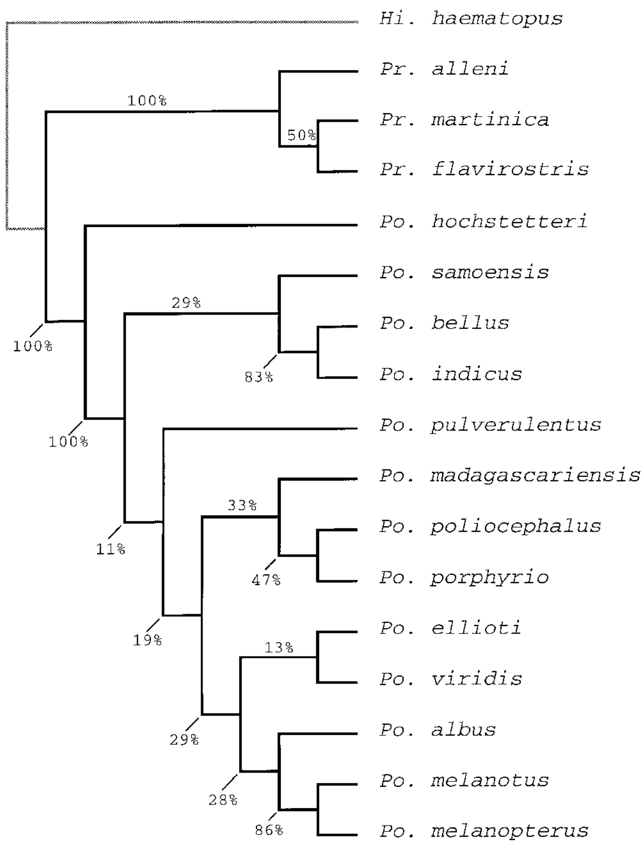

Figure 6. Majority-rule consensus tree for the 1304 shortest trees recovered in a branch-and-bound analysis for diagnosable partitions of modern *Porphyrio* (*Po.*; including '*Notornis*'), and *Porphyrula* (*Pr.*). Trees were rooted using *Himantornis haematopus*; percentages are given for nodes conserved in the majority of the solution set and nodes compatible with the majority-rule nodes. See table 1 and Appendix C for details concerning delimitation of terminal taxa.

The smaller of the two major clades of remaining rallids comprised the flufftails (*Sarothrura*) and the closely related genera *Rallina* and *Rallicula* (figure 3). The consensus tree indicated that the four species of *Rallina* are paraphyletic to *Rallicula* and *Sarothrura*, and that the latter two genera are sister groups and each monophyletic. Within *Rallina*, the solution set failed to resolve unambiguously the relationships of *R. eurizonoides* and *R. amauroptera*, although 75% of the 20 000 shortest trees placed the former as the sister group of the rest of the three-genus clade. The remaining two species, *R. canningi* and *R. fasciata*, were inferred to be sister species in all trees recovered (figure 3). Within *Rallicula*, only *R. rubra* and *R. mayri* were grouped as sister species in all shortest trees (figure 3); *R. leucospila* was placed as the sister species of the latter clade in 89% of the sample of shortest trees. *Sarothrura* was completely resolved in all topologies summarized in the consensus tree, in which *S. pulchra*, *S. elegans* and *S. rufa* formed a basal grade paraphyletic to a terminal clade of six species (figure 3). Within the latter, *S. ayresi* and *S. watersi* comprised the sister group of the remaining four terminal taxa, which in turn were partitioned into two couplets of sister groups, *S. lugens* with *S. boehmi*, and *S. insularis* with the *S. affinis*-group. Successive weighting applied to the Grues reversed the order of

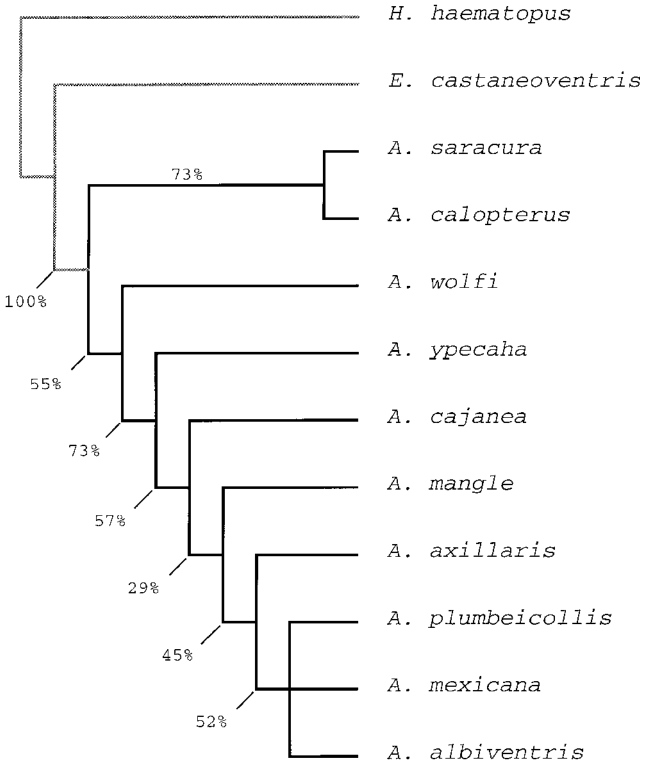

Figure 7. Majority-rule consensus tree for the 56 shortest trees recovered in a branch-and-bound analysis for diagnosable partitions of modern *Aramides*. Trees were rooted using *Himantornis* and *Eulabeornis*; percentages are given for nodes conserved in the majority of the solution set and nodes compatible with the majority-rule nodes. See table 1 and Appendix C for details concerning delimitation of terminal taxa.

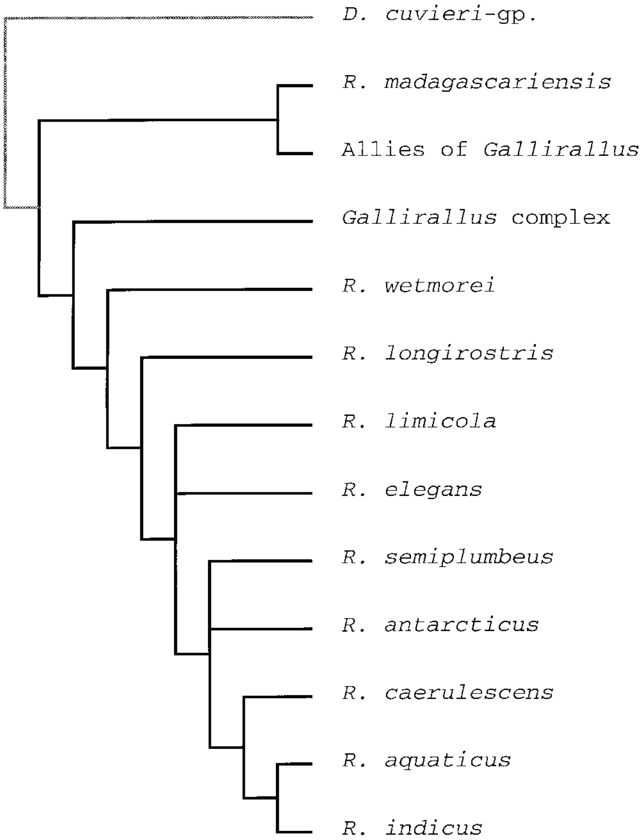

Figure 8. Single shortest tree recovered in a branch-and-bound analysis for modern species of *Rallus* (*sensu stricto*). Trees were rooted using *Dryolimnas*; also included were '*Rallus*' *madagascariensis* and merged taxa representing *Gallirallus* (exclusive of *torquatus*-group) and allies of *Gallirallus* (*Tricholimnas*, *Nesoclopeus*, *Aramidopsis*, *Cabalus*, *Habropteryx* and the '*G.*' *torquatus*-group). See table 1 and Appendix C for details concerning delimitation of terminal taxa.

branching of *Rallina tricolor* and the clade comprising *R. canningi* and *R. fasciata*, and collapsed the two nodes uniting the members of *Rallicula*.

The sister clade to the preceeding trigeneric group comprises a small clade composed of two species of *Ortygonax* and the monotypic genera *Cyanolimnas* and *Pardirallus*, and a large clade comprising the long-billed rails (*Rallus* and allies), crakes, moorhens and coots (figure 3). A majority (75%) of the sample of shortest trees under equal weighting of characters placed *Cyanolimnas* as the sister group of *Pardirallus* and *Ortygonax*, and a majority (88%) also confirmed the monophyly of *Ortygonax* within this narrower group. All shortest trees recovered following two iterations of successive weighting, however, placed *Pardirallus* as the sister group of *Cyanolimnas* and *Ortygonax*, and confirmed the latter as monophyletic.

The 'long-billed' rails (including *Rallus*, *Gallirallus* and allies) were inferred to be monophyletic in 88% of the shortest trees examined; however, a minority of shortest trees partitioned several genera of large, flightless rails and the '*Gallirallus*' *torquatus*-group separately from the more typical members, resulting in a trichotomy of these two groups in the strict consensus tree (figure 3) with that comprising crakes, moorhens and coots (figures 3 and 4). In the larger of the two clades of 'long-billed' rails, '*Rallus*' *madagascariensis*, *Dryolimnas cuvieri*-group and *R. caerulescens* form a basal grade which subtends a poorly resolved group of Eurasian and neotropical members of *Rallus* and a clade comprising most members of *Gallirallus* (figure 3). Within the latter clade, the *G. pectoralis*-group, *G. striatus* (polytomously with poorly known *G. sharpei*) and the *Gallirallus australis*-group are paraphyletic to a clade comprising two subgroups: the *G. philippensis* complex with sister species *G. dieffenbachii*; and the three flightless species *G. owstoni*, *G. rovianae* and *G. wakensis* (figure 3). The smaller clade of 'long-billed' rails was partitioned into two major subclades: an unresolved group of large, flightless rails (*Tricholimnas* and *Nesoclopeus*); and a five-member clade in which *Aramidopsis plateni*, *Cabalus modestus* and *Habropteryx insignis* are paraphyletic to the '*Gallirallus*' *torquatus*-group and its sister species '*G.*' *okinawae*. Two iterations of successive weighting of characters altered this arrangement in several ways: *Dryolimnas* and '*Rallus*' *madagascariensis* were placed as sister groups; the genera of large, flightless rails allied with *Gallirallus* (*Tricholimnas*, *Nesoclopeus*, *Aramidopsis*, *Habropteryx*, *Cabalus* and the '*Gallirallus*' *torquatus*-group) were arrayed as a grade paraphyletic to *Rallus* and typical *Gallirallus*; and *Gallirallus striatus* and *G. pectoralis* were paraphyletic to *Rallus* (*sensu stricto*), the latter being monophyletic.

A branch-and-bound analysis for Eurasian and neotropical *Rallus* in which the *Gallirallus* complex and allies were merged into two composite lineages discovered a

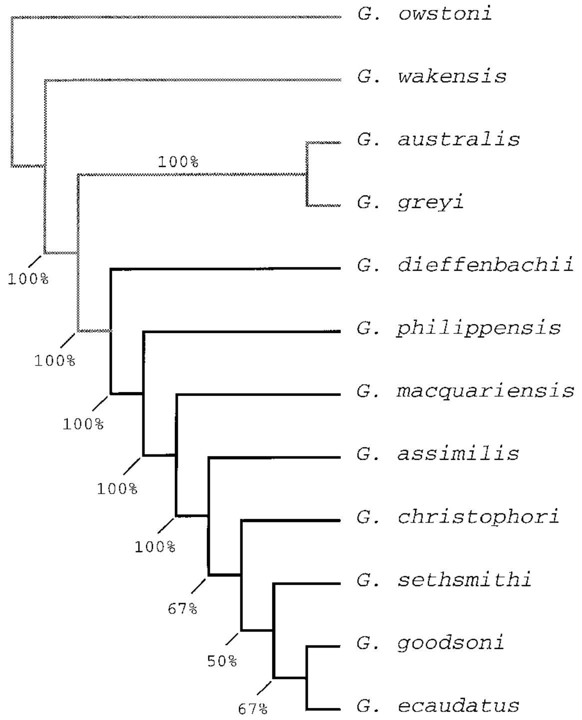

Figure 9. Majority-rule consensus tree for 12 shortest trees recovered in a branch-and-bound analysis for diagnosable partitions of the modern *Gallirallus philippensis*-group and *G. dieffenbachii*. Trees were rooted using a paraphyletic series of closely related rallids; percentages are given for nodes conserved in the majority of the solution set and nodes compatible with the majority-rule nodes. See table 1 and Appendix C for details concerning delimitation of terminal taxa.

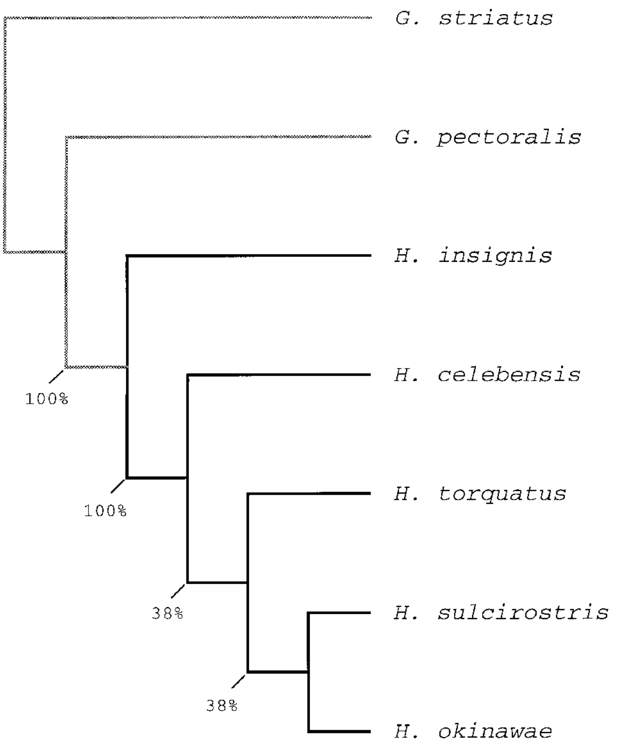

Figure 10. Majority-rule consensus tree for the eight shortest trees recovered in a branch-and-bound analysis of diagnosable partitions of the modern '*Gallirallus*' *torquatus*-group and '*G.*' *okinawae*, here labelled as congeneric with *Habropteryx insignis*. Trees were rooted using a paraphyletic series of closely related rallids; percentages are given for nodes conserved in the majority of the solution set and nodes compatible with the majority-rule nodes. See table 1 and Appendix C for details concerning delimitation of terminal taxa.

single shortest tree in which *Rallus* was monophyletic (figure 8). Furthermore, the genus was resolved as (in order of increasingly close relationship): *R. wetmorei*; *R. longirostris*; a trichotomy comprising *R. elegans*, *R. limicola* and a nested trichotomy comprising *R. antarcticus*, *R. semiplumbeus* and clade including the three remaining species (figure 8). Successive weighting of characters failed to improve resolution in this group.

A branch-and-bound analysis treating seven diagnosably distinct groups within the *G. philippensis*-group (Appendix C) identified *G.* (*p.*) *philippensis* and *G.* (*p.*) *macquariensis* as basal branches in all 12 shortest trees; the remaining five members were sequenced as *G.* (*p.*) *assimilis*, *G.* (*p.*) *christophori*, *G.* (*p.*) *sethsmithi*, *G.* (*p.*) *goodsoni* and *G.* (*p.*) *ecaudatus* in a majority of the solution set (figure 9). A similar assessment of the eight shortest trees for three diagnosable subgroups of '*G.*' *torquatus* and closest relatives indicated that the '*G.*' *torquatus* complex may be paraphyletic to flightless '*Gallirallus*' *okinawae* (figure 10). Successive weighting of characters failed to improve resolution in either of these groups.

The third component of the terminal trichotomy in the strict consensus of shortest trees comprised the crakes, moorhens and coots (figure 4). The 'crakes' are a polyphyletic assemblage of comparatively small, short-billed rallines coloured in varying proportions of chestnut, yellow, white, grey and black; this diverse group of taxa may be diagnosed best as comparatively short-billed rails lacking the significant specializations for aquatic habits characteristic of *Amaurornis*, *Gallinula* and allies and *Fulica*. A number of flightless species are included among the genera of 'crakes', and at least one of the several included genera appears to be polyphyletic. Unique *Atlantisia rogersi* was placed as the first branch of this large clade (figure 4), indicative of the combination of comparatively primitive '*Rallus*-like' characters and derived characters shared with 'crakes' shown by this taxon. Successive weighting, however, placed *Atlantisia* as the sister group of *Laterallus*.

The next node in this large, diverse clade represents the divergence of a small distinctive subgroup of blackish *Laterallus* (*L. jamaicensis*-group and *L. spilonotus*) from other *Laterallus* and the remaining rallid genera (figure 4). One of the few losses in resolution resulting from exclusion of selected flightlessness-related characters was the node supporting monophyly of *Laterallus*, an effect notable because the genus includes no flightless members. The sample of shortest trees revealed only three unanimously supported subgroups among the remaining members of *Laterallus*, which were included with the remaining taxa of crakes, moorhens and coots in a polytomy: *L. fasciatus* as a separate lineage; a trichotomy comprising *L. viridis*, *L. ruber* and *L. levraudi*; and a totipectinate, six-taxon clade comprising (in order of increasingly close relationship) *L. melanophaius*, *L. cinereiceps*, *L. albigularis*, *L. exilis*, *L. leucopyrrhus* and *L. xenopterus* (figure 4). Successive weighting for all Grues confirmed monophyly of *Laterallus*, but indicated several marginally

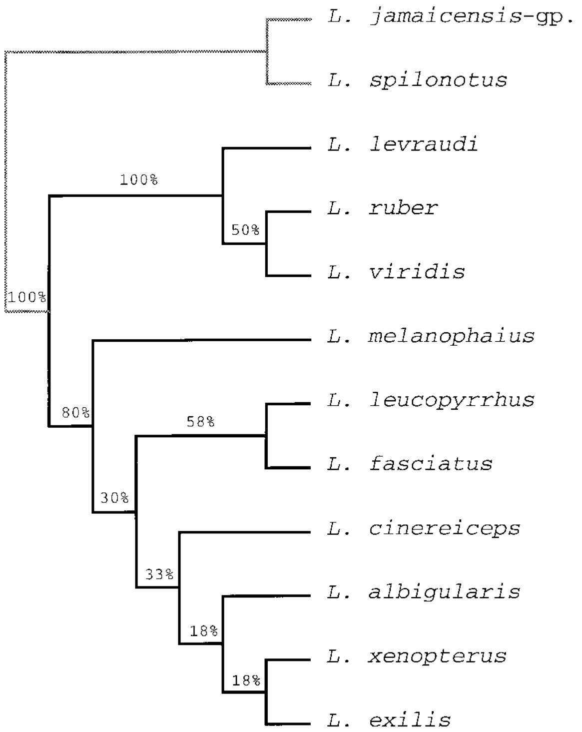

Figure 11. Majority-rule consensus tree for the 40 shortest trees recovered in a branch-and-bound analysis for the primary clade of *Laterallus*. Trees were rooted using congeneric sister groups, *L. spilonotus* and *L. jamaicensis*-group; percentages are given for nodes conserved in the majority of the solution set and nodes compatible with the majority-rule nodes. See table 1 and Appendix C for details concerning delimitation of terminal taxa.

supported groupings within *Laterallus* which differed from those found under equal weighting. A majority-rule consensus tree of the 40 shortest trees for *Laterallus* recovered in a taxonomically restricted, branch-and-bound analysis indicated the monophyly of the genus (exclusive of the rooting *L. jamaicensis*-group and *L. spilonotus*), and indicated several other subgroups within the genus which were shared by or compatible with a majority of the shortest trees (figure 11). Successive weighting of characters in the single-genus analysis failed to improve resolution within *Laterallus*, but confirmed a close relationship among *L. viridis*, *L. ruber* and *L. levraudi*.

The basal grade of remaining rallids—those comprising *Porzana*, *Coturnicops*, *Micropygia* and *Crex*, and paraphyletic to waterhens (*Amaurornis*), moorhens (*Gallinula* and allies) and coots (*Fulica*)—present the most challenging inferences to reconcile with existing generic taxonomy in the Rallidae (figure 4). Apparent polyphyly of *Porzana* and closely related taxa is the primary source of these difficulties, and species assigned to *Porzana* fell into two broad topological groups: 15 species, some of which are considered by some authorities to be generically distinct (e.g. *Poliolimnas*, *Aenigmatolimnas*, *Porzanula* and *Crecopsis*), that were interposed among several other small, but widely accepted genera (*Coturnicops*, *Micropygia* and *Crex*); and seven other species or species groups (including taxa assigned by some to the genera *Neocrex*, *Limnocorax* or included in *Amaurornis*) which are paraphyletic to the waterhens, moorhens and coots (figure 4).

In the analysis based on equal weighting of characters, the large, first group of '*Porzana*' consists of a poorly resolved, basal grade of three chestnut, comparatively '*Laterallus*-like' forms (*P. sandwichensis*, *P. fusca* and *P. paykullii*), followed by (in order of increasingly close relationship) *Coturnicops*; highly autapomorphic *Micropygia* and sister group *Porzana flaviventer*; sister species *P.* ('*Poliolimnas*') *cinerea* and *P.* ('*Aenigmatolimnas*') *marginalis*; and a ten-branch terminal clade of 'olive' crakes including as deeply nested members *P.* ('*Crecopsis*') *egregia* and the monotypic genus *Crex* (figure 4). Two iterations of successive weighting indicated a sister relationship between *P. fusca* and *P. paykullii*.

The smaller group of '*Porzana*' comprise seven species of largely 'blackish' crakes which are weakly supported as paraphyletic to *Amaurornis*, *Gallinula* and allies, and *Fulica* (figure 4). This grade comprises, in order of increasingly close relationship to the latter genera: *P. tabuensis* (intermediate between the 'olive' crakes and the following 'blackish' forms), *P. monasa*, *P. atra*, *P. flavirostra*, *P. olivieri* and a sister lineage of *P. bicolor* and the *P.* ('*Neocrex*') *erythrops*-group. Two iterations of successive weighting indicated the monophyly of the 'blackish' crakes, while maintaining their placement as more closely related to the moorhens and allies than to other *Porzana*, and grouped *P. flavirostra*, *P. atra* and *P. monasa* as especially closely related.

The waterhens (*Amaurornis*), a group of comparatively large, 'crake-like' rallids considered by some to include also several species of '*Porzana*' (Olson 1973*a*; Ripley 1977; Sibley & Monroe 1990; Taylor 1996), were placed as closely related to the moorhens and coots (figure 4). The genus, as constituted here, was supported as monophyletic under equal weighting of characters, and comprised five species or species-groups (in order of increasingly close relationship): *A. olivaceus*-group, *A. phoenicurus*, *A. akool* and the sister species *A. isabellinus* and flightless *A.* ('*Megacrex*') *ineptus* (figure 4). Successive weighting of characters, however, rendered *Amaurornis* paraphyletic to the moorhens and coots, wherein *A. ineptus* was segregated from its congeners; also, the nested relationships among the latter were reversed.

Moorhens and allies, long considered to comprise a natural group closely related to the coots (*Fulica*), have been assigned to at least seven genera (Peters 1934; Olson 1973*a*, 1975*a*,*b*,*d*); most recent classifications recognized only two or three genera (e.g. Olson 1973*a*; Ripley 1977; Taylor 1996). The present analysis placed two South Pacific forms—*Pareudiastes pacificus* and *Edithornis silvestris*—as sister species comprising the basal branch of four in the assemblage (figure 4). This basal group is followed by two pairs of taxa (figure 4)—*Gallicrex cinerea* and *Porphyriops melanops*, and two species of *Tribonyx*—included in a trichotomy with the terminal clade comprising the typical moorhens (comprising *Porphyriornis* and *Gallinula sensu stricto*) and *Fulica*. *Gallinula* was resolved sequentially as *G. tenebrosa*, *G. angulata* and the *G. chloropus*-group (figure 4). Successive weighting produced a similar consensus tree, but interposed the clade comprising *Pareudiastes* and *Edithornis* and that for *Tribonyx* as a grade between *Gallicrex* and *Porphyriops*. A majority-rule consensus tree for all 18 shortest trees for the moorhens and coots based on a branch-and-bound analysis confirmed most placements (including all nodes within *Amaurornis* and *Fulica*), but favoured the placement of the

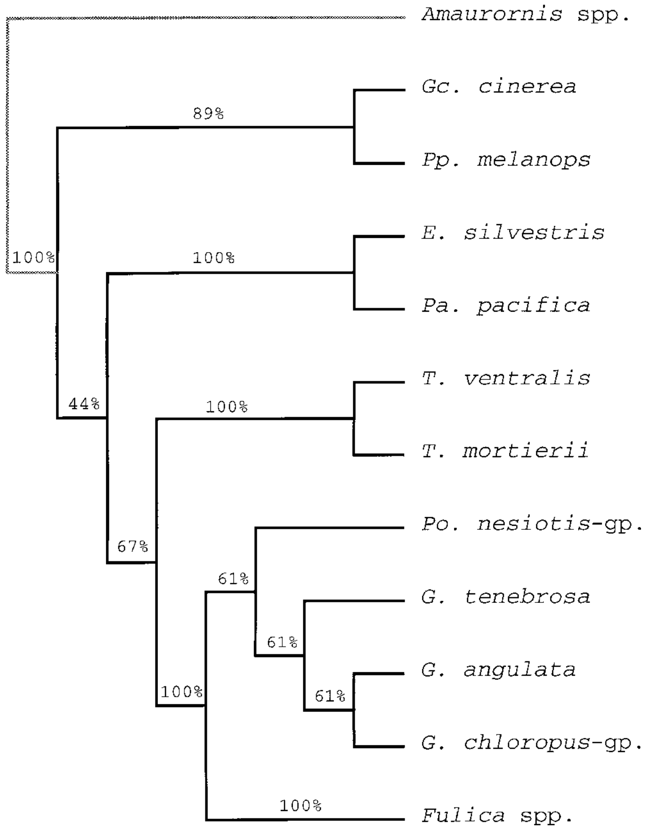

Figure 12. Majority-rule consensus tree for the 18 shortest trees recovered in a branch-and-bound analysis for the moorhens and coots. Trees were rooted using the six taxa of *Amaurornis* as monophyletic outgroup; percentages are given for nodes conserved in the majority of the solution set and nodes compatible with the majority-rule nodes. See table 1 and Appendix C for details concerning delimitation of terminal taxa.

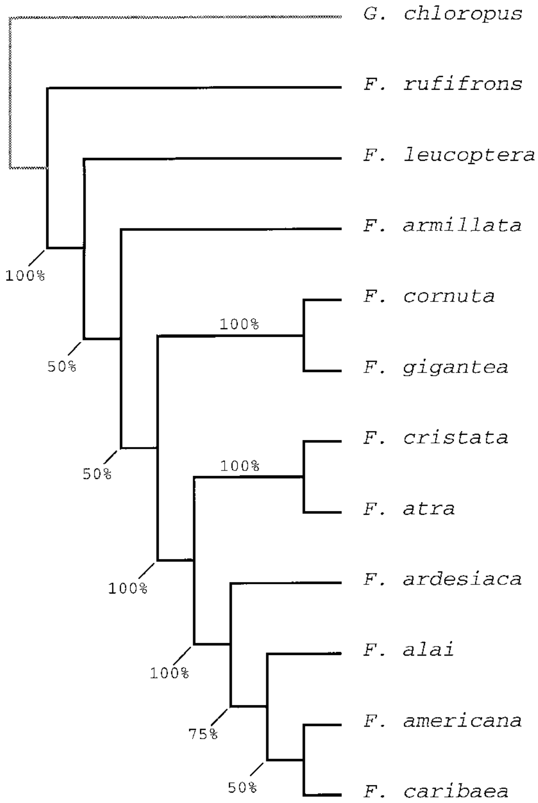

Figure 13. Majority-rule consensus tree for the eight shortest trees recovered in a branch-and-bound analysis for *Fulica*. Trees were rooted using *Gallinula chloropus*; percentages are given for nodes conserved in the majority of the solution set and nodes compatible with the majority-rule nodes. See table 1 and Appendix C for details concerning delimitation of terminal taxa.

clade comprising *Gallicrex* and *Porphyriops* as basal to that comprising *Pareudiastes* and *Edithornis* (figure 12). A further branch-and-bound analysis in which the several allospecies within the *Gallinula chloropus*-group were distinguished revealed that all dichotomous arrangements were equally frequent in the total solution set.

Fulica rufifrons was placed as the basal-most member of the coots (figure 4). The remaining species comprised two major groups: two large, Andean endemics as sister species (*F. cornuta* and *F. gigantea*); and a clade comprising five lineages. The last group comprised a basal pair of neotropical species (*F. armillata* and *F. leucoptera*) and clade in which the *F. americana*-group subtends the sister species *F. atra* and *F. cristata* (figure 4). A majority-rule consensus tree for the eight shortest trees from a branch-and-bound analysis (including a finely partitioned *F. americana*-group) indicated that *F. leucoptera* and *F. armillata* may be paraphyletic to the remaining species (an arrangement also favoured under successive weighting), and revealed that the most frequent reconstruction within the *F. americana*-group placed *F.* (*am.*) *ardesiaca* as the sister group of *F.* (*am.*) *alai* and the sister species of *F.* (*am.*) *americana* and *F.* (*am.*) *caribaea* (figure 13).

(iii) *Assessments of support*

Nodes establishing interfamilial relationships and the basal bifurcation within the Gruidae were well supported (figure 2); lesser but significant evidence supported terminal, intergeneric nodes within the Gruidae, whereas most other nodes within the family were only weakly supported (figure 5). Relationships among the three genera of Heliornithidae remain unresolved (figure 2). Diagnostic synapomorphies for well supported nodes are given in table 3.

Within the Rallidae, nodes supporting monophyly of the Rallidae, rallids exclusive of *Himantornis*, the swamphens (*Porphyrio* and *Porphyrula*) and the sister group relationship between *Canirallus* and *Mentocrex* were strongly supported (figure 2). Moderately robust nodes delimited the rallids exclusive of *Himantornis* and the swamphens, the clade comprising the flufftails and allies (*Rallina*, *Rallicula* and *Sarothrura*), the clade comprising *Rallicula* and *Sarothrura*, supported monophyly of the genera *Porphyrio*, *Gymnocrex*, *Aramides*, *Sarothrura*, *Amaurornis* and *Fulica*, and a number of couplets of taxa within *Porzana*, the gallinules and the coots (figures 2–4).

A number of other nodes were robust to bootstrapping but had support indices of lesser magnitude; these marginally robust nodes include those supporting the genus *Porphyrula*, two couplets within '*Gallirallus*', and several nodes within *Rallina*, *Rallicula*, *Sarothrura*, *Porzana* and *Amaurornis* (figures 2–4). Nodes conserved in all shortest trees sampled but not robust to bootstrapping were found to have support (Bremer) indices of one, a pattern mirrored by the genus-level analysis of the Gruiformes (figure 1).

Table 3. *Branch-length ranges and diagnostic apomorphies* (*i.e. those having* CI = 1.0) *for selected robust nodes in phylogenetic tree of species of Grues* (*figures 2–4*)

(See Appendices A and B for character descriptions, and Appendix C for delimitation of taxonomic groups. Apomorphies shown in boldface were also diagnostic in ordinal analysis (figure 1).)

taxonomic group(s)	branch-length range	diagnostic apomorphies
Grues	7–23	98b, **184b**
Gruoidea	13–24	32c, 89b, 111b, 115b, 134b, **137b**, 202b, **242b**, **272b**, **321b**
Psophiidae	27–45	**27b**, **90b**, **130b**, 205b, **221b**, **229c**, **238b**, **244b**, 248b, **291b**, **309b**, 361b, **378b**, **475b**
Aramidae and Gruidae	24–40	33b, 43b, 87b, 140b, **141b**, **156b**, **171b**, **178b**, 185b, **187b**, 196b, 198b, **210b**, **211b**, **223b**, 237b, **257b**, 267b, **324b**, 533b
Aramidae	4–12	**101b**, 538b
Gruidae	12–21	**59b**, **155b**, **224b**, **234b**, **325b**, **341b**, 476b, 533c
Balearicinae	12–17	**68b**, 407b, 454b, 464b, 466b, 532b, 548b, 560b
Gruinae	12–18	**28b**, **102b**, **158b**, **168b**, **172b**, **174b**, **190b**, 196c
Ralloidea	24–44	9a, 104a, 107a, 125c, 132a, 153b, 201a, **215b**, 218a, 222b, **236b**, **238c**, **244c**, 249b, **253b**, **254b**, **273b**, 308b, **327b**, **354b**
Heliornithidae	32–48	**160b**, **183b**, 218c, **260b**, **276b**, 278a, 283b, 284b, **290b**, 294b, **296b**, **306b**, **315b**, **334b**, **350b**, 421b, 444b, 520b, 529b, 565b
Rallidae	15–23	62b, 194b, 286b, **293b**, **301b**, **336b**, 345b
Rallinae	9–19	17b, **117b**, 167b, 373b, 559b
Porphyriornithini	28–37	2b, **60b**, **331b**, 333b, 342b, **347b**, **356b**, **369c**, 420b, 472b, 488c, 511b, 540b, 549b
Sarothrura	8–9	485c, 510b
Fulica	17–21	97b, **124b**, 125d, **216b**, 274c, **298b**, **311b**, **343b**, **364b**, **367b**, **369d**, 567b

Table 4. *Positions of subfossil Rallidae in strict and majority-rule consensus trees, based on individual analyses in which strict consensus tree for modern taxa was used as a backbone constraint*

(See table 1 for taxa included in species groups.)

subfossil taxon	position in strict consensus tree with that for modern taxa as backbone constraint
Porphyrio kukwiedei	sister group of *Porphyrio hochstetteri*
Porphyrio mantelli	sister group of *Porphyrio hochstetteri*
Aphanocrex podarces	sister group of clade comprising *Porphyrula* and *Porphyrio*
Hovacrex roberti	included within polytomy comprising rallids exclusive of *Himantornis*, *Porphyrio* and *Porphyrula*
Nesotrochis debooyi	sister group of *Canirallus* (including *Mentocrex*)
Nesotrochis steganinos	included within polytomy of rallids exclusive of *Himantornis*
Rallus Bermuda-group	included within polytomy comprising *Rallus* and *Gallirallus* (*sensu lato*)
Capellirallus karamu	sister group of *Cabalus modestus*
Aphanapteryx bonasia	sister group of *Cabalus modestus*
Aphanapteryx leguati	sister group of *Cabalus modestus*
Diaphorapteryx hawkinsi	sister group of *Cabalus modestus*
'*Atlantisia*' *elpenor*	included within Rallidae exclusive of *Himantornis*, *Porphyrio*, *Porphyrula*, *Gymnocrex*, *Habroptila*, *Eulabeornis*, *Aramides*, *Canirallus* (including *Mentocrex*) and *Anurolimnas*
Porzana Bermuda-group	included within polytomy comprising the crakes, moorhens, coots, and allied genera, exclusive of *Atlantisia*, some *Porzana*, and some *Laterallus*
Porzana astrictocarpus	Iincluded within polytomy comprising the crakes, moorhens, coots and allied genera, exclusive of *Atlantisia*
Porzana Hawaii-group	included within polytomy comprising the crakes, moorhens, coots and allied genera, exclusive of *Atlantisia* and *Laterallus*
Tribonyx hodgenorum	included within polytomy comprising *Tribonyx*, *Pareudiastes*, *Edithornis*, *Porphyriornis*, *Gallinula* and *Fulica*
Fulica newtonii	included within *Fulica* exclusive of *F. rufifrons*
Fulica chathamensis-group	included within *Fulica* exclusive of *F. rufifrons*

(iv) *Placements of fossil taxa*

Rallidae known only from subfossil skeletal elements were placed individually using heuristic searches in which the strict consensus tree for modern taxa (figures 2–4) was used as a backbone constraint tree. Exclusion of flightlessness-related characters was considered especially critical in analyses of these extinct species because most or all were obviously flightless and, in combination with the numerous missing data for these taxa, the resultant placements were liable to be affected disproportionately by skeletal homoplasy of this kind. Provisional placements of subfossil taxa, some of which were merged for analysis (table 1), were summarized by positions in strict consensus trees of the solution sets (table 4). Although some of these extinct taxa are so synapomorphically distinctive and adequately represented to permit confident assignments to modern genera (*Porphyrio kukwiedei*, *P.* (*m.*) *mantelli*, *Tribonyx hodgenorum*, *Fulica chathamensis*-group and *Fulica newtonii*), a number either only could be placed within broad suprageneric groups (e.g. *Hovacrex roberti*, *Nesotrochis debooyi*, *N. steganinos*, extinct Bermuda *Rallus*, '*Atlantisia*' *elpenor*, *Porzana astrictocarpus*, extinct Bermuda *Porzana* and extinct Hawaiian *Porzana*). Other subfossil forms (*Capellirallus karamu*, *Aphanapteryx bonasia*, *A. leguati* and *Diaphorapteryx hawkinsi*), some of which are among the most unusual osteologically in the Rallidae, were placed with other flightless genera, a pattern indicated in the analysis of gruiform genera (figure 1). Although the position of *Capellirallus* with *Cabalus* was supported by several characters and those of all four included characters not obviously associated with flightlessness, the potential for homoplasy related to large body size and flightlessness (see below) renders these associations tentative.

4. DISCUSSION

(a) *Phylogenetic inferences and support*

(i) *Well-supported groups*

Given the paucity of comparable phylogenetic reconstructions, most aspects of the present analysis are amenable only to internal assessments of support. Fortunately, many groupings were based on substantial evidence, including those establishing relationships among most gruiform families and those confirming monophyly and basal-most bifurcations of all families (figures 1–4). Particularly noteworthy is the overwhelming evidence in support of close relationships between the following groups: modern Cariamidae and fossil phorusrhacoids; *Eurypyga* and the clade comprising *Rhynochetos* and *Aptornis*; *Aramus* and the Gruidae; and the Heliornithidae and Rallidae (figure 1). Other strongly supported nodes include those uniting (figures 1–4) gruiforms exclusive of *Pedionomus* and the Turnicidae; Gruidae exclusive of *Balearica*; Rallidae; Rallidae exclusive of *Himantornis*; *Porphyrio* and *Porphyrula*; *Canirallus* and *Mentocrex*; *Rallina*, *Rallicula* and *Sarothrura*; and the eight species of *Sarothrura*.

(ii) *Moderately supported inferences*

Most other groupings of non-rallid genera were supported by less, but nonetheless significant character evidence (figures 1 and 5). This intermediate level of support includes nodes uniting *Pedionomus* as the sister group of the Turnicidae and two nodes delimiting fundamental subgroups of gruiform families (figure 1). Within the Rallidae, comparable support was marshalled to unite the following modern taxa: *Gymnocrex*; *Aramides*; '*Gallirallus*' *okinawae* and the '*G.*' *torquatus*-group; several subgroups within the genera *Sarothrura*, *Porzana* and *Fulica*; *Coturnicops*; *Amaurornis*; and *Fulica* (figures 2–4). Although not strictly comparable to nodes in the unconstrained analyses of modern taxa, the placements of many of the subfossil taxa were supported by moderately strong evidence (e.g. those in the *Porphyrio* complex or in *Fulica*). Although consensus placements of many of the other subfossil taxa were at disappointingly high taxonomic levels (e.g. Bermuda *Rallus* and '*Atlantisia*' *elpenor*) or possibly compromised by homoplasy related to flightlessness (e.g. *Aphanapteryx* and *Diaphorapteryx*), some of these also were supported by moderately high levels of empirical evidence (table 4).

(iii) *Weakly supported groups and unresolved relationships*

Unfortunately, marginally supported nodes include one suggestive of paraphyly of the Charadriiformes; that justifying the membership of the clade comprising the Pedionomidae and Turnicidae among the Gruiformes; and one germane to the position of the Otididae with respect to the other major subgroups of the order (figure 1). Most nodes within the Rallidae were only marginally supported; many nodes in the sample of shortest trees (those for which support statistics were not given in figures 2–4) were favoured by only a single step in total tree length. Some polytomies in the strict consensus tree of shortest trees were shown to be resolved most frequently in specific topologies by narrower, exhaustive searches (figures 5–12) and favoured by successive weighting of characters.

(b) *Flightlessness-related homoplasy*

Special treatment of several characters known *a priori* to be related to flightlessness did not correct completely the analytical effects of such homoplasy in that several other characters (e.g. skeletal character 152 and integumentary character 519) also showing significant correlation with flightlessness in rallids were retained because these also showed important variation among higher-level taxa in the family. Consequently, residual concern attends groupings of flightless rallids that hinged, at least in part, on characters showing indications of such homoplasy. Groupings which fall under this suspicion (figures 2–4) include several modern taxa (e.g. some subgroups within *Gallirallus*, and the alliance among *Tricholimnas*, *Nesoclopeus*, *Cabalus*, *Habropteryx*, and '*Gallirallus*' *torquatus* and allies) as well as the association among 'aberrant', subfossil forms (*Diaphorapteryx* and *Aphanapteryx*). However, several genera (*Porzana*, *Amaurornis* and the moorhens) having more than one flightless member showed negligible tendencies to cluster included flightless forms (figure 4), and several monotypic flightless genera (*Habroptila*, *Cyanolimnas* and *Atlantisia*) were allied most closely with flighted lineages (figures 2–4). Finally, several groupings of flightless taxa (*Notornis* complex with *Porphyrio*; *Capellirallus* and *Cabalus*) appear to have been based on a sufficient diversity of characters as to preclude relegation to mere artefacts of independently derived flightlessness.

(c) *Comparison with previous assessments*

This study provides modest support for the return of the Pedionomidae to its traditional association with the Turnicidae, and weak support for the inclusion of both families among the Gruiformes (figure 1), as advocated by Peters (1934). These inferences suggest that the similiarities among the Turnicidae, Pedionomidae and Charadriiformes cited by Olson & Steadman (1981) are symplesiomorphic and that the differences between the

Turnicidae and Pedionomidae largely reflect uninformative autapomorphy. Inclusion of the Otididae and Mesitornithidae as basal members of the Gruiformes is supported strongly by this analysis; the former contradicts the reassignment of the Otididae to the Charadriiformes advocated by Olson (1985). A close relationship between *Eurypyga* and *Rhynochetos*, first proposed by Bartlett (1862), is also supported by this assessment. The position of *Aptornis* inferred here agrees with that suggested by Olson (1975*a*, 1985) and Cracraft (1980), but opposes an alliance with the Rallidae (Oliver 1945; Houde *et al.* 1997) and strongly contradicts the suggestion of anseriform affinities by Hesse (1990) and Weber & Hesse (1995). The present study also supports the widely accepted alliance between the fossil phorusrhacids and modern Cariamidae (Sinclair & Farr 1932; Cracraft 1968*a*, 1971, 1973*a*; Mourer-Chauviré 1981, 1982, 1983; Peters 1987, 1991). This analysis argues against a close relationship between the Cariamidae and Psophiidae (Cracraft 1968*a*, 1982), and suggests that similarities between these two families are probably symplesiomorphic.

Placement of *Aramus* as the sister group of the Gruidae in the present study reflects the essential accuracy of the grouping advocated by Verheyen (1957*b*) and the conclusion by Olson (1985, p. 164) that '. . . the Aramidae are no more than a subgroup of the Gruidae'. Findings of the present work show considerable concordance with a recent molecular analyses of the Gruidae (Krajewski 1989*b*, 1990; Krajewski & Wood 1995; Krajewski & King 1996); in the latter studies, however, positions of *Anthropoides* and *Bugeranus* rendered *Grus* polyphyletic, an inference at odds with the present assessment (figure 5). The present study failed to confirm the inference by Ingold *et al.* (1989) that *L. leucogeranus* is especially closely related to *Grus americana* (figure 5). Also, the present study does not support unequivocally the subfamilial segregation of *Podica* and *Heliopais* advocated by Brooke (1984), in that the ordinal analysis suggested that these genera were paraphyletic to *Heliornis* (figure 1) and relationships among the three genera of Heliornithidae were unresolved in the subordinal analysis (figure 2).

The groupings among gruiforms depicted by Sibley & Ahlquist (1990, fig. 363) contrast with those inferred herein (figures 1–4). Furthermore, there are important discrepancies between the groupings depicted by Sibley & Ahlquist (1990) and the classification proposed by Sibley & Monroe (1990), and the empirical basis for the latter remains unclear; therefore the classification by Sibley & Monroe (1990) is excluded from further discussion here. With the exception of the familial integrity of bustards, cranes and rails, a basal bifurcation within cranes, and the lower-order groupings of *Porphyrio* and *Porphyrula* and the clade comprising *Gallicrex*, *Gallinula* and *Fulica*, the differences between the analysis by Sibley & Ahlquist (1990) and the present work are complete. Higher-order points of disagreement between the two studies are numerous, as reflected by the following conclusions by Sibley & Ahlquist (1990, fig. 363): position of the Turnicidae as unresolved within Aves; *Pedionomus* as the sister group of seedsnipe (Charadriiformes: Thinocoridae); *Eurypyga* as the sister group of all other non-rallid genera of Gruiformes sampled and only distantly related to *Rhynochetos*; and *Aramus* as the sister group of *Heliornis*.

The subsequent reassessment by Sibley *et al.* (1993) permitted few firm conclusions, but the authors recommended the following departures from the earlier study based on DNA hybridization, both of which represented moves toward consensus with the present study: the sample previously labelled as *Heliornis* was considered of uncertain identity and excluded from further consideration, a decision supported by Houde (1994); and *Psophia* was judged to be the sister group of *Aramus* and *Grus*. However, the reanalysis by Sibley *et al.* (1993) maintained the uncertain and basal position of *Turnix*, repeated the proposed alliance between *Pedionomus* and *Thinocorus*, precluded comparisons of groupings within the Rallidae through the elimination of all rallid genera except *Porphyrio* and *Fulica* from analysis, and recommended no modifications of the companion classification by Sibley & Monroe (1990). Finally, Houde *et al.* (1995) performed a reanalysis using DNA hybridization and concluded that the Heliornithidae are monophyletic and that *Heliopais* and *Heliornis* are sister genera.

The recent phylogenetic analysis of 17 genera of Gruiformes using sequence data by Houde *et al.* (1997) proved challenging to compare with the present study for several reasons: *Gallus* was used to root trees because attempts to use charadriiform taxa as outgroups rendered the gruiform taxa polyphyletic; *Pedionomus* was excluded *a priori* from analysis; sampling of the Rallidae was limited to single representatives of *Rallus*, *Laterallus* and *Gallinula*; alignments of sequences and associated reconstructions were based in part by the recovery of selected groups considered *a priori* to be valid, a process admitted (p. 133) to be circular; at least 7 out of 17 nodes in the preferred tree (fig. 5.6) were not robust to bootstrapping; and standard summary statistics (e.g. CI and total length) were not given for most trees depicted. Nevertheless, Houde *et al.* (1997) found three robust groups common to all analytical variants presented, all of which were consistent with clades recovered in the present study: *Eurypyga* and *Rhynochetos*; Gruidae exclusive of *Balearica*; and *Heliornis* and *Podica*. Houde *et al.* (1997) also included the Psophiidae, Aramidae, Gruidae, Heliornithidae and Rallidae in a single clade in most reconstructions and consistently included *Turnix* among the Gruiformes sampled; however, topological positions of *Turnix*, *Ardeotis* (Otididae), *Mesitornis*, *Cariama* and *Psophia* were affected significantly by the methods employed.

Perhaps the most marked point of disagreement between the study by Houde *et al.* (1997) and the present analysis involved the position of *Aptornis* relative to the clade comprising *Rhynochetos* and *Eurypyga*, genera inferred herein to be closely related (figure 1). Houde et al. (1997) placed the former as the sister group of the Rallidae and the latter as the sister group of all other Gruiformes sampled, although the empirical basis for this inference may have been compromised by substantially incomplete sequences for *Aptornis* and *Rhynochetos* (missing 23% and 55% of domains analysed, respectively; p. 128). Using the present data set, positioning *Aptornis* as sister group of the Rallidae alone added 40 steps to minimal tree length, almost a 5% increase in length (excluding uniformative characters); if four flightlessness-related characters are excluded, 38 additional steps were required (4% increase in tree length). Alternatively, substitution of the topology of *Aptornis*, *Rhynochetos* and *Eurypgya* inferred in the present study (figure 1) using the matrix of Houde *et al.* (1997) entailed an approximate increase in total tree length of 2% (P. Houde, personal communication).

A basal position for *Himantornis* among the Rallidae inferred herein agrees with several classifications (Verheyen 1957*a*,*b*; Wolters 1975; Ripley 1977; Taylor 1996) and the anatomical assessment by Olson (1973*a*). At least two other broad groups recognized by Verheyen (1957*a*,*b*) were confirmed here: the higher-order divergence of *Porphyrio* and allies; and that of *Sarothrura*. The classic work by Peters (1934) also included several groupings (some only implied by adjacency in the generic sequence) corroborated here, including an alliance between *Canirallus* and *Mentocrex*, genera merged even earlier by Sharpe (1894). The relationships among species of *Sarothrura* inferred here correspond remarkably well with an intuitive tree presented by Keith *et al.* (1970, fig. 15) in which a '*pulchra* group' (*S. pulchra* and *S. elegans*) was depicted as distinct from other members, the latter being subdivided into an '*ayresi* group' (*S. ayresi* and *S. watersi*), '*affinis* group' (*S. affinis* and *S. insularis*) and '*rufa* group' (*S. rufa*, *S. boehmi* and *S. lugens*).

A number of taxonomic groupings suggested by Olson (1973*a*) also received support from the present study, including the basal divergence of *Canirallus* and *Mentocrex*; an alliance among *Rallina*, *Rallicula* and *Sarothrura*; possible polyphyly of *Laterallus* and *Porzana*; a close relationship between *Habropteryx insignis* and '*Gallirallus*' *torquatus*, first suggested by Sclater (1880); and the possibility of an especially close relationship between *Amaurornis ineptus* and *A. isabellinus*. Also striking is the confirmation in the present analysis of the monophyly of four of five members of a subgroup of *Porzana* (*pusilla*, *carolina*, *porzana* and *fluminea*) delimited by Olson (1973*a*, p. 404) and implied in the sequence proposed by Peters (1934). The inference of *Pareudiastes* and *Edithornis* as sister groups among other moorhens (figures 4 and 12) also was foreseen by Olson (1975*d*). However, several other phylogenetic relationships depicted by Olson (1973*a*, fig. 7) contrast with those inferred here; some seem at odds with his own narrative, underscoring the challenges of interpretation of such informal diagrams. Points of disagreement include placements of *Canirallus* (including *Mentocrex*), *Amaurolimnas*, *Eulabeornis*, *Anurolimnas*, *Sarothrura*, *Porphyrio*, *Habroptila* and *Amaurornis ineptus*. The present study also provides no support for the following proposals: referral of *Porzana flavirostra* and *P. olivieri* to *Amaurornis* (Olson 1973*a*); an especially close relationship between *Porzana flaviventer* and *P. cinereus* (Olson 1970, 1973*a*); or a close relationship of *Atlantisia* to *Rallus* (Olson 1973*a*,*b*). This analysis indicates a closer relationship between *Atlantisia* and the crakes, with weak evidence from successive weighting that the most likely sister group of the genus is *Laterallus*.

Olson (1973*b*) referred subfossil *Aphanocrex podarces* to the modern genus *Atlantisia*, and described in the same genus the subfossil species *elpenor*. The present study, however, indicates that *Aphanocrex* is closely related to (if not synonymous with) *Porphyrula*, and the intrafamilial relationships of '*Atlantisia*' *elpenor*, like those of most rallids known only from subfossil elements, remain only broadly demonstrable on the basis of available evidence (table 4). These classifications by Olson (1973*b*) seem to have been based, at least in part, on geographical considerations and underscore the importance of the comparative approach (Cracraft 1974*a*) and the fundamental differences between the 'intuitive' and phylogenetic paradigms (Livezey 1997*b*). However, inferences by Olson (1975*a*,*b*) concerning the generic affinities of subfossil *Gallirallus*, *Tribonyx*, *Gallinula* and *Fulica* from Australasia were consistent with inferences presented here. Also, given the uniquely derived skeletons of *Diaphorapteryx* and *Capellirallus* and persistent uncertainties regarding the effects of flightlessness-related homoplasy, differences in inferred positions of these taxa proposed by Olson (1975*a*,*b*) and the present analysis are not surprising. Similar considerations attend the retention of *Aphanapteryx bonasia* and '*A.*' *leguati* as congeners by Olson (1977), a decision evidently also influenced by geographical distributions of the two taxa.

The present study contradicts a number of other generic allocations proposed by Ripley (1977), including merging *Gymnocrex*, *Amaurolimnas* and *Aramides* with *Eulabeornis*; merging *Dryolimnas* with *Canirallus* (including *Mentocrex*); inclusion of *Habroptila*, *Pardirallus*, *Ortygonax*, *Tricholimnas*, *Aramidopsis*, *Nesoclopeus*, *Habropteryx* and '*Hypotaenidia*' within *Rallus*, while retaining *Gallirallus* solely for the *australis* complex; treatment of *Gallirallus dieffenbachii* as a subspecies within the already unwieldy '*Rallus*' *philippensis* complex; merging *Rallicula*, '*Porzana*' *paykullii* and (especially) *Anurolimnas* with (paraphyletic) *Rallina*; merging of *Sarothrura* with *Coturnicops* and *Micropygia*, begun in part by Peters (1934); and inclusion of *Porphyrula* in *Gallinula*.

There is poor correspondence between the phenetic subgroups of *Laterallus* proposed by Storer (1981) and the groups indicated by this analysis (figure 11), but the genus may be paraphyletic and support for included nodes is marginal at best. Based on external similarities, Benson & Winterbottom (1968) suggested that *P.* (*Crecopsis*) *egregia* and *P. albicollis* are sister groups. Using similar comparative arguments, Benson & Wagstaffe (1972) suggested that *Porzana olivieri* and *P.* (*Limnocorax*) *flavirostra* were sister species, a proposal with which Olson (1973*a*) only partly concurred. The hypothesis presented here (figure 4) indicates that the latter proposal reflects symplesiomorphy between adjacent members of a grade, whereas the former proposal is supported by synapomorphy.

Fjeldså (1985, fig. 9) presented an intuitive tree of relationships for *Fulica*, based in part on the inference by Ridgway & Friedmann (1941) that *F. rufifrons* was intermediate between gallinules and coots. Inferences made herein for the genus (figures 4 and 13) differ from the hypothesis of Fjeldså (1985), with the exception of the sister relationship between *F. cornuta* and *F. gigantea*, monophyly of the *F. americana*-group exclusive of *F.* (*am.*) *ardesiaca*, and a sister relationship between *F. atra* and *F. cristata*.

Sibley & Ahlquist (1990, fig. 363) arrived at a number of inferences for the Rallidae which differ from those proposed herein, including *Rallus* and *Gallirallus* as paraphyletic to other rails sampled; and *Porphyrio* and *Porphyrula* as comparatively deeply nested within the

Rallidae. One notable point of concurrence between the two analyses was the placement of the swamphens (*Porphyrio* and *Porphyrula*) and coots (*Fulica*) as only distantly related within the Rallidae, a departure from a long-standing taxonomic tradition (Sharpe 1894; Peters 1934; Ripley 1977; Taylor 1996). In the only other molecular study involving more than three species of Rallidae, Trewick (1997) marshalled variable support for grouping *Porphyrula* with *Porphyrio*, *Rallus* with *Gallirallus*, and *Gallinula* with *Fulica*, while positions inferred for several other genera (*Eulabeornis*, *Anurolimnas*, *Porzana* and *Amaurornis*) varied significantly with the combinations of analytical methods employed. Although possibly an artefact of flightlessness-related homoplasy, the present analysis offers no support for the morphometric hypothesis of Trewick (1996) that the several flightless forms of *Porphyrio* from the New Zealand region ('*Notornis*') are polyphyletic (table 4).

(d) *Summary trees and classification*

The foregoing analyses were used as the basis for a phylogenetic classification (Appendix C). In light of the modest support for inclusion of the Pedionomidae and Turnicidae among the Gruiformes, an alternative would be to classify these two families within a separate order Turniciformes, sequenced between the orders Charadriiformes and Gruiformes, perhaps under a common superorder Charadriimorphae. The recent DNA-based study by Houde *et al.* (1997), however, supported the inclusion of *Turnix* among the Gruiformes; unfortunately, *Pedionomus* was not included in that analysis.

Notable aspects in the proposed classification of the Rallidae that differ from conventional schemes include transfer of *Porphyrio* and allied genera from a terminal position with *Fulica* and relatives to a separate tribe immediately following the uniquely primitive *Himantornis*; segregation of *Rallina*, *Rallicula* and *Sarothrura* as a separate tribe; generic transfer of the '*Gallirallus*' *torquatus*-group and '*G.*' *okinawae* to *Habropteryx*, inferred herein to comprise a clade with *H. insignis*; treatment of *Rallus antarcticus* and *R. semiplumbeus* as members of a superspecies; and a concession regarding the uncertainty of the generic assignment of '*Rallus*' *madagascariensis*. The proposed classification follows recent taxonomic practice in merging *Mentocrex* with *Canirallus*. Formal naming of well-supported subgroups of *Sarothrura* was waived (in part) because the only available, non-nominate genus-group name—*Lemurolimnas* Salomonsen, 1934 (type, *watersi*)—would apply to but a single couplet of species. Similar conservatism was adopted within *Fulica*, wherein the only non-nominate, genus-group names available—*Phalaria* Reichenbach, 1853 (type, *gigantea*) and *Lycornis* Bonaparte, 1856 (type, *cornuta*)—also pertain to a single, two-species clade. Subdivision of *Gallirallus* and allies into subgenera was deemed premature; moreover, available names—*Hypotaenidia* Reichenbach, 1853 (type, *pectoralis*) and *Sylvestrornis* Mathews, 1928 (type, *sylvestris*)—would be largely redundant with recognized genera and species-groups.

Profound problems attend the reconciliation of reconstructed subgroups within the 'crakes' (especially '*Porzana*'), difficulties which are exacerbated considerably by the complex taxonomic history of the group and the tenuous support afforded many of the pertinent nodes in the present study (figures 4 and 11). Perusal of the plates in Ripley (1977) or Taylor (1996) reveals the complex of continuously varying patterns of the integument in these taxa. The number of generic names synonymized with *Porzana* by most authors (Olson 1973*a*; Ripley 1977; Taylor 1996)—including *Aenigmatolimnas* Peters, 1932 (type, *marginalis*), *Crecopsis* Sharpe, 1893 (type, *egregia*), *Porzanula* Frohawk, 1892 (type, *palmeri*), *Aphanolimnas* Sharpe, 1892 (type, *monasa*) and *Nesophylax* Murphy, 1924 (type, *atra*)—is indicative of the taxonomic morass surrounding the group. Concerns regarding the marginal support for many nodes in the analysis depicted (figures 4 and 11) are deepened by a consideration of the impact of flightlessness-related characters or the exclusion of all taxa but those having essentially complete data on recovered groups. These uncertainties argue for a conservative treatment of *Porzana* and allied genera for the present that preserves old, widely recognized generic names where these are broadly consistent with nodes which were afforded significant support or were retained in most or all methodological variations employed. As is indicated by the numerous annotations of '*incertae sedis*' which follow the subgroups defined (Appendix C), many of the subdivisions of 'crakes' exclusive of *Atlantisia* and *Laterallus* are of doubtful monophyly and are proposed only as provisional conveniences. It is hoped that special attention will be given this important segment of the rallid phylogeny by future investigators.

At least one revision concerning subfossil Rallidae, the inclusion of *Aphanocrex* among the Porphyriornithini, represents a noteworthy departure from recent classifications by Olson (1973*b*, 1977). I deferred several generic reallocations of several other flightless rails in the absence of firmly supported alternative placements and the likelihood of flightlessness-related homoplasy in associated groupings; similar conservatism prompted the retention of several modern genera of flightless rail (e.g. *Tricholimnas*, *Nesoclopeus* and *Aramidopsis*). However, based on this study, it could be argued that *Capellirallus* should be merged with *Cabalus* and that the generic affinities of '*Atlantisia*' *elpenor* and '*Aphanapteryx*' *leguati* are yet to be determined. For provisional classifications of additional fossil Rallidae, especially taxa from Tertiary and continental Quaternary deposits, see Olson (1977).

(e) *Biogeographic patterns*

Although incomplete resolution of the phylogenetic relationships within a number of genera of Rallidae precludes a formal cladistic analysis of historical biogeography (Wiley 1981, 1988*a*,*b*; Cracraft 1988*c*), several broad patterns can be discerned. A simple tally of gruiform families reveals a preponderance of southern-hemisphere groups, although the fossil Messelornithidae are known only from Europe and several other families (e.g. Gruidae and Rallidae) are widely distributed. A southern-hemispheric origin appears likely for the Rallidae, at least on the basis of distributions of modern representatives of closely related families: the austral distributions of Cariamidae, Eurypygidae, Rhynochetidae and Aptornithidae; the neotropical distribution of the Psophiidae and Aramidae; the African distribution of *Balearica*; and the 'circumequatorial' distribution of the

Heliornithidae. An austral origin and radiation of several gruiform families—e.g. Eurypygidae, Rhynochetidae and Aptornithidae—was intuited prior to the proposal of formal phylogenetic hypotheses (Cracraft 1973*b*, 1980).

Evidence for austral origins is augmented within the Rallidae, wherein a number of basal genera (*Himantornis*, *Gymnocrex*, *Eulabeornis*, *Canirallus*, *Mentocrex* and *Anurolimnas*) are strictly equatorial or southern-hemispheric in distribution. In addition, most species of *Porphyrio* and *Porphyrula* are limited to the southern hemisphere, and *Aramides* is most diverse in South America with only a few representatives in the northern neotropics. A number of comparatively derived genera or larger clades of rallids are limited to or predominantly distributed in the southern hemisphere (e.g. *Dryolimnas*, *Rallina*, *Rallicula* and *Sarothrura*), and at least one widely distributed genus is characterized by a basal grade of austral representatives (*Fulica*). Of modern Rallidae, only a minority of genera (*Porphyrio*, *Porphyrula*, *Rougetius*, *Rallus*, *Gallirallus*, *Rallina*, '*Laterallus*', *Crex*, *Coturnicops*, '*Porzana*', *Amaurornis*, *Gallicrex*, *Gallinula* and *Fulica*) include members having distributions incorporating (at least seasonally) significant northern-hemispheric components.

The unprecedented proposal of a sister relationship between *Gymnocrex* and *Habroptila* is at least plausible on biogeographic grounds (Ripley 1977; Taylor 1996). The poorly resolved phylogenetic relationships among the 'long-billed' rails—*Rallus*, *Gallirallus* and close relatives—render detailed biogeographic assessments problematic, despite previous attempts (Schodde & Naurois 1982; Beauchamp 1989; Olson 1997). Similar limitations prevent biogeographic reconstructions for the crakes, notably the widespread '*Porzana*'. Although closely related subgroups can be interpreted within narrow geographical contexts—e.g. allospecies of *Gallirallus* in the New Zealand region—integration of phylogeny with available biogeographic data for the pertinent regions (Mayr 1943; Rand 1955; Fleming 1962, 1975, 1979; Moreau 1966; McDowall 1969; Craw 1988; Pauley 1990) must await better-resolved hypotheses for many groups of rallids. Such fine-scale analyses of the phylogeny and distribution of the *P. porphyrio*-group, *G. philippensis*-group, *G. striatus*-group and *G. pectoralis*-group would provide important insights into the history and mechanisms of allopatric speciation, dispersal and historical patterns of flightlessness in South Pacific rallids.

5. CONCLUSIONS

Although the present study succeeded in resolving some interfamilial relationships for the Gruiformes and delimiting a number of subgroups of the Rallidae on the basis of morphological characters, the mediocre resolution of many rallid taxa lends some credence to the pessimistic summary by Olson (1973*a*, p. 381): 'one of the difficulties of rallid taxonomy arises from the relative homogeneity of the family, rails for the most part being rather generalized birds with few groups having morphological modifications that clearly define them.' Furthermore, the alternative treatments of 'flightlessness-related' characters presented here confirm in some respects the suspicions expressed by Mayr (1949) and Olson (1973*a*, p. 381) concerning the 'instability of morphology' related to flightlessness and the reflection of such apomorphy in the proliferation of monotypic genera in the family. Homoplasy of several osteological characters related to flightlessness is especially vexing in that several flightless rallids are known only from subfossil remains, limiting assessments to osteological data.

Considered treatment of the issue of homoplasy (Sanderson & Donoghue 1989, 1996), however, does not justify assumptions of pervasive effects of flightlessness and giantism on phylogenetic reconstruction. Houde *et al.* (1997, p. 142) suggested that an earlier proposal of a close relationship between *Aptornis* and *Rhynochetos* is based on the 'obliteration' of the informativeness of postcranial morphological characters related to changes in locomotion and body size. Although any data set may be misleading, this dismissal assumes an unknown mechanism of sufficient generality to affect a diversity of osteological characters with no obvious relationship to either size or locomotion in both *Rhynochetos* and *Aptornis* and shared (in part) by smaller, flighted *Eurypyga*. Although homoplasy associated with flightlessness was inferred in the present study, there is no indication that such effects were important for higher-order inferences. Also, such homoplasy appears not to have overwhelmed the phylogenetic informativeness of anatomical characters in the ratites, birds of larger size and more profound pectoral reduction (Lee *et al.* 1997). Speculative detractions of this kind can be offered as readily for molecular studies, especially in light of doubts recently raised concerning the most commonly cited advantages of sequence data for phylogenetic inference, including selective neutrality and clock-like, unbiased and independent evolutionary rates (Sheldon 1987; Sheldon & Bledsoe 1993; Naylor & Brown 1997; Omland 1997). Clearly, however, an improved understanding of relationships lies not in partisan rationalization of contrasting inferences but in the reasoned combination and augmentation of diverse data sets to address problems of common concern (Bull *et al.* 1993; Chippindale & Wiens 1994; de Queiroz *et al.* 1995; Wiens & Reeder 1995).

Missing data—whether associated with modern taxa represented only by study skins (lacking osteological characters) or fossils (lacking integumentary characters)—also imposed substantial limitations on analyses of the Rallidae performed in the present study. Such limitations have given rise to a new, more critical perspective on the use of fossils for phylogenetic reconstruction, in which fossils in some cases can be analytically burdensome while inferentially unimportant for phylogenetic reconstruction (Huelsenbeck 1991*b*; Platnick *et al.* 1991; Livezey 1996*a*, 1997*b*; Shaffer *et al.* 1997). On the other hand, the inclusion of fossils in cladistic analyses may be critical for the resolution of key nodes in phylogenetic trees (Gauthier *et al.* 1988). Also, phylogenetic assessments of fossils provide instructive contrasts with the intuitive classifications of the past, despite vulnerabilities of both approaches to fallable character analyses and limitations imposed by missing data.

Most anatomical systems of gruiforms remain unexplored for purposes of phylogenetics. Comparisons of tracheal anatomy, pelvic myology and pterylography seem promising, although none of these would shed light on positions of subfossil taxa or recently extirpated species lacking anatomical material. DNA sequences, in addition to confirming or countering groupings indicated by morphological characters, hold potential for resolving heretofore impenetrable nodes. Although molecular data are afflicted by the same problems and limitations as anatomical characters for phylogenetic reconstruction (Hillis 1987; Bledsoe & Raikow 1990; Moritz & Hillis 1990; Swofford 1991; Novacek 1994; Smith & Littlewood 1994; Doyle 1996; Hillis *et al.* 1996; Lee 1997; Omland 1997), sequences showing moderately fast evolutionary rates (e.g. mitochondrial cyt-*b*) may prove especially powerful for resolving relationships among the several large, superspecific radiations in the Rallidae (e.g. *Rallus longirostris elegans*-groups and *Gallirallus philippensis*-group).

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APPENDIX A. DESCRIPTIONS OF CHARACTERS

Characters 1–381 coded for outgroups, all higher-order taxa of Gruiformes, and species of Grues; characters 382–570 coded only for species of Grues. Unless indicated otherwise, all multistate characters were analysed as unordered; default plesiomorphous state is 'a', and those characters for which basal polarity is uncertain are so annotated.

Osteologia

Cavitas nasalis

001. Apertura nasi ossea, caudal terminus, caudal extent relative to zona flexoria craniofacialis and shape: (a) extending caudally to zona flexoria craniofacialis, slit-like, producing 'schizorhinal' aspect; (b) terminating rostrad to zona flexoria craniofacialis, rounded, producing 'holorhinal' aspect; (c) terminating rostrad to zona flexoria craniofacialis, variably slit-like, producing 'pseudoschizorhinal' aspect. Note: Mesitornithidae comparatively rounded, unique appearance due to apomorphic, abrupt broadening of processus frontalis of os nasale at posterior terminus of apertura *Gymnocrex plumbeiventris* tending to state 'a' in single specimen available; *Gallirallus* (including *dieffenbachii*) tending to state 'b'.

002. Apertura nasi ossea, shape and length: (a) long, often narrow, length typically at least one-half length of maxilla; (b) subovate, length significantly less than one-half length of maxilla.

003. Septum nasale osseum: (a) absent or incomplete; (b) complete.

004. Apertura nasi ossea, dorsoventrally orientated osseous vestige of concha nasalis bridging anterior symphyses, blocking dorsally divided canalis neurovascularis: (a) absent; (b) present.

005. Apertura nasi ossea, craniocaudally orientated osseous vestige of concha nasalis bridging margo ventralis 1 mm posterior to anterior symphyses: (a) absent; (b) present.

006. Apertura nasi ossea, irregularly, rectanguloid osseous vestige of concha nasalis, continued caudomediodorsally to fuse on midline (os nasale, facies ventralis) in anterodorsal vertex: (a) absent; (b) present.

007. Apertura nasi ossea, position in maxilla: (a) extending (variably) to both the proximal and distal halves of the maxilla); (b) confined to proximal half of maxilla.

Ossa faciei

Mandibula

008. Ramus mandibulae, pars intermedia, ventral decurvature: (a) slight; (b) obsolete; (c) moderate; (d) strong, extending rostrally to produce strongly decurved symphysis mandibulae.

009. Ramus mandibulae, angulus ventralis mandibulae (new term; variably pronounced angularity of ventral margin of ramus in lateral view): (a) absent or indistinct; (b) distinct. Note: basal polarity indeterminate.

010. Fenestra rostralis mandibulae: (a) slit-like; (b) moderately large, subovate, due to position of os prearticulare; (c) obsolete. Note: polarity tentatively assigned using secondary outgroups. Fragility of margins of bordering elements contributes to intraspecific variation. Perhaps should reject character, especially given variation among outgroups. Messelornithidae possibly possess state 'd'; Otididae variable, comparatively elongate anteroposteriorly.

011. Fenestra caudalis mandibulae: (a) small, distinctly smaller than fenestra rostralis mandibulae; (b) large, approximating in dorsoventral dimension that of fenestra rostralis mandibulae.

012. Fossa aditus canalis neurovascularis, conformation as a long, narrow opening in margo dorsalis of pars intermedia mandibulae: (a) absent; (b) present.

013. Fossa articularis quadratica, tuberculum intercotylare (crista intercotylaris): (a) present; (b) obsolete.

014. Fossa articularis quadratica, margo caudalis, deep ovate fovea: (a) absent; (b) present.

015. Fossa articularis quadratica, recessus caudalis (new term; a variably distinct depression caudal or caudomedial to cotylae quadraticum mandibulae, not associated with condylus caudalis quadrati): (a) absent; (b) present.

016. Os dentale, pars symphysialis, symphysis mandibularis: (a) anteroposteriorly relatively short ($\leqslant$25% mandibular length) and (typically) dorsoventrally thin; (b) anteroposteriorly relatively long ($\geqslant$25% mandibular length) and dorsoventrally thick; (c) anteroposteriorly relatively long ($\geqslant$25% mandibular length) and dorsoventrally thin.

017. Os angulare, angulus caudoventralis mandibulae (new term; variably conformed caudoventral margin of element and ramus mandibulae): (a) rounded, comparatively truncate; (b) produced into variably knobbed process.

018. Os angulare, hamulus retroarticularis (new term; comparatively small, hook-shaped, dorsally orientated processus on caudal margin of element and ramus mandibulae): (a) present, variably conformed, sometimes diminutive; (b) obsolete. Note: not to be confused with large, prominent, blade-like (true) processus retroarticularis of Anseriformes. Stercorariidae, Laridae, and Rynchopidae variable.

019. Os articulare, processus mandibulae medialis, dorsal prominence: (a) moderate; (b) extreme.

Ossa maxillae et palati

020. Os nasale, processus rostralis premaxillaris: (a) not abruptly broadened; (b) abruptly broadened, forming angular 'shield' at rostral margin of zona elastica craniofacialis.

021. Os premaxillare, processus frontalis, at anterior terminus of apertura nasi ossea: (a) continuously tapered; (b) with distinct, dorsally concave depression.

022. Os premaxillare, anterior terminus (tip of maxilla), strong ventral hooking: (a) absent; (b) present.

023. Ossa premaxillare, maxillare, et palatinum; ramus of maxilla, cross-sectional shape: (a) lateromedially broad, dorsoventrally compressed throughout; (b) dorsoventrally (relatively) broad, lateromedially compressed, basally. Note: *Habropteryx insignis* tending to state 'a'.

024. Ossa premaxillare, maxillare, et nasale, amphikinesis involving both proximal and distal zonae flexoriae (ordered): (a) absent; (b) present, only moderately pronounced, lacking distinct structural modification of distal zona; (c) present, pronouced, involving distal torsion of os maxillare, processus maxillaris of approximately 90°, in which distal ramus is broader lateromedially than high dorsoventrally. Note: see Zusi (1984); *Dryolimnas* provisionally coded as state 'a'.

025. Os premaxillare, density of foramina neurovascularia distally: (a) low; (b) high.

026. Os premaxillare, processus maxillaris: (a) extending posteriorly, synostotic with os nasale, processus maxillaris dorsal to its synostosis with os maxillare; (b) terminating immediately posterior to the anterior terminus of apertura nasi ossea, joining os nasale, processus maxillaris well ventroanterior to the synostosis between os nasale, processus maxillaris and os maxillare.

027. Os maxillare, dorsally orientated flange at posterior terminus of each apertura nasi ossea: (a) absent; (b) present.

028. Os maxillare, processus maxillopalatinus: (a) variably margined, often pneumatic, laterally convex, typically of moderate size; (b) large, ovate, single-layered, nonpneumatic, laterally concave plate.

029. Ossa maxillares, processi maxillopalatini, medial synostosis resulting in partitioning of fenestra ventromedialis (new term; a variably conformed medial opening between the ossa maxillae in the osseous palate) from fenestra choanalis: (a) absent; (b) present, producing 'desmognathy'. Note: fenestra ventromedialis referred to as *Oberschnabellucke* by Hofer (1949). Most Gruiformes are schizognathous *sensu lato*.

030. Os maxillare, processus nasalis (dorsocaudal extension of bone to os nasale, processus maxillaris, interposed between ossa lacrimale et frontale): (a) absent; (b) present.

031. Os maxillare, processus jugalis, position relative to apertura nasi ossea, margo ventralis: (a) ventral, arcus jugalis conforming in arc with that of ramus maxillare; (b) dorsal, arcus jugalis orientated dorsad to that of ramus maxillare. Note: some *Porzana* and *Laterallus* approach state 'b'. Some intraspecific variation.

032. Os palatinum, processus rostralis (new term; anterior or rostral portion of element, variably articulating or synostotic with os maxillare): (a) anterior portion distinctly tapering anterior to anterior terminus of lamella choanalis; (b) anterior portion broadening anteriorly, fusing broadly with os maxillare, processus palatinus, occluding (in ventral view) most of os premaxillare, processus frontalis; (c) anterior portion remaining of approximately uniform width to point immediately posterior to synostosis with os maxillare.

033. Os palatinum, pars choanalis, lamina choanalis, margo (ala) ventralis, position of caudal terminus relative to that of pars lateralis, margo lateralis: (a) rostral; (b) coincident.

034. Os palatinum, pars choanalis, lamina choanalis, margo (ala) ventralis, processus interpalatinus: (a) absent or obsolete; (b) small but distinct.

035. Os palatinum, pars lateralis, truncate conformation, defining distinct angulus caudolateralis, with precursor of processus transpalatinus approximately equal to processus pterygoideus in posterior extent: (a) absent; (b) present. Note: some Charadriiformes (e.g. Burhinidae) problematical.

036. Os palatinum, pars lateralis: (a) with deep trough-like depression between crista ventralis and crista lateralis; (b) without deep trough between crista ventralis and crista lateralis. Note: state 'a' limited to posterior portion in Otididae.

037. Ossa palatini, fissura interpalatina: (a) relatively long; (b) relatively short.

038. Vomer, rostral terminus (in articulatio): (a) comparatively posterior, typically coinciding with posterior margin of apertura nasi ossea; (b) comparatively anterior, typically extending to midpoint of apertura nasi ossea.

039. Vomer, caudal terminus (modal): (a) divided medially, laterally; (b) undivided medially.

040. Vomer et os palatinum, synostosis (complete) vomeropalatina: (a) absent; (b) present.

041. Ossa jugale et maxillare, sutura jugomaxillaris: (a) bounded posteriorly by osseus lamina, enclosing (typically) ventrally exposed, often recessed fenestra; (b) without posterior osseus lamina or enclosed fenestra. Note: Laridae variable, Pedionomidae deeply recessed, Psophiidae and Heliornithidae ventrally obstructed by lamina, Otididae variable.

042. Ossa jugale et palatinum, sutura jugomaxillaris, angulus of synostosis of arcus: (a) moderately great; (b) shallow.

043. Zonae flexoriae craniofaciales, development and relative position producing rhynchokinesis: (a) absent, prokinetic condition; (b) present. Note: see Zusi (1984). Subgroup of Rallidae shows amphikinesis.

044. Zona flexoria craniofacialis: (a) inconspicuous, with more or less rounded or angular posterior terminus, dorsal surface merging gradually with ossa frontales; (b) well demarcated across rostrum, straight, with defined dorsal crease with ossa frontales. Note: difficult codings frequent, with aspect confounded by dorsal contour of facies immediately caudal to zona.

045. Maxilla, dorsolateral compression: (a) not as follows; (b) dorsoventally compressed, lateromedially broad.

046. Maxilla, lateromedial compression: (a) not dorsoventrally deep; (b) dorsoventrally deep and lateromedially moderately compressed, with dorsal profile of culmen strongly convex; (c) dorsoventrally very deep and lateromedially greatly compressed, culmen strongly convex. Note: see characters of bill shape under 'integumentum commune'.

047. Maxilla, relative length: (a) less than or approximately equal to that of postmaxillary length of skull; (b) significantly longer than postmaxillary length of skull. Note: basal polarity indeterminate.

048. Os quadratum, corpus quadrati, facies lateralis, facies articularis zygomaticus: (a) absent; (b) present, laterocranial to processus oticus quadrati, articulating with caudomedial surface of os squamosum, processus zygomaticus.

049. Os quadratum, foramen pneumaticum, modal location: (a) 'caudale', in processus oticus, facies caudalis; (b) 'mediale', in corpus quadrati, facies medialis. Note: polarity tentatively confirmed using secondary outgroups. Significant ontogenetic plasticity within some species, with some specimens having both foramina (but 'characteristic' one typically is larger); this modal condition of mutual exclusivity of two states in all taxa but Glareolidae led to treatment as single character. Alcidae not comparable, apneumatic, coded as missing.

050. Os quadratum, processus orbitalis quadrati, significant anterodorsal elongation and mediodorsal deflection: (a) absent; (b) present.

051. Os quadratum, processus mandibularis quadrati, condylus medialis, conformation as ventrally prominent and knob-like, with deep, adjacent sulcus intercondylaris: (a) absent; (b) present.

052. Os quadratum, processus mandibularis quadrati, condylus caudalis, significant enlargement obscuring sulcus intercondylaris: (a) absent; (b) present.

053. Os quadratum, processus mandibularis quadrati, condylus lateralis: (a) not prominent ventrally; (b) very prominent ventrally, with deep sulcus intercondylaris clearly distinguishing more-posterior condylus caudalis from condylus lateralis proper. Note: for Messelornithidae, see Hesse (1990, p. 33, fig. 8).

054. Os quadratum, processus mandibularis quadrati, sulcus intercondylaris (dividing condylus medialis from variably conformed, more-lateral condyla), if present: (a) comparatively shallow, typically relatively broad; (b) comparatively deep, typically lateromedially constricted, distinguishing prominent condylus medialis.

055. Os quadratum, processus mandibularis quadrati, condylus pterygoideus, position relative to condylus lateralis: (a) slightly dorsal; (b) well dorsal.

056. Os quadratum, processus oticus, conformation in which capitulum [condylus] oticum is markedly ventral to capitulum [condylus] squamosum and intervening bone presents a pronounced, subangular sloping profile (anteromedial view in articulatio): (a) absent; (b) present.

Ossa cranii

057. Os lacrimale: (a) present; (b) vestigial or absent. Note: all other characters of os lacrimale coded as missing for non-comparability for taxa having state 'b'. Taxa having state 'b' were considered to lack the element by Cracraft (1968*b*), but present study indicates a vestige may remain; reduction in some Charadriiformes approaches this extreme condition.

058. Os lacrimale, processus orbitalis: (a) does not directly articulate with os jugale; (b) directly articulates with os jugale. Note: small tuberculum on arcus suggests short ligamentous connection in *Diaphorapteryx*.

059. Os lacrimale, processus orbitalis: (a) not highly pneumatic; (b) highly pneumatic, having one or more conspicuous foramina pneumatica on facies lateralis.

060. Os lacrimale, position and synostosis with ossa frontale et nasale: (a) relatively rostral, articulates dorsomedially with both os frontale and os nasale for significant segments lateral to zona elastica craniofacialis; (b) relatively caudal, articulates dorsomedially principally or only with os frontale.

061. Os lacrimale, processus orbitalis, foramen lacrimalis: (a) absent; (b) present.

062. Os lacrimale, processus supraorbitalis: (a) small or obsolete; (b) present, variably shaped and orientated.

063. Os lacrimale, processus supraorbitalis, conspicuous caudolateral elongation: (a) absent; (b) present.

064. Os lacrimale, processus orbitalis, articulatio lacrimo-ectethmoidalis: (a) present, by means of ventrolateral (typically strut-like) margin of os ectethmoidale; (b) absent. Note: Cariamidae and Phorusrhacoidea possess os uncinatum and non-comparable; Eurypygidae lack os ectethmoidale and non-comparable.

065. Os ectethmoidale: (a) present, variably conformed; (b) absent. Note: taxa possessing state 'b' considered non-comparable for characters involving os ectethmoidae.

066. Os ectethmoidale: (a) not expanded; (b) greatly expanded, occupying entire anterior end of orbit.

067. Septum interorbitale, fonticulus interorbitalis (new term; variably expansive and conformed perforation in septum): (a) present, but restricted peripherally to less than one-half the orbital diameter; (b) present, large, diameter approaching that of entire orbit; (c) obsolete. Note: intraspecifically variable in some taxa.

068. Os frontale, conspicuous, medial interorbital ridge and paired prominences at posterolateral vertices of cranial dome: (a) absent; (b) present.

069. Os frontale, margo supraorbitalis, dorsolateral expansion into rima: (a) present; (b) absent. Note: feature in Charadriiformes variably evident due to sulcus glandulae nasalis.

070. Os frontale, facies dorsalis: (a) flat or (more typically) slightly concave; (b) moderately convex; (c) inflated along midline interorbitally, evidently age-related or sexual variation present. Note: problematic comparability in *Eulabeornis* caused by sulci glandulae nasales.

071. Os frontale, margo supraorbitalis: (a) laterally straight or concave; (b) laterally convex, related to expansion of region into subcircular 'shield'.

072. Os frontale, facies dorsalis, sulcus glandulae nasalis: (a) present, distinct, deep, typically with ventral fenestra to orbit or lacking ventral partition entirely; (b) absent; (c) present, without lateral margins evident. Note: basal polarity indeterminate. Not evident in Messelornithidae, but see Hesse (1990).

073. Ossa frontales, facies cerebralis, crista frontalis interna: (a) prominent, dividing medially the bilateral fonticuli orbitales in posterodorsal facies of orbita; (b) obsolete rostrally, not dividing medially the fonticulus orbitalis in posterodorsal facies of orbita. Note: fragile structure.

074. Os laterosphenoidale, processus postorbitalis: (a) relatively long, approximately equal in ventral extent to cotyla quadratica otici et squamosi; (b) short or obsolete.

075. Os laterosphenoidale, processus postorbitalis, ossification of ligamentum postorbitale (accessory attachment), producing narrow osseus lamina joining it with os squamosum, processus zygomaticus: (a) absent; (b) frequent, if not typical. Note: rare in *Cariama*.

076. Os parasphenoidale, rostrum sphenoidale, processus basipterygoideus (functional in adults): (a) present; (b) absent. Note: vestiges of embryonic processus basipterygoideus are detectable in most or all of the taxa included in state 'b' above.

077. Os parasphenoidale, lamina paraspheniodale, ala parasphenoidalis, processus lateralis parasphenoidalis: (a) absent or indistinct; (b) distinct. Note: basal polarity indeterminate. Apparently involved in the more lateral of two possible articulationes mandibulosphenoidales, termed 'lateral basitemporal process' by Bock (1960).

078. Os parasphenoidale, lamina paraspheniodale, tuberculum basilare, processus medialis parasphenoidalis: (a) small to moderately developed, variably conformed crista, not exceeding (articulated) os quadratum in ventral extent; (b) ventrally very prominent, exceeding (articulated) os quadratum in ventral extent, with prominent, convex crista caudally. Note: apparently involved in the more medial of two possible articulationes mandibulosphenoidales, termed 'medial basitemporal process' by Bock (1960).

079. Os squamosum, large tenda ossea of musculi mandibulae: (a) absent; (b) present.

080. Os squamosum, fossa temporalis: (a) distinct, variably deep, but separated medially from each other by significantly broad, elevated expanse of os frontale; (b) distinct, deep, almost meeting medially; (c) indistinct, shallow, limited to region immediately ventral to processus postorbitalis. Note: Alcidae variable, *Porzana* problematic.

081. Os squamosum, facies articularis quadratica, enclosure of condylus squamosus et proöticus by ventral elongation of processus suprameaticus laterally and posterolateral elongation of os squamosum medially, on ventral margin of cavitas tympanica: (a) absent; (b) present.

082. Os squamosum, processus zygomaticus: (a) short and broad, but variably conformed; (b) long and thin, and approximating processus postorbitalis of os laterosphenoidale in length; (c) long and broad, and approximating processus postorbitalis of os laterosphenoidale in length. Note: Eurypygidae tending to state 'c'; Messelornithidae may be state 'c' (Hesse 1990). Apternithidae especially well developed, possibly reaching arcus jugalis directly or via short ligamentum.

083. Os squamosum, ala tympanica, pronounced ventral enlargement that largely conceals articulatio quadratosquamosa in ventral view: (a) absent; (b) present.

084. Cavitas tympanica, foramen pneumaticum caudale (immediately posterior to condylus proöticus of processus oticus quadrati): (a) absent; (b) present. Note: not to be confused with widespread, typically large foramina pneumatica in cavitas tympanica (slightly medial or lateral to former) cited by Cracraft (1988*a*) as synapomorphy for Gruiformes. Some intraspecific variation in conspicuousness (e.g. *Rhynochetos*).

085. Os basioccipitale, fossa subcondylaris: (a) not as follows; (b) trough-like, deeply concave medially (in ventral perspective) but ventrally protrusive anterolaterally. Note: distinct but convergent condition also in *Diaphorapteryx*.

086. Os basioccipitale, condylus occipitalis, modal conformation in caudal view: (a) essentially globular; (b) distinctly bilobate, bilaterally elongate. Note: see Goebloed (1958).

087. Os exoccipitale, fonticulus occipitalis: (a) absent; (b) present (Rostratulidae, Haematopodidae, Ibidorhynchidae, Recurvirostridae, Charadriidae, Scolopacidae,

Phalaropodidae, Alcidae; Aramidae, Gruidae). Note: polarity tentatively assigned using secondary outgroups.
088. Os exoccipitale, processus paroccipitalis: (a) not laterocaudally prominent; (b) laterocaudally prominent.
089. Os supraoccipitale, facies nuchalis, crista nuchalis, marked angulus: (a) absent, crista essentially continuous lateromedially and lacking prominent, convex eminence or marked caudal convexity; (b) present, bowed ventrally, markedly convex caudally and forming defining a dorsomedial vertex, or with prominent convex eminence and defining dorsolateral angulus.

Ossa accessoria cranii

090. Ossa supraorbitalia: (a) absent; (b) present.
091. Os uncinatum, articulating dorsally with os lacrimale, processus orbitalis and ventrally with os jugale: (a) absent; (b) present.

Note on nomenclature of ossa sclerae

Lateral views of elements of selected taxa are shown in figure 14. Because most rings are free from the cranium in prepared specimens, many rings (especially those approaching symmetry dorsally) are classified as 'left' and 'right' by a presumption of parsimony of pattern differences within and among species. Numbers of elements in adjacent imbricated series probably related in some cases by a positional shift of interposed lateral or medial ossicles.
092. Ossa sclerae, configuration (after Lemmrich 1931): (a) type A, having two ossa sclerae laterales with two interposed ossa sclerae mediales, defining four, variably long series of unidirectional ossa sclerae imbricales (new term); (b) type B, having one os sclera laterale and one os sclera mediale, defining two variably long series of unidirectional ossa sclerae imbricales. Note: taxa having type B may not homologous because of relative lengths of imbricated series, hence both are coded as missing for non-comparability for scleral characters 93–96.
093. Ossa sclerae, imbricated series I, modal number of incorporated elements (primitive state in bold, ordered): (a) two; **(b) three;** (c) four; (d) five. Note: intraspecifically variable, limited asymmetry within individuals.
094. Ossa sclerae, imbricated series II, modal number of incorporated elements (primitive state in bold, ordered): (a) one; (b) two; **(c) three**. Note: intraspecifically variable, limited asymmetry within individuals. Possible confusion in some species approaching antero-posterior symmetry of scleral elements in imbricated series II and III.
095. Ossa sclerae, imbricated series III, modal number of incorporated elements (primitive state in bold, ordered); (a) zero; **(b) one**. Note: intraspecifically variable, limited asymmetry within individuals. Possible confusion in some species approaching antero-posterior symmetry of scleral elements in imbricated series II and III.
096. Ossa sclerae, imbricated series IV, modal number of incorporated elements (primitive state in bold, ordered): (a) three; **(b) four**. Note: intraspecifically variable, limited asymmetry within individuals.
097. Ossa sclerae, shape of ring: (a) comparatively narrow, not distinctly concave laterally with marked lateral prominence of internal margin, with comparatively great internal diameter; (b) comparatively wide, concave laterally, with marked lateral prominence of internal margin producing subconical profile, with comparatively small internal diameter.

Apparatus hyobranchialis (hyoideus)

098. 'Os' entoglossum, corpus: (a) ossified, at least cornu; (b) unossified.

Systema respiratorium

099. Os cricoideum, rounded caudal flange: (a) absent; (b) typically present. Note: for state of Messelornithidae, see Hesse (1990, fig. 12).
100. Ossa tracheales: (a) shallow, height significantly less than width; (b) deep, height approximately equal to width.
101. Ansae tracheales, extrasternal, coiled: (a) absent; (b) present.
102. Ansae tracheales, intrasternal, looped (ordered): (a) absent; (b) present, single loop; (c) present, partial loop nested within a larger loop; (d) present, complete loop nested within a larger (typically very large) loop, in some the outer loop extending to caudal terminus of carina. Note: see Berndt (1938).

Columna vertebralis

103. Vertebrae cervicales, modal number (primitive in bold; ordered): (a) 14; **(b) 15**; (c) 16 or 17; (d) 18; (e) 19 or 20. Note: state for Messelornithidae based on Hesse (1990:41). Intraspecific variation in *Aramides* sufficiently large to necessitate polymorphic codes.
104. Vertebrae cervicales speciales, axis, arcus axis, ansa costotransversaria, foramen transversarium: (a) absent; (b) present. Note: related in part to prominence of processus costalis.
105. Vertebrae cervicales speciales, axis, corpus axis, processus ventralis corporis, elaboration as elongated, bilaterally compressed, craniocaudally truncated carina: (a) absent; (b) present, variably prominent. Note: significant variation in some Charadriiformes.
106. Vertebrae cervicales speciales, axis, arcus axis, zygopophysis cranialis: (a) distinct; (b) obsolete, facies articularis atlantica structurally indistinguishable from craniodorsal margin of arcus.
107. Vertebrae cervicales speciales, axis, arcus axis, lamina lateralis arcus, foramen pneumaticum: (a) absent; (b) present. Note: polarity problematic, based on broad survey of other orders (B. C. Livezey and R. L. Zusi, unpublished data).
108. Vertebrae cervicales communis, section I of Zusi & Storer (1969), processus costalis: (a) well developed; (b) vestigial.
109. Vertebrae cervicales communis, notably section II of Zusi & Storer (1969), processus postlateralis (for attachment of M. longus colli ventralis): (a) absent; (b) present.
110. Vertebrae cervicales, arcus vertebrae, lamina arcocostalis (ordered): (a) absent; (b) present, variably extensive, and in many enclosing one or two lateral foramina, but lacking a ventral lamina; (c) present, well developed, enclosed ventrally by an osseus lamina, producing a foramen transversarium caudalis (new term; caudal

opening between lamina arcocostalis and corpus vertebrae).

111. Vertebrae cervicales, marked heterogeneity of form involving relative elongation of intermediate elements, section II of Zusi & Storer (1969): (a) absent; (b) present.

112. Vertebrae cervicales, especially section III of Zusi & Storer (1969), corpus vertebrae, facies ventralis corporis, processus caroticus, arcus caroticus: (a) absent; (b) present.

113. Vertebrae cervicales, section III of Zusi & Storer (1969), corpus vertebrae, facies lateralis corporis, concavitas lateralis, recessus corporis caudolateralis (new term; apparently apneumatic recess on caudolateral aspect of corpus), continued caudally by distinct bilateral depressio ovalis (new term; distinctly ovate depression on lateral facies of corpus, delimited by rounded rim) in vertebrae thoracicae: (a) absent; (b) present.

114. Vertebrae thoracicae with costae completae verae, modal number (primitive in bold, ordered): (a) four; **(b) five or six;** (c) seven; (d) eight.

115. Vertebrae thoracicae, notarium: (a) absent; (b) present, involving three vertebrae; (c) present, involving four vertebrae. Note: homologies of incorporated vertebrae in state 'c' appear the same, i.e. first four vertebrae thoracicae with costae incompletae (vertebrae thoracicae III–VI).

116. Vertebrae thoracicae, pneumaticity: (a) moderate, foramina typically limited to cranioventral surface of processus transversus; (b) great, foramina typically in cranioventral surface of processus transversus and in corpus, facies lateralis.

117. Vertebrae thoracicae, freely articulating vertebra (not incorporated in notarium or synsacrum) with costae completae spuriae, between vertebrae with costae completae verae and synsacrum: (a) absent; (b) present.

118. Vertebrae thoracicae, facies ventralis, processus ventrolateralis: (a) absent or very poorly developed, typically limited in occurence to cranial-most elements; (b) present, well developed in several elements immediately cranial to synsacrum.

119. Vertebrae thoracicae, facies ventralis, processus ventralis: (a) limited in occurence to cranial elements; (b) retained on caudal elements, including cranial-most element in synsacrum.

120. Vertebrae thoracicae et synsacrales, modal number of synostotic elements, exlcuding variably adherent cranial-most vertebrae caudales (ordered): **(a) 13 or 14;** (b) 15 or 16; (c) 17. Note: see van Oort (1905), Boas (1934).

121. Vertebrae synsacrales, synsacrum, crista spinosa synsacri: (a) not greatly elevated, height approximating width of associated processus transversus; (b) greatly elevated, height significantly greater than width of associated processus transversus.

122. Vertebrae synsacrales, synsacrum, interacetabular and postacetabular elements, facies dorsalis, processus transverses: (a) significantly broader between acetabula than in postacetabular elements, forming essentially flat or shallowly concave surface with ala postacetabularis ilii; (b) constricted lateromedially, only slightly broader between acetabula than in postacetabular elements, deeply concave and forming narrow, elongate, medial depression with ala postacetabularis ilii.

123. Vertebrae synsacrales, synsacrum, postacetabular elements, lateral termina of processus transverses (and sutura iliosynsacralis): (a) shortening markedly caudad; (b) remaining of approximately uniform lateral extent from acetabulae to margo caudales of alae postacetabulares ilii, appearing mutually parallel in dorsal view.

124. Vertebrae synsacrales, synsacrum, crista dorsalis of caudal postacetabular elements, crista spinosa synsacri: (a) variably evident, vertebrae not dorsally concave, segment not dorsally concave with elongate, medial depression, foramina intertransversaria remaining distinct; (b) obsolete, vertebrae typically dorsally concave, producing shallow, elongate, broad, medial depression, foramina intertransversaria largely or completely occluded.

125. Vertebrae synsacrales, synsacrum, processus transverses, at articulation with ala postacetabularis ilii, margo medialis (vertebralis) (ordered): (a) no vertebrae modified as follows; (b) one vertebrae craniocaudally broadened, ventrally prominent, accomodating dorsally (with margo medialis) a caudal extension of fossa renalis, recessus iliacus; (c) two vertebrae craniocaudally broadened, ventrally prominent, accomodating dorsally (with margo medialis) a caudal extension of fossa renalis, recessus iliacus; (d) three vertebrae craniocaudally broadened, ventrally prominent, accomodating dorsally (with margo medialis) a caudal extension of fossa renalis, recessus iliacus. Note: count does not include first (cranial-most), variably synostotic vertebra caudalis.

126. Vertebrae synsacrales, synsacrum, extremitas caudalis synsacri, element(s) opposite ala postacetabularis ilii, facies ventralis, crista iliaca caudalis, distinct processus costalis: (a) absent; (b) present. Note: processi costales and transverses separated at least partly by enclosed fenestrae.

127. Vertebrae caudales liberae (excluding pygostylus), modal number (primitive in bold, ordered): (a) five; (b) six; **(c) seven**; (d) eight or nine. Note: see van Oort (1905).

128. Vertebrae caudales liberae, processus transversus: (a) not laterally elongate; (b) laterally elongate.

Costae

129. Costae vertebrales, extremitas proximales, facies medialis, foramina pneumatica: (a) typically absent; (b) typically present.

130. Costae vertebrales, processus uncinatus: (a) essentially straight, forming approximate 45° angle with corpus costae, margo caudalis; (b) sharply dorsally hooked, forming comparatively acute angle with corpus costae, margo caudalis.

131. Costae vertebrales, first pair of costae incompletae cervico-thoracicae: (a) not exceptionally conformed relative to other costae; (b) uniquely craniocaudally broadened to approximately twice the normal width (largely through dorsoventral elongation and craniocaudal broadening of processus uncinatus), typically enclosing one to two foramina, and apparently acted as a surface of support for the corpus scapulae and (perhaps) extremitas omalis coracoideum.

132. Costae sternales, extremitas sternales, facies mediales, foramina pneumatica: (a) obsolete; (b) typical.

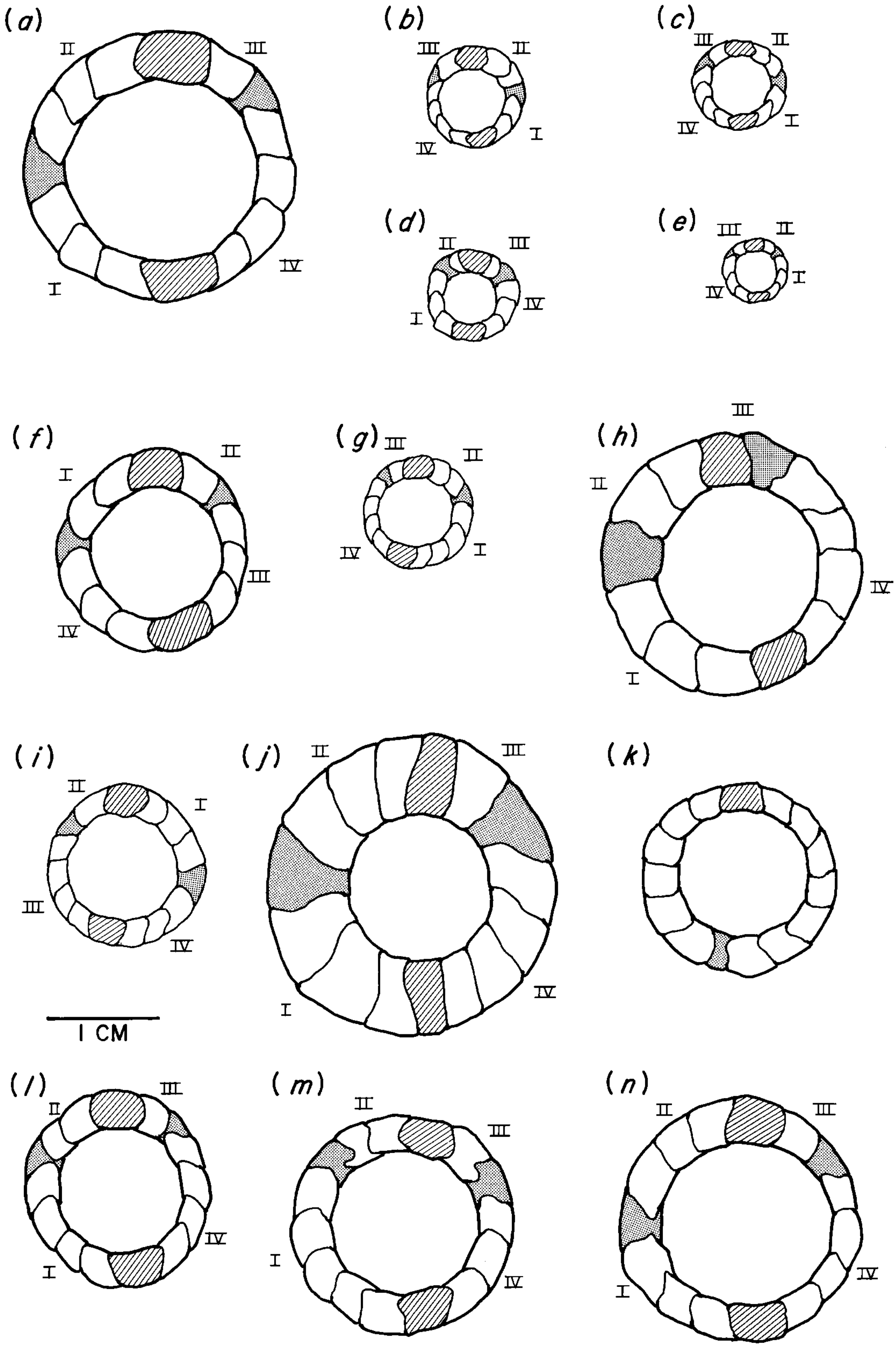

Figure 14. (*a*–*n*). Diagrams (lateral view) of scleral rings of two taxa of Charadriiformes and selected Gruiformes, lateral ossicles are shown in diagonal hatching, medial ossicles are stippled and imbricated ossicles are plain: (*a*) *Burhinus bistriatus* (USNM 432021); (*b*) *Jacana spinosa* (CM 10249); (*c*) *Pedionomus torquatus* (BMNH 1970.12.13); (*d*) *Turnix nigricollis* (USNM 488643); (*e*) *Ortyxelos meiffreni* (BMNH 1944.8.19.1); (*f*) *Eupodotis afra* (USNM 558479); (*g*) *Monias benschi* (BMNH 1968.30.15); (*h*) *Cariama cristata* (USNM 19492); (*i*) *Eurypyga helias* (USNM 613747); (*j*) *Rhynochetos jubatus* (after Lemmrich 1931, fig. 27); (*k*) *Psophia crepitans* (USNM 429974); (*l*) *Aramus guarauna* (USNM 614588); (*m*) *Balearica pavonina* (USNM 558265; variant showing short segment I and long segment IV); (*n*) *Grus monacha* (USNM 429723).

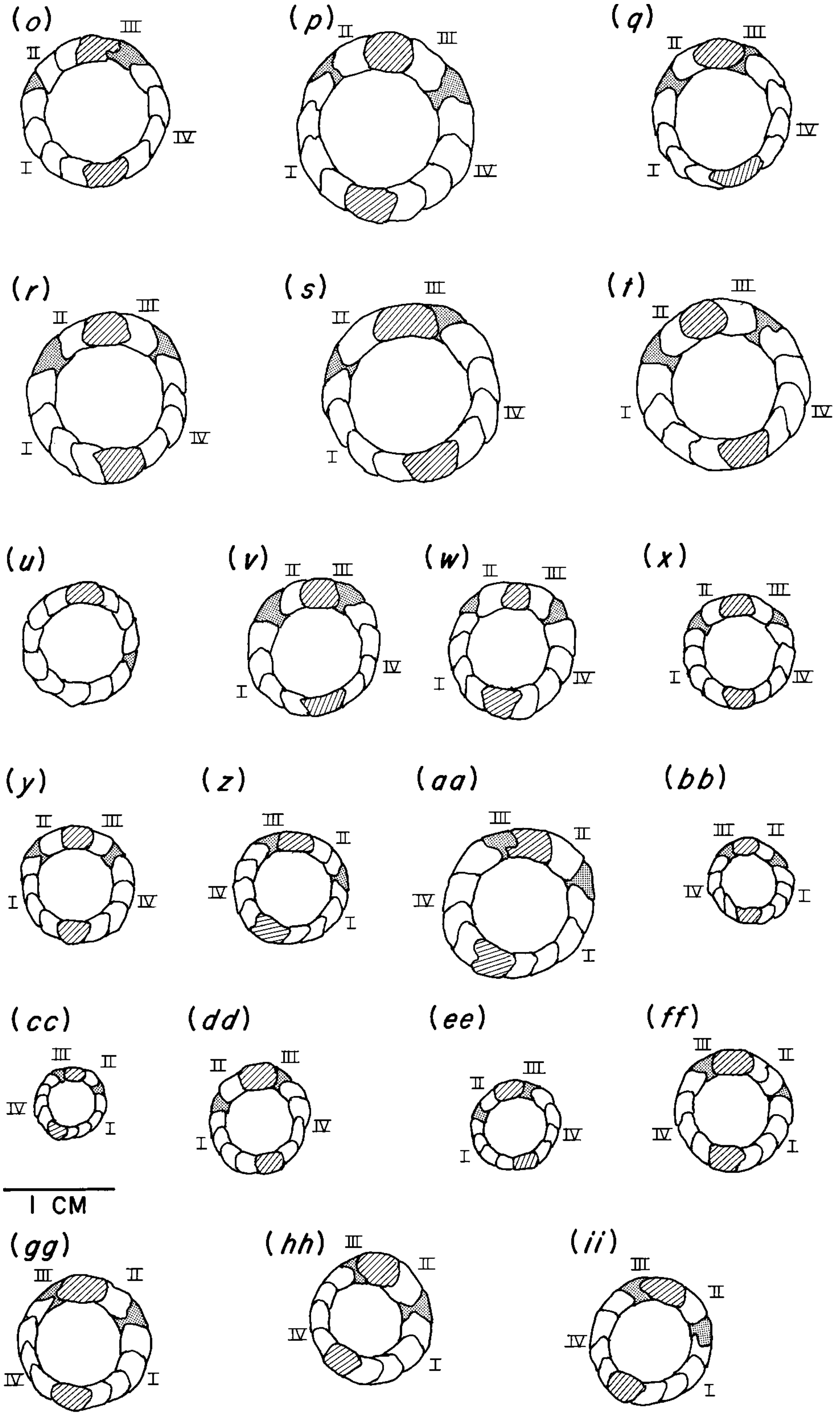

Figure 14. (*o–ii*). (*o*) *Podica senegalensis* (BMNH 1928.5.3.1); (*p*) *Himantornis haematopus* (AMNH 4183); (*q*) *Porphyrio madagascariensis* (UMMZ 227833); (*r*) *Gymnocrex plumbeiventris* (USNM 505787); (*s*) *Habroptila wallacii* (USNM 560792); (*t*) *Aramides ypecaha* (USNM 614590); (*u*) *Amaurolimnas concolor* (USNM 613961); (*v*) *Rallina eurizonoides* (AMNH 17718); (*w*) *Cyanolimnas cerverai* (USNM 343159); (*x*) *Ortygonax sanguinolentus* (USNM 227903); (*y*) *Rallus longirostris* (USNM 553301); (*z*) *Nesoclopeus poecilopterus* (BMNH 1940.12.8.82); (*aa*) '*Gallirallus*' *okinawae* (UMMZ 225360); (*bb*) *Laterallus melanophaius* (USNM 612029); (*cc*) *Coturnicops novaboracensis* (USNM 556931); (*dd*) *Crex crex* (USNM 490304); (*ee*) *Porzana atra* (USNM 562788); (*ff*) *Amaurornis olivaceus* (USNM 560653; variant showing long segment II); (*gg*) *Porphyriornis comeri* (BMNH 1922.12.6.221); (*hh*) *Gallinula* [*chloropus*] *cachinaans* (USNM 347871); (*ii*) *Fulica rufifrons* (USNM 614603). See Appendix A for explanation of segments and nomenclature, Acknowledgments for institutional acronyms. In presumptive right rings, imbricated series progress in clockwise fashion; in

Sternum

133. Corpus sterni, processus (trabecula) lateralis: (a) present; (b) absent. Note: Mesitornithidae with obscured processus caudolaterales because of closure of associated incisurae; Pedionomidae and Turnicidae retain processus lateralis but lack (distinct) processus caudolateralis because of narrowing of corpus sterni caudally.
134. Corpus sterni, distinct trabecula intermedia: (a) present; (b) absent, through occlusion of incisura medialis; (c) absent, through attenuation of corpus sterni caudally. Note: Cariamidae uniquely short relative to trabecula medialis.
135. Corpus sterni, trabecula intermedia, if present and distinct: (a) does not extend significantly caudad to trabecula mediana; (b) extends significantly caudad to trabecula mediana.
136. Corpus sterni, facies muscularis sterni, linea intermuscularis: (a) not cranially restricted; (b) cranially restricted, defining indistinct impressio m. suprcoracoideus and more-craniolateral, deeper, and more-distinct impressio m. coracobrachialis caudalis at caudomedial base of processus craniolateralis.
137. Corpus sterni, facies visceralis sterni, sulcus medianus, pori pneumatici: (a) absent or limited to cranial depression; (b) numerous, widespread.
138. Corpus sterni, facies visceralis sterni, on midline immediately caudal to margo cranialis, foramen pneumaticum: (a) present; (b) absent. Note: polarity tentatively assigned using secondary (ordinal) outgroups.
139. Corpus sterni, facies visceralis, pila coracoidea: (a) not supported caudally by medial strut (evidently secondarily lost in flightless rallids); (b) supported caudally by large, cranially divergent, medial strut, which is dorsal to foramen pneumaticum, if present.
140. Corpus sterni, facies visceralis, margo cranialis, pori pneumatici lateral to midline: (a) absent; (b) present.
141. Corpus sterni, processus craniolateralis: (a) elongate, comparatively acuminate; (b) short, subrectangular.
142. Corpus sterni, processus craniolateralis, caudal deflection: (a) absent; (b) present.
143. Corpus sterni, processus craniolateralis, processus costales: (a) absent or (rarely) one caudally; (b) three or four, distributed along most of processus craniolateralis, margo lateralis.
144. Corpus sterni, margo cranialis, sulcus articularis coracoideus, tuberculum labri ventralis: (a) not ventrally prominent; (b) prominent ventrally, continuous with base of pila carinae.
145. Corpus sterni, margo costalis: (a) relatively restricted, occupying roughly the cranial one-half of margo lateralis craniad to processus caudolateralis (if present) or homologous point (if not distinct); (b) relatively extensive, occupying essentially all of margo lateralis craniad to processus caudolateralis (if distinct) or homologous point.
146. Corpus sterni, marked narrowing caudally: (a) absent, modal ratio of width across processus caudolaterales divided by minimal width $\gg 1.5$ for freed, dried elements having typical proportions of trabecula intermedia; (b) present, modal ratio of width across processus caudolaterales divided by minimal width $\leqslant 1.5$ for freed, dried elements having typical proportions of trabecula intermedia. Note: *Amaurornis ineptus* problematic. *In situ* elements of spirit specimens underestimate caudal width.
147. Corpus sterni, margo costalis, incisurae intercostales, pori pneumatici: (a) absent; (b) present.
148. Corpus sterni, trabecula mediana: (a) tapers, typically to a rounded terminus; (b) broad, not tapered significantly.
149. Corpus sterni, (apparent) trabecula mediana: (a) not as follows; (b) laterally widened opposite processus caudolaterales and continuing caudad in semiovate extension, resulting from occlusion of incisurae and incorporation of processus caudolaterales.
150. Corpus sterni, trabecula mediana: (a) not as follows; (b) tapered sharply for caudal three-quarters of length.
151. Corpus sterni, trabecula mediana, margo caudalis: (a) approximately opposite or only moderately caudal to caudal termina of processus caudolaterales (if present); (b) significantly caudal to processus caudolaterales. Note: Rhynochetidae, Aptornithidae, Psophiidae, Aramidae, Gruidae not comparable.
152. Corpus sterni, margo lateralis, facies lateralis, prominent ('true') processus costales, modal number per side (primitive state in bold; ordered): (a) three; (b) four; **(c) five;** (d) six; (e) seven. Note: variable, subjective; see Olson (1975) concerning *Tribonyx hodgenorum*.
153. Corpus sterni, facies muscularis, sulcus ventrolateralis (new term; longitudinal trough on ventral surface of element immediately medial to processus costales): (a) absent or indistinct; (b) distinct, typically for length of margo costalis.
154. Corpus sterni, incisura medialis (if present), angulus cranialis: (a) rounded; (b) pointed. Note: Rhynochetidae, Aptornithidae, Psophiidae, Aramidae, Gruidae not comparable.
155. Carina sterni, margo cranialis, sulcus carinae: (a) absent or shallow; (b) deep, ventrally extensive.
156. Carina sterni, margo cranialis, foramen pneumaticum: (a) absent; (b) typically present in dorsal part of pila carinae.
157. Carina sterni, margo cranialis, sulcus carinae, if present) (ordered): (a) lacking prominent depressions or enclosures; (b) with deep cranial depression that partially encloses single ansa tracheale; (c) greatly enlarged, opening into corpus sterni, enclosing ansae tracheales.
158. Carina sterni, margo cranialis, pila carinae, rounded dorsal prominence (delimited ventrally by sulcus): (a) absent; (b) present.
159. Carina sterni, continued cranioventrally as thin, fenestrated, ossified membrane: (a) absent; (b) present, enclosing ansae tracheales.
160. Carina sterni, apex carina, tuberositas ligamenti sternoclavicularis and facies articularis clavicularis: (a) indistinct; (b) prominent.
161. Carina sterni, apex and margo ventralis (cranially): (a) not laterally thickened; (b) typically laterally thickened relative to more dorsal parts of carina.
162. Rostrum sterni, spina externa: (a) present; (b) absent or obsolete, loss evidently begining medially. Note: shape of spina externa differs modally between *Fulica chathamensis* (rounded point) and *F. prisca* (truncated point, invaginated cranially).
163. Rostrum sterni, spina communis (dorsoventral synostosis of spinae interna et externa): (a) present; (b) absent.

164. Rostrum sterni, spina communis (if present) or spinae interna and externa: (a) not greatly elongate cranially; (b) greatly elongate cranially.

165. Rostrum sterni, spina communis (if present) or spina externa, prominent ventral processus: (a) absent; (b) present.

Ossa cinguli membri thoracici

Clavicula

166. Claviculae: (a) present, synostotic ventrally to form furcula; (b) vestigial, largely cartilaginous, not fused ventrally; (c) vestigial but ossified, probably (but not certainly) fused ventrally into furcula.

167. Scapus (corpus) claviculae, craniocaudal curvature (especially extremitas sternalis): (a) pronounced; (b) modest.

168. Extremitas sternalis claviculae, synostosis with carina sterni, apex carina: (a) absent; (b) present.

169. Extremitas sternalis claviculae, apophysis furculae (hypocleideum): (a) prominent; (b) obsolete. Note: Mesitornithidae not comparable.

170. Extremitas sternalis claviculae, apophysis furculae, processus interclavicularis dorsalis (new term; variably distinct, dorsally orientated tuberculum or processus on dorsal aspect of apophysis): (a) absent; (b) present. Note: Mesitornithidae not comparable. See Fürbringer (1888).

171. Extremitas omalis claviculae, facies articularis acrocoracoidea, foramina pneumatica: (a) absent (rare in Otididae); (b) present.

172. Extremitas omalis claviculae, processus acromialis, dorsal conformation: (a) rounded; (b) acuminate.

173. Extremitas omalis claviculae, processus acrocoracoideus: (a) distinct; (b) obsolete.

Scapula

174. Corpus scapulae, ventral curvature: (a) significant; (b) obsolete, blade essentially straight.

175. Corpus scapulae, relative lateromedial compression: (a) moderate; (b) great.

176. Extremitas cranialis scapulae, acromion, facies costalis, deep ovate depressio: (a) absent; (b) present.

177. Extremitas cranialis scapulae, acromion, cranially elongate processus: (a) absent; (b) present.

178. Collum scapulae, facies costalis, foramen pneumaticum: (a) absent; (b) present.

179. Corpus scapulae, pars caudalis, distinct ventral angling: (a) present, typically marked by angularity in margo dorsalis; (b) absent, corpus monotonically curved.

Coracoideum

180. Extremitas omalis coracoidei, processus acrocoracoideus, orientation with respect to corpus coracoidei: (a) essentially aligned; (b) perpendicular, impressio ligamentum acrocoracohumeralis uniquely deep.

181. Extremitas omalis coracoidei, processus procoracoideus: (a) present; (b) obsolete.

182. Extremitas omalis coracoidei, processus procoracoideus: (a) cranially prominent; (b) cranially truncated. Note: tentative state for *Messelornis* based in part on Hesse (1990).

183. Extremitas omalis coracoidei, processus procoracoideus, ventral prominence: (a) subequal to that of corpus coracoidei; (b) significantly ventral to corpus coracoidei.

184. Extremitas omalis coracoidei, processus procoracoideus, foramen pneumaticum: (a) absent; (b) present. Note: not to be confused with more caudal, apneumatic fenestra n. supracoracoidei that occurs in some Aptornithidae (AMNH 7300) and *Gallirallus australis* (USNM 19021, BMNH 1896.2.16.40).

185. Extremitas omalis coracoidei, facies ventralis, ventral margin of corpus: (a) not cranioventrally prominent; (b) cranioventrally prominent, lateromedially compressed.

186. Extremitas omalis coracoidei, facies dorsalis immediately caudal to processus acrocoracoideus, foramina pneumatica: (a) absent; (b) present.

187. Extremitas omalis coracoidei, processus acrocoracoideus, facies articularis clavicularis: (a) medially prominent, distinctly undercut, terminus caudally orientated, overhanging sulcus m. supracoracoideus, articulating directly with clavicula, extremitas omalis claviculae, facies articularis acrocoracoidei; (b) medially obsolete, failing to articulate directly with clavicula, extremitas omalis claviculae, facies articularis acrocoracoidei, syndesmosis completed by elongate ligamentum acrocoracacromiale.

188. Extremitas omalis coracoidei, processus procoracoideus and processus acrocoracoideus: (a) in close proximity to each other, but separated medially by small gap; (b) typically fused, forming within coracoideum a circumosseus canalis supracoracoideus; (c) well separated. Note: illustration of Phorusrhacoidea in Sinclair & Farr (1932) may not pertain, but specimen indicates simple strut-like bone lacking both processi.

189. Extremitas omalis coradoidei, processus procoracoideus: (a) not continued caudally along margo medialis by crista procoracoidei (new term; variably prominent and extensive crista forming medial margin or element); (b) continued caudally along margo medialis by variably prominent crista, i.e. crista procoracoidei present.

190. Corpus coracoidei, facies ventralis, linea intermuscularis ventralis: (a) passing lateral to ventral prominence or ridge; (b) approximately following ventral prominence or ridge. Note: Phorusrhacoidea non-comparable.

191. Corpus coracoidei (sternalis), facies dorsalis, foramen pneumaticum: (a) absent; (b) present.

192. Corpus coracoidei, length relative to width of facies articularis sternalis: (a) generally less than three times width; (b) greater than four times the width.

193. Corpus coracoidei, cross-sectional shape: (a) cranially roughly circular, caudally essentially flat or slightly concave dorsally; (b) cranially roughly circular, caudally strikingly angular, dorsally deeply concave.

194. Extremitas sternalis coracoidei, margo medialis: (a) lacking medial crista medialis (new term; sternal portion of crista procoracoidei, defined above) (b) with medial, variably prominent crista medialis, continued cranially by crista procoracoidei.

195. Extremitas sternalis coracoidei, facies dorsalis, impressio m. sternocoracoidei: (a) indistinctly margined; (b) distinctly rimmed, variably deep. Note: not comparable in Turnicidae; secondarily reduced in some flightless Rallidae, obsolete in *Capellirallus.*

196. Extremitas sternalis coracoidei, facies articularis sternalis, approximate angle with respect to long axis of corpus coracoidei: (a) perpendicular; (b) moderately obtuse; (c) strongly obtuse.

197. Extremitas sternalis coracoidei, facies articularis sternalis, distinct fovea enclosing foramina neurovascularia: (a) absent; (b) present.

198. Extremitas sternalis coracoidei, facies articularis sternalis, crista dorsalis: (a) significantly cranial to crista ventralis, producing dorsally angled facies articularis; (b) approximately equal to crista ventralis in caudal extent, producing facies articularis essentially perpendicular to corpus.

199. Extremitas sternalis coracoidei, synostosis with sternum, margo cranialis, sulcus articularis coracoideus, braced mediodorsally by narrow osseus, bridging lamina (typically with open canalis ventral to lamina): (a) absent; (b) frequent, probably modal in adults.

Ossa alae (membri thoracici)

Humerus

200. Extremitas proximalis humeri, fossa pneumotricipitalis: (a) single-parted, essentially confined to region ventral to crus dorsalis fossae; (b) two-parted, with prominent fossae dorsal (pars dorsalis) and ventral (pars ventralis) to crus dorsalis fossae. Note: see Bock (1962); Jacanidae variable.

201. Extremitas proximalis humeri, fossa pneumotricipitalis: (a) lacking enclosed foramina pneumatica; (b) including enclosed foramina pneumatica.

202. Extremitas proximalis humeri, fossa pneumotricipitalis, crus dorsale fossae: (a) dorsoventrally narrow; (b) dorsoventrally broad.

203. Extremitas proximalis humeri, prominent tuberculum m. scapulohumeralis cranialis obstructing distal terminus of incisura capitis on corpus humeri, facies caudalis: (a) absent; (b) present.

204. Extremitas proximalis humeri, crista deltopectoralis, margo dorsalis (ordered): (a) rounded, essentially continuously curving, lacking distinct angulus cristae; (b) intermediate between squared off and rounded; (c) squared off, with distinct angulus cristae. Note: *Turnix* uniquely conformed, *Capellirallus* having crista obsolete, non-comparable. Aptornithidae deeply incised, possibly non-comparable.

205. Extremitas proximalis humeri, crista deltopectoralis, terminus distalis: (a) positioned on corpus humeri, margo dorsalis; (b) deflected cranially, positioned on corpus humeri, facies cranialis.

206. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis: (a) essentially flat or convex; (b) distinctly concave. Note: problematic to evaluate for some taxa; *Capellirallus* crista obsolete, non-comparable.

207. Extremitas proximalis humeri, crista deltopectoralis, tuberculum dorsalis: (a) not bordered dorsally by deep sulcus; (b) bordered dorsally by deep sulcus.

208. Extremitas proximalis humeri, crista deltopectoralis, angulus cristae, prominent ventrally directed tuberculum: (a) absent; (b) present.

209. Extremitas proximalis humeri, crista bicipitalis, crus distale fossae (new term; variably pronounced, often caudally concave extension of distal portion of crista bicipitalis): (a) present, merging more or less smoothly with margo cristalis, typically with concavity in facies caudalis; (b) obsolete, typically forming roughly right angle with margo ventralis.

210. Extremitas proximalis humeri, crista bicipitalis, incisura cristae (new term; variably distinct notch at dorsocranial terminus of crista bicipitalis): (a) absent; (b) present. Note: problematical quasi-incisura in some flightless rails.

211. Extremitas proximalis humeri, crista bicipitalis, terminus on corpus humeri, margo ventralis: (a) not continued along corpus humeri, margo ventralis; (b) continued by shallow low but distinct ridge along corpus humeri, margo ventralis.

212. Extremitas proximalis humeri, crista bicipitalis, tuberculum ventrale, and extremitas distalis humeri, processus flexorius, ventral prominence relative to corpus humeri, facies ventralis: (a) negligible; (b) pronounced.

213. Extremitas proximalis humeri, tuberculum dorsale (minus): (a) prominent, distinct distally from crista deltopectoralis; (b) indistinct on facies caudalis, attachment site on proximal margin of element.

214. Extremitas proximalis humeri, facies bicipitalis: (a) slightly to moderately convex proximally; (b) moderately concave proximally.

215. Corpus humeri, facies caudalis, margo caudalis, conformation: (a) essentially rounded; (b) angular, marked by longitudinal eminentia. Note: see 'capital shaft ridge' of Livezey (1986).

216. Extremitas proximalis humeri, planum intertuberculare, intumescentia humeri: (a) outline essentially circular or equilaterally triangular; (b) outline approximating a distally elongate, roughly right triangle. Note: *Aptornis* and *Gallirallus* problematical, possibly non-comparable.

217. Corpus humeri, dorsoventral curvature: (a) moderate; (b) pronounced.

218. Extremitas distalis humeri, epicondylus ventralis (entepicondylus), distal prominence relative to that of condylus ventralis: (a) roughly equal; (b) significantly less; (c) substantially greater.

219. Extermitas distalis humeri, processus flexorius: (a) not distally elongate; (b) distally elongate.

220. Extremitas distalis humeri, tuberculum supracondylaris dorsalis: (a) comparatively proximal in position and prominent; (b) comparatively distal in position and not prominent.

221. Extremitas distalis humeri, tuberculum supracondylaris dorsalis, position relative to condylus dorsalis: (a) opposite or slightly proximal; (b) distinctly distal.

222. Extremitas distalis humeri, sulcus m. humerotricipitis: (a) short, shallow; (b) long, deep.

Ulna

223. Extremitas proximalis ulnae, tuberculum m. extensor longus alulae: (a) not conspicuous; (b) prominent, delimiting an ovate depressio immediately distal to incisura radialis.

224. Extremitas proximalis ulnae, depressio m. brachialis: (a) without prominent, crista brachialis (new term; variably distinct, proximal, undercutting ridge); (b) with prominent crista brachialis proximally.

225. Extremitas proximalis ulnae, processus cotylaris dorsalis: (a) present; (b) obsolete.
226. Extremitas proximalis ulnae, processus cotylaris dorsalis, sulcus radialis (new term; variably deep sulcus undercutting processus along entire margin): (a) present, distinct; (b) absent, evidently caused by continuity between tuberculum m. extensor longus alulae with margin of cotyla.
227. Extremitas proximalis ulnae, olecranon, margo caudalis, tuberculum m. scapulotriceps: (a) indistinct; (b) distinct, blunt, triangular.
228. Extremitas proximalis ulnae, olecranon: (a) essentially rounded or slightly pointed; (b) elongate, acuminate.
229. Extremitas distalis ulnae, trochlea carpalis, sulcus intercondylaris: (a) distinct, rounded; (b) deep, subangular; (c) shallow, indistinct, especially proximally. Note: Aptornithidae not comparable.
230. Extremitas distalis ulnae: (a) typically conformed; (b) truncate, trochlea carpalis, sulcus intercondylaris obsolete.
231. Extremitas distalis ulnae, sulcus radialis: (a) distinct; (b) obsolete.

Radius

232. Corpus radii, distal half, facies ventralis, depressio ligamentosis: (a) shallow, limited to distal one-quarter of corpus; (b) deep, extending almost to midpoint of corpus, producing comparatively flattened facies ventralis.
233. Corpus radii, distal half: (a) not strongly bowed or dorsoventrally compressed; (b) strongly bowed, dorsoventrally compressed.
234. Extremitas distalis radii, margo dorsalis, expansion producing approximate symmetry with tuberculum aponeurosis: (a) absent; (b) present.

Carpometacarpus

235. Carpometacarpus: (a) typical, comprising ossa metacarpale alulare, metacarpale majus, and metacarpale minus, the latter two fused proximally and distally to enclose spatium intermetacarpale; (b) vestigial, ossa metacarpale majus et minus truncated distally, synostosis metacarpalis distalis and extremitas distalis carpometacarpi lacking.
236. Extremitas proximalis carpometacarpi, trochlea carpalis, sulcus trochlearis (new term): (a) shallow, rounded in cranial or caudal view; (b) deep, subangular in cranial or caudal view. Note: Aptornithidae not comparable.
237. Extremitas proximalis carpometacarpi, trochlea carpalis, facies articularis ulnocarpalis, labrum dorsalis (new term; dorsal rim of trochlea), extent relative to labrum ventralis (new term; ventral rim of trochlea): (a) terminates well proximad, extends only to proximal margin of fovea carpalis caudalis; (b) subequal, reaching point opposite midpoint of fovea carpalis caudalis. Note: Aptornithidae not comparable.
238. Extremitas proximalis carpometacarpi, trochlea carpalis, labrum dorsalis, apex proximalis (new term; proximal terminus of dorsal rim of trochlea): (a) weakly angular; (b) rounded; (c) strongly angular, almost pointed, elongated proximally. Note: Aptornithidae not comparable.
239. Extremitas proximalis carpometacarpi, os metacarpale alulare, processus extensorius: (a) not prominent; (b) prominent, typically rugose, dorsoventrally thickened into 'spur'. Note: Aptornithidae not comparable.
240. Extremitas proximalis carpometacarpi, fovea carpalis cranialis: (a) shallow, indistinct; (b) deep, distinct.
241. Extremitas proximalis carpometacarpi, fovea carpalis caudalis (ordered): (a) shallow, indistinct; (b) moderately deep, distinct; (c) very deep, comparatively extensive, forming distinct sulcus immediately dorsal to trochlea carpalis, facies articularis ulnocarpalis. Note: intraspecific variation, e.g. some *Gallinula* (especially *tenebrosa*) atypically deep *Habropteryx insignis* and *Nesoclopeus* (*p.*) *woodfordi* tending to state 'c'; Aptornithidae not comparable.
242. Extremitas proximalis carpometacarpi, facies ventralis, crista infratrochlearis (new term; ridge between processus pisiformis and trochlea carpalis): (a) narrow, not prominent; (b) thick, prominent. Note: Aptornithidae not comparable.
243. Extremitas proximalis carpometacarpi, synostosis metacarpalis proximalis: (a) well distal and caudal to processus pisiformis; (b) immediately distal to processus pisiformis. Note: Aptornithidae not comparable.
244. Extremitas proximalis carpometacarpi, os metacarpale minus, tuberculum intermetacarpalis (new term; small tuberculum on os metacarpale minus, facies ventralis, immediately distal to synostosis metacarpalis proximalis): (a) distinct; (b) elongate; (c) obsolete. Note: Aptornithidae not comparable. Character referred to by Hesse (1990) as '*Fortsatz*'.
245. Extremitas proximalis carpometacarpi, os metacarpale minus, tuberculum intermetacarpalis (if present), marked elongation: (a) absent; (b) present, typically protruding over spatium intermetacarpale, in some fusing to os metacarpale majus to form arcus intermetacarpalis (new term; ossified tendinous loop between proximodorsal portions of oss metacarpalia majus et minus), thereby occluding spatium intermetacarpale immediately distal to synostosis proximalis. Note: Aptornithidae not comparable.
246. Extremitas proximalis carpometacarpi, os metacarpale minus, proximal half, facies caudalis: (a) essentially coplanar with that of os metacarpale majus; (b) markedly rotated ventrally, at approximately 45° angle with that of os metacarpale majus. Note: Aptornithidae not comparable.
247. Extremitas proximalis carpometacarpi, os metacarpale minus, dorsoventral depth at synostosis proximalis: (a) broad, subequal to that of os metacarpale; (b) narrowed, reduced dorsally, approximately half of that of os metacarpale majus. Note: Aptornithidae not comparable.
248. Extremitas proximalis carpometacarpi, collum carpometacarpi (new term; region between processus alularis and synostosis metacarpalis proximalis): (a) not proximodistally compressed; (b) proximodistally foreshortened. Note: Aptornithidae not comparable.
249. Corpus carpometacarpi, os metacarpale majus, processus intermetacarpalis: (a) present; (b) obsolete.

Note: associated with insertion of m. flexor carpi ulnaris. Aptornithidae not comparable.

250. Corpus carpometacarpi, os metacarpale majus, facies ventrocaudalis (bordering spatium intermetacarpale): (a) angular, distinctly convex, with centrally aligned, longitudinally continuous prominence; (b) essentially flat. Note: Aptornithidae not comparable.

251. Corpus carpometacarpi, os metacarpale minus, craniocaudal curvature: (a) virtually absent, ossa metacarpalia majus et minus essentially parallel throughout majority of lengths; (b) distinct throughout lengths, in some (marked by asterisks) variably obscured by craniocaudal broadening of extremitas distalis carpometacarpi. Note: Aptornithidae not comparable. Some flightless rallids tend to state 'b' with shortening of element.

252. Corpus carpometacarpi, os metacarpale minus, facies caudalis: (a) proximally flat; (b) distinctly concave, trough-like. Note: Aptornithidae not comparable.

253. Extremitas distalis carpometacarpi, synostosis metacarpalis distalis, sulcus interosseus ventralis: (a) absent; (b) present, but shallow. Note: problematic determinations numerous; Aptornithidae not comparable.

254. Extremitas distalis carpometacarpi, synostosis metacarpalis distalis, sulcus interosseus dorsalis (variable): (a) broad, deep, bounded cranially and caudally by distally extensive cristae; (b) narrow, shallow, not bounded caudally by crista. Note: Otididae variable, Aptornithidae not comparable.

255. Extremitas distalis carpometacarpi, facies articularis digitalis major: (a) not distally prominent; (b) distally prominent. Note: Aptornithidae not comparable.

Ossa digitorum manus

256. Phalanges digitorum manus: (a) present; (b) absent.

257. Phalanx digiti alulae, tuberculum aponeurosis distocaudalis (new term; variably distinct tuberculum on distocaudal portion of element associated with insertion of mm. abductor alulae et extensor brevis alulae): (a) absent; (b) present. Note: Aptornithidae not comparable.

258. Phalanx proximalis digiti majoris, processus distocaudalis (new term; variably prominent, angular eminentia at distocaudal margin of element): (a) prominent, extending farther distally than facies articularis phalangealis; (b) small or obsolete, in rallids sometimes resulting in phalanx proximalis being slightly shorter than phalanx distalis. Note: Aptornithidae not comparable.

259. Phalanx distalis digiti majoris, tuberculum aponeurosis (new term; variably distinct tuberculum on caudal margin of distal end of element, associated with insertion of mm. interosseus ventralis et dorsalis): (a) present; (b) absent. Note: character states weakly defined in some taxa; Charadriiformes variable, Aptornithidae not comparable.

Ossa cinguli membri pelvici

Os coxae

260. Fenestra ischiopubica: (a) comparatively large; (b) reduced to narrow slit. Note: intraspecifically variable; *Gallirallus dieffenbachii* approaches state 'b'.

261. Foramen ilioischiadicum, modal shape (lateral perspective): (a) distinctly oblong, major axis craniocaudally orientated; (b) distinctly oblong, cranial extreme distinctly dorsal to caudal extreme; (c) approximately circular.

262. Canalis iliosynsacralis: (a) present; (b) obsolete. Note: intraspecifically variable.

263. Fossa renalis, recessus caudalis fossae (ordered): (a) essentially absent; (b) present, comparatively shallow, ventral enclosure by ilium terminating well caudad to foramen ilioischiadicum; (c) present, deep, ventral enclosure by ilium terminating at caudal margin of foramen ilioischiadicum; (d) present, very deep, ventral enclosure by ilium extending medially to point cranial to caudal terminus of foramen ilioischiadicum. Note: Hesse (1990) used this term to refer to incisura marginis caudalis; for Jacanidae, see Lowe (1925).

264. Fossa renalis, recessus iliacus, pars pudenda, cranial terminus (recessus dorsolateral to corpus ilii, crista iliaca intermedia) and caudal terminus (recessus iliacus), pori pneumatici: (a) absent; (b) present. Note: intraspecific variation in *Aramides* necessitated polymorphic coding.

265. Incisura marginis caudalis: (a) shallow; (b) deep. Note: Hesse (1990) united *Eurypyga*, *Rhynochetos*, and *Messelornis* (but not *Aptornis*) by apparently same character, under the name 'recessus iliacus'.

Ilium

266. Corpus ilii, processus antitrochantericus, relative lateral prominence: (a) moderate; (b) great.

267. Corpus ilii, processus antitrochantericus, mediocaudal surface (cranial border of foramen ilioischiadicum), foramina pneumatica: (a) absent; (b) typical.

268. Corpus ilii, crista iliaca intermedia, dorsoventral position of terminus on facies lateralis of fossa renalis: (a) significantly dorsal to acetabulum; (b) coplanar with acetabulum, margo dorsalis.

269. Corpus ilii, tuberculum preacetabulare, sulcus preacetabularis (new term; sulcus immediately craniodorsal to tuberculum preacetabulare), enclosed foramina pneumatica: (a) absent; (b) typical. Note: Otididae variable.

270. Corpus ilii, tuberculum preacetabulare: (a) present; (b) obsolete. Note: intraspecifically variable.

271. Corpus ilii, dorsoventral curvature: (a) moderate; (b) pronounced.

272. Ala preacetabularis ilii, margo cranialis: (a) essentially straight; (b) with rounded indentation.

273. Ala preacetabularis ilii, margo cranialis, processus cranioventralis (new term; cranioventral vertex of terminis of ala): (a) rounded or squared; (b) an elongate, laterally prominent, angular flange.

274. Ala preacetabularis ilii, relative interacetabular width (ordered, primitive in bold): (a) great, exceeds one-half synsacral length; **(b) moderate**, one-half to one-third synsacral length; (c) small, approximately one-quarter synsacral length; (d) extremely small, approximately one-sixth synsacral length. Note: in states 'c' and 'd', antitrochanter lateral to ilium, ala postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis.

275. Ala preacetabularis ilii, margo medialis, crista iliaca dorsalis, dorsal prominence: (a) equals or exceeds dorsal prominence of vertebrae thoracicae, synsacrum, crista dorsalis; (b) significantly less than dorsal prominence of vertebrae thoracicae, synsacrum, crista dorsalis. Note: evidently equivalent to differently coded 'interparapophyseal area of the preacetabular sacrum' of Olson & Steadman (1981). Problematic codings frequent.

276. Ala preacetabularis ilii, margo medialis, crista iliaca dorsalis: (a) variably dorsal to vertebrae thoracicae, synsacrum, facies dorsalis, crista dorsalis; (b) articulates with vertebrae thoracicae, synsacrum, facies dorsalis, processus transverses.

277. Ala preacetabularis ilii, margo medialis, crista iliaca dorsalis, pronounced lateromedial compression with synostosis of alae medially to synsacrum: (a) absent; (b) present, in those with alae dorsal to synsacrum, synostotic where also. Note: see preceeding characters, which alters appearance of synostosis.

278. Ala preacetabularis ilii, margo medialis, crista iliaca dorsalis (in some paralleled by underlying synsacrum, crista dorsalis): (a) essentially flat; (b) convex, conspicuously bowed.

279. Ala postacetabularis ilii, facies dorsalis, fossa iliocranialis (new term; depression immediately caudomedial to craniolateral vertex of ala): (a) absent; (b) present.

280. Ala postacetabularis ilii, facies dorsalis, fossa iliocaudalis: (a) present; (b) absent. Note: Charadriiformes somewhat variable, Pedionomidae weakly differentiated.

281. Ala postacetabularis ilii, facies dorsalis, elements immediately caudal to acetabula and adjacent to vertebrae thoracicae, synsacrum, pronounced convexity: (a) absent; (b) present, forming lateromedially narrow depressio along midline of synsacrum.

282. Ala postacetabularis ilii, margo lateralis, crista dorsolateralis ilii, vertex craniolateralis (new term; variably angular or tubercular craniolateral terminus of ala dorsal to acetabulum): (a) not prominent; (b) prominent, forming ventrally concave surface overhanging ala ischii, facies lateralis.

283. Ala postacetabularis ilii, margo lateralis, crista dorsolateralis ilii, vertex craniolateralis (see above), tuberculum craniolateralis (new term; elongation of vertex craniolateralis, defined above): (a) absent; (b) present.

284. Ala postacetabularis ilii, margo lateralis, crista dorsolateralis ilii: (a) prominent; (b) indistinct or obsolete at caudal margin; (c) indistinct or obsolete significantly cranial to caudal margin. Note: Alcidae variable, Pedionomidae weakly differentiated.

285. Ala postacetabularis ilii, margo lateralis, crista dorsolateralis ilii, angulus caudolateralis (new term; variably angular eminentia at caudolateral margin of element): (a) absent; (b) present.

286. Ala postacetabularis ilii, margo lateralis, crista dorsolateralis ilii, angulus caudolateralis (where present): (a) marked by a comparatively small, rounded, laterally directed prominence; (b) marked by a comparatively prominent, ventrally curved flange, undercut by a deep concavitas infracristalis.

287. Ala postacetabularis ilii, margo lateralis, crista dorsolateralis ilii, between angulus caudolateralis (where present) and processus dorsolateralis: (a) essentially straight or slightly concave; (b) deeply concave, giving angulus caudolateralis the appearance of a caudally prominent processus.

288. Ala postacetabularis ilii, processus terminalis ilii, spina dorsolateralis: (a) not medially directed; (b) medially directed, margo mediocaudalis concave, forming lyre-shaped spatium between ilia.

289. Ala postacetabaluris ilii, processus terminalis ilii, spina dorsolateralis: (a) not medially deflected so as to enclose vertebrae caudales in ventral direction; (b) medially deflected so as to enclose vertebrae caudales in ventral direction.

290. Ala postacetabularis ilii, processus terminalis ilii, processus (spina) dorsolateralis: (a) essentially coplanar with facies dorsalis; (b) dorsally recurved.

291. Ala postacetabularis ilii, facies dorsalis, caudal extent relative to fossa renalis, recessus iliacus, terminus caudalis: (a) small, roughly length of two synsacral vertebrae; (b) great, roughly length of four or five synsacral vertebrae.

292. Ala postacetabularis ilii, facies ventralis, caudal to fossa renalis, recessus iliacus: (a) shallow cranially; (b) deep cranially, with pori pneumatici. Note: Otididae prominently pneumatic.

293. Ala postacetabularis ilii, facies ventralis, facies renalis ilii: (a) concave, sloping, delimiting comparatively shallow fossa renalis, recessus iliacus; (b) flat or convex, delimiting comparatively dorsoventrally deep fossa renalis, recessus iliacus.

Ischium

294. Corpus ischii, processus obturatorius, synostosis with corpus pubis: (a) absent; (b) present, forming circumosseus foramen obturatum.

295. Ala ischii, processus terminalis ischii: (a) conspicuously greater in caudal extent than ala postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis, processus (spina) dorsolateralis; (b) subequal to or only moderately greater in caudal extent than ala postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis, processus (spina) dorsolateralis. Note: Rostratulidae intermediate, Otididae unique.

296. Ala ischii, processus terminalis ischii, orientation: (a) ventrocaudal; (b) conspicuously ventral.

297. Ala ischii, processus terminalis ischii, margo ventralis: (a) essentially continuous with margo ventralis of cranial portion of ala ischii; (b) distinctly angled dorsally.

298. Ala ischii, processus terminalis ischii, ventrocaudally directed flange: (a) absent; (b) present.

Pubis

299. Corpus pubis, medial curvature: (a) slight to moderate, apices not closely approaching each other; (b) great, apices virtually touching each other medially.

300. Apex pubis, margo dorsalis, small subterminal tuberculum opposite ischium, ala ischii, processus terminalis ischii, tuberculum ischiacus (new term; small prominence on margo dorsalis of apex pubis, evidently marks ligamentous attachment to ischium): (a) absent; (b) present. Note: for taxa showing state 'b', variable intraspecifically, significantly affected by differences in preparation and wear, and proportional to body size.

Ossa membri pelvici

Femur

301. Extremitas proximalis femoris, trochanter femoris, crista trochanteris, facies caudalis distal to facies articularis antitrochantericus: (a) lacking distinct, distal thickening; (b) thickening weakly developed.

302. Extremitas proximalis femoris, trochanter femoris, crista trochanteris, facies craniomedialis, great proximal elongation (height from facies articularis antitrochanterica exceeding dorsoventral depth of caput femoris) and foramen pneumaticum: (a) absent; (b) present.

303. Extremitas proximalis femoris, trochanter femoris, crista trochanteris, cranial prominence: (a) moderate; (b) great.

304. Corpus femoris, craniocaudal curvature (medial perspective): (a) negligible; (b) moderate.

305. Extremitas distalis femoris, fossa poplitea: (a) shallow; (b) deep, in part related to caudal prominence of caudomedial extremity of condylaris medialis.

306. Extremitas distalis femoris, facies cranialis, immediately proximal to cranioproximal terminus of condylaris lateralis, crista tibiofibularis: (a) grading smoothly on to corpus femoris, facies cranialis; (b) distinctly depressed relative to corpus femoris, facies cranialis, forming shallow trough toward laterally bowed margin of corpus femoris.

307. Extremitas distalis femoris, condylus medialis (medial perspective): (a) rounded or weakly angular; (b) prominently angular, with vertex directed distally. Note: variable, weakly differentiated character in some taxa.

308. Extremitas distalis femoris, epicondylus medialis, cranioproximal terminus on corpus femoris, facies cranialis: (a) prominently elevated, typically tubercular; (b) not prominently elevated, grading essentially smoothly.

309. Extremitas distalis femoris, crista supracondylaris medialis, tuberculum m. gastrocnemialis medialis: (a) moderately prominent; (b) very prominent caudally, perpendicular to corpus femoris, facies caudalis.

310. Extermitas distalis femoris, crista supracondylaris medialis: (a) without prominent, rugose, proximally extensive ridge; (b) with prominent, rugose, proximally extensive, typically straight ridge.

311. Extermitas distalis femoris, crista supracondylaris medialis, tuberculum m. gastrocnemialis medialis: (a) small, with concavity between epicondylaris medialis and corpus femoris; (b) prominent, with essentially straight or convex slope between epicondylaris medialis and corpus femoris.

312. Extremitas distalis femoris, impressio ansae m. iliofibularis: (a) immediately proximal to condylaris lateralis on facies laterocranialis; (b) separated from condylaris lateralis by conspicuous area of smooth bone on facies laterocranialis.

Patella

313. Patella (as osseus element): (a) absent; (b) present.

Tibiotarsus

314. Extremitas proximalis tibiotarsi, crista patellaris: (a) prominent, with distally directed tuberculum; (b) obsolete, lacking tuberculum.

315. Extremitas proximalis tibiotarsi, crista cnemialis (tibialis) cranialis, linea extensoria: (a) not raised into medially slanting crista along corpus tibiotarsi, facies cranialis; (b) a distinct, medially slanting crista along corpus tibiotarsi, facies cranialis.

316. Extremitas proximalis tibiotarsi, crista cnemialis (tibialis) cranialis, proximal extent (ordered): (a) moderate; (b) of intermediate size; (c) comparatively great, well proximal to extremitas proximalis tibiotarsi, facies articulares medialis et lateralis throughout its width. Note: purported difference between *Fulica chathamensis* and *F. prisca* in prominence and orientation of crista cnemialis (tibialis) lateralis (Millener 1980).

317. Extremitas proximalis tibiotarsi, area intercondylaris: (a) present; (b) obsolete.

318. Extremitas proximalis tibiotarsi, fossae retrocristales (especially medialis): (a) comparatively shallow; (b) very deep, frequently almost perforating element proximally.

319. Corpus tibiotarsi, crista fibularis: (a) moderately prominent; (b) obsolete.

320. Corpus tibiotarsi, foramen interosseum distale, length relative to that of foramen interosseum proximale: (a) short, little longer than foramen interosseum proximale; (b) long, significantly longer than foramen interosseum proximale.

321. Corpus tibiotarsi, linea extensoria, tuberositas distalis retinaculi mm. extensorum: (a) small, located at medioproximal terminus of extremitas distalis tibiotarsi, condylaris lateralis; (b) conspicuously enlarged, located well medial to extremitas distalis tibiotarsi, condylus lateralis.

322. Corpus tibiotarsi, sulcus extensorius: (a) deep, mediodistally delimited by distinct, typically laterally concave wall; (b) shallow, mediodistal border indistinct.

323. Corpus tibiotarsi, sulcus extensorius, canalis extensorius: (a) not strongly medially deflected; (b) strongly medially deflected.

324. Corpus tibiotarsi, facies cranialis: (a) variably rounded (convex) for much of its length; (b) flat or slightly concave for much of its length.

325. Extremitas distalis tibiotarsi, condylus lateralis: (a) essentially rounded; (b) flattened or (typically) 'notched' distally.

326. Extremitas distalis tibiotarsi, condylus medialis, margo medialis: (a) variably flattened distally, with shallow, distal 'notch'; (b) rounded distally, lacking distal 'notch'.

327. Extremitas distalis tibiotarsi, tuberositas retinaculi m. fibularis (peronei): (a) only moderately developed; (b) prominent, typically ossified cranially to form arcus. Note: intraspecifically variable.

328. Extremitas distalis tibiotarsi, trochlea cartilaginis tibialis, crista sulci: (a) prominent, termination as thin, distinct rim, proximal terminus forming abrupt angulus with corpus tibiotarsi, facies caudalis; (b) not prominent, caudally rounded, proximal terminus sloping gradually at shallow angulus with corpus tibiotarsi, facies caudalis. Note: intraspecific variation frequent.

329. Extremitas distalis tibiotarsi, relative cranial prominence (relative to corpus tibiotarsi, facies cranialis) of condyla medialis et lateralis: (a) condylus medialis not conspicuously more cranially prominent than condylus lateralis; (b) condylus medialis conspicuously more cranially prominent than condylus lateralis.

330. Extremitas distalis tibiotarsi, incisura intercondylaris, area intercondylaris: (a) limited to central area; (b) extends medially, especially deep immediately proximal to condylus medialis. Note: depressio accommodates (at maximal flexion) the tarsometatarsus, extremitas proximalis tarsometatarsi, eminentia intercondylaris.

Fibula

331. Corpus fibulae, spina fibulae: (a) essentially cylindrical throughout; (b) papery thin, slightly curved, craniocaudally compressed, cranially concave distal to tuberculum m. iliofibularis.

Tarsometatarsus

Homologies of hypotarsal tendons interpreted using Hudson (1937), Berger (1956*a*), Strauch (1978) and Rosser *et al.* (1982).

332. Extremitas proximalis tarsometatarsi, cotyla lateralis, sulcus craniocotylaris (new term; sulcus in labrum dorsalis immediately lateral to eminentia, associated with relative proximal prominence of cotylae lateralis et medialis: (a) shallow or obsolete, cotylae lateralis et medialis essentially equally prominent; (b) comparatively deep, cotyla lateralis less prominent proximally than cotyla lateralis. Note: basal polarity indeterminate.

333. Hypotarsus, crista lateralis hypotarsi, spina lateralis hypotarsi (new term; distally directed spina from crista lateralis): (a) absent or miniscule; (b) prominent.

334. Hypotarsus, crista intermedia hypotarsi, spina intermedia hypotarsi (new term; distally directed spina from crista intermedia): (a) absent; (b) present.

335. Hypotarsus, crista medialis hypotarsi, crista plantaris mediana, spina medialis hypotarsi (new term; distally directed spina from crista medialis): (a) absent; (b) present (sometimes extending distodorsally to fuse with corpus tarsometatarsi, facies plantaris by ligamentum ossificans in Aptornithidae).

336. Hypotarsus, lamina medialis hypotarsi (new term; refers to total dorsoplantar lamina, including exposed crista, plantar to corpus tarsometatarsi, facies plantaris), plantar prominence relative to corpus tarsometatarsi, facies plantaris (associated with lateromedial compression of hypotarsus and enlargement of fossae parahypotarsalis medialis et lateralis): (a) greater than or equal to that of lamina lateralis hypotarsi; (b) less than or equal to that of lamina lateralis hypotarsi.

337. Hypotarsus, dorsomedial passage for M. flexor digiti longus (tendinal canal 1 of Strauch (1978)), plantar closure (modal): (a) present, producing closed canalis; (b) absent, producing open sulcus. Note: character states weakly defined in some taxa. Basal polarity indeterminate.

338. Hypotarsus, dorsolateral passage for M. flexor hallicus longus (tendinal canal 3 of Strauch (1978)), plantar closure (modal): (a) absent, producing open sulcus; (b) present, producing closed canalis.

339. Hypotarsus, within plantar closure of dorsolateral passage (if present), lamina partitioning canalis for M. flexor perforatus digiti IV and M. flexor perforans et perforatus digiti II (tendinal canal 2 of Strauch (1978)), and M. flexor hallicus longus (tendinal canal 3 of Strauch (1978)) from canalis for M. flexor digiti longus (tendinal canal 1 of Strauch (1978)): (a) present; (b) absent.

340. Hypotarsus, uniformly elevated, block-like plantar prominence lacking distinct sulcus or canalis: (a) absent; (b) present.

341. Fossa parahypotarsalis medialis, distal extent relative to hypotarsus, crista medialis hypotarsi: (a) significant; (b) narrow or obsolete.

342. Fossa parahypotarsalis medialis, conformation: (a) moderately developed; (b) conspicuously enlarged (associated with apparent lateral shift of hypotarsus), deep, length being greater than or equal to one-half that of corpus tarsometatarsi, and width being greater than or equal to one-half that of corpus tarsometatarsi; (c) markedly deep, narrow, short, roughly triangular, with irregular margins.

343. Fossa infracotylaris dorsalis, tuberositas m. tibialis cranialis: (a) comparatively small, outline indistinct, with dorsal surface rounded; (b) comparatively large, distinct, with dorsal surface flat.

344. Corpus tarsometatarsi, general aspect: (a) not as follows; (b) lateromedially broad, dorsoplantad thick, short.

345. Corpus tarsometatarsi, sulcus extensorius, arcus extensorius: (a) absent; (b) present. Note: variation associated with age and preparation of specimen, and wear (especially subfossil specimens).

346. Corpus tarsometatarsi, sulcus extensorius: (a) well defined both medially and laterally by ridges of bone for most of corpus; (b) not defined distomedially, associated with evident torsion of corpus about long axis.

347. Corpus tarsometatarsi, sulcus extensorius, deep medial depression: (a) absent; (b) present.

348. Corpus tarsometatarsi, sulcus flexorius, crista plantaris lateralis, prominence immediately distal to extremitas proximalis tarsometatarsi, area intercondylaris, sulcus ligmentosus, and merging distally with sulcus flexorius, crista plantaris medialis just proximal to bases of trochlea metatarsi: (a) absent; (b) present.

349. Extremitas distalis tarsometatarsi, foramen vasculare distale: (a) present; (b) obsolete through loss of distal margin.

350. Extremitas distalis tarsometatarsi, foramen vasculare distale (where present), facies plantaris: (a) not marked by distal sulcus; (b) continued distally by sulcus to incisura intertrochlearis lateralis. Note: Aptornithidae non-comparable.

351. Extremitas distalis tarsometatarsi, trochlea metatarsi secundi, eminentia plantaris (new term; wing-like flange on plantar surface): (a) moderately developed; (b) conspicuously enlarged.

352. Extremitas distalis tarsometatarsi, trochlea metatarsi secundi, plantar prominence: (a) equal to that of trochlea metatarsi quarti; (b) exceeds that of trochlea metatarsi quarti.

353. Extremitas distalis tarsometatarsi, trochlea metatarsi secundi, distal prominence: (a) subequal to that of trochlea metatarsi quarti, distal terminus opposite the middle of trochlea metatarsi quarti; (b) essentially equal to that of trochlea metatarsi quarti; (c) significantly less than that of trochlea metatarsi quarti, distal terminus opposite base of trochlea metatarsi quarti. Note: basal polarity indeterminate.

354. Extremitas distalis tarsometatarsi, trochlea metatarsi secundi, facies articularis phalangealis, sulcus trochlearis (new term; narrow groove between lateral and medial rims of trochlea): (a) obsolete on facies dorsalis, terminating medially toward fovea ligamentorum collateralium at distal apex of trochlea; (b) remains distinct on facies dorsalis.

355. Extremitas distalis tarsometatarsi, trochlea metatarsi quarti, lateral prominence relative to corpus tarsometatarsi, margo lateralis (ordered): (a) well lateral, trochlea secundi et quarti symmetrical in lateral deflection from corpus; (b) only slightly to moderately lateral; (c) colaterally aligned, lateral divergence negligible. Note: variable intraspecifically, subtle modal difference only evident in comparisons of series.

356. Extremitas distalis tarsometatarsi, trochlea metatarsi quarti, eminentia plantaris (new term; wing-like crista on facies plantaris): (a) not prominent, palmar extent significantly less than that of trochlea metatarsi secundi; (b) conspicuously prominent, palmar extent subequal to that of trochlea metatarsi secundi. Note: not to be confused with flange on plantar surface of trochlea metatarsi secundi, common in many genera.

Ossa digitorum pedis

357. Hallux: (a) present; (b) absent. Note: in state ‘b’, all parts of the digit (os metatarsale I and phalanges proximalis and distalis) are lost. Polarity supported also by reference to secondary (ordinal) outgroups.

358. Digiti tertius, phalanx intermedialis (secundi): (a) modally shorter than phalanx distalis (tertius); (b) equal to or (typically) longer than phalanx quartus.

359. Digiti quartus, phalanges tertius et quartus, relative lengths (ordered): (a) tertius shorter than quartus; (b) tertius essentially equal to quartus, but tending toward state ‘c’; (c) tertius longer than quartus. Note: Alcidae variable. Proposed as synapomorphy for Charadriiformes by Hesse (1992).

360. Phalanges ungulares, relative length: (a) moderately short, stout, and curved; (b) long (approaching in length that of articulating, penultimate phalanx in length of corpus), slender, less curved.

361. Phalanges ungulares, curvature: (a) moderately stout, curved; (b) sharply hooked, raptorial.

Myologia

362. Musculi membri pelvici, tendo ossificans: (a) absent or limited to partial ossification of tendo of M. flexor digitorum longus; (b) typical in several or most musculi. Note: basal polarity indeterminate. States for Charadriiformes based on M. C. McKitrick (unpublished data). Especially conspicuous in species with large body size.

Integumentum natalis

363. Corona, single, broad naked area: (a) absent; (b) present.

364. Corona, three longitudinal, naked strips: (a) absent; (b) present.

365. Plumae, corona, bilaterally paired crown stripes, convergent or confluent on nape: (a) present; (b) absent. Note: basal polarity indeterminate.

366. Plumae, facies, regio orbitalis, contrastingly dark orbital stripe: (a) present; (b) absent. Note: basal polarity indeterminate.

367. Plumae, facies, short, orange plumae at base of bill: (a) absent; (b) present.

368. Plumae, facies, regio gularis, bilateral, dark throat stripes: (a) absent; (b) present.

369. Plumae, long, filamentous, white filoplumae: (a) absent; (b) present, limited to facies; (c) present, limited to facies and dorsum; (d) present, distributed throughout.

370. Plumae, dorsum, contrasting, longitudinal band(s), often paired and variably curved: (a) present; (b) absent. Note: basal polarity indeterminate. Relative darkness and homologies of bands and intervening spaces problematic. States for Charadriiformes based in part on Jehl (1968) and P. C. Chu (unpublished data).

371. Plumae, dorsum, ground colour (unform with ventrum in most Rallidae): (a) medium or dark brown; (b) pale grey; (c) bright cinnamon; (d) silver; (e) black. Note: Charadriiformes variable, and Pedionomidae, Turnicidae and Otididae heavily mottled with pale. Blackish brown of *Gallirallus,* and allies suggestive of distinct state but problematic as it is confounded with foxing in older skins.

372. Plumae, dorsum, contrastingly pale mottling (often including ventrum): (a) present; (b) absent.

373. Plumae, ventrum: (a) distinctly paler than dorsum; (b) only negligibly paler than dorsum or uniformly dark.

374. Condition at hatching: (a) precocial; (b) altricial.

Integumentum definitivum

Glandulae cutaneae

375. Glandula uropygialis: (a) present; (b) absent. Note: see Johnston (1988).

Plumae

376. Pulviplumae (powder down); (a) absent; (b) present, confined to five paired regions; (c) present, diffuse.

Pennae contourae

377. Pennae contourae, hypopenna (aftershaft): (a) present; (b) absent.

378. Collum, pennae contourae, vexilla loose, having filmentous, almost hirsute aspect: (a) absent; (b) present.

379. Qualitative sexual dichromatism: (a) absent; (b) present, andro-apomorphic or typical, i.e. derived plumage (i.e. most divergent from juvenile condition) limited to males, often seasonally manifested; (c) present, gyno-apomorphic or 'reversed', i.e. derived plumage (i.e. most divergent from juvenile condition) limited to females, often seasonally manifested. Note: basal polarity indeterminate. Negligible in *Ortyxelos*. Whether *Monias* is state 'b' or state 'c' is problematic, in part because of poor representation of specimens and comparatively weak development. Variation within *Porzana pusilla*, *P. porzana*, and *P. carolina* apparently age-related and limited to variably subtle quantitative differences and confounded by comparatively marked seasonal and age-related variation.
380. Pteryla alae, remiges secundarii, diastema remigum secundarium: (a) present, producing diastataxy; (b) absent, producing eutaxy. Note: see Miller (1924), Steiner (1956, 1958), review by Sibley & Ahlquist (1990). *Laterallus* and *Sarothrura* reportedly polymorphic, but these and supposed absence in *Anurolimnas*, *Rallicula* and *Gallirallus dieffenbachii* considered errors stemming from superficial assessments of study skins.
381. Remiges primarii et secundarii, moult: (a) sequential; (b) synchronous. Note: based largely on Stresemann & Stresemann (1966); limited variation is some taxa (e.g. *Leucogeranus*), especially captives.

Rhamphotheca

382. Ground colour: (a) 'yellow', with variably pronounced green or orange tones (*Psophia crepitans* comparatively brownish, *Grus americana* comparatively greenish, *Gymnocrex rosenbergii* blackish, *Nesoclopeus poecilopterus* bright orange, *Edithornis* comparatively red, *Fulica* variably patterned); (b) 'brown', including 'greyish' (*Anthropoides virgo* problematic, *Gallirallus sharpei* apparently comparatively orange, *G. australis* pinkish); (c) 'black' or 'blackish' (*Rallicula*, *Sarothrura*, and *Micropygia* brownish, *Laterallus leucopyrrhus* with yellow base of mandibula; some *Porzana* dark greenish gray); (d) 'red' or 'reddish orange' (*Rougetius* blackish, '*Rallus*' *madagascariensis* rosy). Note: problematic to characterize for many taxa, relied most heavily on photographs of living specimens, label data, text descriptions and illustrations.
383. Contrasting white colour: (a) absent; (b) present, restricted to dorsal basal part of maxilla; (c) present, encompassing entire bill.
384. Maxilla, depressio naris, conformation as broad and deep, contrasting blackish colouration: (a) absent; (b) present.
385. Maxilla and mandibula, blurred, variably distinct, reddish basal suffusion: (a) absent; (b) present. Note: see following characters.
386. Maxilla, basal, contrasting suffusion of orange: (a) absent; (b) present.
387. Mandibula, sharply contrasting red subterminal spot: (a) absent; (b) present.
388. Maxilla and mandibula, contrastingly pinkish basal region: (a) absent ('*Rallus*' *madagascariensis* obscured by uniformly 'rosy' colour); (b) present.
389. Maxilla, bilateral patches of small whitish caruncles: (a) absent; (b) present.
390. Maxilla, contrastingly black culmen stripe: (a) absent; (b) present.
391. Maxilla, culmen immediately anterior to aperturae nasales, slight but distinct dorsal concavity or recurvature: (a) absent; (b) present.
392. Maxilla and mandibula, contrasting subterminal reddish-brown bars: (a) absent; (b) present.
393. Crista cornea frontalis (ordered): (a) absent; (b) present, but short, thin, dorsally concave, posteriorly rounded, a 'false' frontal shield; (c) present, well developed, but variably shaped in adults, a 'true' frontal shield (*Fulica chathamensis* coded by condition of maxilla). Note: raised, roughened area at base of maxilla in some large specimens of *Diaphorapteryx* suggests that adult males possessed some kind of shield or caruncle at base of the bill.
394. 'True' crista cornea frontalis (if present), margo posterior: (a) rounded (*Gallicrex* excluding crista or 'horn'); (b) squared; (c) acuminate.
395. Maxilla and crista cornea frontalis (if present), proximal suffusion of orange: (a) absent; (b) present, but not encompassing entire 'crista cornea frontalis'; (c) present, but 'true' crista frontalis lacking; (d) present, encompassing entire 'crista cornea frontalis'; (e) present, 'crista cornea frontalis' lacking. Note: *Tribonyx mortierii* may rarely approach state 'b' (photograph).
396. Crista cornea frontalis (if present), bright yellow colour in sharp contrast to white of maxilla and mandibula: (a) absent; (b) present.
397. Crista cornea frontalis (if present), margo caudalis, contrasting red coloration: (a) absent; (b) present.
398. Crista cornea frontalis (if present), distinctly swollen, uniquely convex dorsal surface: (a) absent; (b) present.
399. Crista cornea frontalis (if present), margo caudalis, bilateral, contrastingly red-coloured caruncles: (a) absent; (b) present.
400. Crista cornea frontalis (if present), contrasting blue colour: (a) absent; (b) present.
401. Crista cornea frontalis, prominent, red, elongate, and horn-like: (a) absent; (b) present in males.
402. Fleshy rostral 'horn' (lobus carnosus frontale), blackish, largely feathered: (a) absent; (b) present.
403. Fleshy rostral 'horn' (lobus carnosus frontale), bright yellow (breeding males only): (a) absent; (b) present.
404. Naris, position in depressio nasalis: (a) ventroanterior; (b) ventromedial, variably proportioned.
405. Cere, extension anteriorly, coloured red, with small rounded excresences: (a) absent; (b) present.

Pennae contourae

Caput

406. Frons and corona, uniformly pale, contrasting with darker sides of head: (a) absent; (b) present.
407. Frons and corona, short, velvet-like feathers that are contrastingly jet black: (a) absent; (b) present.
408. Corona, sharply and contrastingly coloured black (defining 'cap'): (a) absent; (b) present.
409. Frons, lorum, and regio suborbitalis, sharply contrasting black colour: (a) absent; (b) present.
410. Frons, corona, unfeathered region (variable in extent ventroposteriorly): (a) absent; (b) present, reddish;

(c) present, grey on frons, red on corona; (d) present, grey.

411. Corona, pennae with conspicuous, blackish longitudinal stripes on olive or brownish ground colour (not limited to frons): (a) absent; (b) present (*Gallirallus wakensis* weak, *G. dieffenbachii* obsolete).

412. Corona (and to varying extent, nucha), dull, mottled, chestnut colour, comparatively narrow in extent, and contrasting with regio auricularis: (a) absent; (b) present.

413. Corona et regio auricularis, uniform chestnut colour (variably extending to nucha, regio gularis, pectus), lacking dorsal countershading, producing uniform 'hooded' effect: (a) absent; (b) present, males only; (c) present, both sexes.

414. Corona, contrasting rufous-olive ground colour: (a) absent; (b) present.

415. Corona, contrastingly black: (a) absent; (b) present.

416. Corona, olive-brown colour (if present) extending ventrally to regio malaris: (a) absent; (b) present.

417. Corona, fine, sharp, whitish spotting: (a) absent; (b) present.

418. Corona, regio auricularis and pectus, fine darkish barring: (a) absent; (b) present.

419. Corona, lorum, mentum and regio gularis (extending caudally to tectrices caudae ventrales), contrasting black colour: (a) absent; (b) present.

420. Corona and nucha, blue (structurally produced) ground colour: (a) absent; (b) present, purplish-grey (*Porphyrula flavirostris* weak); (c) present, essentially grey; (d) present, greyish-blue; (e) present, essentially blackish. Note: *Porphyrio albus* non-comparable due to leucisticism.

421. Corona, narrow blackish strip with distinct greenish-purple iridescence: (a) absent; (b) present, extending to nucha (*Heliopais*), pars caudalis of collum (*Heliornis*), or mantle (*Podica*, males only).

422. Corona, regio auricularis, lorum and (in some) regio gularis but not (in most) including nucha, uniform (unstreaked) pale grey: (a) absent; (b) present. Note: similar, possibly related character of *Ortygonax*, *Cyanolimnas*.

423. Corona, frons, pale-grey pennae with fine black stripes along rachises: (a) absent; (b) present.

424. Regio circumrostralis ('base of bill') blackish, broadening dorsally to include lorum and joining a black corona (all of which contrasting with surrounding grey): (a) absent; (b) present (*Gallicrex* obscured frontally by crista cornea).

425. Regiones oralis et gularis, and lorum, unfeathered and red: (a) absent; (b) present.

426. Lorum, narrow chestnut stripe: (a) absent; (b) present.

427. Lorum, sparsely feathered, yellow-orange area from base of maxilla to orbit: (a) absent; (b) present.

428. Lorum, contrasting black colour: (a) absent; (b) present.

429. Lorum et regio orbitalis, narrow unfeathered 'regio circumorbitalis': (a) absent; (b) present, blackish, flesh-coloured or reddish, or cobalt blue.

430. Regio orbitalis, palpebrae ventralis et dorsalis ('eye ring'), bright orange coloration: (a) absent; (b) present.

431. Regio orbitalis, palpebra ventralis, contrasting white colour (white, ventral hemi-ring): (a) absent; (b) present.

432. Regio orbitalis, pale supraorbital stripe, bilaterally delimiting dorsally a well-defined, darker medial stripe on the corona: (a) absent; (b) present.

433. Regio orbitalis, pale supraorbital stripe (if present), caudal continuation and ventral confluence with pale regio gularis, delimiting dark regio auricularis caudally: (a) absent; (b) present.

434. Regio orbitalis, pale supraorbital stripe (if present), distinct dorsal angling posteriorly: (a) absent; (b) present.

435. Regio orbitalis, short (typically terminating at posterior margin of orbit), pale, comparatively indistinct, supraorbital stripe, meeting medially across frons: (a) absent; (b) present.

436. Regio orbitalis, palpebra ventralis and regio immediately ventral: (a) feathered and/or skin not yellow; (b) essentially unfeathered, yellow. Note: see loral character for *Himantornis*.

437. Regio orbitalis, bilateral pale supraorbital stripes extending well caudad to orbit: (a) absent; (b) present.

438. Regio orbitalis, short, narrow, whitish supraloral stripe: (a) absent; (b) present. Note: distinct from chestnut loral stripe of *Rougetius*.

439. Regio orbitalis, short, broad, white, caudally attenuated (teardrop-shaped), supraorbital stripe, terminating at caudal margin of orbit: (a) absent; (b) present.

440. Regio orbitalis, broad, chestnut orbital stripe: (a) absent; (b) present.

441. Regio orbitalis, broad, black orbital stripe: (a) absent; (b) present.

442. Regio orbitalis, broad, white suborbital stripe: (a) absent; (b) present.

443. Regio orbitalis, oculus, iris, ground colour: (a) 'brown'; (b) 'bluish-white'; (c) 'red' (*Aramidopsis plateni* comparatively orange); (d) 'yellow'. Note: basal polarity indeterminate. Some state assigments were problematic because of limited data from photographs, descriptions, illustrations and specimen labels.

444. Regio orbitalis, conspicuous white, caudally extensive, postorbital stripe: (a) absent; (b) present (cranial portion chestnut in female *Heliornis*).

445. Regio orbitalis, broad, brownish, dark-streaked orbital stripe: (a) absent; (b) present.

446. Regio orbitalis, contrastingly dark orbital stripe, without adjacent pale supraorbital stripe (both sexes): (a) absent; (b) present (*Sarothrura watersi* restricted to lorum).

447. Regio orbitalis, contrasting white postorbital spot: (a) absent; (b) present.

448. Regiones orbitalis et auricularis, contrastingly olive-brown with darker mottling: (a) absent; (b) present.

449. Regio auricularis, contrasting pale tannish-brown: (a) absent; (b) present.

450. Regio auricularis, lorum, and extending to upper pectus and sides, bright tawny-yellow ground colour: (a) absent; (b) present.

451. Regio auricularis ('cheeks'), medium grey colour, contrasting sharply with adjacent plumage: (a) absent; (b) present, confined to regio auricularis; (c) present, including corona.

452. Regio auricularis, contrasting, caudally broadening olive wash extending to lateral sides of pectus: (a) absent; (b) present.

453. Regio auricularis, contrastingly rufous-black patch: (a) absent; (b) present.
454. Regio auricularis, unfeathered, largely white: (a) absent; (b) present.
455. Regio auricularis, contrastingly white, elongate tufts: (a) absent; (b) present.
456. Regio auricularis, unfeathered and red-coloured region: (a) absent; (b) present.
457. Mentum and regio gularis, fine whitish transverse barring: (a) absent; (b) present, conspicuous; (c) present, faint.
458. Mentum and regio gularis, white, sharply demarcated from surrounding chestnut: (a) absent; (b) present.
459. Mentum and regio gularis, black spots forming border for restricted, distinct pale region: (a) absent; (b) present.
460. Mentum, regio gularis and upper breast, pure white sharply bordered on all margins by chestnut: (a) absent; (b) present.
461. Mentum and regio gularis, narrow whitish patch grading into surrounding darker colour, forming blurred border: (a) absent (Heliornithidae problematic; in *Sarothrura* and *Gallicrex* conspicuous only in breeding males); (b) present, comparatively extensive and broadening caudally; (c) present, confined, caudally narrowing.
462. Regiones malaris et orbitalis, dark, dorsally orientated malar stripe extending to surround orbit: (a) absent; (b) present.
463. Regio gularis, black colour contrasting with regio auricularis: (a) absent; (b) present.
464. Regio gularis, palear: (a) absent; (b) present, unfeathered; (c) present, largely feathered, bilobate.

Collum

465. Nucha, chestnut colour (often contrasting with corona and collum, pars intermedia): (a) absent; (b) present (continuous with corona, mantle in *Laterallus xenopterus*).
466. Crista nuchalis pennarum, hemispherical and composed of black-tipped filoplumae: (a) absent; (b) present. Note: excludes non-homologous cristae in some Otididae, *Rhynochetos*, Cariamidae.
467. Pars intermedia et caudalis, contrastingly bright lateral, chestnut stripes: (a) absent; (b) present.
468. Pars caudalis (base of neck), facies dorsalis, change in colour from dark grey of corona, nucha, and collum craniodorsalis to medium grey of dorsum trunci, regio cranialis: (a) absent; (b) present, comparatively gradual; (c) present, comparatively abrupt.
469. Pars intermedia et caudalis, contrasting black region, completely circumcollumnar and terminating craniad to pectus (extension of black facial region, if present): (a) absent; (b) present.
470. Pars caudalis, margo ventralis, pennae elongate, pointed, forming a shaggy fringe cranial to pectus: (a) absent; (b) present.

Dorsum trunci

471. Dorsum, typically including tectrices secundariae dorsales, ground colour: (a) brown, with variable olive or reddish tones; (b) grey or black (*Habroptila* with faint olive wash, *Sarothrura* based on males); (c) white; (d) blue-green, structurally produced; (e) chestnut (*Rallicula rubra* based on males); (f) grey with variably pronounced olive-brown cast medially (*Gallinula* especially pronounced).
472. Dorsum (variably extending into other regions), structurally produced blue-green ground colour (if present), secondary tones: (a) structurally produced ground colour and secondary tones absent; (b) tones present, brown or bronze (*Porphyrula flavirostris* weak); (c) tones present, purplish; (d) tones present, blackish (*Porphyrio albus*, although largely white, scattered black feathers remain). Note: basal polarity in this restricted character, which pertains only to those taxa showing state 'f' in previous character, is problematic.
473. Dorsum, regio interscapularis, scapularis, and continuing ventrally to sides, a sharply defined, contrastingly black mantle: (a) absent; (b) present.
474. Pennae of dorsum (including mantle, regio interscapularis, tectrices primariae et secundariae dorsales), blackish stripes along rachises, facies dorsalis: (a) absent; (b) present, lateromedial breadth less than or equal to combined widths of paler margins (vestigial in *Dryolimnas* (*c.*) *aldabranus*); (c) present, lateromedial breadth greater than combined widths of paler margins.
475. Regio scapularis, pennae ('scapulars') contrastingly pale, non-metallically coloured, elongate, and loosely structured (plumaceous): (a) absent; (b) present, buffy craniodorsally and medium grey caudoventrally (*Psophia crepitans*), white (*P. leucoptera*), or olive (*P. viridis*). Note: see scapular characters of some Gruidae.
476. Regio scapularis, pennae (scapulars), conspicuous elongation combined with ventral curvature: (a) absent; (b) present.
477. Omus, regio scapularis et regio interscapularis (typically extending to tectrices secundariae dorsales), large, single, medial, black-bordered white spots on feathers (females): (a) absent; (b) present.
478. Omus, regio scapularis, regio interscapularis, et regio synsacralis (typically extending to tectrices secundariae dorsales), small pairs of black-bordered, white spots (tending to short streaks caudally) on vexilla of pennae: (a) absent; (b) present (*Laterallus* (*jamaicensis*) *tuerosi* prominent, tending to bars).
479. Omus, regio scapularis, et regio interscapularis, paired, pale (typically whitish) spots or bars on vexilla of pennae: (a) absent; (b) present, bars throughout, typically with several pairs per penna (*Gallirallus dieffenbachii* bars olive brown; *G. pectoralis* and *G.* (*p.*) mirificus obsolete cranially); (c) present, barred caudally, spotted cranially; (d) present, spotted throughout (*G.* (*p.*) *macquariensis* weak).
480. Omus, regio scapularis, regio interscapularis, regio synsacralis, and (typically) pyga and tectrices secundariae dorsales, fine, white, V-shaped, subterminal bars on pennae: (a) absent; (b) present (comparatively crescent-shaped in *Coturnicops notata*).
481. Omus, regio scapularis, regio interscapularis, regio synsacralis, et tectrices secundariae dorsales, single, black, subterminal spot on rachis of penna: (a) absent; (b) present.
482. Mantle (omus et regio interscapularis), typically terminating cranial to pyga (rump) and typically

excluding dorsum of collum, nucha and corona, uniformly rich chestnut colour: (a) absent; (b) present (*Aramides* (*c.*) *plumbeicollis* restricted to caudal portion; *Rallina canningi* approaching maroon; *Rallicula* especially rich, almost maroon; *Sarothrura* based on males).

483. Mantle (omus et regio interscapularis), contrastingly grey colour: (a) absent; (b) present (*Aramides axillaris* comparatively sharply demarcated). Note: continuous with grey collumnar region, forming collar in *Aramides mangle*, *A. cajanea*-group.

484. Omus, regio scapularis, regio interscapularis, regio synsacralis and (in some pyga) tectrices secundariae et primariae dorsales of females (sexually dichromatic taxa only), bold spotting with buff or white: (a) absent; (b) present.

485. Omus, regio scapularis, regio interscapularis, regio synsacralis, pyga and tectrices secundariae et primariae dorsales of females (sexually dichromatic taxa only), buffy markings on vexilla: (a) absent; (b) present, as variably sloping bars (*Sarothrura watersi* weak); (c) present, as prominent spots; (d) present, as irregular spots.

486. Omus, regio scapularis, regio interscapularis, regio synsacralis, pyga and tectrices secundariae et primariae dorsales of males (sexually dichromatic taxa only), prominent white or buffy marks: (a) absent; (b) present, as single, longitudinal white stripes along rachises; (c) present, as spots (*Sarothrura pulchra* white, *S. elegans* buffy).

Latus et ventrum trunci

487. Mentum caudally to upper pectus, ground colour (paler on mentum, especially in taxa having whitish regio gularis), often with additional markings, and variably contrasting with adjacent regions: (a) brown, including chestnut (*'Rallus' madagascariensis* wine-coloured, *Amaurornis ineptus* paler medially); (b) black with purplish iridescence; (c) medium grey, often silvery (*Grus vipio* and *G. monacha* comparatively dark); (d) dark grey (*Gallicrex* males barred; *Amaurornis phoenicurus* interrupted medially); (e) white (Heliornithidae problematic because of sexual and seasonal variation); (f) black; (g) blue, structurally produced; (h) dark plumbeous grey; (i) pale rufous or tawny (*Rallus limicola* pale rufous; *R. wetmorei* tawny; *Crex* tawny); (j) rufous yellow. Note: unordered step matrix optionally employed, in which transitions within two sets of states ({a, i, j},{c, d, f, h}) were assigned one step, whereas transitions between other pairs of states were assigned two steps.

488. Regio gularis and pectus (variably extending into other regions), structurally produced blue ground colour (if present), secondary tones: (a) structurally produced ground colour and secondary tones absent; (b) tones absent, colour essentially blue; (c) tones present, purplish. Note: basal polarity in this restricted character, which pertains only to those taxa showing state 'h' in previous character, is problematic. Ventrum white by paedomorphosis (*Porphyrula flavirostris*) or entire plumage leucistic (*Porphyrio albus*) considered non-comparable.

489. Pectus, sharply contrasting black bilateral stripes at caudal margin: (a) absent; (b) present.

490. Pectus, variably including regio gularis and mentum, pennae medium greyish-brown basally with subterminal white band and cinnamon terminus: (a) absent; (b) present.

491. Pectus, variably including regio gularis and mentum, white spots (if present) with black borders: (a) absent; (b) present.

492. Pectus and regio abdominalis, distinctive chestnut-washed olive ground colour (with black-and-white spotting): (a) absent; (b) present.

493. Pectus et regio abdominalis, pennae pale grey with broad, whitish margins, producing scalloping: (a) absent; (b) present.

494. Pectus and regio abdominalis, pennae dark with broad grey margins, producing 'scalloped' aspect: (a) absent; (b) present.

495. Pectus, variably narrow, chestnut or olive-brown band: (a) absent; (b) present, rudimentary, medially incomplete, and/or significantly 'faded'; (c) present, typically complete, chestnut; (d) present, typically complete, olive-brown.

496. Pectus (variably extending to nucha, collum, corona et regio abdominalis), deep, bright, uniform, unmarked chestnut colour: (a) absent (includes tawny-breasted *Rallus limicola*, *R. elegans*); (b) present, both sexes (*Eulabeornis* pinkish, intraspecifically variable; *Aramides ypecaha* pale*; Rallina canningi* autapomorphically maroon-coloured; *Amaurolimnas* uniquely extensive, uniform throughout corpus); (c) present, males only (*Sarothrura* (*a.*) *antonii* variable and typically limited to upper breast; most extensive caudally in *S. rufa*).

497. Margin between (chestnut) pectus and (black) regio abdominalis, white band: (a) absent; (b) present.

498. Pectus, lateral margins, significant white spotting ventral to olive of dorsum: (a) absent; (b) present.

499. Regio abdominalis, variably extended to pectus, alternating dark (typically relatively broad) and pale (typically relatively narrow, whitish to chestnut), transverse barring: (a) absent (*Pardirallus maculatus* spotted); (b) present, discernable in both sexes, confined to regio abdominalis (*Heliopais* and *Podica* weak, laterally restricted, sexually variable; *Cyanolimnas* and *Ortygonax* faint; *Pardirallus maculatus* broad, tending to spotting; *Rougetius* and *Nesoclopeus* (*p.*) *immaculatus* faint; *Gallirallus australis*-group variable; *G. sharpei* problematic; *Rallina victa* weak; *Porzana sandwichensis*, *P. tabuensis* faint); (c) present, discernable only in females, barring restricted to regio abdominalis (*Sarothrura watersi* vestigial); (d) present, discernable in both sexes, restricted to regio abdominalis, but distinctly tri-toned, involving pale, medium and dark bars; (e) present, discernable in both sexes, extending cranially to include pectus (*Aramidopsis plateni* and *Rallus caerulescens* faint; *Gallicrex*, obscured in breeding males). Note: pale margins of feathers in some adults (possibly wear-related) and 'vestiges' in juveniles of some species indicate that absence in 'black' *Porzana*, *Gallinula* and *Fulica* represent reversal(s). Barring of some Heliornithidae may represent unique state.

500. Regio abdominalis, sharp demarcation of uniform grey coloration from caudal part of pectus, with irregular black medial area: (a) absent; (b) present.

501. Regio abdominalis, craniolateral parts with contrasting olive ground colour with scattered, typically obliquely aligned, large, white spots: (a) absent; (b) present.

502. Regio abdominalis, variably extensive, irregular whitish medial region: (a) absent; (b) present, confined to regio abdominalis; (c) present, extending cranially to regio gularis. Note: not homologous to white belly band within *Aramides*.

503. Regio abdominalis et crus, uniform coloration with distinct demarcation of colour from that of pectus: (a) absent; (b) present, grey or black (only partly black in *Aramides 'guttularis'*); (c) present, olive. Note: non-comparable, white in *Porphyrio albus*.

504. Crus, plumage grey, contrasting with chestnut of ventrum: (a) absent; (b) present. Note: blackish crus of some *Aramides* can be greyish-olive in juveniles, and can fade or wear to grey in adults.

505. Crus, plumage pale chestnut, contrasting with pale grey of ventrum: (a) absent; (b) present.

Tectrices caudae

506. Tectrices dorsales caudae and pyga, black colour contrasting with mantle: (a) absent; (b) present.

507. Tectrices dorsales caudae et pyga, contrastingly vinaceous chestnut: (a) absent; (b) present.

508. Tectrices dorsales caudae et pyga, contrasting, deep chestnut colour, extending to calami rectrices (but not vexillae) and scattered variably to tectrices dorsales secundarii: (a) absent; (b) present.

509. Tectrices dorsales caudae, profuse, white markings: (a) absent; (b) present, as paired spots (*Gallirallus sharpei* with slanting bars); (c) present, as transverse bars.

510. Tectrices dorsales et ventrales caudae: (a) distinguishable from rectrices by shorter length, different shape or lesser stiffness; (b) essentially indistinguishable from rectrices.

511. Tectrices ventrales caudae, pure white coloration: (a) absent (including largely white state in *Cyanolimnas*, *Dryolimnas*, *Rougetius*, *'Rallus' madagascariensis*, and separate state in coots and gallinules); (b) present.

512. Tectrices ventrales caudae: (a) not as follows; (b) white dorsolaterally, black ventromedially; (c) buff dorsolaterally, black ventromedially. Note: state for *Laterallus xenopterus* uncertain; rectrices and associated tectrices missing.

513. Tectrices ventrales caudae: (a) not as follows; (b) white dorsolaterally, coloured medially like flanks, belly.

514. Tectrices ventrales caudae, white dorsally, pale chestnut ventrally: (a) absent; (b) present.

515. Tectrices ventrales caudae (typically including caudal regio abdominalis), alternately pale-and-dark barring (typically pale is finer): (a) absent; (b) present (*Ortygonax* faint; *Laterallus murivagans* and *L. tuerosi* weak; *Porzana bicolor* and *sandwichensis* weak). Note: 'barring of belly' coded as above except extremely weak in *Ortygonax*, *Nesoclopeus poecilopterus-woodfordi*, males of some *Sarothrura*. Inclusion of *Porzana monasa* in state 'b' based on Ripley (1977).

516. Tectrices ventrales caudae, chestnut ground colour, typically without transverse barring: (a) absent; (b) present (*Laterallus jamaicensis* barred; *Porzana marginalis* pale; *Amaurornis olivaceus* obsolete). Note: damage to tail rendered coding for *Laterallus xenopterus* tentative.

517. Tectrices ventrales caudae, uniformly black colour: (a) absent (*Grus vipio* dark grey, *Amaurolinas* olive); (b) present.

518. Tectrices ventrales caudae, white coloration with black stripes along rachises: (a) absent; (b) present.

Rectrices

519. Modal number of pairs, exclusive of moult (ordered, plesiomorphic state is 'c'): (a) four; (b) five; **(c) six**; (d) eight.

520. Great, relative elongation with pronounced lateromedial gradation in lengths of rectrices, producing attenuated tail: (a) absent; (b) present.

521. Moderate, relative elongation of rectrices and (typically) tectrices ventrales caudae, producing tail extending to or beyond distal terminus of tarsometatarsus or (in some) digiti pedis, without marked lateromedial gradation in lengths of rectrices: (a) present; (b) absent.

522. Profound truncation: (a) absent, rectrices typically developed, forming obvious tail; (b) present, rectrices very short, barely emergent beyond tectrices ventrales et dorsales caudae, tail obsolete on external inspection.

523. Narrow, acuminate, with fine, white margins of vexilla, especially medial rectrices: (a) absent; (b) characteristic, but comparatively ephemeral.

524. Narrow, acuminate, steeply graduated lateromedially: (a) absent; (b) present.

525. Whitish, transverse barring, in rallids tending to paired, irregular spots: (a) absent; (b) present (*Tricholimnas sylvestris* and *Nesoclopeus poecilopterus* vestigial, variable; *Gallirallus australis*-group buff, vestigial in *greyi*). Note: similar states to 'b' occur in Burhinidae, Pedionomidae, Turnicidae, Otididae, Cariamidae and Eurypygidae.

526. Ground colour: (a) brown; (b) dark grey or black; (c) chestnut (*Sarothrura*, at least males, including *watersi*); (d) white.

527. Black, transverse bars across vexilla (widths of bars vary interspecifically, in some taxa almost obscuring chestnut or white ground colour, giving appearance of pale bars on black): (a) absent; (b) present, both sexes (obsolete in *Gallirallus greyi*); (c) present, females only (*Rallicula rubra* faint).

528. Dark brown along rachis with olive-brown or buffy scalloping on margins: (a) absent; (b) present (*Micropygia* problematic because of central white spot).

529. Contrasting whitish apices: (a) absent; (b) present. Note: obscured by wear.

Ala (membrum thoracicum)

530. Axillar-metapatagial marsupium: (a) absent; (b) present, for aerial transport of altricial young. Note: see Brooke (1984).

531. Pennae brachiales dorsales ('tertials'), and (in some) the proximal-most remiges secundariae, conspicuous elongation (typically equalling or exceeding the tips of remigii primariae in folded wing): (a) absent; (b) present.

532. Pennae brachiales dorsales ('tertials'), and (in some) the proximal-most remiges secundariae, vexillae differing from those of adjacent remiges in greater breadth, length, loose structure and chestnut colour: (a) absent; (b) present.

533. Remiges secundarii (including 'remiges tertii'), modal full-complement number (ordered): (a) 9–15; (b) 16 or 17; (c) 19–25.
534. Remiges secundarii, central remiges, white patches on vexilla: (a) absent; (b) present.
535. Remiges secundarii, pars pennaceae, apices (only), contrasting white colour: (a) absent; (b) present.
536. Remiges primarii, modal number, exclusive of remicle and moult (ordered, primitive is state 'b'): (a) nine; **(b) 10;** (c) 11. Note: some *Porzana atra* show state 'a'.
537. Remiges primarii, distal members, white apices: (a) absent; (b) present.
538. Remiges primarii, distal-most (tenth) remex, vexillum internum: (a) without deep, distally extensive incisura vexilli; (b) with deep, distally extensive incisura vexilli.
539. Remiges secundarii et primarii, relative darkness: (a) similar (others, including); (b) primarii distinctly and uniformly darker than secundarii; (c) primarii distinctly and uniformly paler than secundarii.
540. Remiges (especially primarii), contrasting colour of vexillum externum (outer, anterior): (a) absent (including those in which these are blackish like the vexilla externum); (b) present, green; (c) present, purple; (d) present, dark blue; (e) present, pale caerulean. Note: *Porphyrio albus* non-comparable, remiges white.
541. Remiges primarii, vexilla internum et externum, transverse barring: (a) absent, uniformly coloured (including non-homologously marked Eurypygidae and Rhynochetidae); (b) present, marked with four pairs of broad whitish bars (*Canirallus oculeus* especially conspicuous, including facies dorsalis and involving tectrices primariae dorsales); (c) present, marked with (typically) more than four pairs of narrow white or largely white bars, sometimes shortened and appearing as elongated spots; (d) present, marked with (typically) more than four pairs of largely chestnut bars.
542. Remiges primarii, vexilla, contrasting, central chestnut patches ('flashes'): (a) absent; (b) present.
543. Remiges primarii, vexilla, white speckling: (a) absent; (b) present.
544. Remiges primarii, 'remex primaris distalis' ('outermost primary'), vexillum externum with whitish speckling tending to form broad white band (covering much of vexillum in some), both sexes: (a) absent; (b) present (*Sarothrura insularis* weak).
545. Remiges primarii, 'remex primaris distalis' ('distalmost primary'), vexillum externum, margo externum ('leading edge of primaries'), narrow white margin (most conspicuous ventrally; evidently stiffening edge, perhaps related to flight): (a) absent; (b) present (*Gallinula tenebrosa* conspicuous in juveniles, weak and variable in adults; *Porphyriornis* narrow, variable; *Fulica cristata* narrow, proximally restricted; *F. gigantea* narrow, proximally restricted, variable; *F. cornuta* vestigial proximally). Note: variation from wear frequent, especially difficult in *Porzana*.
546. Tectrices primariae et secundariae dorsales, contrasting chestnut or tawny colour: (a) absent; (b) present (*Rallus caerulescens* dark, *R. longirostris*-group variable).
547. Tectrices primariae et secundariae dorsales, contrasting bright buffy ground coloration: (a) absent; (b) present.
548. Tectrices primariae et secundariae dorsales, pure white colour in sharp contrast with jet-black remiges: (a) absent; (b) present.
549. Tectrices primariae et secundariae dorsales, structurally produced ground colour of blue, green or purple: (a) absent; (b) present, distinctly greenish with variably pronounced black or bronze tones (*Porphyrula flavirostris* comparatively pale); (c) present, essentially completely black; (d) present, distinctly purple; (e) present, bright blue. Note: *Porphyrio albus* leucistic, non-comparable.
550. Tectrices primariae et secundariae dorsales, black-and-white barring (in some accompanied by profuse, laterodorsally conspicuous barring of remiges primarii): (a) absent; (b) present (*Tricholimnas lafresnayanus*, *Habroptery insignis*-*torquatus*-group, *Cabalus* and *Rallina canningi* vestigial; *Gallirallus sharpei* with paired white spots; *Laterallus xenopterus* prominent).
551. Tectrices primariae et secundariae dorsales, scattered pale barring and/or subterminal spots: (a) absent; (b) present.
552. Tectrices primariae et secundariae dorsales, scattered white tips: (a) absent; (b) present.
553. Tectrices secundariae et primariae dorsales, iridescent purple colour, contrasting with adjacent pterylae: (a) absent; (b) present.
554. Tectrices primariae et secundariae ventrales, with large, ovate, white spots: (a) absent (*Podica* with multiple, irregular stripes and spots); (b) present (*Himantornis* comparatively indistinct).
555. Tectrices primariae et secundariae ventrales (typically also axillaries), ground colour (generally similar to that of adjacent remiges, often variably patterned with paler markings): (a) medium brown (*Porphyrula martinica* suffused with greenish-blue; *Micropygia* buffy; *Porphyriops* tending to state 'b'; *Gallicrex* sexually dichromatic, tending to state 'b'); (b) dark grey, blackish or black (*Porphyrio* with vexilla internum variable; *Porzana erythrops*-group variably marked with white, extreme in *colombianus*); (c) white; (d) pale grey; (e) chestnut.
556. Tectrices primariae et secundariae ventrales (typically including axillaries), transverse barring: (a) absent (*Himantornis* scalloped; *Crex*, *Micropygia*, *Coturnicops*, *Poliolimnas* and *Aenigmatolimnas* 'smudgy' pale); (b) present, white, very narrow, sparse, typically confined to terminal margins of pennae; (c) present, white, broad, numerous (*Gallirallus* (*pectoralis*) *muelleri* faint; *Sarothrura lugens* faint; *Fulica rufifrons* vestigial); (d) present, chestnut (at least largely), numerous.
557. Tectrices primariae et secundariae ventrales, very pale brown with indistinct, pale-buff or whitish margins: (a) absent; (b) present.
558. Tectrices primariae et secundariae ventrales (and to a lesser degree, tectrices dorsales), distally contrasting white ('whitish bend of wing'): (a) absent; (b) present, more or less conspicuous (*Fulica atra*-group weak).

Ungues digitorum manus

559. Ungue digiti majoris: (a) typically retained in adults; (b) typically lacking in adults. Note: ungue digiti alulae, widespread in Rallidae, seemed to be absent in Burhinidae and 'non-Grues'.

Podotheca

560. Regio tarsalis, facies dorsalis, scuta or scutella, composing an acrometatarsium: (a) present; (b) absent, covered with reticula. Note: basal polarity indeterminate. Some Charadriiformes and Otididae also state 'b'.

561. Regio tarsalis, trochlea tarsalis tertius, facies dorsalis: (a) covered by row of single scutella extending (undivided) across trochlea lateromedially; (b) covered by reticula, or (at the very least) lateromedial pairs of reticula. Note: intraspecific variation, and degree of interspecific variation in state 'b' problematic. *Balearica* non-comparable.

562. Regio tarsalis, facies plantaris: (a) covered lateral to midline by variably extensive series of moderately large scutella, but covered medially by reticula of variable size; (b) covered (at least proximally) by single row of 'true' scuta (large, undivided, rectanguloid scales) centred along midline, in many taxa extending distally to base of trochlea (*Gallirallus* reduced distally, variable; *Tricholimnas* variable); (c) covered completely by reticula; (d) covered proximally by row of lateromedially paired, moderately large scutellae. Note: basal polarity indeterminate. Relative extent of reticulate integument in state 'c' variable.

563. Crus, regio tarsalis and digiti, ground colour: (a) 'yellow'; (b) 'grey or black', some with greenish overtones; (c) 'brown' (*Tricholimnas* greyish; *Amaurornis akool* reddish); (d) 'orange' or 'red(dish)' (*Himantornis* dull, *Rougetius* blackish); (e) 'green'. Note: basal polarity indeterminate. Problematic codings and marginal data frequent. Often differ from predefinitive colours (e.g. juveniles of most species of Gruinae have flesh-coloured legs). Storer (1981) described *Laterallus xenopterus* as 'bluish-grey'. *Porphyriornis nesiotis* difficult, may be 'yellow'.

564. Crus, immediately proximal to articularis intertarsalis, contrasting reddish band ('garter'): (a) absent; (b) present (*Fulica armillata* and *F. americana*-group variable).

565. Tele interdigitalis pedis, broad cutaneous lobi, with shallow, rounded incisurae interphalangeales, on lateral and medial sides of digitales II–IV (single lobus ventralis on hallux): (a) absent; (b) present.

566. Zonae interphalangeales digitales, contrasting black bands ('knuckle marks'): (a) absent; (b) present.

567. Tele interdigitalis pedis, moderately broad cutaneous lobi, with deep, essentially complete incisurae interphalangeales, on lateral and medial sides of digitales II–IV (single lobus ventralis on hallux): (a) absent; (b) present.

568. Tele interdigitalis pedis, narrow cutaneous plicae, without incisurae interphalangeales, on lateral and medial sides of digitales I–IV: (a) absent; (b) present.

Ungues digitorum pedis

569. Hallux (excluding unguis), distal extent relative to proximal phalanges of digiti quartus (ordered): (a) substantially less than that of phalanx proximalis, in some cases barely extending beyond trochlea; (b) approximating (typically subequal to) that of phalanx proximalis (*Micropygia* barely); (c) significantly greater than that of phalanx proximalis, but not exceeding that of phalanx II; (d) approximating or exceeding that of phalanx II.

570. Unguis digiti pedis III, conspicuous elongation, comparatively straight, dagger-like shape relative to ungues digitorum pedis II et IV: (a) absent; (b) present.

APPENDIX B. CHARACTER MATRICES

Copies of all matrices—genera of Gruiformes ('Gruiformes', 76 taxa by 381 characters), species of Grues unmerged ('Grues', 224 taxa by 570 characters) and species of Grues partly merged ('Grues—M', 161 taxa by 570 characters)—are accessible at the Royal Society Web site (http://www.pubs.royalsoc.ac.uk/publish/phi_bs/dec98tb.htm); copies also are available on Macintosh diskette from the author on request. Matrices were constructed using MACCLADE and are suitable for importation into PAUP for analysis. Characters and states in all matrices correspond to those identified in Appendix A.

APPENDIX C. PHYLOGENETIC CLASSIFICATION OF GRUIFORMES

Higher-order classification of non-rallid Gruiformes is based primarily on generic analysis (figure 1); intergeneric relationships within Rallidae and Gruidae were based on complete-matrix assessments (figures 2–4), and finer-scale groupings were based on ancillary analyses (figures 5–13). Subfossil Rallidae were placed conservatively using constrained analyses (table 2). The sequencing convention of Wiley (1981) for nested series of taxa was employed to avoid proliferation of non-conventional taxonomic ranks. Taxonomic groups of uncertain phylogenetic integrity (e.g. possibly paraphyletic or polyphyletic, provisional groups) are annotated *incertae sedis*; where the relationships among member taxa within a group are uncertain, the taxon is annotated *sedis mutabilis*. Taxa not examined but placed based on available descriptions are enclosed by square brackets; these include two rallids recently described by Lambert (1998*a*,*b*). Citations of authorship of taxa correspond to the synonymies presented by Peters (1934), Brodkorb (1967), Wolters (1975), Olson (1977), Ripley (1977); complete bibliographic citations for author-year citations for taxa are given by del Hoyo *et al.* (1996). Adoption of the ordinal name Gruiformes (Bonaparte, 1854), instead of apparently senior taxon Ralliformes (Reichenbach, 1852), is intended to conform with standard usage in the absence of formal rules of nomenclature for ordinal-group names. Generic and familial names for *Aptornis* follow the ruling by International Commission on Zoological Nomenclature (1997). Where species recognized by Ripley (1977) were subdivided, the original species taxon is indicated parenthetically and subspecies included are listing without individual authorships. Taxa known only from fossil or subfossil remains are preceeded by daggers, and typically listed following extant members. I exclude from formal consideration the *Rallus pacificus* Gmelin, 1789 (Ripley 1977) and *Rallus nigra* Miller, 1784 (Walters 1988, 1989), both of which are based solely on historical illustrations and lack documentary specimens. Capitalization of common names follows conventions of Parkes (1978).

- **Order Gruiformes (Bonaparte, 1854)**
  - **Suborder Turnices (Huxley, 1868)**
    - **Family Pedionomidae (Bonaparte, 1852)—collared hemipodes**
      - **Genus** *Pedionomus* Gould, 1841
    - **Family Turnicidae (G. R. Gray, 1840)—buttonquails**
      - **Genus** *Turnix* Bonnaterre, 1791
      - **Genus** *Ortyxelos* Vieillot, 1825
  - **Suborder Otidides Wagler, 1830**
    - **Family Otididae (Rafinesque, 1815 [alternatively, G. R. Gray, 1840])—bustards**
  - **Suborder Mesitornithes Wetmore, 1960**
    - **Family Mesitornithidae Wetmore, 1960—mesites**
      - **Genus** *Mesitornis* Bonaparte, 1855
      - **Genus** *Monias* Oustalet & Grandidier, 1903
  - **Suborder Cariamae Fürbringer, 1888**
    - **Family Cariamidae Bonaparte, 1850—seriemas**
      - **Genus** *Cariama* Brisson, 1760
      - **Genus** *Chunga* Hartlaub, 1860
    - **[†Family Bathornithidae Wetmore, 1933]**
    - **[†Family Idiornithidae Brodkorb, 1965]**
    - **†Family Phorusrhacidae (Ameghino, 1899)**
  - **Suborder Eurypygae Fürbringer, 1888**
    - **Superfamily Eurypygoidea (Selby, 1840)**
      - **Family Eurypygidae Selby, 1840—sunbitterns**
        - **Genus** *Eurypyga* (Illiger, 1811)
      - **†Family Messelornithidae Hesse, 1988**
        - **Genus** *Messelornis* Hesse, 1988
    - **Superfamily Rhynochetoidea (Sharpe, 1891)**
      - **Family Rhynochetidae Newton, 1868—kagus**
        - **Genus** *Rhynochetos* Verreaux & Des Murs, 1860
      - **†Family Aptornithidae Bonaparte, 1856—adzebills**
        - **Genus** *Aptornis* Owen, 1848
  - **Suborder Grues Bonaparte, 1854**
    - **Superfamily Gruoidea (Vigors, 1825)**
      - **Family Psophiidae Bonaparte, 1831—trumpeters**
        - **Genus** *Psophia* Linnaeus, 1758
          - *P. crepitans* Linnaeus, 1758—grey-winged trumpeter
          - *P. leucoptera* Spix, 1825—white-winged trumpeter
          - *P. viridis* Spix, 1825—green-winged trumpeter
      - **Family Aramidae Bonaparte, 1854—limpkins**
        - **Genus** *Aramus* Vieillot, 1816
          - *A. guarauna* (Linnaeus, 1766)—limpkin
      - **Family Gruidae Vigors, 1825—cranes**
        - **Subfamily Balearicinae Brasil, 1913**
          - **Genus** *Balearica* Brisson, 1760—crowned cranes
            - *B. pavonina* (Linnaeus, 1758)—black-crowned crane
            - *B. regulorum* (Bennett, 1833)—grey-crowned crane
        - **Subfamily Gruinae (Vigors, 1825)**
          - **Tribe Anthropodini (Bonaparte, 1855)**
            - **Genus** *Anthropoides* Vieillot, 1816—crested cranes
              - *A. paradisea* (Lichenstein, 1793)—blue crane
              - *A. virgo* (Linnaeus, 1758)—demoiselle crane
          - **Tribe Gruini (Vigors, 1825)**
            - **Genus** *Bugeranus* Gloger, 1841
              - *B. carunculatus* (Gmelin, 1789)—wattled crane
            - **Genus** *Leucogeranus* Bonaparte, 1855
              - *L. leucogeranus* (Pallas, 1773)—Siberian crane
            - **Genus** *Grus* Pallas, 1766—typical cranes
              - *G. canadensis* (Linnaeus, 1758)—sandhill crane
              - *G. vipio* Pallas, 1811—white-naped crane
              - *G. rubicunda* (Perry, 1810)—Australian crane
              - *G. antigone* (Linnaeus, 1758)—Sarus crane

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G. monacha Temminck, 1835—hooded crane
G. grus (Linnaeus, 1758)—Eurasian crane
G. nigricollis Prezhwalsky, 1876—black-necked crane
G. japonensis (Müller, 1776)—Japanese crane
G. americana (Linnaeus, 1758)—whooping crane
Superfamily Ralloidea (Vigors, 1825)
Family Heliornithidae G. R. Gray, 1841—finfoots; *sedis mutabilis*
Genus *Heliopais* Sharpe, 1893
H. personata (Gray, 1849)—masked finfoot
Genus *Podica* Lesson, 1831
P. senegalensis (Vieillot, 1817)—African finfoot
Genus *Heliornis* Bonnaterre, 1791
H. fulica (Boddaert, 1783)—American finfoot
Family Rallidae (Rafinesque, 1815), alternatively Vigors, 1825
Subfamily Himantornithinae (Bonaparte, 1856)
Genus *Himantornis* Hartlaub, 1855
H. haematopus Hartlaub, 1855—Nkulenga rail
Subfamily Rallinae (Rafinesque, 1815)
Tribe Porphyriornithini (Reichenbach, 1849)—swamphens
Genus *Porphyrio* Brisson, 1760—greater swamphens
Subgenus *Porphyrio* Brisson, 1760—typical swamphens; *sedis mutabilis*
P. (*p.*) *bellus* Gould, 1840—West Australian swamphen
P. (*p.*) *indicus* Horsfield, 1821—Indonesion swamphen (includes *palliatus*)
P. (*p.*) *samoensis* Peale, 1848.—Samoan swamphen (includes *pelewensis*, *vitiensis*, *aneiteumensis*, '*tongensis*')
P. (*p.*) *pulverulentus* Temminck, 1826—brown-backed swamphen
P. (*p.*) *porphyrio* (Linnaeus, 1758)—Mediterranean swamphen
P. (*p.*) *poliocephalus* (Latham, 1801)—ashy-headed swamphen (includes *seistanicus*)
P. (*p.*) *madagascariensis* (Latham, 1801)—African swamphen (includes *aegyptiacus*)
P. (*p.*) *viridis* Begbie, 1834—Malaysian swamphen (includes *edwardsi*)
P. (*p.*) *ellioti* Salvadori, 1879—Admiralty Islands swamphen (includes *neobritanicus*, *caledonicus*)
P. (*p.*) *albus* (White, 1790)—Lord Howe Island swamphen
P. (*p.*) *melanotus* Temmick, 1820—Australasian swamphen (includes *stanleyi*, *fletcherae*, '*norfolkensis*', *chathamensis*)
P. (*p.*) *melanopterus* Bonaparte, 1856—Moluccan swamphen (includes *mertoni*)
[†*P. paepae* Steadman, 1988—Marquesan swamphen]
Subgenus *Notornis* Owen, 1848—takahes; *sedis mutabilis*
†*P.* (*m.*) *mantelli* (Owen, 1848)—North Island takahe
P. (*m.*) *hochstetteri* (Meyer, 1883)—South Island takahe
†*P. kukwiedei* Balouet & Olson, 1989—New Caledonian takahe
Genus *Porphyrula* Blyth, 1852—lesser swamphens; *sedis mutabilis*
P. alleni (Thompson, 1842)—Allen's swamphen
P. martinica (Linnaeus, 1766)—American swamphen
P. flavirostris (Gmelin, 1789)—azure swamphen
†**Genus** *Aphanocrex* Wetmore, 1963
A. podarces Wetmore, 1963—St Helena swamphen
Tribe Gymnocrecini, new taxon
Genus *Gymnocrex* Salvadori, 1875—bare-faced rails
G. rosenbergii (Schlegel, 1866)—bald-faced rail
G. plumbeiventris (G. R. Gray, 1862)—bare-eyed rail
[*G. talaudensis* Lambert, 1998—Talaud Islands rail]
Genus *Habroptila* G. R. Gray, 1860
H. wallacii G. R. Gray, 1860—Wallace's rail
Tribe Eulabeornithini, new rank; *incertae sedis*
Genus *Eulabeornis* Gould, 1844
E. castaneoventris Gould, 1844—chestnut rail
Genus *Aramides* Pucheran, 1845—wood-rails
A. saracura (Spix, 1825)—slate-breasted wood-rail
A. calopterus Sclater & Salvin, 1878—chestnut-winged wood-rail
A. wolfi Berlepsch & Taczanowski, 1883—brown wood-rail
A. ypecaha (Vieillot, 1819)—giant wood-rail
A. mangle (Spix, 1825)—little wood-rail

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A. axillaris Lawrence, 1863—rufous-necked wood-rail
A. (*c.*) *cajanea* (Müller, 1776)—grey-necked wood-rail (includes *latens*, *morrisoni*, *gutturalis*)
A. (*c.*) *plumbeicollis* Zeledon, 1888—rufous-backed wood-rail
A. (*c.*) *mexicana* Bangs, 1907—northern wood-rail (includes *pacifica*)
A. (*c.*) *albiventris* Lawrence, 1867—white-bellied wood-rail (includes *vanrossemi*)
Genus *Canirallus* Bonaparte, 1856—pale-throated rails
C. oculeus (Hartlaub, 1855)—grey-throated rail
C. kioloides (Pucheran, 1845)—white-chinned rail
†**Genus** *Nesotrochis* Wetmore, 1918—West Indian cave-rails; *incertae sedis*
N. debooyi Wetmore, 1918—Antillean cave-rail
N. steganinos Olson, 1974—Haitian cave-rail
[*N. picapicensis* (Fischer & Stephan, 1971)—Cuban cave-rail]
Genus *Anurolimnas* Sharpe, 1893
A. castaneiceps (Sclater & Salvin, 1868)—chestnut-headed rail
Genus *Amaurolimnas* Sharpe, 1893
A. concolor (Gosse, 1847)—rufous rail
Genus *Rougetius* Bonaparte, 1856
R. rougetii (Guérin-Méneville, 1843)—Rouget's rail
Tribe Sarothrurini (Verheyen, 1957)—flufftails and allies
Genus *Rallina* G. R. Gray, 1846—chestnut-rails; *incertae sedis*
R. (*e.*) *eurizonoides* (Lafresnaye, 1845)—banded chestnut-rail (includes *minahasa*, *alvarezi*)
R. (*e.*) *amauroptera* (Eyton, 1845)—white-throated chestnut-rail (includes *amauroptera*=*nigrolineata*, *telmatophila*, *sepiaria*, *formosana*)
R. canningi (Blyth, 1863)—Andaman chestnut-rail
R. fasciata (Raffles, 1822)—red-legged chestnut-rail
R. (*t.*) *tricolor* G. R. Gray, 1858—bar-bellied chestnut-rail
R. (*t.*) *victa* Hartert, 1901—red-necked chestnut-rail (includes *convicta*)
Genus *Rallicula* Schlegel, 1871—forest-rails
R. forbesi Sharpe, 1887—Forbes' forest-rail
R. leucospila (Salvadori, 1875)—white-striped forest-rail
R. rubra Schlegel, 1871—New Guinea forest-rail
R. mayri Hartert, 1930—Mayr's forest-Rail
Genus *Sarothrura* Heine, 1890—flufftails
S. pulchra (J. E. Gray, 1829)—white-spotted flufftail
S. elegans (Smith, 1839)—buff-spotted flufftail
S. rufa (Vieillot, 1819)—red-chested flufftail
S. ayresi (Gurney, 1877)—white-winged flufftail
S. watersi (Bartlett, 1879)—Waters' flufftail
S. lugens (Böhm, 1884)—African flufftail
S. boehmi Reichenow, 1900—streak-breasted flufftail
S. insularis (Sharpe, 1870)—Madagascan flufftail
S. (*a.*) *affinis* (Smith, 1828)—chestnut-tailed flufftail
S. (*a.*) *antonii* Madarasz & Neumann, 1911—chestnut-breasted flufftail
Tribe Rallini (Rafinesque, 1815)—true rails
Subtribe Pardirallina, new taxon; *sedis mutabilis*
Genus *Cyanolimnas* Barbour & Peters, 1927
C. cerverai Barbour & Peters, 1927—Zapata rail
Genus *Pardirallus* Bonaparte, 1856
P. maculatus (Boddaert, 1783)—spotted rail
Genus *Ortygonax* Heine, 1890
O. sanguinolentus (Swainson, 1838)—plumbeous rail
O. nigricans (Vieillot, 1819)—blackish rail
Subtribe Rallina (Rafinesque, 1815)—long-billed rails; *incertae sedis*
Genus *Dryolimnas* Sharpe, 1893—white-throated rails
D. (*c.*) *cuvieri* (Pucheran, 1845)—Madagascan rail
D. (*c.*) *aldabranus* (Günther, 1879)—Aldabra Islands rail
D. (*c.*) *abbotti* (Ridgway, 1894)—Assumption Island rail
Genus *Rallus* Linnaeus, 1758—typical rails; *incertae sedis*
'*R.*' *madagascariensis* (Verreaux, 1833)—wine-breasted rail
R. caerulescens Gmelin, 1779—kaffir rail
R. (*a.*) *aquaticus* Linnaeus, 1758—water rail (includes *hibernans*, *korejewi*)

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  - *R.* (*a.*) *indicus* Blyth, 1849—brown-cheeked rail
  - *R. wetmorei* Zimmer & Phelps, 1944—Wetmore's rail
  - *R.* (*a.*) *antarcticus* King, 1828—Patagonian rail
  - *R.* (*a.*) *semiplumbeus* Sclater, 1856—Bogotá rail
  - *R. limicola* Vieillot, 1819—Virginia rail
  - *R.* (*l.*) *longirostris* Boddaert, 1783—clapper rail complex (provisionally includes all grey-bellied forms: *crepitans*, *waynei*, *coryi*, *pallidus*, 'pale morph' *insularum*, possibly 'pale morph' *caribeus*)
  - *R.* (*l.*) *elegans* Audubon, 1834—king rail complex (provisionally includes all tawny-bellied forms: *elegans*, *obsoletus*, *beldingi*, *levipes*, except possibly 'dark morph' *scottii*, 'dark morph' *caribeus*, and all other forms included by Ripley [1977] within *longirostris* complex)
  - †*Rallus* sp. (Olson & Wingate, in preparation)—large Bermuda rail
  - †*Rallus* sp. (Olson & Wingate, in preparation)—small Bermuda rail

- **Genus** *Gallirallus* Lafresnaye, 1841—lesser Pacific rails
  - *G.* (*p.*) *pectoralis* (Temminck, 1831)—slate-breasted rail (includes *insulsus*, *captus*, *mayri*, *alberti*, *exsul*, *brachipus*)
  - *G.* (*p.*) *muelleri* (Rothschild, 1893)—Auckland Islands rail
  - *G.* (*p.*) *mirificus* (Parkes & Amadon, 1959)—brown-banded rail
  - *G. striatus* (Linnaeus, 1766)—blue-breasted rail
  - *G. sharpei* (Büttikofer, 1893)—Sharpe's rail
  - *G.* (*a.*) *australis* (Sparrman, 1786)—South Island weka (includes *scotti* [small morph, Stewart Island]; *hectori* [yellowish morph, South Island], *troglodytes* [dark morph, South Island])
  - *G.* (*a.*) *greyi* (Buller, 1888)—North Island weka
  - *G.* (*p.*) *philippensis* (Linnaeus, 1766)—Philippine banded-rail (includes all other subspecies recognized by Ripley [1977] within *philippensis* complex)
  - *G.* (*p.*) *macquariensis* (Hutton, 1879)—Macquarie Island banded-rail
  - *G.* (*p.*) *assimilis* (G. R. Gray, 1843)—austral banded-rail (includes *norfolkensis*)
  - *G.* (*p.*) *christophori* (Mayr, 1939)—Solomon Islands banded-rail (includes *wilkinsoni*, '*chandleri*')
  - *G.* (*p.*) *sethsmithi* (Mathews, 1911)—Fijian banded-rail (includes *swindellsi*)
  - *G.* (*p.*) *goodsoni* (Mathews, 1911)—Somoan banded-rail
  - *G.* (*p.*) *ecaudatus* (Miller, 1783)—Tongan banded-rail
  - *G. dieffenbachii* (G. R. Gray, 1843)—Chatham Islands banded-rail
  - *G. owstoni* (Rothschild, 1895)—Guam rail
  - *G. rovianae* Diamond, 1991—Roviana rail
  - *G. wakensis* (Rothschild, 1903)—Wake Island rail
  - [†*G. ripleyi* Steadman, 1986—Mangaian rail]
- **Genus** *Tricholimnas* Sharpe, 1893—greater Pacific rails
  - *T. lafresnayanus* (Verreaux & Des Murs, 1860)—New Caledonian rail
  - *T.* (*s.*) *sylvestris* (Sclater, 1869)—Lord Howe Island rail
  - *T.* (*s.*) *conditicius* Peters & Griscom, 1928—Gilbert Islands rail (possibly synonymous with *T. sylvestris*)
- **Genus** *Nesoclopeus* Peters, 1932—bar-winged rails
  - *N.* (*p.*) *poecilopterus* (Hartlaub, 1866)—Fiji bar-winged rail
  - *N.* (*p.*) *woodfordi* (Ogilvie, 1889)—Guadacanal bar-winged rail
  - *N.* (*p.*) *immaculatus* Mayr, 1949—Ysabel bar-winged rail
- **Genus** *Aramidopsis* Sharpe, 1893
  - *A. plateni* (Blasius, 1886)—Platen's rail
- **Genus** *Cabalus* Hutton, 1874
  - *C. modestus* (Hutton, 1872)—Chatham Island rail
- †**Genus** *Capellirallus* Falla, 1954
  - *C. karamu* Falla, 1954—snipe-billed rail
- **Genus** *Habropteryx* Stresemann, 1932—barred-rails
  - *H. insignis* (Sclater, 1880)—New Britain barred-rail
  - *H.* (*t.*) *celebensis* (Quoy & Gaimard, 1830)—Celebes barred-rail
  - *H.* (*t.*) *torquatus* (Linnaeus, 1766)—Philippine barred-rail
  - *H.* (*t.*) *sulcirostris* (Wallace, 1862)—Eastern barred-rail (includes *kuehni*, *limarius*, *remigialis*)
  - *H. okinawae* (Yamashina & Mano, 1981)—Okinawan barred-rail
- †**Genus** *Aphanapteryx* Frauenfeld, 1868—Mascarene Islands rails; *incertae sedis*
  - *A. bonasia* (Sélys-Longchamps, 1848)—Mauritius rail
  - '*A.*' *leguati* (Milne-Edwards, 1874)—Rodriguez rail
- †**Genus** *Diaphorapteryx* Forbes, 1892
  - *D. hawkinsi* Forbes, 1892—Hawkins' rail

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Subtribe Crecina (Olphe-Galliard, 1887)—crakes; *incertae sedis*
Genus *Atlantisia* Lowe, 1923—South Atlantic flightless crakes; *incertae sedis*
A. rogersi Lowe, 1923—Inaccessible Island crake
†*‘A.’ elpenor* Olson, 1973—Ascension Island crake
Genus *Laterallus* G. R. Gray, 1855—blackish and ruddy crakes; *incertae sedis*
Subgenus *Creciscus* Cabanis, 1857—blackish crakes
L. (*j.*) *jamaicensis* (Gmelin, 1789)—black crake (includes *salinasi*, *coturniculus*)
L. (*j.*) *tuerosi* Fjeldså, 1983—Junín crake
L. (*j.*) *murivagans* (Riley, 1916)—cinnamon-vented crake
L. spilonotus (Gould, 1841)—Galápagos crake
Subgenus *Laterallus* G. R. Gray, 1855—ruddy crakes
L. levraudi (Sclater & Salvin, 1868)—rusty-flanked ruddy-crake
L. viridis (Müller, 1776)—russet-crowned ruddy-crake
L. ruber (Sclater & Salvin, 1860)—black-headed ruddy-crake
L. melanophaius (Vieillot, 1819)—rufous-sided ruddy-crake
L. fasciatus (Sclater & Salvin, 1867)—black-banded ruddy-crake
L. leucopyrrhus (Vieillot, 1819)—white-breasted ruddy-crake
L. (*a.*) *albigularis* (Lawrence, 1861)—white-throated ruddy-crake (includes *cerdaleus*)
L. (*a.*) *cinereiceps* (Lawrence, 1875)—grey-headed ruddy-crake
L. xenopterus Conover, 1934—rufous-faced ruddy-crake
L. exilis (Temminck, 1831)—grey-breasted ruddy-crake
Genus *Coturnicops* G. R. Gray, 1854—barred-backed crakes
C. (*n.*) *noveboracensis* (Gmelin, 1789)—American yellow crake (includes *goldmani*)
C. (*n.*) *exquisitus* (Swinhoe, 1873)—Chinese yellow crake
C. notatus (Gould, 1841)—Darwin’s crake
Genus *Micropygia* Bonaparte, 1856—yellow-breasted crakes
M. schomburgkii (Schomburgk, 1848)—ocellated crake
M. flaviventer (Boddaert, 1783)—yellow-breasted crake
Genus *Crex* Bechstein, 1803—greater crakes
C. crex (Linnaeus, 1758)—corn crake
C. egregia (Peters, 1854)—African crake
C. albicollis (Vieillot, 1819)—white-necked crake
Genus *Porzana* Vieillot, 1816—grey crakes and allies; *incertae sedis*
Subgenus *Corethrura* G. R. Gray, 1846—reddish crakes; *incertae sedis*
P. sandwichensis (Gmelin, 1789)—Hawaiian crake
P. fusca (Linnaeus, 1766)—ruddy-breasted crake
P. paykullii (Ljungh, 1813)—band-bellied crake
Subgenus *Poliolimnas* Sharpe, 1893—pale-browed crakes
P. cinerea (Vieillot, 1819)—white-browed crake
P. marginalis Hartlaub, 1857—striped crake
Subgenus *Porzana* Vieillot, 1816—grey crakes; *incertae sedis*
Species-group *incertae sedis*:
P. parva (Scopoli, 1769)—little crake
P. palmeri (Frohawk, 1892)—Laysan crake
P. spiloptera Durnford, 1877—dot-winged crake
Species-group *porzana*:
P. porzana (Linnaeus, 1766)—spot-breasted crake
P. carolina (Linnaeus, 1758)—Sora crake
P. pusilla (Pallas, 1776)—Baillon’s crake
P. fluminea Gould, 1842—spotted crake
Subgenus *Limnocorax* Peters, 1854—black crakes; *incertae sedis*
P. tabuensis (Gmelin, 1789)—spotless crake
P. monasa (Kittlitz, 1858)—Kosrae crake
P. atra North, 1908—Henderson Island crake
P. flavirostra (Swainson, 1837)—black crake
P. olivieri Grandidier & Berlioz, 1927—Madagascan crake
P. bicolor Walden, 1872—black-tailed crake
Subgenus *Neocrex* Sclater & Salvin, 1868—red-billed crakes
P. erythrops Sclater, 1867—paint-billed crake
P. columbiana (Bangs, 1898)—Colombian crake

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- **Subgenus undetermined**
  - †*P.* sp. (Olson & Wingate, in preparation)—Bermuda crake
  - †*P. astrictocarpus* Olson, 1973—St Helena crake
  - †*P. rua* Steadman, 1986—Mangaian crake
  - †*P. ziegleri* Olson & James, 1991—lesser Oahu crake
  - †*P. menehune* Olson & James, 1991—lesser Molokai crake
  - †*P. keplerorum* Olson & James, 1991—lesser Maui crake
  - †*P. ralphorum* Olson & James, 1991—greater Oahu crake
  - †*P. severnsi* Olson & James, 1991—greater Maui crake

- **Subtribe Amaurornithina, new rank**
  - **Genus** *Amaurornis* Reichenbach, 1853—waterhens
    - *A.* (*o.*) *olivaceus* (Meyen, 1834)—rufous-tailed waterhen
    - *A.* (*o.*) *moluccanus* (Wallace, 1865)—rufous-vented waterhen (includes *nigrifrons*, *frankii*, *ultimus*)
    - *A.* (*o.*) *ruficrissus* (Gould, 1869)—red-fronted waterhen
    - [*A.* (*o.*) *magnirostris* Lambert, 1998—Talaud waterhen]
    - *A. phoenicurus* (Pennant, 1769)—white-breasted waterhen
    - *A. akool* (Sykes, 1832)—brown waterhen
    - *A. isabellinus* (Schlegel, 1865)—Isabelline waterhen
    - *A. ineptus* (D'Albertis & Salvadori, 1879)—New Guinea flightless waterhen
- **Subtribe Fulicarina (Nitzsch, 1820)—moorhens and coots**
  - **Genus** *Gallicrex* Blyth, 1852
    - *G. cinerea* (Gmelin, 1789)—watercock
  - **Genus** *Porphyriops* Pucheran, 1845
    - *P. melanops* (Vieillot, 1819)—spot-flanked moorhen
  - **Genus** *Pareudiastes* Hartlaub & Finsch, 1871
    - *P. pacificus* Hartlaub & Finsch, 1871—Samoan moorhen
    - *P. silvestris* (Mayr, 1933)—San Cristobal moorhen
  - **Genus** *Tribonyx* Du Bus, 1840—native-hens
    - *T. ventralis* (Gould, 1836)—black-tailed native-hen
    - *T. mortierii* Du Bus, 1840—Tasmanian native-hen
    - [†*T.* (*m.*) *repertus* (De Vis, 1888)—De Vis' native-hen]
    - †*T. hodgenorum* (Scarlett, 1955)—New Zealand native-hen
  - **Genus** *Gallinula* Brisson, 1760—moorhens
    - **Subgenus** *Porphyriornis* Allen, 1892—South Atlantic moorhens
      - *G.* (*n.*) *nesiotis* (Sclater, 1861)—Tristan moorhen
      - *G.* (*n.*) *comeri* (Allen, 1892)—Gough Island moorhen
    - **Subgenus** *Gallinula* Brisson, 1760—typical moorhens
      - *G. tenebrosa* Gould, 1846—dusky moorhen
      - *G. angulata* Sundevall, 1850—lesser moorhen
      - *G.* (*c.*) *chloropus* (Linnaeus, 1758)—Eurasian moorhen (includes *indica*, *orientalis*, *correiana*, *guami*)
      - *G.* (*c.*) *pyrrhorrhoa* Newton, 1861—Madagascan moorhen (includes *seychellarum*)
      - *G.* (*c.*) *cachinnans* Bangs, 1915—North American moorhen (includes *cerceris*)
      - *G.* (*c.*) *galeata* (Lichtenstein, 1818)—South American moorhen (includes *garmani*, *pauxilla*)
      - *G.* (*c.*) *sandvicensis* Streets, 1877—Hawaiian moorhen
  - **Genus** *Fulica* Linnaeus, 1758—coots
    - *F. rufifrons* Philippi & Landbeck, 1861—red-fronted coot
    - *F. armillata* Vieillot, 1817—red-gartered coot
    - *F. leucoptera* Vieillot, 1817—white-winged coot
    - *F. cornuta* Bonaparte, 1853—horned coot
    - *F. gigantea* Eydoux & Souleyet, 1841—giant coot
    - *F.* (*a.*) *americana* Gmelin, 1789—American coot (includes *columbiana*)
    - *F.* (*a.*) *ardesiaca* Tschudi, 1843—Andean coot (includes *atrura*; polymorphic)
    - *F.* (*a.*) *alai* Peale, 1848—Hawaiian coot
    - *F.* (*a.*) *caribaea* Ridgway, 1884—Caribbean coot
    - *F. atra* Linnaeus, 1758—black coot
    - *F. cristata* Gmelin, 1789—red-knobbed coot
    - †*F.* (*c.*) *chathamensis* Forbes, 1892—Chatham Islands coot
    - †*F.* (*c.*) *prisca* Hamilton, 1893—New Zealand coot
    - †*F. newtoni* Milne-Edwards, 1867—Mauritius coot

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