

An Exploratory Phylogenetic Analysis of the Genera of the Accipitridae, with Notes on the Biogeography of the Family

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ABSTRACT

An exploratory phylogenetic analysis of osteological characters for most of the genera of the Accipitridae resulted in a single tree. The Osprey *Pandion haliaetus* was as far from the main accipitrid stem as was the designated outgroup, the Secretarybird (*Sagittarius serpentarius*). The 'kites' *Elanus* and *Elanoides* were basal but separated on the tree, and the Old World vultures and serpent and snake eagles formed a clade distinct from all other accipitrids. *Geranospiza* appears to be the sister-group of *Circus* and only convergently similar to *Polyboroides*. Within the main accipitrid clade, the milvine 'kites' and sea eagles formed a major basal clade. The harpy eagles appear to be paraphyletic. *Morphnus* is placed closer to the *Accipiter/Buteo* clade than to the harpies. *Ictinia* and *Harpagus*, two genera that have been allied to other small 'kites', are shown to be part of the *Accipiter/Buteo* radiation, along with several other 'sub-buteonines'. Although there was little agreement between patterns of parasite infection and higher (above Family) level systematics among the diurnal birds of prey, the major branches of the tree were broadly consistent with the distribution of infection with species-groups in the genus *Degeeriella* (Mallophaga). A biogeographic analysis suggests a long-standing dichotomy between the evolutionary histories of Old and New World accipitrids.

INTRODUCTION

The relationships within the family Accipitridae are poorly understood (de Boer & Sinoo 1984; Jollie 1976, 1977a, 1977b, 1977c; Olson 1985). Amadon (in Stresemann & Amadon 1979: 272) declined to recognise formal divisions within the Accipitridae, although Stresemann had recognised eleven in his original manuscript for the Checklist. Kemp & Crowe (1990) recognised two major clades within the Accipitridae, but found it difficult to resolve the relationships between genera within the major clades. Their work was unusual in being based on a variety of characters, including external morphology, behaviour, and karyology. Apart from early workers such as Milne-Edwards (1867-1871), Fürbringer (1888), and Suschkin (1899, 1900, 1905), and the

selective work of Jollie (1976, 1977a, 1977b, 1977c), most classifications are based primarily on external morphology (Brown & Amadon 1968; Stresemann & Amadon 1979; Swann 1924-1945) or on biochemical characters (Sibley & Ahlquist 1972, 1990). There has been little interest in the comparative analysis of skeletal characters in the group.

Families and subfamilies within the Accipitridae have been diagnosed on external characters (e.g., Witherby *et al.* 1939). Osteological diagnoses of subfamilial groups in the Accipitridae often do not allow different groups to be distinguished. Friedmann (1950) gave identical osteological diagnoses for several of his subfamilial groups. Osteological characters continued to be omitted from most recent diagnoses and systematic treatments (Amadon 1953, 1964, 1978, 1982a, 1982b; Brown & Amadon 1968; Friedmann 1950; Stresemann & Amadon 1979), despite their potential (Jollie 1976, 1977a, 1977b, 1977c). It is not surprising, therefore, that it is difficult to incorporate fossil accipitrids into these classifications (Olson 1985). Even when the fossil material is copious and well-preserved, the paucity of knowledge of skeletal characters within the Accipitridae has hampered progress in determining relationships (Ballmann 1969, 1973). Haast's Eagle (*Harpagornis moorei*), a huge extinct accipitrid from the late Quaternary of New Zealand, is represented by material comparable to that held for living taxa. The relationships of Haast's Eagle have, however, remained obscure since Haast described it in 1872 (Haast 1872; Oliver 1930, 1945, 1955; Owen 1879; Shufeldt 1896).

The phylogenetic analysis reported here was undertaken as part of research on the roles that phylogeny, ecology, and historical constraints (Seilacher 1979) played in the evolution of structural traits and functional morphology in this eagle. It was part of a wider study whose prime emphasis was the palaeobiology of the eagle. The limitations in the treatment must be seen in this light.

Level of treatment

The history of the taxonomy and systematics of the Falconiformes [=Accipitriformes] has been reviewed at length by Sibley & Ahlquist (1972, 1990) and Jollie (1976, 1977a, 1977b, 1977c), and summarised by Kemp & Crowe (1990). The reviews include extensive literature citations and comparisons of previous classifications, and only a brief summary of recent views pertinent to the scope of the present study is presented here.

Problems remain with identifying the higher taxonomic levels within the diurnal birds of prey. The main problem until recently has been of what groups to include within the traditional order Falconiformes. As generally conceived (e.g., Brown & Amadon 1968; Stresemann & Amadon 1979), the Order Falconiformes includes diverse groups whose major features in common are a hooked beak and a generally carnivorous diet. Stresemann & Amadon (1979) accepted four suborders: Cathartae (Vulturidae [Cathartidae *auct.*]; the 'New World' vultures); Accipitres (Accipitridae; hawks, eagles, kites, and Old World vultures); Sagittarii (Sagittariidae; *Sagittarius serpentarius*); and Falcones (Falconidae: falcons and caracaras). They listed two subfamilies in the Accipitridae: the Pandioninae (containing only the osprey (*Pandion haliaetus*); and the Accipitrinae (Stresemann & Amadon 1979).

The profound differences between the major groups have been appreciated for many years (Beddard 1898; Hudson 1948; Friedmann 1950). Jollie (1953) countered Clay's (1951) suggestion that the order was monophyletic - based on the distribution of several genera of bird lice (Mallophaga) on hosts in the different bird families - with strong evidence for polyphyly.

Recent work supports Jollie's contention. Of the four suborders recognised by Stresemann & Amadon, there is now compelling osteological (Emslie 1988; Jollie 1976, 1977a, 1977b, 1977c; Ligon 1967; pers. obs.), karyological (de Boer 1976), behavioural (König 1982), and biochemical (Sibley & Ahlquist 1990) evidence that the Vulturidae are related to the storks (Ciconiidae) and do not belong with the accipitrids. The evidence was acknowledged by Friedmann (1950), Brown & Amadon (1968), and Amadon (in Stresemann & Amadon 1979), but was not followed in the classifications of any of these workers.

Sagittarius differs from the Accipitridae in several ways, including its gross karyotype (de Boer 1975) and thigh muscle formula (BXY as against A, Beddard (1898)). It has been accorded various ranks, up to subordinal level (Brown & Amadon 1968), and even excluded from the Falconiformes altogether (Jollie 1977c).

The falconid karyotype differs greatly from that of the Accipitridae (de Boer 1976), and Jollie (1976, 1977a, 1977b, 1977c) concluded on osteological, pterylogical, and other morphological

grounds that the Falconidae are not related to the accipitrids.

Despite the differences in detail between the karyotypes of the Falconidae, Sagittariidae, and Accipitridae, Kemp & Crowe (1990) pointed out that the families are the only ones lacking large macrochromosomes. This is apparently a derived character (de Boer & Sinoo 1984; Rytman *et al.* 1987). Other characters used by Kemp & Crowe (1990) to support monophyly of the three groups are variable within the groups.

Whatever the higher relationships of the Accipitridae, de Boer (1975, 1976) and de Boer & Sinoo (1984) have stressed the uniqueness of the accipitrid karyotype. The peculiarity of the karyotype strongly suggests that the group is monophyletic and does not include *Pandion* or *Sagittarius*.

The object of the present study was to determine the relationships between as many genera of the Accipitridae as possible, using osteological characters, so that fossil taxa could be incorporated into the phylogeny. The sister group of *Harpagornis moorei* could then be established amongst the apparently homogeneous assemblage of about 60 genera currently recognised in the family.

My use of the genus as the basic OTU assumed that generic level systematics of the Accipitridae were well founded. This is probably not a valid assumption because the limits of several genera are blurred by frequent changes in taxonomy, particularly in *Spizaetus* and African forest eagles (e.g., Amadon 1982a). However, my sample represented most of the major variation amongst c 220 species in the family (Stresemann & Amadon 1979).

Phylogenetic analysis

There have been three recent attempts to produce a non-linear arrangement of species within the Accipitridae. Two of these left open the connections between major branches (Brown & Amadon 1968; Jollie 1977c). Although he examined osteological features in his systematic work on the Accipitridae, Jollie (1976, 1977a, 1977b, 1977c) rejected the use of phylogenetic (cladistic) techniques as inappropriate. In the most recent study, however, Kemp & Crowe (1990) analysed a variety of behavioural, karyological, anatomical, and skin characters, using a computer-aided cladistic approach.

I used phylogenetic analysis because it is based on the assumption that shared derived characteristics are the best indicators of common ancestry (Hennig 1966; Wiley 1981). The use of derived characters reduces the effects of shared primitive features (symplesiomorphies) and of convergent features (homoplasies) (Wiley 1981). The development of several computer programs (e.g., HENNIG, MACCLADE, PAUP, PHYLIP) have simplified the analysis of large character suites for many operational taxonomic units (OTUs).

I rejected the phenetic approach of seeking a measure of overall similarity as inappropriate because there was strong evidence for convergence (e.g., between *Ictinia* and the *Elanus* kites (Shufeldt 1896)) in the Accipitridae. Like Raikow (1985), I believe that the traditional eclectic systematic method, as used by Amadon, Brown, Jollie, and Stresemann cannot generate a classification based on phylogeny (Amadon 1953, 1964, 1977, 1978, 1982a, 1982b, Brown 1982, Brown & Amadon 1968, Jollie 1976, 1977a, 1977b, 1977c, Stresemann & Amadon 1979).

Only those genera generally accepted as belonging in the Accipitridae were included in my analysis. Neither the falcons nor the New World vultures are considered further here, for the reasons outlined above. However, I included *Sagittarius* as an outgroup for analysis of the relationships within Stresemann & Amadon's (1979) Accipitrinae. *Pandion* was also included because of its subfamilial rank within the Accipitridae in Stresemann & Amadon (1979), although other authors have accorded it familial (Brown & Amadon 1968) or even subordinal rank (Hudson 1948). The phylogenetic hypothesis for the Accipitridae represented by the tree reported here is further interpreted by means of a formal, unambiguous (Raikow 1985) classification.

Biogeography of the Accipitridae

The most recent discussion of the biogeography of diurnal raptors is that of Kemp & Crowe (1990). They concluded, in part, that the biogeography of clades "offers little insight to their areas of origin." I report here also the results of an analysis of the global distribution of species of Accipitridae. Species density was analysed cladistically (Brooks 1985), to see if any patterns

congruent with phylogenetic patterns could be discerned.

METHODS

Taxa and specimens

A full survey of all species in the Accipitridae was not attempted. Instead, each monotypic genus and up to three species from polytypic genera were studied. Some genera of Accipitridae are not well-defined, for example there is considerable discussion as to the limits of *Aquila*, *Accipiter*, and *Gyps* (Amadon & Brown 1968; Amadon, in Amadon & Stresemann 1979; Amadon 1978, 1982a), so species unequivocally assigned to those genera were used.

I examined skeletal material of *Pandion haliaetus*, *Sagittarius serpentarius*, and 66 species representing 51 of the approximately 60 genera and 215-220 species presently included in the Accipitridae (Appendix 1). Eight genera were represented by two species, and one genus by three species.

Several taxa were represented in collections only by part skeletons, or a few bones removed from study skins. Material of others (*Dryotriorchis*, *Megatriorchis*, *Harpyopsis*, *Eutriorchis*, *Oroaetus*, *Hamirostra*, *Lophoictinia*, *Henicopernis*) was either not available in the collections visited, or was not held in collections at the time (e.g., Blandamer & Burton 1979). *Sarcogyps* and *Torgos* are sometimes recognised as monotypic genera, but were included in *Aegyptius* by Amadon (1977) and Stresemann & Amadon (1979). Only *Aegyptius* was examined in this study.

South-east Asian species of *Spizaetus* were poorly represented in collections, so that genus, as presently understood (Stresemann & Amadon 1979), was represented by the American *Spizaetus ornatus*. The absence of south-east Asian taxa is unfortunate, because they are geographically one of the closest groups of forest eagles to *Harpagornis moorei*, and have been suggested as possibly being similar to it morphologically (Brathwaite & Holdaway 1987).

Analysis of characters

I used only qualitative, multi-state osteological characters so that *Harpagornis moorei* could be scored for all characters used in the analysis. Most characters were defined after examination of series of homologous elements from as full a range of taxa as possible. Other characters had already been defined or illustrated, primarily by Jollie (1976, 1977a, 1977b, 1977c) and Olson (1982, 1987).

Of 273 characters assessed, 188 were used in the analysis of 45 taxa, including the outgroup (mean 4.2 features per OTU). The other characters either could not be assessed for sufficient taxa, or their different states could not be surveyed adequately. The unused characters are here included as a basis for future work (Appendix 2).

All skeletal characters were discrete features having at least two definable states. Character states were tabulated for each OTU. Characters were assumed to be homologous if they involved similar structures in corresponding positions on the same elements. Most could be described using standard terminology (Ballmann 1969; Baumel 1979; Howard 1929), and are therefore subject to the least possible error in assumed homology as present knowledge of avian osteology permits. Most difficulty was experienced in reconciling some characters, especially of the pelvis, femora, and tibiotarsi of *Sagittarius* and *Pandion* with those in similar anatomical positions in accipitrids.

Whenever possible, characters were checked for intraspecific and interspecific variation; where this was found, the feature was reassessed or omitted if the variation was considered to be too great.

Characters were weighted equally because there was no reliable information on the conservativeness of any particular feature. Characters were coded as missing if no material was available, or if an element was damaged and the state was difficult to determine.

Characters are listed and described in Appendix 2. The OTU-character state matrix is available from the author.

Trees

I used the program PAUP (Swofford 1985) to generate phylogenetic trees for 42 living genera, *Harpagornis*, *Pandion* and *Sagittarius*. PAUP uses parsimony to produce one or more shortest trees; those in which fewest changes of character state are required. The MULPARS (multiple parsimony) option was invoked, in which all equal length trees are kept until a shorter tree is found. This procedure avoids the possibility that one tree may be accepted from several trees of different topology and the same length. It also helps to reduce the possibility that searching may be limited when rearrangement of a single tree does not result in a shorter tree. If several trees are kept in the computer's memory, it is possible that another equal-length tree will be found from which a shorter tree can be derived (Swofford 1985).

To maximise the chance of finding the shortest tree, the GLOBAL branch swapping option was used. Global swapping involves removing every possible subtree and inserting it at all other positions in search of a shorter tree.

The Accipitridae is apparently so isolated phylogenetically that it is difficult to determine the higher taxon with which it shares its most recent common ancestor (Olson 1985). In alternative recent classifications, *Sagittarius* is considered to be a subclade of either the major clade Order Falconiformes (Stresemann & Amadon 1979) or the Parvorder Accipitrida (Sibley & Ahlquist 1988). I did not use the Falconidae as an outgroup because it was more difficult to assess the homology of characters between the Accipitridae and Falconidae than between the accipitrids and *Sagittarius*. The outgroup was chosen from within the small group of postulated closest relatives, because it was not an object of this study to investigate the relationships of the accipitrids with other families.

Polarities of character state changes were not assumed, and I did not attempt to derive transformation series for the character states. With the data unordered option in effect, PAUP algorithms develop transformation series for the features, and do not assume that transformation series were known. Primitive and derived states were generated by PAUP by outgroup comparison, using *Sagittarius* as the outgroup. Examination of the characters used suggests that it should be possible to derive transformation series for them on outgroup and ontological criteria when a full analysis of the Accipitridae is undertaken.

Pandion was tried as the outgroup, and the trees produced were similar, but not identical, in topology to those produced using *Sagittarius*. *Sagittarius* was the preferred outgroup because its separation from the Accipitridae is supported by a range of evidence (de Boer & Sinoo 1984; Jollie 1976, 1977a, 1977b, 1977c). On the other hand, there is some support for the hypothesis that *Pandion* and the accipitrids share a most recent common ancestor (Sibley & Ahlquist 1972; Tyler 1966).

No ontogenetic information was available for most characters used and as a consequence developmental data could not be used to determine character state polarities. I did not use the criterion of wide representation of a character indicating plesiomorphy (primitiveness), because of the apparent homogeneity of morphology and the high level of plesiomorphy within the family suggested by karyological data (de Boer & Sinoo 1984).

All taxa compared were taken as belonging to a single, natural clade because all species in the family that have been studied so far share the derived condition, apparently unique within Aves, of having only 6-12 microchromosomes (de Boer & Sinoo 1984).

Comparisons with other data

Trees were assessed by making comparisons with published classifications, and with morphological and other data available in the literature. Trees were also compared with information on host-parasite relationships of bird lice (Mallophaga) and results of a biogeographic analysis (see below). It was not possible to use data from fossils (Olson 1985), but the presence of Vulturidae in Europe during the Tertiary (Cracraft & Rich 1972), and of accipitrid vultures in North America until the late Pleistocene (Rich 1980), was taken into account.

Biogeography of the Accipitridae

Patterns of distribution of living accipitrids were analysed by using genera as characters, and numbers of species in each genus as character states. This is a modification of the method discussed

by Brooks (1985). OTUs were geographic regions that usually coincided with boundaries and sub-boundaries of biogeographic regions. Numbers of species in each genus in each of 18 areas were compiled from distributional data and maps provided by Brown & Amadon (1968) and Stresemann & Amadon (1979). Numbers of species were arrayed against area (Appendix 3) and trees produced using PAUP (Swofford 1985), with MULPARS and GLOBAL branch swapping options selected, and character states unordered. The tree topologies were then compared with those obtained from the phylogenetic study.

RESULTS AND DISCUSSION

General

Two shortest trees were found with almost identical topologies (consistency index 0.217). They differed only in the position of *Gypaetus* in the accipitrid vulture clade (see below). The main branches of the second tree are shown in Fig. 1, and details of its branches are shown in Figs 2-13.

The results confirmed the monophyly of several groups that have been recognised at various taxonomic levels in different classifications.

Basal branches

Sagittarius was separated from the other taxa by changes in 59 of 188 characters, including 11 unambiguous autapomorphies. My results supported karyological evidence that *Sagittarius* is not close to the Accipitridae (de Boer 1976).

Pandion branched off first in the main sequence, and was almost as far from the accipitrids as was the outgroup (*Sagittarius*). Forty-six characters, including 13 autapomorphies, supported its distinction. Ten characters were unique to *Pandion* (Fig. 2). The separation of *Pandion* from the Accipitridae agreed with conclusions based on pterylosis (Compton 1938), karyology (Ryttman *et al.* 1987), and osteology (Jollie 1976, 1977a, 1977b, 1977c), but some degree of relationship is indicated by eggshell structure (Tyler 1966).

My results confirmed the polyphyly of the 'kites' *sensu* Brown & Amadon (1968). *Elanus* and *Elanoides* were separate clades (Fig. 1, 2). *Elanoides* was defined by 23 characters, but no autapomorphies. *Elanus*, however, had five autapomorphies among 31 characters. Osteological characters confirmed the separation of these genera; Friedmann (1950) and Brown & Amadon (1968) also separated them on claw morphology.

I had insufficient data to test whether *Gampsonyx* and *Chelictinia* are sister groups of *Elanus* as is implied by Friedmann's (1950) grouping of the three genera in the subfamily Elaninae. *Gampsonyx* was long included in the Falconidae, as it superficially resembles small falcons. Osteologically, however, it is clearly an accipitrid (Brodkorb 1960).

Accipitrid vultures and the serpent eagles

Monophyly of the accipitrid vultures and the so-called 'serpent eagles' was supported by 17 characters, including two autapomorphies, within the Accipitridae as accepted here (one was shared with *Pandion*, Fig. 2).

The clade included two major branches, with 14 characters defining the vultures, and nine the serpent eagles (Fig. 3, 4, 5). The vultures (Fig. 4, 5) included three genera (*Gypaetus*, *Neophron*, and *Gypohierax*), whose proximity to the typical vultures has been questioned (Brown & Amadon 1968; Jollie 1977c), and one (*Pernis*) which has usually been included with the elanoidid kites (Jollie 1977c). The serpent eagle branch included *Polyboroides* (African Harrier-Hawk) and *Terathopius* (Bateleur Eagle), in addition to *Spilornis* (Asiatic Serpent Eagles) and *Circaetus* (Snake Eagles of Eurasia and Africa).

Inclusion of *Polyboroides* with the serpent eagles was based on 29 characters (Fig. 3). Three of 17 convergences were with *Geranospiza* (South American Crane Hawk), whose relationship to *Polyboroides* has been debated for many years (Burton 1978; Brown & Amadon 1968; Friedmann 1950; Jollie 1977c).

Friedmann (1950) thought that they were closely related, whereas Brown & Amadon (1968: 21) stated that *Polyboroides* is "definitely related to the snake-eagles and might be regarded as only

a specialised member of that group". They based this view partly on the similarity of the plumage of the young to that of *Spilornis*. Burton (1978) concluded that the shared derived characters of the intertarsal joint seemed to support a relationship but could not exclude the possibility of convergence of these characters. He noted, however, that if the intertarsal joint criterion was omitted, then there was little evidence for a close relationship between the two taxa. Jollie (1977c) placed *Polyboroides* with the accipitrid vultures and serpent eagles, and *Geranoospiza* grouped them with South American 'sub-Buteos'. Beddard (1889) noted that *Polyboroides* was similar in its myology to *Gypohierax*.

My data confirmed a relationship between *Polyboroides* and the serpent eagles, but as a plesiomorphic taxon within the group rather than a highly specialised (derived) one as suggested by Brown & Amadon (1968). Nevertheless, it did exhibit four autapomorphies.

Terathopius did not possess any autapomorphies, but was defined by a suite of 24 characters, including 17 convergences, 6 reversals, and one complex character. The inclusion of *Terathopius* with the serpent eagles supports Brown & Amadon's (1968) interpretation. Jollie (1977c) concluded that it was intermediate between the serpent eagles and the accipitrid vultures.

The clade of serpent eagles was defined by 17 characters (Fig. 3). *Spilornis* lacked an autapomorphy among a suite of 30 distinguishing characters. *Circaetus*, however, had one autapomorphic character among the 25 that separated it from *Spilornis*. Brown & Amadon (1968) and Jollie (1977c) considered the two genera were closely related.

de Boer & Sinoo (1984) found that *Circaetus gallicus* had a karyotype identical to that of the accipitrid vultures, and only slightly different from that of *Pernis*. The karyological data provide some support for the branching pattern found here.

In the vulturine branch, the separation of *Gypohierax* (Palmnut Vulture) was supported by 28 characters, but no autapomorphies (Fig. 4). *Gypohierax* was included with the vultures by Brown & Amadon (1968), who suggested that it linked them to the sea eagles (*Haliaeetus*). Brown & Amadon (1968) also suggested that it most resembled *Neophron* (Egyptian Vulture) amongst the other vultures, a view also held by Jollie (1977c) and Suschkin (1899), but not confirmed here.

The monophyly of a group consisting of *Pernis* (honey buzzards) and *Neophron* was supported by 13 characters, but none of these was an unambiguous autapomorphy (Fig. 4). As noted above, *Pernis* has usually been placed near *Elanoides* (Brown & Amadon 1968; Jollie 1977c) and not with the accipitrid vultures. However, Brown & Amadon (1968) implied that there was at least a distant relationship by suggesting that the vultures had evolved from kites, and Jollie (1977c) noted that *Neophron* is " 'kite-like' in many respects", although it superficially resembles *Necrosyrtes*. *Pernis* was characterised by four autapomorphies, and *Neophron* by three and another character shared with *Pandion* (Fig. 4).

The position of the Bearded Vulture, *Gypaetus*, in the branching sequence of the accipitrid vultures was the only difference between the two shortest trees. In the first tree, *Gypaetus* was the sister group of a clade containing *Necrosyrtes* (African Hooded Vulture), *Gyps* (Griffon Vultures), and *Aegypius* (Black and Lappet-faced Vultures of Africa and Eurasia) (Fig. 5). In the second tree (Fig. 4), *Gypaetus* was the sister group of all the vultures except *Gypohierax*.

de Boer (1976) concluded that the differences between the karyotypes of *Gypaetus* and the other vultures did not support a close relationship between the former and the vultures, and more recently de Boer & Sinoo (1984) also rejected the relationship. Instead, they proposed that *Gypaetus* was near *Circus* (harriers), *Pernis*, and the so-called booted eagles (including *Aquila* and *Spizaetus* (de Boer & Sinoo 1984)). However, they also noted that the condition in *Gypaetus*, *Pernis*, and the booted eagles could have evolved independently from an 'original' condition, namely that found in *Circaetus*. Such thinking is more in line with my second tree than my first.

Clay (1951) proposed that the Accipitridae and the Vulturidae constitute a monophyletic group because they share the same taxa of bird lice (Mallophaga). However, in 1951 it was not clear that accipitrid ('Old World') and vulturid ('New World') vultures had been sympatric in Europe and North America for millions of years, and until as recently as the late Pleistocene in North America (Cracraft & Rich 1972; Howard 1932; Olson 1985; Rich 1980). There was ample time for lice to have colonised new hosts, particularly when both host groups probably fed at the same carcasses, and their presence on both cannot be considered indicative of a close relationship between the hosts.

Monophyly of the remaining three genera (*Necrosyrtes*, *Gyps*, and *Aegypius*) was supported

by 26 characters (19 convergences, 6 reversals, 1 synapomorphy) (Fig. 5). *Gyps* and *Aegypius* were linked by 21 characters; *Gyps* was characterised by three autapomorphies. Jollie (1977c) recognised a similar grouping of these three genera, as did Brown & Amadon (1968).

Circus and Geranospiza

Circus was found to be the sister group of *Geranospiza* (Fig. 6), and not a sub-buteonine (Amadon 1982b). Nor was it close to *Accipiter* as suggested by Jollie (1977c), despite the apparent close resemblance of its postcranial anatomy (Olson & James 1991). The monophyly of the clade consisting of *Geranospiza* and *Circus* was supported by two synapomorphies. As noted above, *Geranospiza* was not close to *Polyboroides*. The karyotype of *Geranospiza* (Williams & Benirschke 1976) differs from the unique *Circus* karyotype (de Boer & Sinoo 1984). This feature supports the likelihood of an early separation of the two genera.

Sibley & Ahlquist (1972) found that the egg white proteins of *Circus* were similar to those of *Elanus*. The similarity is probably plesiomorphic, because the egg white proteins of these genera were similar to those of *Pandion*.

Machaerhamphus

Brown & Amadon (1968) regarded the bat kite *Machaerhamphus* as an aberrant elanoidid kite. However, Jollie concluded that the skeletal evidence was equivocal and suggested that it is "an extreme type without close relatives ... [that had] ... a long and independent history" (Jollie 1977c: 121(321)).

My phylogenetic reconstruction indicated that it represented a separate clade, whose monophyly was supported by two autapomorphies, one of which was, however, shared with the outgroups (Fig. 1). It was linked to other 'kites' only by symplesiomorphies.

Milvine kites and sea eagles

The data support a sister group relationship between the milvine 'kites' (*Milvus* and *Haliaeetus*) and the sea and fishing eagles (*Haliaeetus* and *Ichthyophaga*) (Fig. 7). However, *Buteogallus* (the South American black hawks) was an unexpected member of the clade. Jollie (1977c) placed it with *Heterospizias* and *Busarellus* in the same clade as the Harpies, whereas Brown & Amadon (1968) included it with *Heterospizias* and *Leucopternis*. Jollie (1977c: 117-118) grouped *Buteogallus* with *Heterospizias* and summed up the problems of relationships among the Accipitridae when he pointed out that "the Central and South American species of the buteogallin supergenus appear to retain more of the primitive features, a statement that is more of a hope than a defensible hypothesis".

Monophyly of the whole clade was supported by one synapomorphy, the shape of the notch for the *peroneus* nerve in the proximal tarsometatarsus, among 10 defining characters.

Monophyly of the milvines and haliaeetines is supported by 13 characters, including the fusion of the first two phalanges of the second pedal digit. Olson (1982) surveyed the distribution of this derived character in the Accipitridae and reported it in *Ictinia*, *Busarellus*, *Haliaeetus*, *Milvus*, *Haliaeetus*, and *Ichthyophaga*. These genera occurred in three distinct groups on the trees found here (Fig. 1), and the character did not define a small, monophyletic group as proposed by Olson (1982).

It is unclear what functional advantage, if any, is associated with the phalangeal fusion, but at least some members of all three groups take fish, although Olson (1982) rejected any connection with diet or habits. However, he regarded *Ictinia* as a kite, whereas my results indicated that it is related to *Buteo* and *Accipiter* as suggested by Shufeldt (1891) (see below). The absence of fused phalanges in *Pandion*, an obligate fish predator, weakens the argument for their evolution principally for fishing.

As Olson (1982) pointed out, the sequence *Milvus-Haliaeetus-Ichthyophaga* parallels an increasing association with aquatic environments and reliance on a diet of fish. *Buteogallus* is mainly a crab-eater that lives in swampy habitats, and this accords to some extent with its basal position in the clade. The specialised fishing behaviours exhibited by *Busarellus* are, according to my results, convergent on those of the milvine-haliaeetine clade.

Geranoaetus* and *Heterospizias

The isolation of *Geranoaetus* (Grey Eagle-buzzard) as a separate clade is supported by 23 characters, including one autapomorphy (Fig. 8). Despite the 'identity' of its karyotype with that of *Buteo* (de Boer & Sinoo 1984), *Geranoaetus* appears to be an early offshoot from the buteonine-accipitrine lineage rather than a sub-buteonine as concluded by Amadon (1982b). Its resemblance to the buteonines is probably symplesiomorphic.

Heterospizias (Savannah Hawk) is another isolated South American form (Fig. 9) symplesiomorphically similar to the buteonine groups with which it has been linked (Brown & Amadon 1968; Jollie 1977c). It is not close to *Buteogallus*, with which it was synonymised by Amadon (1982b). Following an examination of osteological characters, Plótnick (1956) concluded that *Heterospizias* was similar to *Buteo* and relatively distant from *Accipiter*, a conclusion which is supported by my results if the resemblance to *Buteo* is considered to be plesiomorphic.

Aquila*, *Spizaetus*, and *Harpagornis

Aquila (Golden Eagle group) and *Spizaetus* (South American Hawk Eagles) were independently derived, but adjacent on both trees. Monophyly of the aquiline genera, *Aquila* and *Harpagornis*, was supported by one synapomorphy (Fig. 9). The placement of *Harpagornis* as the sister group of *Aquila* was the major finding of this study, with respect to the primary objective of my thesis research. The proximity of the aquilines to the spizaetines makes an examination of the African and south-east Asian taxa presently placed in *Spizaetus* all the more urgent. Brown & Amadon (1968) suggested that the Asian forms may be a separate group, and Jollie (1977c) showed the genus had two parts, which he thought resembled each other "as much through convergence, as through common ancestry" (Jollie 1977c: 117(317)).

Harpagornis itself was separated from *Aquila* by two autapomorphies within the Accipitridae as accepted here, although both character states were shared with *Pandion*. One character of the femur was convergent with *Ictinia*, another (of the tibiotarsus) was shared with *Elanus*, and a tibiotarsal character was shared with the *Gyps-Aegypius* clade.

Oliver (1930) concluded that *Harpagornis* was most closely related to *Aquila*, but later (Oliver 1945, 1955) changed his mind and suggested that it was related to *Haliaeetus*: "By the form of the skull, however, it should be placed nearer to *Haliaeetus*. In fact, it is further from *Aquila* than is *Haliaeetus*" (Oliver 1945: 137).

Shufeldt (1896) noted similarities to both *Haliaeetus* and *Aquila*, and placed *Harpagornis* "between" them. My results indicate that resemblances to *Haliaeetus* are symplesiomorphic, and that the bird is an aquiline. However, the closeness of the branch point of the clade to that of the South American *Spizaetus*, and the absence of data on Asian *Spizaetus* indicate that further research will be necessary before the group can be understood.

It has been assumed, without substantiation, that *Harpagornis* is most closely to the Australian Wedge-tailed Eagle (*Aquila audax*) (e.g., Duff 1949). Without a detailed study of the relationships within and between *Aquila* and *Haliaeetus*, however, the sister taxon cannot be identified. Insufficient material of some of the rarer taxa precluded my examining this question.

Busarellus*, *Hieraaetus*, and *Polemaetus

The inclusion of *Busarellus* (Fishing Buzzard) in a clade with a group of African and Eurasian eagles (Fig. 10) was unexpected, in view of its present position in the sub-buteonines (Brown & Amadon 1968). The clade is supported by 18 characters, none of which is an unambiguous synapomorphy, however. The clade consisting of *Busarellus* alone is based on 21 characters, of which one is an autapomorphy (Fig. 10), and one the apparently convergent fusion of the pedal phalanges discussed above with respect to the milvine-haliaetine clade. *Hieraaetus* and *Polemaetus* are linked by nine character state changes (Fig. 10).

Brown & Amadon (1968) noted that Ridgway (1873) thought that *Busarellus* was isolated, and perhaps close to *Hamirostra* (Australian Black-breasted Buzzard). However, they concluded that "the resemblance to that genus is superficial and the resemblance to the neo-tropical genera just mentioned [*Heterospizias*, *Buteogallus*, and *Parabuteo*] is real" (Brown & Amadon 1968: 565). Olson (1982) believed that Ridgway's 1873 and 1876 papers were the "last opinion on the matter to be founded on anything other than tradition", and that later works relied on the sequence of

genera in Ridgway's publications rather than his stated conclusions. Olson (1982) also pointed out that no characters had been published that justified the linking of *Busarellus* with the sub-buteonines.

The position of *Hieraaetus*, the genus of Eurasian and African Hawk Eagles, has been debated, including whether it should be recognised at all or whether the constituent species should be included in *Aquila* (Brown & Amadon 1968). Its position in my scheme as the sister group of *Polemaetus* is supported by nine characters, including four examples of convergence (Fig. 10). Brown & Amadon (1968) concluded that *Polemaetus* was not close to *Spizaetus* or any other genus, but Amadon (1982a) merged the two under *Hieraaetus*, citing behavioural similarities in evidence. *Polemaetus* was distinguished by a single unambiguous autapomorphy among 20 characters (Fig. 10).

The "booted eagles"

Nine genera of large eagles with feathered legs have been recognised as a monophyletic group, but the inclusion of taxa such as *Ictinaetus* has been questioned (Amadon 1982a). Amadon (1982a) submerged one genus in *Hieraaetus* and three in *Spizaetus*.

My results suggest that the "booted eagles" is a paraphyletic grouping of taxa, based on a single character that has been demonstrated to vary even within genera (Amadon 1982a). The submergence of *Stephanoaetus* and *Lophaetus* in *Spizaetus* is not supported by the topology of the tree described here.

Harpies

Recognition of *Stephanoaetus* (African Crowned Eagle) as a sister group of *Harpia* (South American Harpy Eagle) is based on 11 characters, but no unambiguous synapomorphies (Fig. 11). *Harpia* exhibited three autapomorphies, but *Stephanoaetus* none.

As noted above, the placement of *Stephanoaetus* in the harpy clade does not support its submergence in *Spizaetus* (Amadon 1982a; Voous & Wijsman 1964) or even a close relationship with *Spizaetus* as suggested by Brown & Amadon (1968). Brown (1982) resurrected *Stephanoaetus*. However, Amadon (1982a) pointed out some similarities between *Harpia* and *Stephanoaetus* in proportions, habits, a two-year breeding cycle, and immature plumage.

Jollie (1977c) grouped *Stephanoaetus* with *Polemaetus* and *Spizaetus*, and apparently separated these and other "aquilins" from the harpies. However, his diagrams are somewhat ambiguous and the aquilins appear as a sister group of the harpies in one that details relationships among the accipitrin and buteonine genera.

Lophaetus, *Pithecophaga* and *Morphnus*

Similarities between these geographically widely separated taxa are apparently symplesiomorphic, because all formed separate clades in my tree (Fig. 1, 11).

My results do not support Amadon's (1982a) lumping of *Lophaetus* and *Spizaetus*. *Lophaetus* (mis-spelled *Lophoaetus* in Brown & Amadon 1968, and in Amadon 1982), the African Long-crested Eagle, was considered to be the sister group of *Spizaetus*, *Polemaetus*, and *Stephanoaetus* by Jollie (1977c).

Pithecophaga forms another monotypic clade. Its karyotype is similar to that of the aegyptiines (de Boer & Sinoo 1984), but its position on my tree suggests that the resemblances may be symplesiomorphic. Shufeldt (1919) concluded that it was related to *Harpia*. Brown & Amadon (1968: 22) also placed it near *Harpia*, although they noted "We do not claim that the New and Old World genera placed in this group [*Pithecophaga*, *Harpyopsis*, *Harpia*, *Morphnus*] have any special or close relationship, but viewed on a worldwide basis they all represent the climax of one line of raptorial evolution". This comment suggests that Brown & Amadon (1968) viewed the harpies as a grade rather than a phylogenetic group. Jollie (1977c) placed *Pithecophaga* near the gypaetins, but left the proximity of the connection unresolved.

Morphnus (Guianan Crested Eagle) also constitutes a separate lineage on my tree, but it is not particularly close to the harpies, with which it was grouped by Brown & Amadon (1968) and Jollie (1977c). It differs from *Harpia* in having short, broad wings, and a long tail, which give it the

proportions of an *Accipiter*. The karyotype is normal for an accipitrid (Williams & Benirschke 1976).

Kaupifalco

Kaupifalco (African Lizard Buzzard) branches off at the base of the accipitrine/buteonine group (Fig. 12). Jollie (1977c) placed it beside *Buteo* and *Butastur* (not dealt with here) which, together with *Leucopternis* and *Parabuteo*, formed his paraphyletic 'buteonin core'. Brown & Amadon (1968) thought it near *Buteo*, and that it resembled 'fortuitous[ly]' some species of *Leucopternis*.

Harpagus* and *Ictinia

Harpagus (Double-toothed Kite) and *Ictinia* (Mississippi Kites) formed a clade supported by 16 characters, including two unambiguous synapomorphies (Fig. 12). Shufeldt (1891) pointed out that the skeleton of *Ictinia* is similar to that of *Buteo*, but Jollie (1977c) included *Ictinia* with the elanin kites, and Brown & Amadon (1968: 20) placed it between the elanin and milvine kites, commenting that it is "like *Milvus* and *Elanus* a classic kite in form". The fused phalanges of the second pedal digit are apparently convergent with those of *Busarellus* and the milvines and haliaetines (see above).

L Miller (1937) pointed out that *Harpagus bidentatus* has been placed in both the Falconidae (by Carriker and Bowdler Sharpe) and the Accipitridae (by Peters). Suschkin (1905) rejected a relationship with the Falconidae, a contention based mainly on the denticulate bill, and Miller (1937) pointed out several osteological features that support its being an accipitrid resembling *Accipiter* more than *Elanus*. He placed it "between" *Elanus leucurus* and *Accipiter cooperii*.

Amadon (1961), however, argued that *Harpagus* is a kite, and he rejected similarities to *Accipiter* as coincidental or the result of mimicry. Later he suggested that, despite reports that the bird hunts like an *Accipiter*, it is probably 'kite-like' in the way it hunts lizards and large insects (Amadon 1964). However, he also pointed out that it resembles *Accipiter* in being strongly sexually dimorphic in size.

Harpagus was separated from *Ictinia* by two autapomorphies among 31 character state changes.

***Melierax*, accipiters, and the buteos**

Melierax (African Chanting Goshawks) and the accipiters and buteos are supported as a monophyletic clade by 10 characters, including one unambiguous synapomorphy (Fig. 12, 13). Brown & Amadon (1968) placed *Melierax* between *Circus* and the accipiters, but noted that its relationships are not obvious.

Buteo (Buzzards) and *Accipiter* (Sparrowhawks and Goshawks) are the most speciose genera in the family (Stresemann & Amadon 1979). Their close relationship was pointed out by Brown & Amadon (1968). Jollie (1977c) also placed them near each other, and included *Leucopternis* (American White Hawks) and *Erythrotriorchis* (Australian Red 'Goshawk') in the group. Both he and Brown & Amadon (1968), however, linked *Erythrotriorchis* with *Accipiter*.

On my tree *Leucopternis* is the sister group of a clade composed of *Buteo*, and *Parabuteo* (American Bay-winged Hawk), and so shares a most recent common ancestor with the clade containing *Accipiter* and *Buteo*. Brown & Amadon (1968) concluded that *Leucopternis* is related to *Buteo*. Jollie (1977c) made it a sister group of *Parabuteo*, judging from his diagram, and together with *Geranospiza*, he linked them with *Buteo* on one side and *Accipiter* on the other.

Parabuteo is the sister group of *Buteo* (Fig. 13). Brown & Amadon (1968) concluded that it was very close to *Buteo*. However, they also raised the possibility of a relationship with *Heterospizias* and *Buteogallus*. Later, Amadon (1982b) chose to ally *Parabuteo* with *Heterospizias*, and he synonymised in turn *Heterospizias* with *Buteogallus*. These genera are widely separated in the tree found here, and their synonymy is not supported.

Olson (1987) discussed the distribution of the procoracoid foramen in the Accipitridae. He found it to be invariably absent in *Accipiter*, nearly or completely absent in some individuals of *Harpagus* and *Circus*, but present in others. Examination of a specimen in the British Museum

(Natural History) labelled as *Erythrotriorchis* and listed as such in Blandamer & Burton (1979) revealed a fully developed procoracoid foramen. This specimen is actually referable to *Haliastur sphenurus* (pers. obs.).

DNA-DNA hybridisation

Sibley & Ahlquist (1990) presented a phylogenetic tree for the class Aves, based on DNA-DNA hybridisation data. The tree included one species of each of seven genera of Accipitridae (*Gyps*, *Aegypius*, *Neophron*, *Gypaetus*, *Harpagus*, *Accipiter*), two species of an eighth (*Buteo*), four of a ninth (*Circus*), *Pandion* and *Sagittarius*. The topology of their tree is very similar to mine, except for the position of *Circus* (put as the sister group of *Harpagus* as against a near-basal clade in mine), and details of the branching within the vultures.

Sagittarius is basal in the Sibley & Ahlquist tree, separated from *Pandion* by $2.6 *T_{50}$ units¹. *Pandion* itself is separated from the accipitrids by 2.6 units. The vultures are then 1.2 units, and the other accipitrids 0.6 units, from the common node with *Pandion*.

In the vultures, the distance between *Gyps* and *Aegypius* is not resolved, and *Neophron* and *Gypaetus* are sister groups. In the other major clade, *Accipiter* is the sister group of the two *Buteo* species as in my tree, and *Harpagus* is a sister group of *Circus*. Given the few taxa involved, the correspondence between the two trees is understandable.

Mallophaga

Clay (1951) used the distribution of taxa of Mallophaga (bird lice) to argue that the Falconiformes is a monophyletic group. Other evidence suggests that this is not correct. The distribution of genera such as *Laemobothrion*, which occurs on both accipitrid and vulturid vultures (Nelson & Price 1965) probably results from the long sympatry of the two vulture groups in North America and Europe (Cracraft & Rich 1972; Rich 1980).

Within the Accipitridae as understood here, however, the distribution of species in the genus *Degeeriella* has been used to elucidate intrafamilial relationships (Clay 1958). Although most genera of Accipitridae appear to have their own species or subspecies of *Degeeriella*, the presence of particular species groups of Mallophaga may indeed reflect major groupings in the Accipitridae (Fig. 14A). This may be so even though it is difficult to relate character differences in the lice to separation times of the host taxa (Clay 1958).

The elanid and elanoidid kites share species of the *D. elani* species group (Clay 1958). Members of this group are also found on *Chelictinia* (African Swallow-tailed Kite) and *Aviceda* (Crested Hawks), which are not included in my phylogenetic tree because of insufficient data, although the *Degeeriella* on *Aviceda* is less certainly related to others of the *elani* group (Clay 1958). A species of the *elani* group also occurs on *Gampsonyx* (American Pearl Kite), which Clay incorrectly included in the Falconidae; *Gampsonyx* was later shown to be an accipitrid (Brodkorb 1960).

Pernis, traditionally placed with the kites, hosts lice of a different species group (*phlyctopygus*) and members of the *elani* species group are absent (Clay 1958). The *phlyctopygus* group apparently shows affinities to the *regalis* species group taxa characteristic of the milvine kites, and *Haliaeetus* (Clay 1958). *Ichthyophaga* and *Buteogallus* have species of the *fulva* group instead, possibly a plesiomorphic condition, as the *fulva* group is the only one known on most genera of the sister clade to the milvines (Fig. 14A). The only exceptions are the presence of lice of the *discocephalus* species group on *Aquila* and one species of *Haliaeetus*, and the *regalis* group on two species of *Buteo* (Clay 1958) (Fig. 14A). The presence of *discocephalus* lice on two northern species of *Haliaeetus* may be the result of contact between *Aquila* and *Haliaeetus* at feeding sites in winter when food supplies are restricted.

Members of the *fulva* group are also found on species of the Serpent Eagle clade (Fig. 14B). The presence of the distinctive *punctifer* group on both *Gyps* and *Gypaetus* (Clay 1958) is a derived character supporting their relationship as depicted in Fig. 4 and 5. However, the presence of a *regalis* louse on *Gypohierax* (Fig. 14C) is apparently either a plesiomorphic feature, or the result of host transfer.

In general, the distribution of the species groups of *Degeeriella* provides independent support

1 $*T_{50}$ is the difference between the temperature at which all DNA is single chain, and the temperature at which 50% of the DNA has formed duplexes.

for the topology of my phylogenetic trees based on osteological data. Species of the *elani* group seem to be associated with taxa isolated by the initial radiation of accipitrids and represented today by the elanin and elanoidin kites and the Crested Hawks.

Possession of the *fulva* group is a plesiomorphic feature of accipitrid genera, and the presence of *regalis*, *discocephalus*, and *punctifer* groups are derived features of the milvins, aquilins, and gypaetins, respectively. The *phlyctopyga* group appears to be autapomorphic for *Pernis*. Its presence on *Neophron* would provide strong supporting evidence for the branching pattern of the tree presented here.

Biogeography

The Accipitridae is a cosmopolitan family, absent only from Antarctica and some remote oceanic islands (Brown & Amadon 1968). An inspection of the species distributions given by Stresemann & Amadon (1979) shows, however, that there is considerable heterogeneity in the representation of different genera in different regions. A tree of the relationships among operational geographic units (OGUs) derived from the taxon distribution matrix (Appendix 3) using PAUP, and South America as the designated ancestor, is shown in Fig. 15. The geographic areas used are shown in Fig. 16.

The tree can be viewed as indicating either that South America and Africa have been the scene of separate radiations of accipitrids, or that formerly more widespread diverse faunas had been disrupted by Tertiary and Quaternary climatic changes, leaving remnant faunas. The inclusion of accipitrid vultures in North American deposits and vulturids in Europe (Olson 1985) tends to support this view, but the high degrees of endemism and low proportion of shared taxa argue strongly against it.

Intermediate areas exhibited mixes of taxa in proportion both to their distance from each centre, and to the relative vagility of the taxa. The second factor is exemplified by the accipitrid faunas of New Zealand, Greenland, and Oceania. The major, or only, groups in these areas are the *Haliaeetus* eagles, *Circus*, and the occasional *Aquila*-type (New Zealand), *Buteo* (Galapagos and Hawaii), and *Accipiter* (Fiji). Fiji is linked by islands to Melanesia and there are no major water crossings involved in reaching the archipelago. *Accipiter* apparently reached at least as far east as Tonga until humans arrived (Olson 1991 - pers. comm. from Steadman), but this record is not included in the present analysis. These are the only genera whose species seem to be able, or willing, to cross large water gaps, and they are the most cosmopolitan of the accipitrids.

South-east Asia and the Indo-Philippine islands are 'sister groups', whose accipitrid faunas are linked to Australia and to Asia north of the Himalayas and from there to Europe, and Africa; but they have little in common with the North American fauna (Fig. 15). The distribution of apparently relict taxa across the now widely separated land masses of the southern hemisphere, and the inability of most accipitrids to cross large water gaps suggest that these taxa have been isolated by movement of land masses during the birds' evolutionary history. A corollary is that the taxa are old. The oldest accipitrids known are late Eocene to early Oligocene in age, but buteonine hawks do not appear in the fossil record until the middle Miocene of Europe (Olson 1985).

If the accipitrids radiated during the Oligocene, then the position and movement of continental blocks from the Oligocene to the present may have influenced or helped drive the evolution of the group. Sea gaps between Australia and Antarctica and Antarctica and South America were very much narrower during the Oligocene than they are today, according to Owen's (1983, map 66) map of continental positions 29 million years BP.² Antarctica and the Falkland Islands had extensive forests at that time (Birnie & Roberts 1986; Rich 1975), and the environment would have favoured the spread of birds from South America to Australia or vice versa. Antarctica itself may have been the site of much bird evolution, of which there is presently no known fossil record apart from that of penguins (Fordyce 1991; Rich 1991).

Africa had separated from both South America and Antarctica millions of years before they separated from each other (Owen 1983), and the faunal links between Africa and the others are much more distant. It was effectively isolated from both South America and Antarctica-Australia by wide oceans or long distances by land during the Oligocene.

2 Owen's reconstructions were rejected by Cox (1990), but Owen (1990) argued strongly that the objections were based on poor cartographic techniques.

Figure 1. Phylogenetic tree of genera of the Accipitridae, based on analysis of 188 osteological characters. Aegyptine clade is shown in Fig. 4 and 5. See Appendix 1 for taxa representing genera and Appendix 2 for characters.

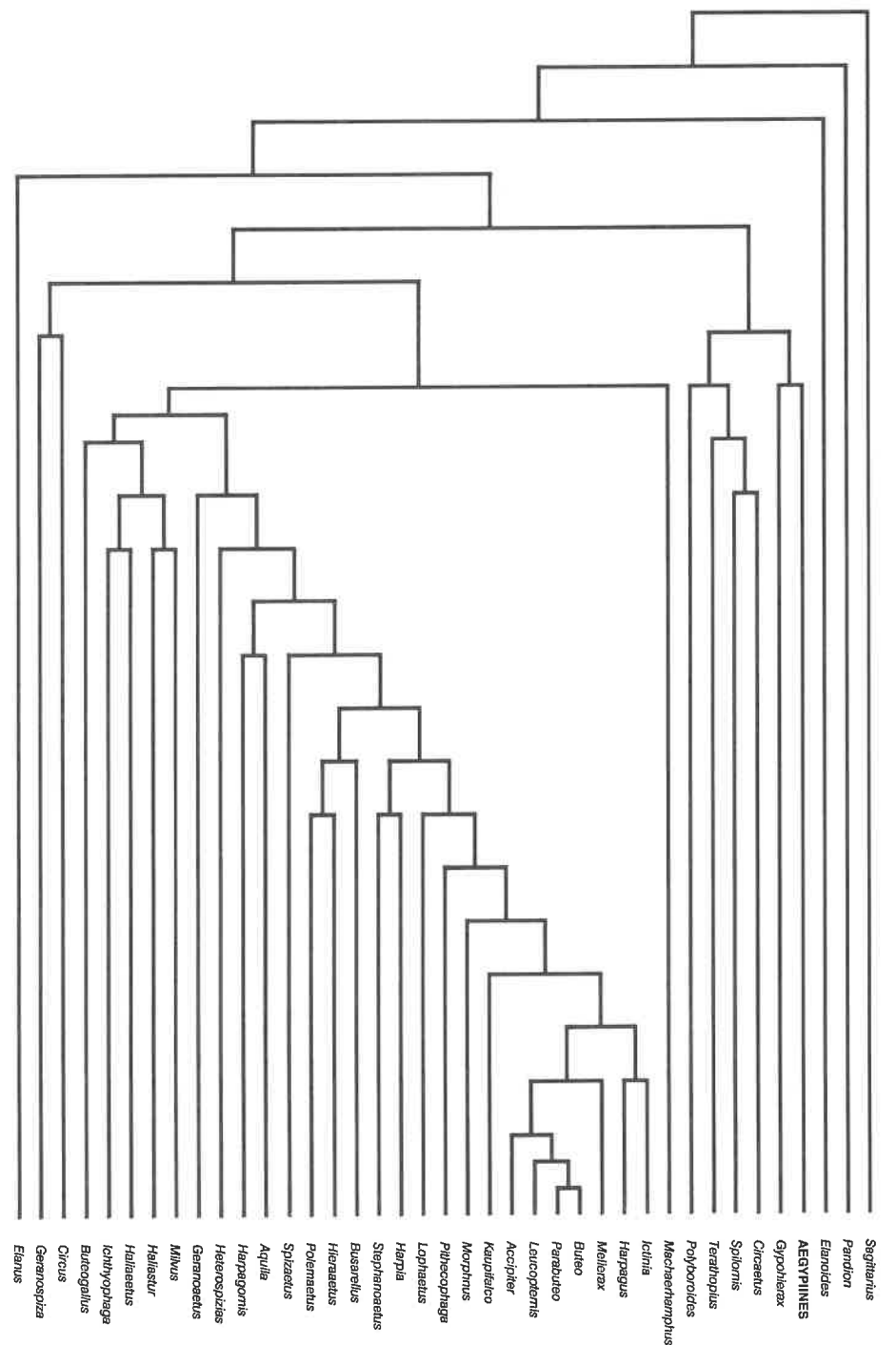


Figure 2. Basal branches of phylogenetic tree of the Accipitridae, including the outgroup (*Sagittarius*) and *Pandion*. The ‘kites’ *Elanoides* and *Elanus* share symplesiomorphic resemblances. Character state changes are shown on each branch. See Appendix 2 for characters.

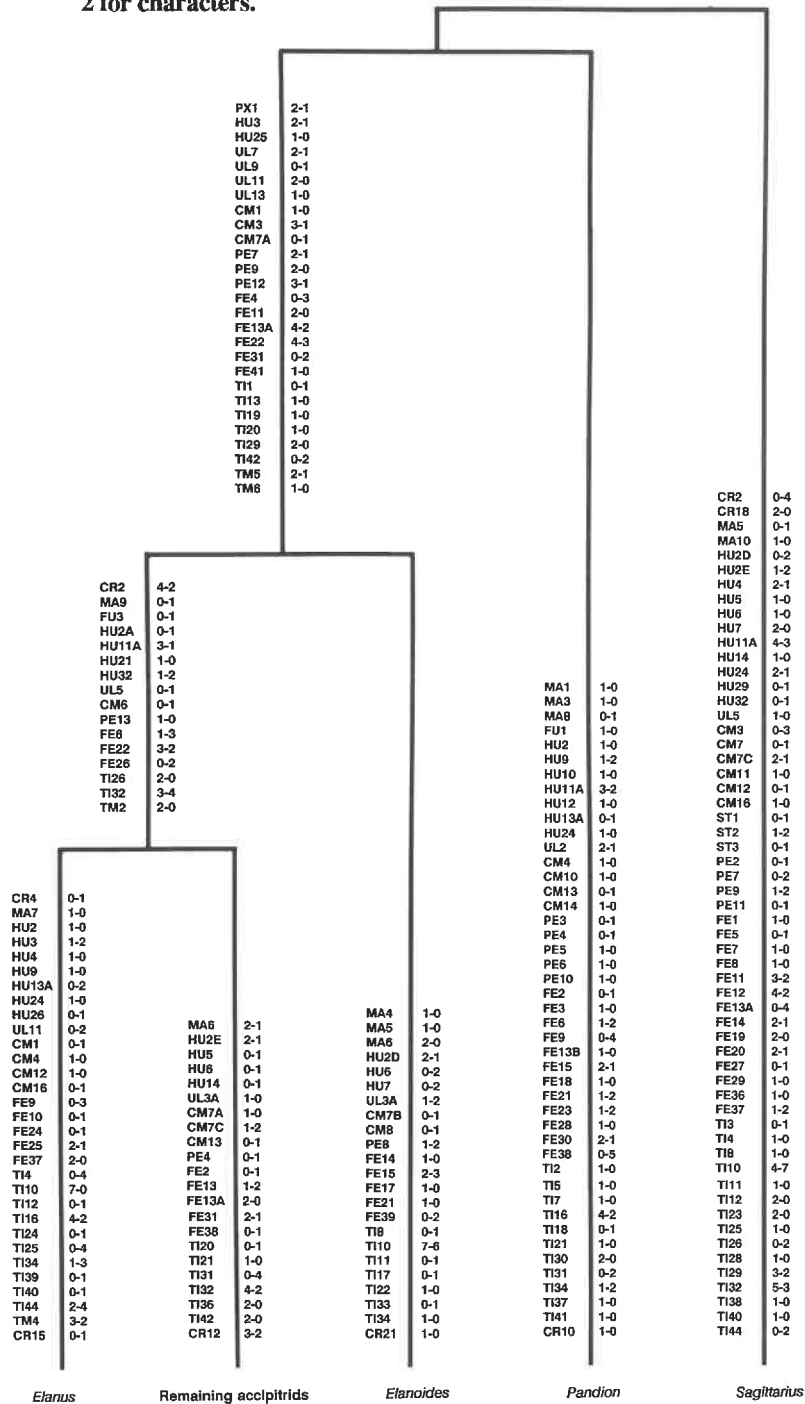


Figure 3. ‘Serpent’ (*Spilornis*) and ‘snake’ (*Circaetus*) eagle, and African Harrier-Hawk (*Polyboroides*) and Bateleur (*Terathopius*) clades, and their relationship to the basal branches of the vulturine clade (including *Gypohierax*). Conventions as in Figure 2.

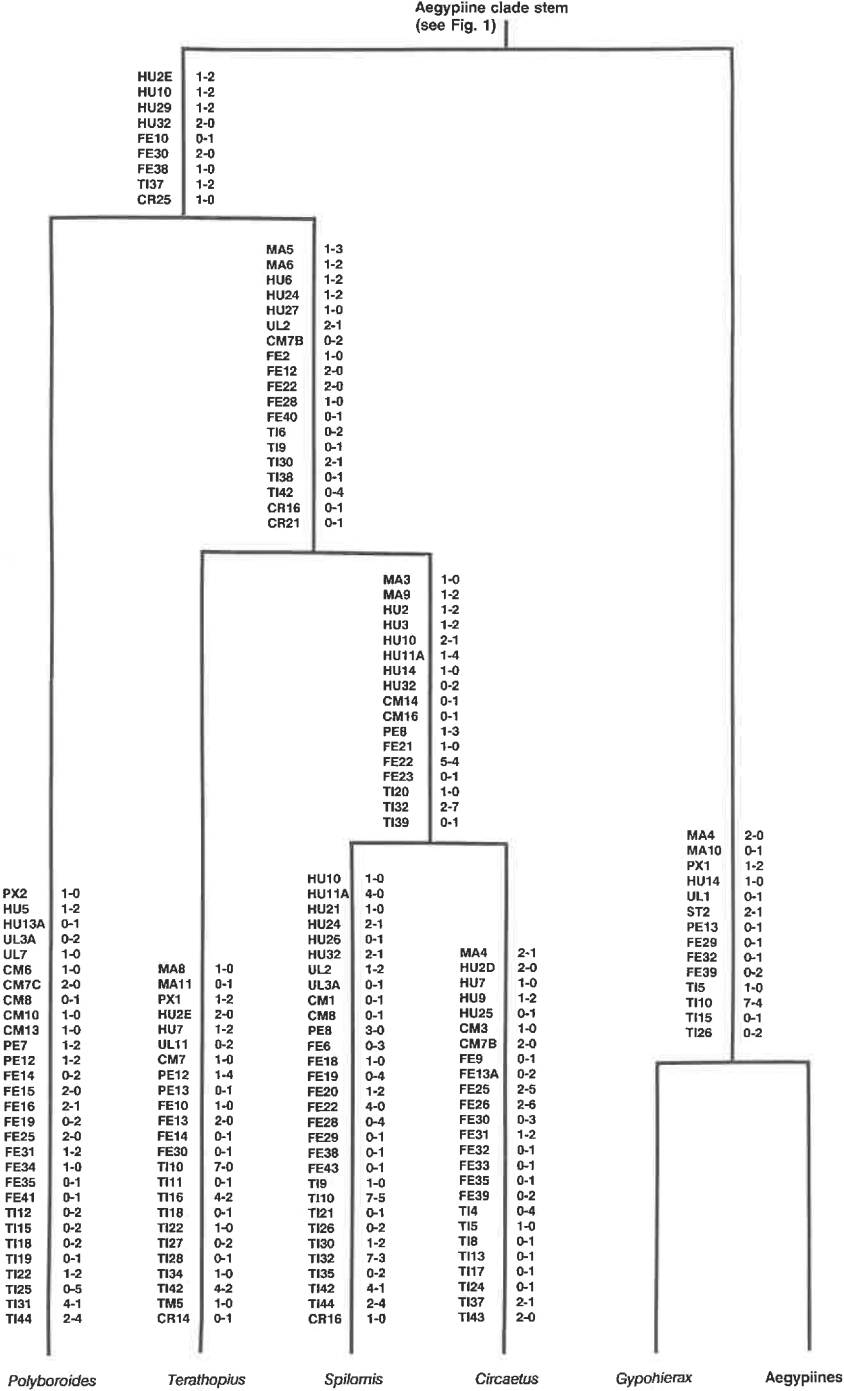


Figure 4. Basal clades of the large vulturines, including the Palm-nut Vulture *Gypohierax*, the Bearded Vulture *Gypaetus*, and the Egyptian Vulture *Neophron*. Note the position of the Honey Buzzard *Pernis* as sister-group of *Neophron* and the that these share a most recent ancestor with the ‘core’ aegyptiines. See Figure 5 for relationships within the ‘core’ clade. Conventions as in Figure 2.

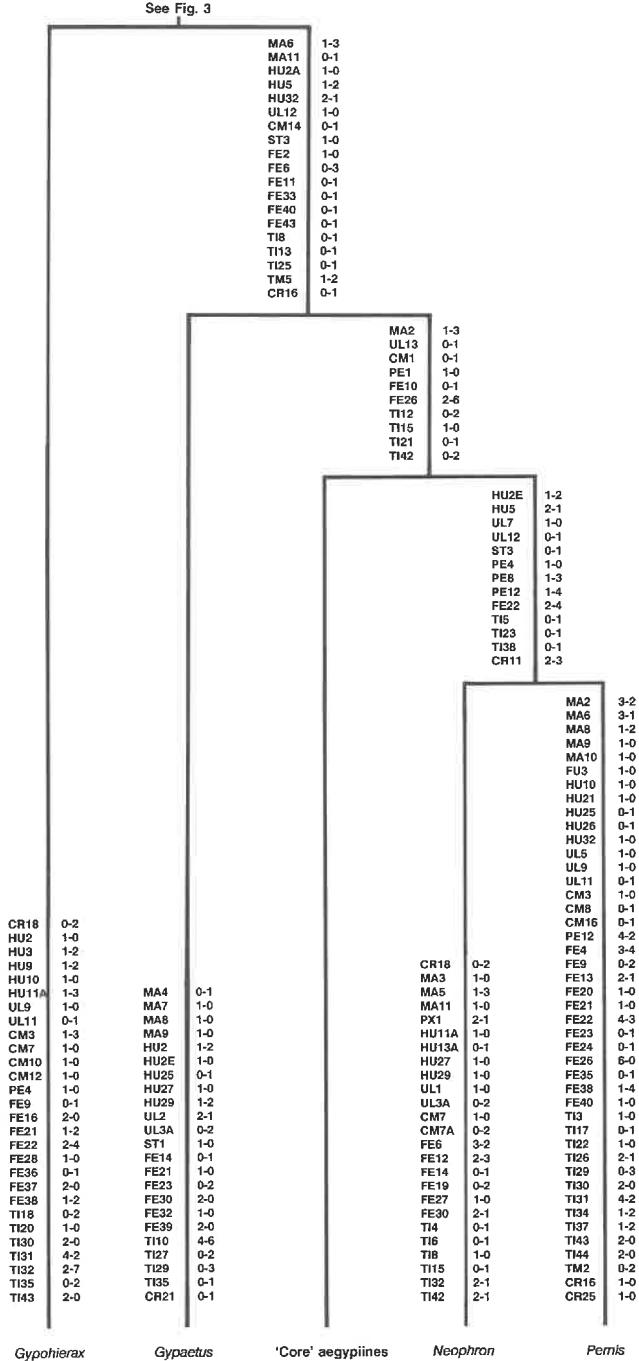


Figure 5. Relationships of the Old World vultures. See Figure 4 for basal branches of the vulturine clade. Conventions as in Figure 2.

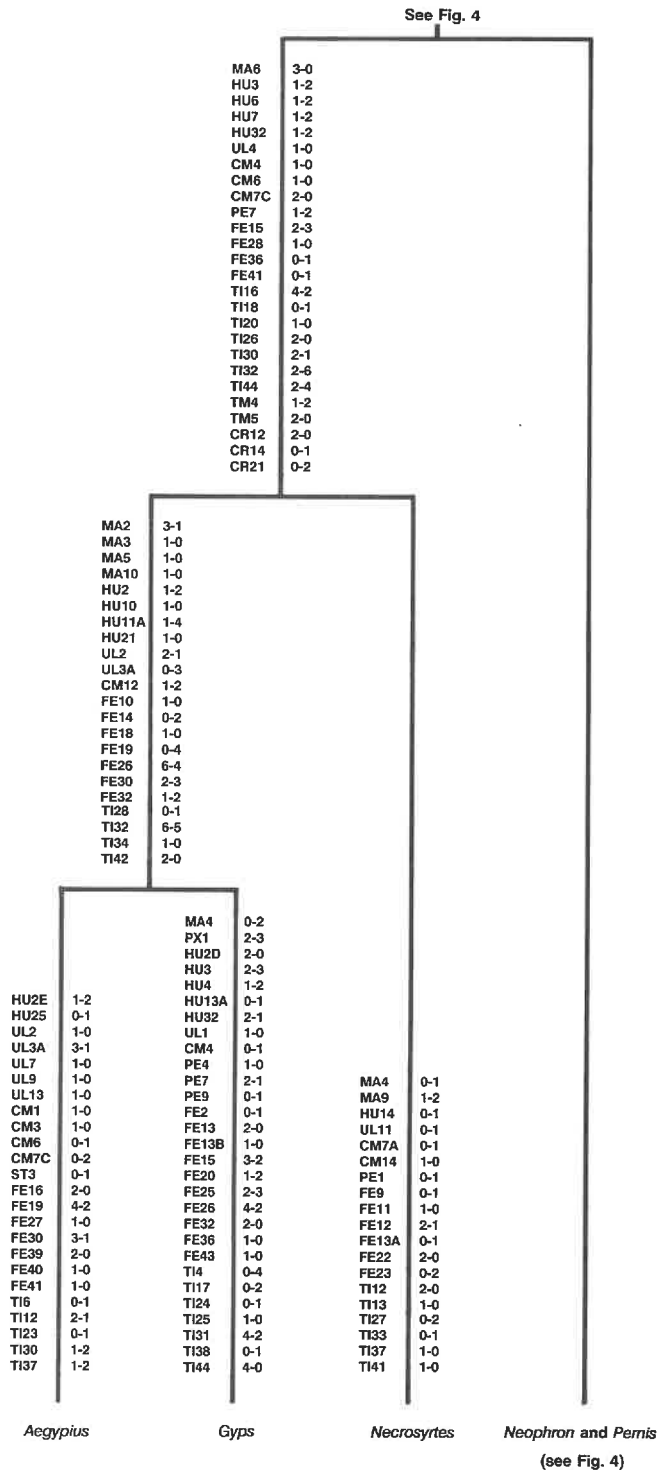


Figure 6. Basal branches of the main accipitrid clade. The Crane Hawk (*Geranospiza*) and the harriers (*Circus*) are sister-groups, and the Bat Hawk (*Machaerhamphus*) is the sister-group of all remaining accipitrids. Conventions as in Figure 2.

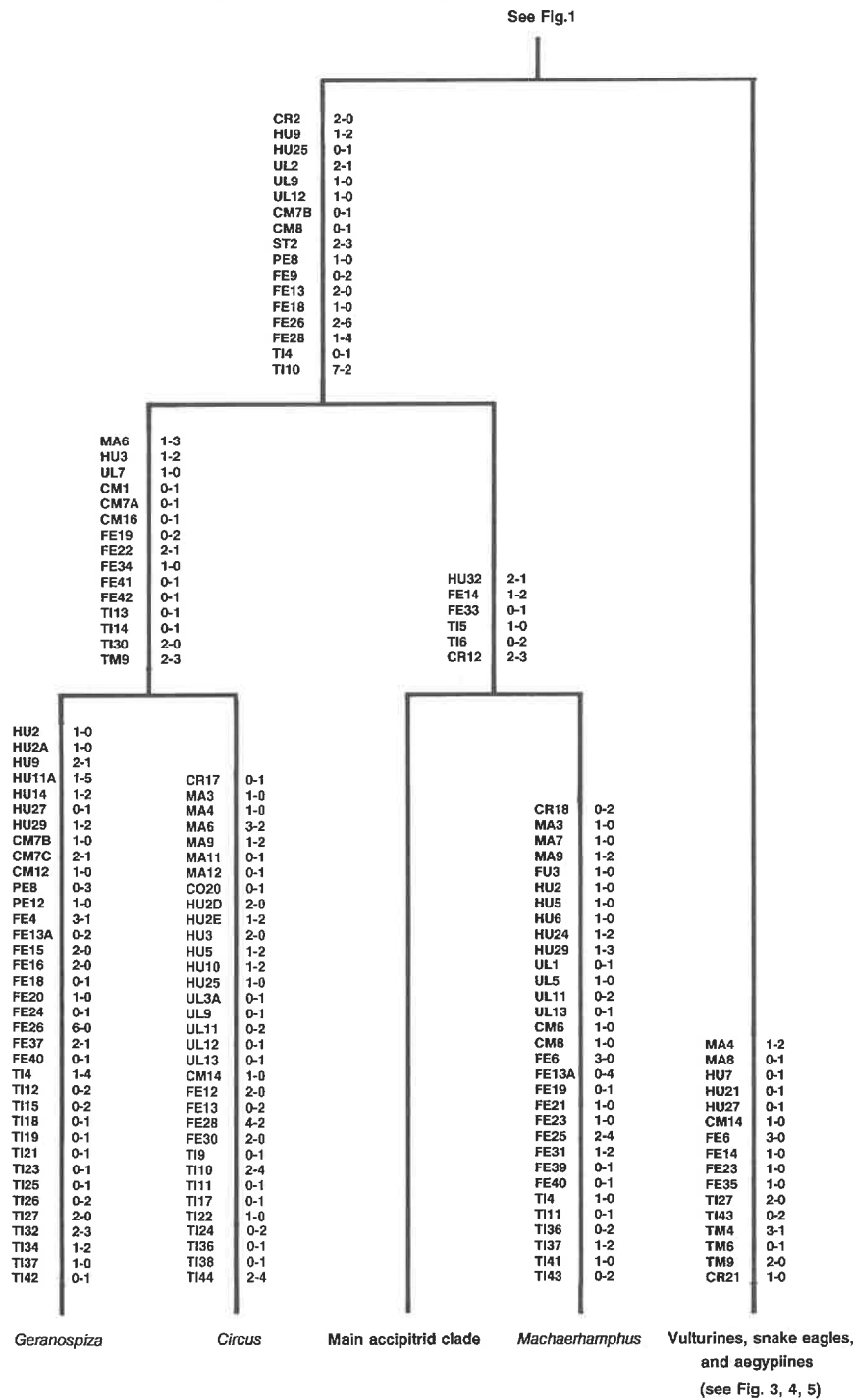


Figure 7. The fish eagles (*Haliaeetus* and *Ichthyophaga*) and milvine kites (*Haliastur* and *Milvus*) clades, showing their sister-group relationship. See Figure 8 for their relationship to *Buteogallus* and the 'core' taxa. Conventions as in Figure 2.

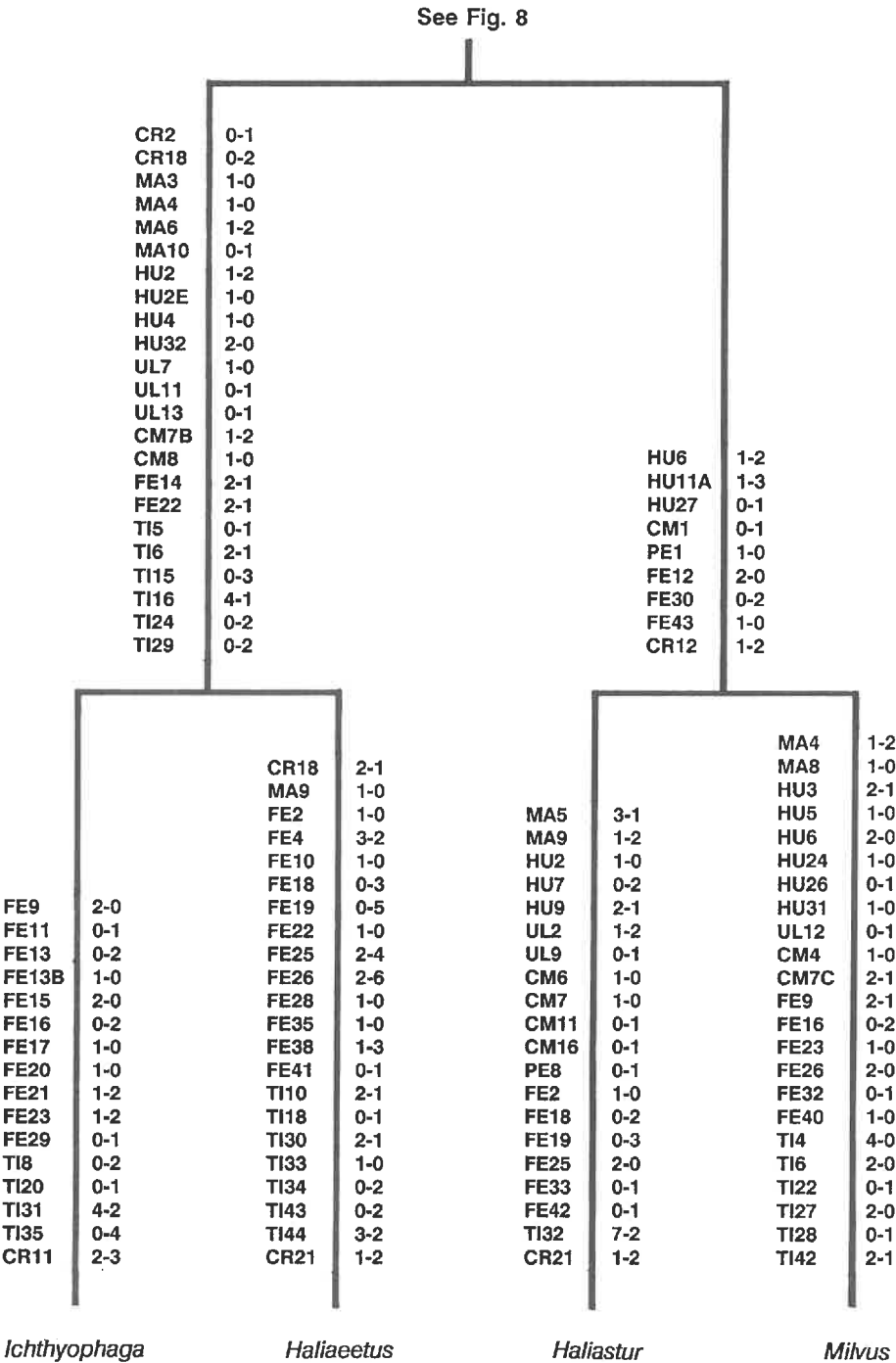


Figure 8. Relationships of the American Black Hawk (*Buteogallus*) and Buzzard Eagle (*Geranoaetus*) to the milvine-haliaeetine clade, and to the accipitrine 'core' taxa. Conventions as in Figure 2.

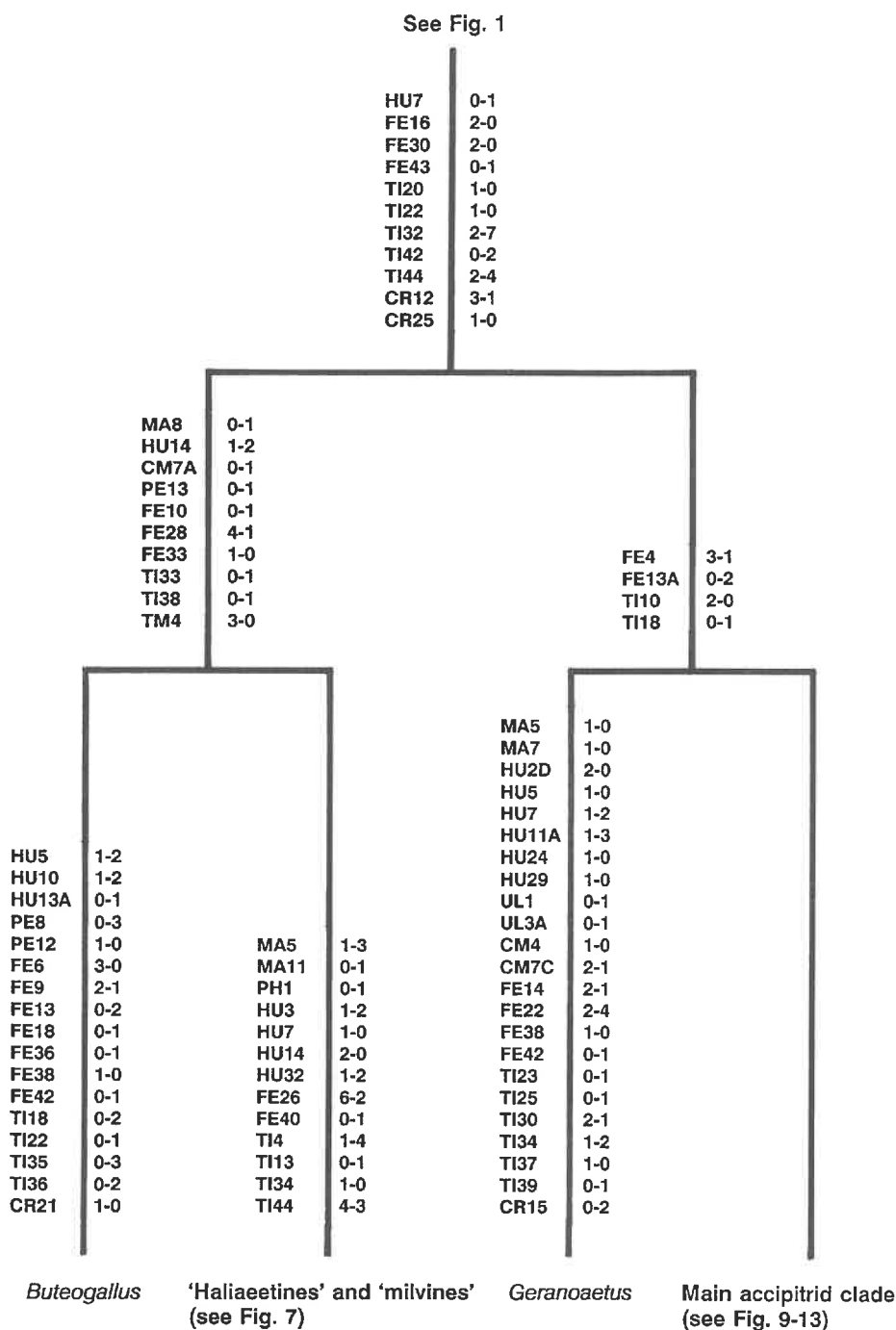


Figure 9. Relationships of the Savannah Hawk (*Heterospizias*) to the aquilines and the accipitrid 'core'. *Harpagornis* is sister-group to *Aquila*. Conventions as in Figure 2.

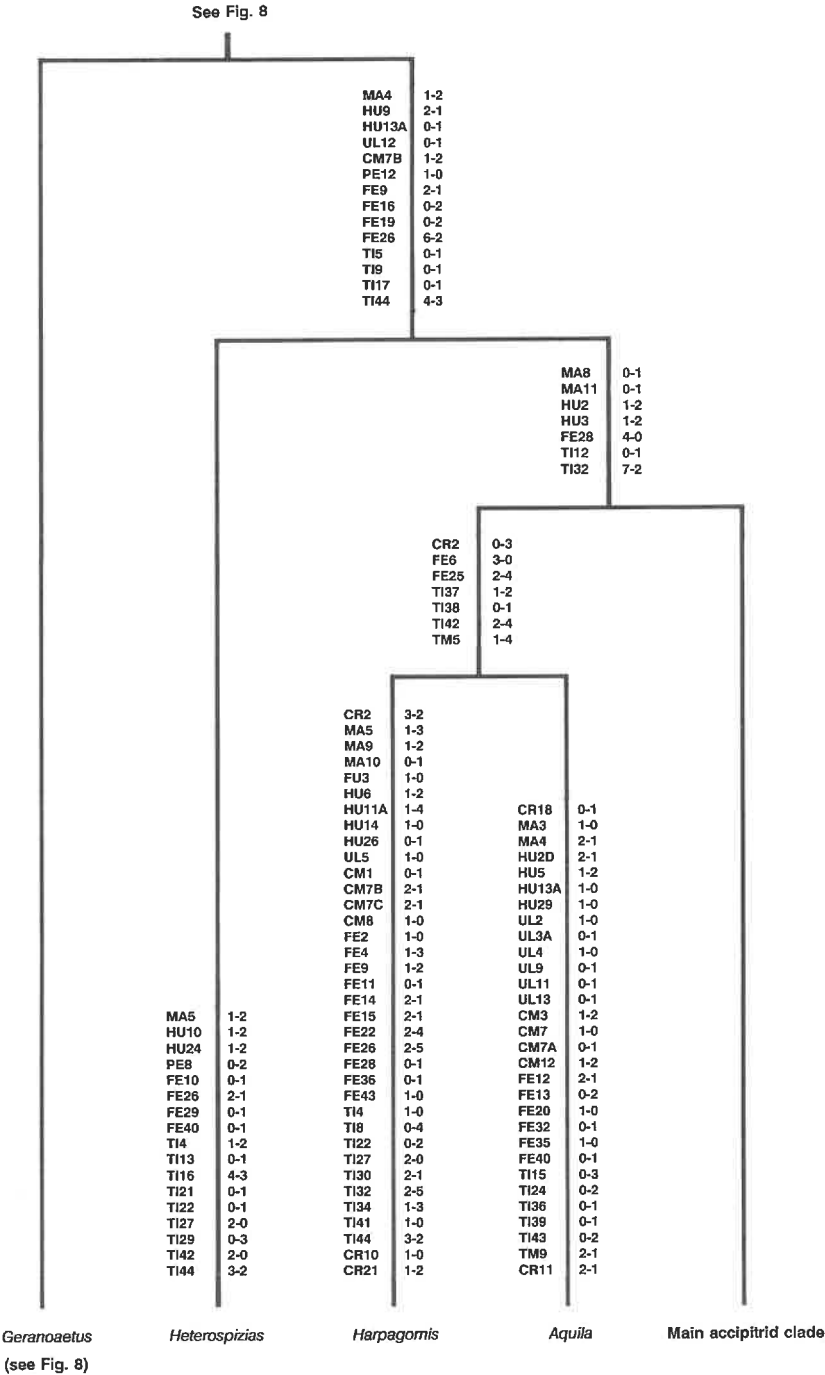


Figure 10. Relationships of the ‘hawk eagles’ of the genera *Spizaetus* and *Hieraaetus*. The African Martial Eagle is sister-group to *Hieraaetus*, and the Black-collared, or Fishing, Hawk (*Busarellus*) shares a most recent ancestor with the Old World hawk eagles. Conventions as in Figure 2.

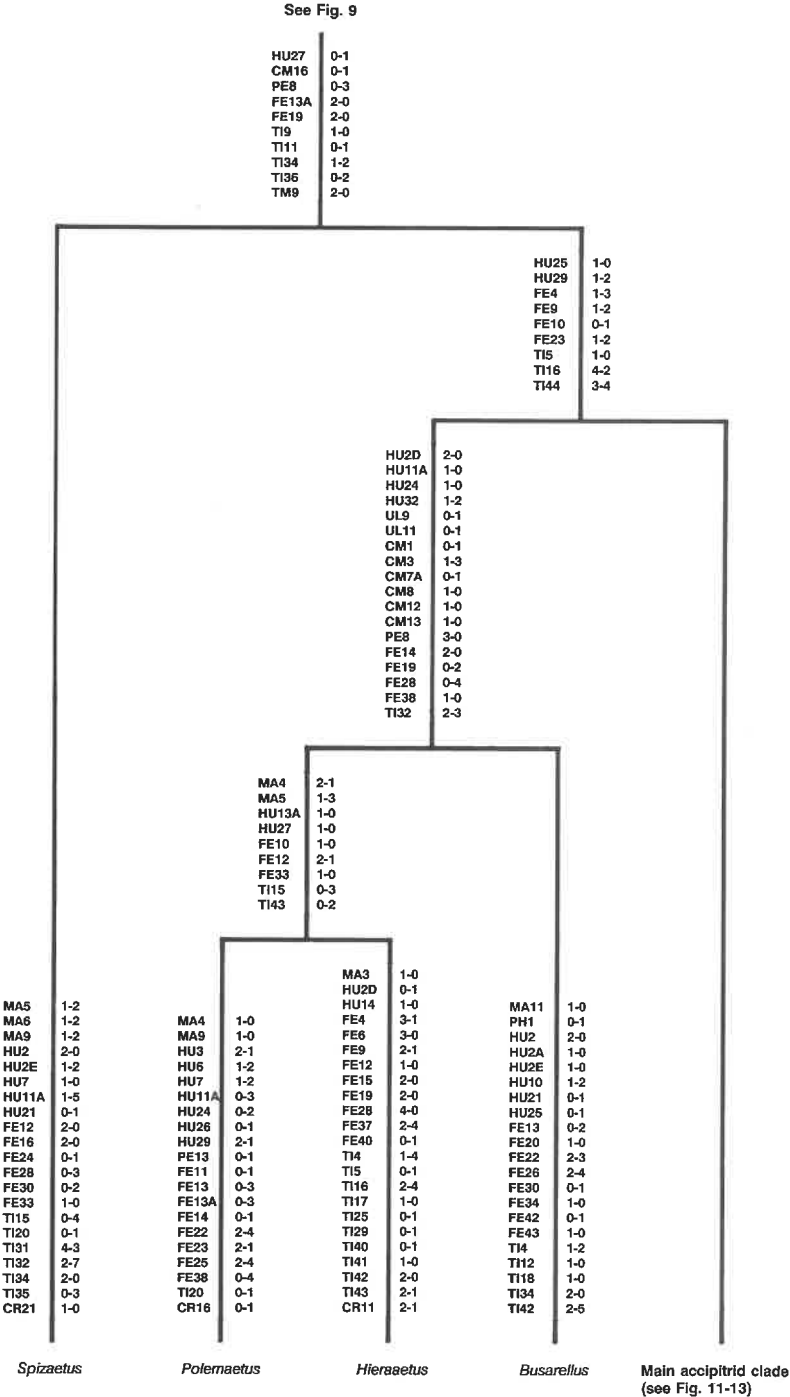


Figure 11. The ‘Harpy’ eagles, showing the sister-group relationship of the African Crowned Eagle (*Stephanoaetus*) and the Neotropical Harpy (*Harpia*), but the paraphyly of the other great forest eagles. In particular, the Guianan Crested Eagle (*Morphnus*) shares a most recent ancestor with the accipitrid ‘core’ taxa (see Figure 12 and 13). Conventions as in Figure 2.

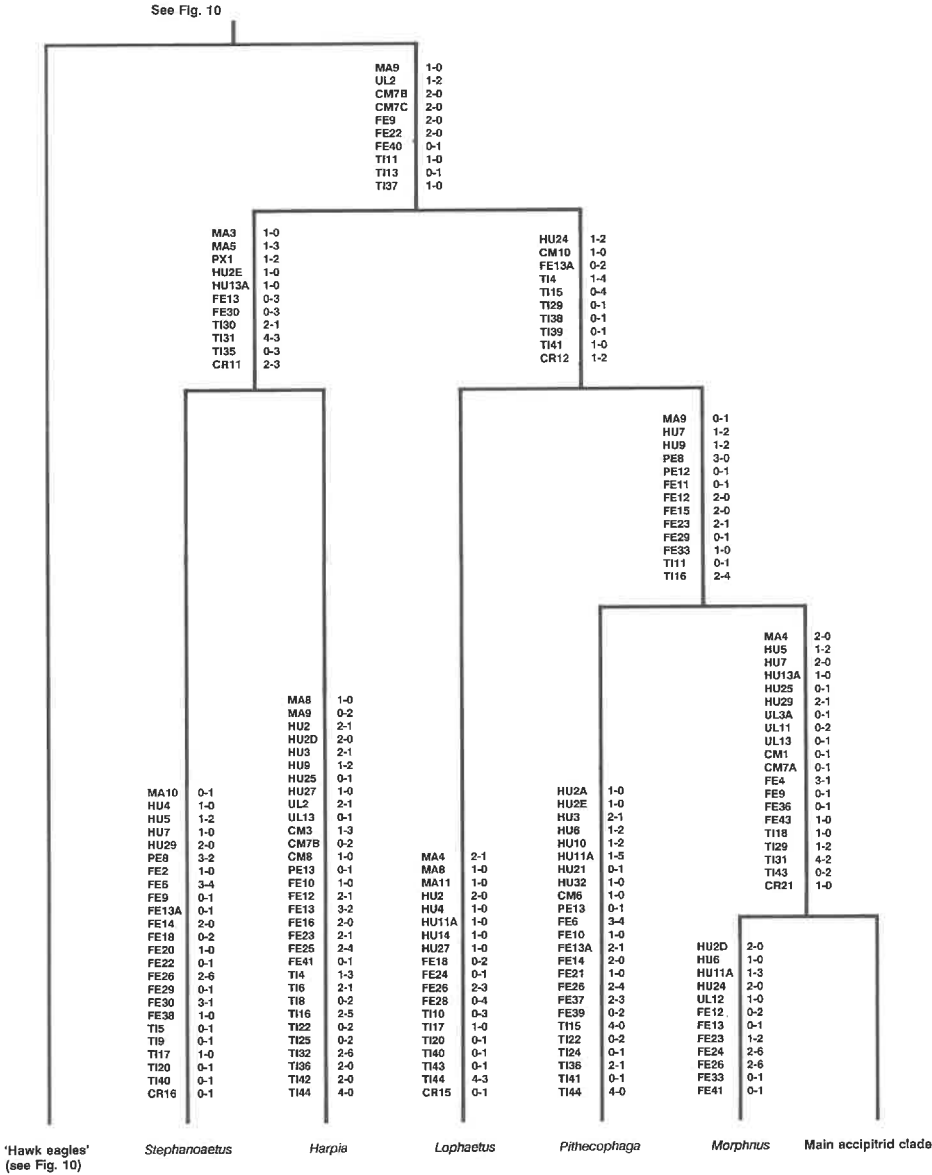


Figure 12. Basal branches of the accipitrid ‘core’. The Tooth-billed Kite (*Harpagus*) and Mississippi Kite (*Ictinia*) are accipitrids near *Accipiter* and *Buteo* and are not ‘elanids’. Conventions as in Figure 2.

See Fig. 11

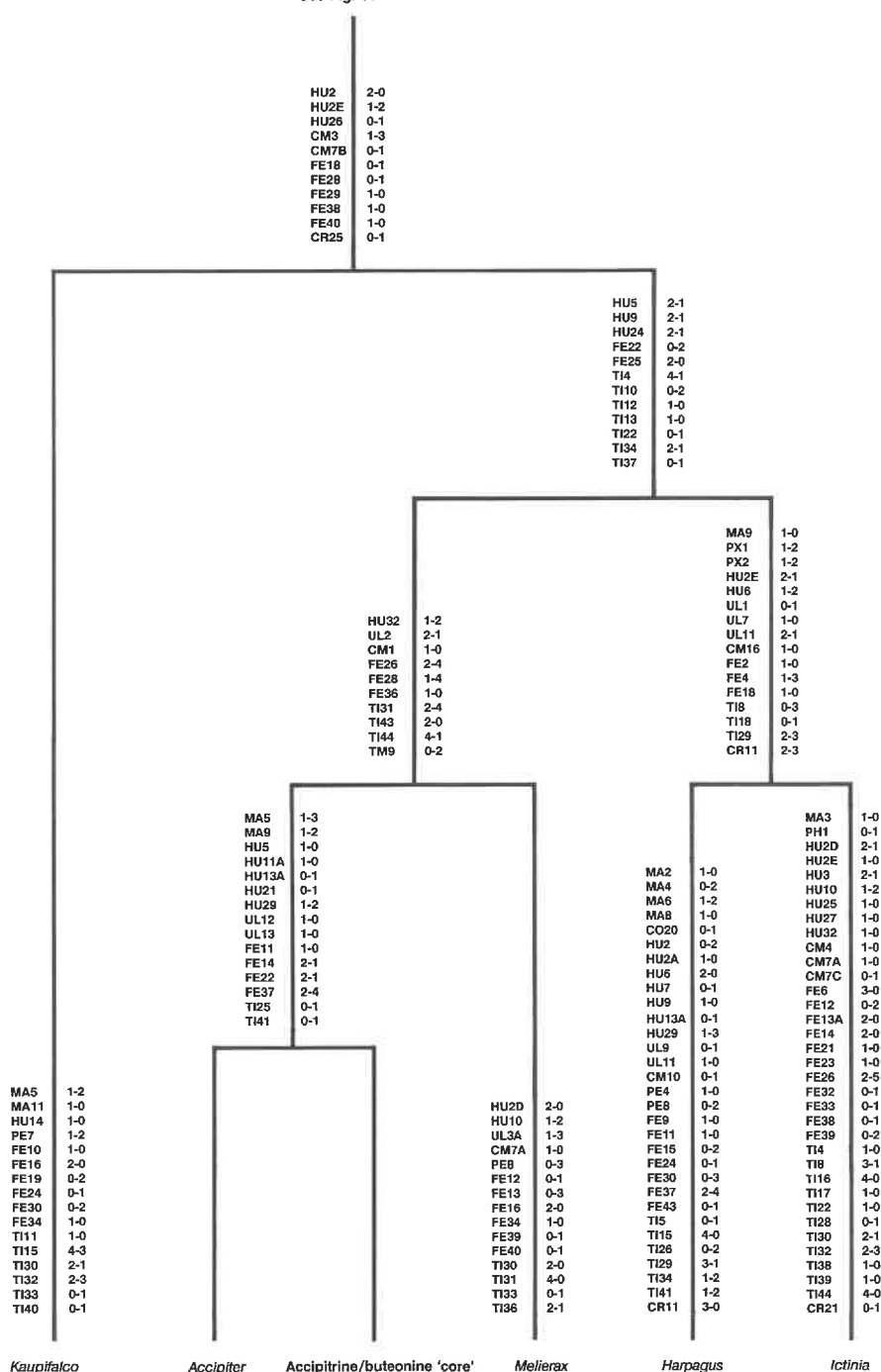


Figure 13. The ‘accipitrid core’, comprising the ‘sub-buteos’ (American White Hawk *Leucopternis* and Harris’s Hawk *Parabuteo*) and the goshawks (*Accipiter*) and buzzards (*Buteo*). *Accipiter* is sister-group to the clade containing the other taxa. Conventions as in Figure 2.

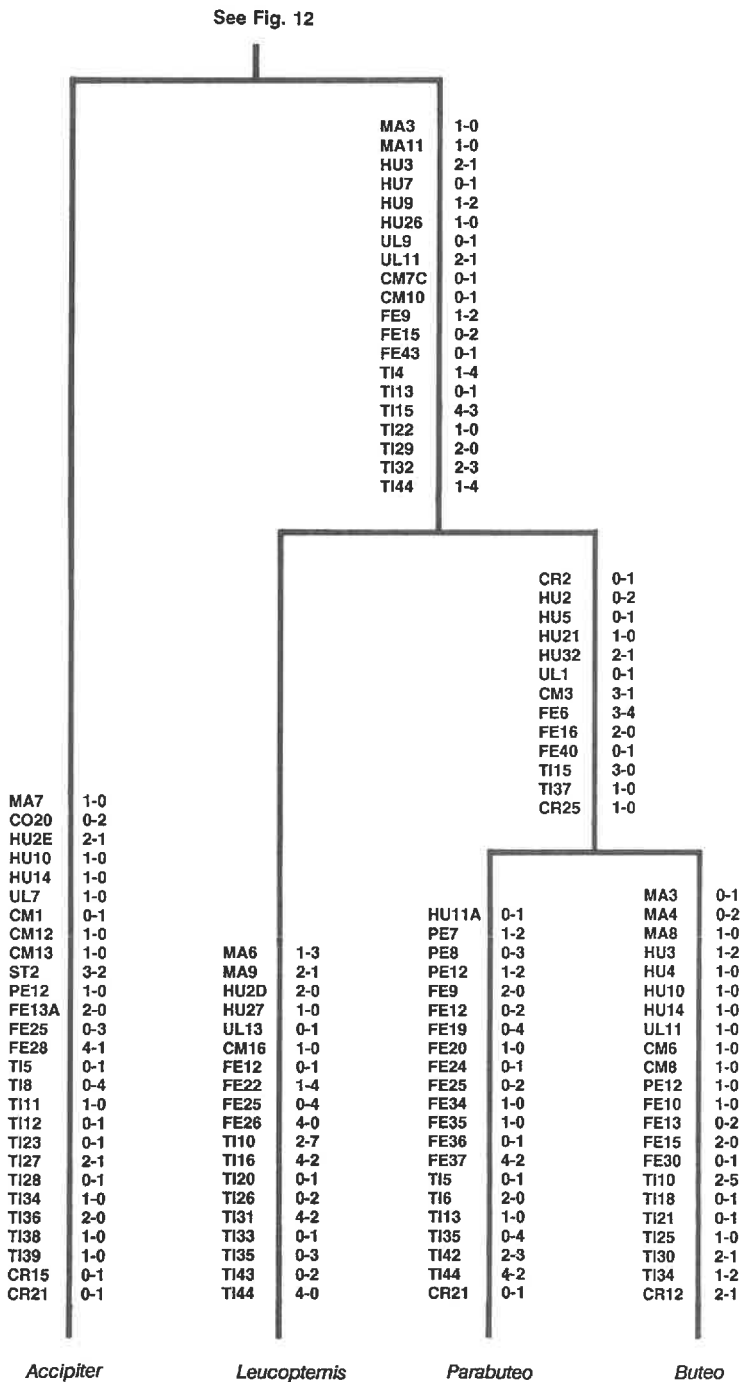


Figure 14A. Phylogenetic tree of the genera of the Accipitridae, showing the species groups (e.g., *elani*) of the feather louse genus *Degeeriella* (Insecta: Mallophaga) to which each genus is known to be host (from Clay 1958). See Figures 1-13 for detailed relationships within the Accipitridae, and Figure 14B and 14C for distribution of louse species-groups within the gypaetiines.

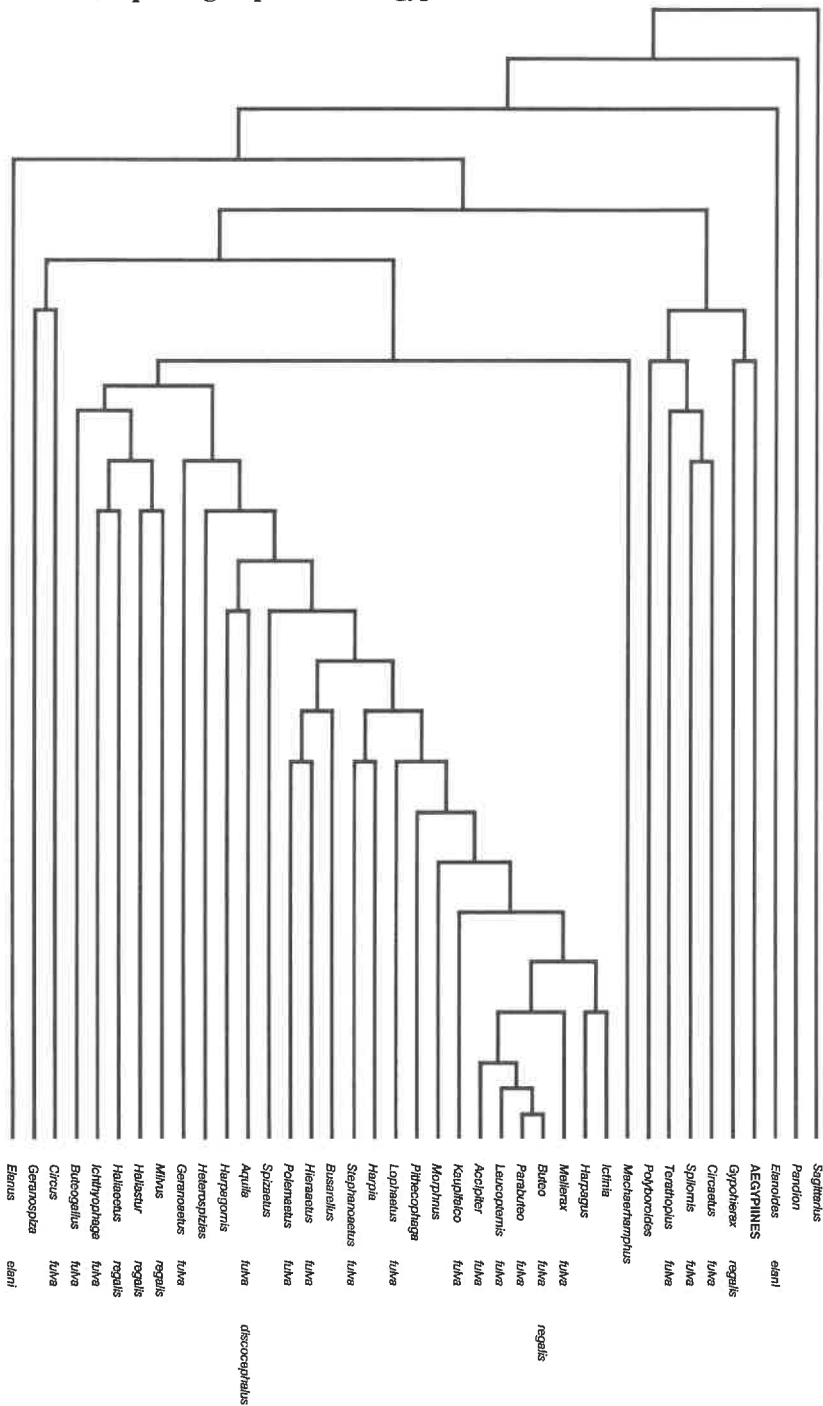


Figure 14B. Phylogenetic tree of the gypaetiines and snake eagles, showing the species groups of the feather louse genus *Degeeriella* (Insecta: Mallophaga) to which each genus is known to be host (from Clay 1958).

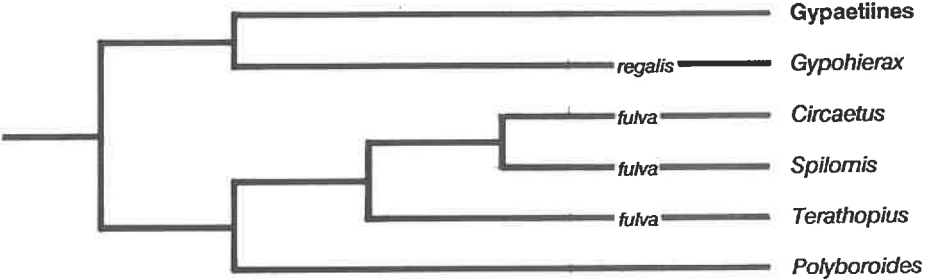


Figure 14C. Phylogenetic tree of the gypaetiines/aegypiines, showing the species groups of the feather louse genus *Degeeriella* (Insecta: Mallophaga) to which each genus is known to be host (from Clay 1958).

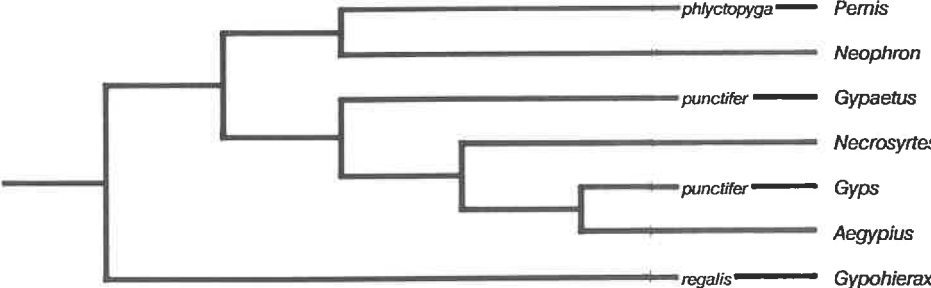


Figure 15. Biogeographic tree of the Accipitridae, using areas as taxa, genera as characters, and number of species in an area as character states. See Appendix 3 for matrix of taxa and areas, and Figure 16 for location of areas used in analysis.

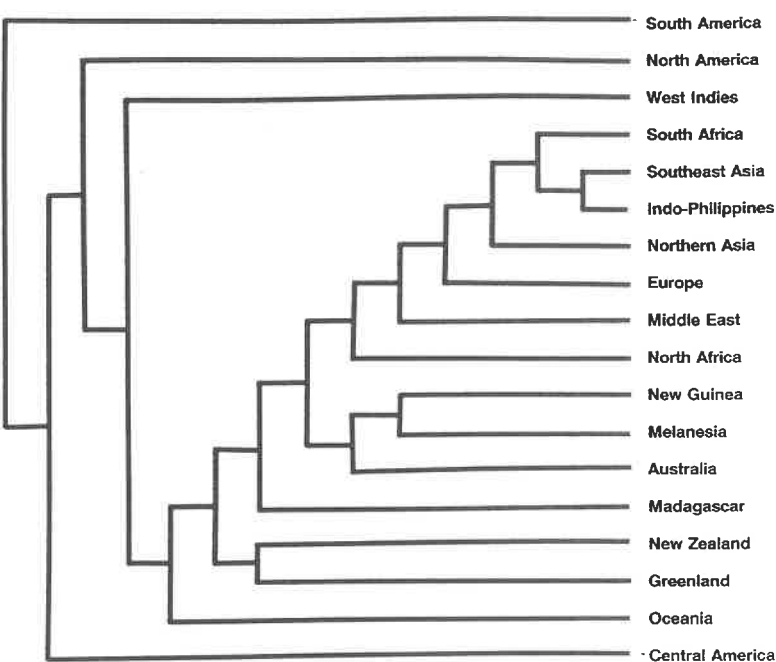
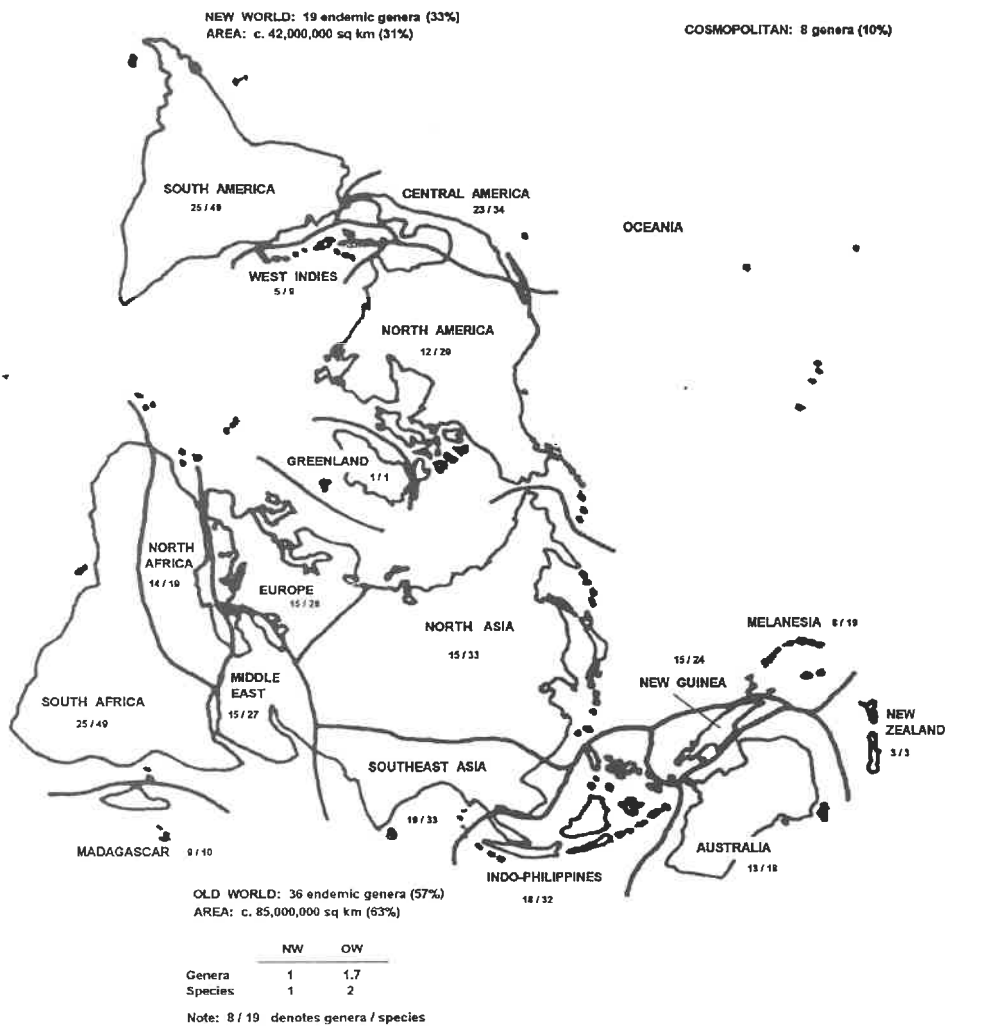


Figure 16 Location of areas used in analysis, Numbers are numbers of genera/number of species. Data from Brown & Amadon (1968). Although the Old World has about twice the land area of the new, the ratio of endemic genera is about 1.7:1



The long-held view that birds colonised Australia from the north (e.g., Mayr 1944) has been refuted by systematic work showing that an independent radiation of the passerines produced groups convergent on Palaearctic families (Sibley & Ahlquist 1985). Much of the evolutionary history of the Accipitridae may have occurred on southern land masses, including Antarctica. The presence of endemic taxa such as *Lophoictinia*, *Hamirostra*, and *Erythroriorchis* suggests that not all accipitrids have colonised Australia from elsewhere.

The Australian fossil record includes several accipitrids of up to mid-Miocene age (Rich & Baird 1986), but these, including a supposed gypaetina vulture, are of uncertain relationships (Rich & van Tets 1982).

Large accipitrids are known from the Australian Quaternary (Rich & van Tets 1982; Rich & Baird 1986), but the association Rich & Baird (1986) make between large size and scavenging habits is unproven.

Australia had extensive rain forests until the late Quaternary (Rich 1975), and the barriers to forest birds formed by the hot desert of Australia and the cold desert of Antarctica are relatively new. Present forest areas in New Guinea, Southeast Asia, and South America were linked by others in the geologically recent past. Links between isolated forest taxa such as *Harpyopsis* of New Guinea and *Pithecophaea* of the Philippines may be better sought to the south rather than the north. Indeed, Rich & van Tets (1982) reported that a small fossil eagle (*Necrastur alacer*) from the Australian Pleistocene resembled *Harpyopsis*.

The poor pre-Quaternary fossil record of accipitrids in Australia (Rich & Baird 1986), and present total absence of such a record in New Zealand (Fordyce 1991) makes a definitive statement on the origin of Haast's Eagle impossible. Its sister group relationship with *Aquila* suggests that it may be a relatively recent immigrant from Australia, but little is known about the time of radiation or dispersal of the *Aquila* eagles, or even how long *Aquila audax* has been in Australia. One of the large Quaternary accipitrids may have been larger than *Aquila audax* (Rich 1991) and perhaps similar in size to Haast's Eagle. Another species, smaller than "*Harpagornis assimilis*", had bones of similar shape to those of Haast's Eagle (Rich & van Tets 1982). This material warrants further study.

The ancestor of Haast's Eagle may have arrived as early as the Early Miocene, when the New Zealand forests were similar to those in highland New Guinea today (Pocknall 1989), and the Tasman Sea was somewhat narrower (Owen 1983).

Relationships of Haast's Eagle

The principal result of my analysis is the placement of Haast's Eagle as sister group of *Aquila*, the genus containing the Golden and Wedge-tailed Eagles (*Aquila chrysaetos* and *A. audax*) (Stresemann & Amadon 1979). A relationship with *Aquila* conflicts with Oliver's (1945, 1955) conclusions, but is in accordance with one popularly held view of the relationships of Haast's Eagle (e.g., Duff 1949). Brathwaite & Holdaway's (1987) suggestion that Haast's Eagle was similar to *Spizaetus* could not be refuted or supported because of the paucity of material of South-east Asian *Spizaetus*. However, a South American *Spizaetus* is close to *Harpagornis* on my phylogenetic tree.

The phylogenetic tree

I did not expect to derive a single principal tree topology from the array of qualitative osteological characters used. Livezey (1986) found 50 equal-length trees for the Anseriformes, using 120 characters that for the most part were established, and ordered transition series. However, Siegel-Causey (1988) obtained one tree from 137 characters for 30 species.

The overall consistency indices for both these studies were much higher than found here. This could have resulted from my characters being less well defined, the complexity of the variation within the group (Jollie 1976, 1977a, 1977b, 1977c), and the short time available to me to assess character states over more species within each genus, and of the large number of taxa. It was less easy to 'mine' the literature for characters, because previous studies (e.g., Amadon 1953, 1978, 1982a, 1982b; Brown 1982; Brown & Amadon 1968; Friedmann 1950) concentrated on details of bill, legs, and wing and tail proportions.

Archie (1989) questioned the value of consistency indices (Kluge & Farris 1969) as measures of the efficiency of the analysis, who emphasised the inverse relationship between the number of

taxa studied and the consistency index, and between the consistency index and the number of characters.

The consistency index obtained here (0.217), although low, is at a level to be expected in analyses of more than 40 taxa, using well over 100 characters (Archie 1989, fig. 5a). The number of steps per character (8.9) was above those given for missing value data, but less than for 2-state data. However, if Archie's (1989) fig. 1 plots are extrapolated to 45 taxa (as used here), there is closer agreement in number of steps per character.

While the low consistency index may result largely from intrinsic properties of large data sets (Archie 1989), examination of the character state changes suggests that evolution within the group has been by changes in suites of minor features within historical, phylogenetic, and broad functional constraints (Seilacher 1979).

Homoplasies and character-state reversals rather than absolute synapomorphies characterise most clades within the Accipitridae. Superficial resemblances in external characters have often formed the basis of classifications within and between genera (Amadon 1982b - sub-buteonines; Wattle 1973 - accipiters), but these were shown to reflect adaptation to a limited range of niches available for raptors. An indication of the ability of different lineages to give rise to ecological correlates is the strong external resemblance of *Ictinia* to the *Elanus* kites in colour pattern, proportions, and behaviour. In its skeleton, as Shufeldt (1891) noted long ago and was confirmed here, *Ictinia* is very close to *Buteo*.

External resemblances of phylogenetically distinct lines have resulted in the complex and fluid higher taxonomy of the Accipitridae (reviewed by Sibley & Ahlquist (1972)). A feature of the tree presented here is the association of groups of species long thought to be related on general resemblances, such as the milvine kites and sea eagles and the accipitrid vultures and serpent eagles.

Although it is comforting that the tree topology incorporates existing arrangements, this is not a valid test of the hypothesised relationships presented here. Indeed, Panchen (1982) has argued that parsimony, the basic assumption of the techniques used here, is inconsistent with the hypothetico-deductive model of science, as championed by Popper (1959) and there is no satisfactory test of such trees. My results, however, support the view of Kemp & Crowe (1990) that a cladistic approach is useful in resolving some of the more controversial aspects of accipitrid relationships, despite Jollie's (1976) doubts. With our present profound ignorance of the relationships within and without the family (Olson 1985), no approach should be dismissed completely. Results of this and Kemp & Crowe's (1990) can now be tested against information from other sources, such as DNA studies.

Choice of characters

The features chosen for this study tended to be those that described the shape and structure of individual elements, so that they could be of maximum use for analysis of fossil taxa. Some were more 'descriptive' than is usual in comparative morphology. All features used displayed recognisable variation within the group, or between the group and the outgroups used and therefore can be considered as characters suitable for analysis by maximum parsimony techniques.

That the analysis converged on two closely similar trees (differing only on the position of a single taxon within a major clade) without a priori or a posteriori weighting of features suggests that noise from 'poorer' characters was overcome by the use of large numbers of features. For an exploratory study such as this, use of many characters can not only result in the discovery of basic pattern as a guide to forming hypotheses on smaller subsets more amenable to analysis, but also allows an evaluation of the variability of new characters.

Raptor ecology and homoplasy

The results revealed the complex nature of the variation in characters among different clades within the family. This was apparent in the few osteological characters such as the procoracoid foramen and fused pedal phalanges whose distribution and taxonomic value have been discussed previously (Olson 1982, 1987), as well as in less well defined characters identified in my examination of the material. The frequent reversals reflect the limited variance in structure within the group, and the way morphologies have been mixed and matched in different lineages.

Symplesiomorphies were found to be a major source of confusion in discerning intrafamilial relationships.

Methodological limitations

Most of the problems with assessing character states for taxa resulted from the state and availability of specimens. Apart from the taxa that were not available in any institution, others were represented by incomplete specimens or sometimes a few bones. Others were incompletely prepared, and characters were obscured. Many taxa, especially of large eagles and vultures, were represented by captive specimens that had evidence of damage or disease associated with captivity. Some had osteoarthritic lesions that obscured characters of the lower leg bones, and several had healed broken wings.

Taxonomic conclusions

Some more general conclusions on the classification within the Accipitridae may be drawn. *Sagittarius* and *Pandion* were found to be sufficiently distinct in their osteology to warrant maintaining them as at least families. My study did not include other non-accipitrids so the proximity of *Sagittarius* to the accipitrids could not be assessed. From the profound differences in osteology, it is likely to be a distant relationship.

As has been suspected, the 'kites' proved to polyphyletic (e.g., Shufeldt 1891) within the family, representing a grade rather than a clade. *Elanus*, *Elanoides*, and *Ictinia* demonstrate how closely convergent external morphologies can be in different clades, through homoplasy and plesiomorphic traits associated with an insectivorous and lower vertebrate diet.

My phylogenetic tree provides at least partial support for Brown & Amadon's (1968) suggestion that omnivorous and scavenging kites and *Pernis*-like species are the least advanced members of the family. Brown & Amadon's (1968) hypothesis that the adaptive radiation of the Accipitridae reached various 'culmination points' in, for example, the accipitrid vultures, the harriers (*Circus*) of open country, bird-catching *Accipiters*, and swift eagles (such as *Spizaetus*), and other large eagles (such as *Harpia*) is supported in that each of these groups represents a clade on my phylogenetic tree. However, the relationships within the *Buteo-Accipiter* clade are more complex, so all the eagles, *Buteos* and *Accipiter* cannot be separated in this way.

To summarise the information in my preferred phylogenetic tree, I include a tentative classification of the Accipitridae. The conventions of Wiley (1981) were followed, so that the order of the branching is reflected by the list, with the earlier major clades recognised by Linnaean-style inclusive group names to tribal level. This classification goes to a much lower taxonomic level (tribe) than other recent treatments to emphasise what I see as potentially the most fruitful areas for future research.

CLASSIFICATION OF THE ACCIPITRIDAE - BASED ON THE PHYLOGENETIC TREE PRESENTED HERE (using conventions suggested by Wiley (1981))

Order Ciconiiformes (sensu Sibley & Ahlquist 1990)

Family Pandionidae (Sclater & Salvin, 1873)

Family Accipitridae (Vieillot, 1816)

Subfamily Elanoidinae Shufeldt, 1891

Elanoides

Subfamily Elaninae Blyth, 1849

Elanus

Gampsonyx (incertae sedis)

Chelictinia (incertae sedis)

Subfamily Gypaetinae Vieillot, 1816

Tribe Gypaetini Vieillot, 1816

Gypohierax
Pernis
Neophron
Gypaetus
Necrosyrtes
Aegypius
Gyps
 Tribe Circaetini Blyth, 1849
Polyboroides
Terathopius
Spilornis
Circaetus
 Subfamily Circinae Bonaparte, 1838
Circus
Geranospiza
 Subfamily Machaerhamphinae **new name**
Machaerhamphus
 Subfamily Milvinae Vigors, 1824
 Tribe Buteogallini new name
Buteogallus
 Tribe Milvinae Vigors, 1824
Milvus
Haliaeetus
Haliaeetus
Ichthyophaga
 Subfamily Accipitrinae (Vieillot, 1816)
Geranoaetus
Heterospizias
Aquila
Harpagornis†
Spizaetus
Busarellus
Hieraaetus
Polemaetus
Harpia
Stephanaetus
Lophaetus
Pithechophaga
Morphnus
Kaupifalco
Ictinia
Harpagus
Melierax
Accipiter
Leucopternis
Parabuteo
Buteo

The higher classification of Haast's Eagle therefore becomes:

Order Ciconiiformes

Family Accipitridae

Subfamily Accipitrinae

Genus *Harpagornis* Haast, 1872

Harpagornis moorei Haast, 1872

If the higher classification of Sibley & Ahlquist (1990) is not followed, the ordinal name should be Accipitriformes (Vieillot), as listed by Brodkorb (1964).

Further progress in morphological studies of the evolutionary history of the accipitrids will involve refining the set of osteological characters and integrating data from other sources such as cytology, as has been done by Kemp & Crowe (1990). Results of biochemical analyses, should be especially illuminating.

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REFERENCES

- AMADON, D. 1953. Remarks on the Asiatic Hawk-eagles of the genus *Spizaetus*. *Ibis* **95**: 492-500.
- AMADON, D. 1961. Remarks on the genus *Buteogallus*. *Novedades Colombianas* **1**(6): 358-360.
- AMADON, D. 1964. Taxonomic notes on birds of prey. *American Museum novitates* **2166**: 1-24.
- AMADON, D. 1977. Notes on the taxonomy of vultures. *Condor* **79**: 413-416.
- AMADON, D. 1978. Remarks on the taxonomy of some Australian raptors. *Emu* **78**: 115-118.
- AMADON, D. 1982a. A revision of the sub-buteonine hawks (Accipitridae, Aves). *American Museum novitates* **2741**: 1-20.
- AMADON, D. 1982b. The genera of booted eagles: *Aquila* and relatives. *Journal of the Yamashina Institute of Ornithology* **14**: 108-121.
- ARCHIE, J.W. 1989. Homoplasy excess ratios: new indices for measuring levels of homoplasy in phylogenetic systematics and a critique of the consistency index. *Systematic zoology* **38**(3): 253-269.
- BALLMANN, P. 1969. Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. *Zitteliana* **1**: 5-60.
- BALLMANN, P. 1973. Fossile Vogel aus dem Neogen der Halbinsel Gargano (Italien). *Scripta geologica* **17**: 1-75.
- BAUMEL, J.J. 1979. Osteologia. In: Baumel, J.J.; King, A.S.; Lucas, A.M.; Breazile, J.E.; Evans, H.E. (ed.) *Nomina anatomica avium: an annotated anatomical dictionary of birds*: 53-119. Academic Press, London.
- BEDDARD, F.E. 1889. On certain points in the anatomy of the Accipitres, with reference to the affinities of *Polyboroides*. *Proceedings of the Zoological Society of London* **59**: 77-82.
- BEDDARD, F.E. 1898. *The structure and classification of birds*. Longmans, Green, London.
- BIRNIE, J.F. & ROBERTS, D.E. 1986. Evidence of Tertiary forest in the Falkland Islands (Islas Malvinas). *Paleogeography, paleoclimatology, paleoecology* **55**: 45-53.
- BLANDAMER, J.S. & BURTON, P.J.K. 1979. Anatomical specimens of birds in the collections of the British Museum (Natural History). *Bulletin of the British Museum (Natural History) (Zoology)* **34**(4): 125-180.

- BRATHWAITE, D.H. & HOLDAWAY, R.N. 1987.** A preliminary reconstruction of *Harpagornis moorei*: top predator in the moa's world [Abstract]. *New Zealand journal of ecology* 10: 162.
- BRODKORB, P. 1960.** The skeleton and systematic position of *Gampsonyx*. *Auk* 77: 88-89.
- BRODKORB, P. 1964.** Catalogue of fossil birds Part 2 (Anseriformes through Galliformes). *Bulletin of the Florida State Museum, Biological sciences* 8: 195-335.
- BROOKS, D.R. 1985.** Historical ecology: a new approach to studying the evolution of ecological associations. *Annals of the Missouri Botanical Garden* 72: 660-680.
- BROWN, L.H. 1982.** Genus *Stephanoaetus*. In: Brown, L.H., Urban, E.K. & Newman, K. (ed.) *The birds of Africa*, vol. 1: 429-433. Academic Press, London.
- BROWN, L.H. & AMADON, D. 1968.** *Eagles, hawks and falcons of the World*. Country Life Books, London. 2 vol.
- BURTON, P.J.K. 1978.** The intertarsal joint of the harrier-hawks *Polyboroides* spp and the Crane Hawk *Geranospiza caerulescens*. *Ibis* 120: 171-177.
- CLAY, T. 1951.** The Mallophaga and relationships within the Falconiformes. *Ibis* 93: 628.
- CLAY, T. 1958.** Revisions of Mallophaga genera. *Degeeriella* from the Falconiformes. *Bulletin of the British Museum (Natural History) (Entomology)* 7(4): 121-207.
- COMPTON, L.V. 1938.** The pterylosis of the Falconiformes with special attention to the taxonomic position of the osprey. *University of California publications in zoology* 42: 173-211.
- COX, C.B. 1990.** New geological theories and old biogeographical problems. *Journal of biogeography* 17: 117-130.
- CRACRAFT, J. & RICH, P.V. 1972.** The systematics and evolution of the Cathartidae in the Old World Tertiary. *Condor* 74: 272-283.
- de BOER, L.E.M. 1975.** Karyological heterogeneity in the Falconiformes (Aves). *Experientia* 31/10 (15.10.1975): 1138-1139.
- de BOER, L.E.M. 1976.** The somatic chromosome complements of 16 species of Falconiformes (Aves) and the karyological relationships of the order. *Genetica* 46: 77-113.
- de BOER, L.E.M. & SINO, R.P. 1984.** A karyological study of Accipitridae (Aves: Falconiformes), with karyotypic descriptions of 16 species new to cytology. *Genetica* 65: 89-107.
- DUFF, R. 1949.** *Pyramid Valley*. Friends of the Canterbury Museum, Christchurch. 48 p.
- EMSLIE, S.D. 1988.** The fossil history and phylogenetic relationships of condors (Ciconiiformes: Vulturidae) in the New World. *Journal of vertebrate paleontology* 8(2): 212-228.
- FORDYCE, R.E. 1991.** A new look at the fossil vertebrate record of New Zealand. In: Rich, P.V.; Monaghan, V.M.; Baird, R.F. Rich, T.H. (ed.) *Vertebrate palaeontology of Australasia*. pp. 1191-1316. Pioneer Design Studio and Monash University, Melbourne.
- FRIEDMANN, H. 1950.** The birds of North and Middle America. Part XI Order Falconiformes: Diurnal birds of prey. *Bulletin of the United States National Museum* 50: 1-527.
- FÜRBRINGER, M. 1888.** *Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane*. van Holkema, Amsterdam. 2 vol. 1751 p.
- HAAST, J. 1872.** On *Harpagornis*, an extinct gigantic bird of prey, containing description of femur, ungual phalanges, and rib. *Transactions and proceedings of the New Zealand Institute* 4 [1871]: 192-196.
- HENNIG, W. 1966.** *Phylogenetic systematics*. University of Illinois Press, Urbana.
- HOWARD, H. 1929.** The avifauna of Emeryville shellmound. *University of California publications in zoology* 32(2): 301-394.
- HOWARD, H. 1932.** Eagles and eagle-like vultures of the Pleistocene of Rancho La Brea. *Carnegie Institute of Washington publication* 429 [Contributions to palaeontology]: 1-111.
- HUDSON, G.E. 1948.** Studies on the muscles of the pelvic appendage in birds II. The heterogeneous Order Falconiformes. *American midland naturalist* 39(1): 102-127.
- JOLLIE, M. 1953.** Are the Falconiformes a monophyletic group? *Ibis* 95: 369-371.
- JOLLIE, M. 1976.** A contribution to the morphology and phylogeny of the Falconiformes, part 1. *Evolutionary theory* 1: 285-298.
- JOLLIE, M. 1977a.** A contribution to the morphology and phylogeny of the Falconiformes, part 1. *Evolutionary theory* 2(4): 285-298.
- JOLLIE, M. 1977b.** A contribution to the morphology and phylogeny of the Falconiformes, part 2. *Evolutionary theory* 2(5): 285-298.
- JOLLIE, M. 1977c.** A contribution to the morphology and phylogeny of the Falconiformes, part 3. *Evolutionary theory* 3(1): 285-298.

- KEMP, A.C. & CROWE, T.M. 1990.** A preliminary phylogenetic and biogeographic analysis of the genera of diurnal raptors. In: Peters, G. & Hutterer, R. (ed.) *Vertebrates in the tropics*: 161-175.
- KLUGE, A.G. & J.S. FARRIS 1969.** Quantitative phyletics and the evolution of anurans. *Systematic zoology* 18: 1-32.
- KÖNIG, C. 1982.** Zur systematische Stellung der Neuweltgeier (Cathartidae). *Journal für Ornithologie* 123(3): 259-267.
- LIGON, J.D. 1967.** Relationships of the cathartid vultures. *Occasional papers of the Museum of Zoology, University of Michigan* 651: 1-26.
- LIVEZEY, B.C. 1986.** A phylogenetic analysis of recent anseriform genera using morphological characters. *Auk* 103: 73-754.
- MAYR, E. 1944.** Timor and the colonization of Australia by birds. *Emu* 46: 113-130.
- MILLER, L.H. 1937.** Skeletal studies of the tropical hawk *Harpagus*. *Condor* 39: 219-221.
- MILNE-EDWARDS, A. 1867-1871.** *Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France*. 4 vol. V. Masson et Fils, Paris.
- NELSON, R.C. & PRICE, R.D. 1965.** The *Laemobothrion* (Mallophaga: Laemobothriidae) of the Falconiformes. *Journal of medical entomology* 2(3): 249-257.
- OLIVER, W.R.B. 1930.** *New Zealand birds*. Fine Arts, Wellington..
- OLIVER, W.R.B. 1945.** Avian evolution in New Zealand and Australia. *Emu* 45: 55-77, 119-152.
- OLIVER, W.R.B. 1955.** *New Zealand birds*, 2nd ed. A.H. & A.W. Reed, Wellington.
- OLSON, S.L. 1982.** The distribution of fused phalanges of the inner toe in the Accipitridae. *Bulletin of the British Ornithologists' Club* 102(1): 8-12.
- OLSON, S.L. 1985.** The fossil record of birds. In: Farner, D.S., King, J.R. & Parkes, K.C. (ed.) *Avian biology*, vol. VIII: 79-252. Academic Press, London.
- OLSON, S.L. 1987.** Variation in the procoracoid foramen in the Accipitridae. *Rivista Italiana ornitologia, Milano* 57(3-4): 1-4.
- OLSON, S.L. 1991.** Patterns of avian diversity and radiation in the Pacific as seen through the fossil record. In: Dudley, E.C. (ed.) *The unity of evolutionary biology*. Vol. 1: 314-318. Dioscorides Press, Portland Oregon.
- OLSON, S.L. & H.F. JAMES 1991.** Descriptions of thirty-two new species of birds from the Hawaiian Islands. Part I. Non-Passeriformes. *Ornithological monographs* 45: 1-88.
- OWEN, H.G. 1983.** *Atlas of continental displacement, 200 million years to the present*. Cambridge University Press, New York. 159 p.
- OWEN, H.G. 1990.** [Letter] Of gaps and globes. Comments on the Guest Essay 'New geological theories and old biogeographical problems' by C.B. Cox (1990). *Journal of biogeography* 17: 693-695.
- OWEN, R. 1879.** Memoir on the trunk and limbs of a gigantic bird of prey (*Harpagornis moorei*, von Haast). In: *Memoirs on the extinct wingless birds of New Zealand; with an appendix on those of England, Australia, Newfoundland, Mauritius, Rodriguez*. J van Voorst, London.
- PANCHEN, A.L. 1982.** The use of parsimony in testing phylogenetic hypotheses. *Zoological journal of the Linnean Society* 74: 305-328.
- POCKNALL, D.T. 1989.** Late Eocene to Early Miocene vegetation and climate history of New Zealand. *Journal of the Royal Society of New Zealand* 19(1): 1-18.
- POPPER, K.R. 1959.** *The logic of scientific discovery*. Hutchinson, London. 479 p.
- RAIKOW, R.J. 1985.** Problems in avian classification. *Current ornithology* 2: 187-212.
- RICH, P.V. 1975.** Antarctic dispersal routes, wandering continents, and the origin of Australia's non-passerine avifauna. *Memoirs of the National Museum of Victoria* 36: 63-125.
- RICH, P.V. 1980.** 'New World vultures' with Old World affinities? *Contributions to vertebrate evolution* 5: 1-115.
- RICH, P.V. 1991.** The Mesozoic and Tertiary history of birds of the Australian plate. In: Rich, P.V.; Monaghan, V.M.; Baird, R.F. & Rich, T.H. (ed.) *Vertebrate palaeontology of Australasia*: 721-808. Pioneer Design Studio and Monash University, Melbourne.
- RICH, P.V. & R.F. BAIRD 1986.** History of the Australian avifauna. *Current ornithology* 4: 97-139.
- RICH, P.V. & G.F. van TETS 1982.** Fossil birds of Australia and New Guinea: their biogeographic, phylogenetic and biostratigraphic input. In: Rich, P.V.; Thompson, E.M. (ed.) *The fossil vertebrate record of Australasia*. pp. 235-384. Monash University, Melbourne.
- RIDGWAY, R. 1873.** Catalogue of the ornithological collection of the Boston Society of Natural History. Part II. Falconidae. *Proceedings of the Boston Society of Natural History* 16: 43-106.
- RYTTMAN, H.; H. TEGELSTROM; K. FREDGA & J. SONDELL 1987.** The karyotype of the osprey,

- Pandion haliaetus* (Aves: Falconiformes). *Genetica* **74**: 143-147.
- SEILACHER, A. 1979. Constructional morphology of sand dollars. *Paleobiology* **5**: 191-221.
- SHUFELDT, R.W. 1891. Some comparative osteological notes on the North-American kites. *Ibis* **6 series** **3**: 228-232.
- SHUFELDT, R.W. 1896. On the affinities of *Harpagornis*: a letter dated 25th January, 1895 to Professor T. Jeffery Parker by R.W. Shufeldt, M.D., Smithsonian Institution, Washington. *Transactions and proceedings of the New Zealand Institute* **28** (1895): 665.
- SHUFELDT, R.W. 1919. Osteological and other notes on the Monkey-eating Eagle of the Philippines, *Pithecopaga jefferyi* Grant. *Philippine journal of science* **15**(1): 33-58.
- SIBLEY, C.G. & J.E. AHLQUIST 1972. A comparative study of the egg white proteins of non-passerine birds. *Peabody Museum of Natural History bulletin* **39**.
- SIBLEY, C.G. & J.E. AHLQUIST 1985. The phylogeny and classification of the Australo-Papuan passerine birds. *Emu* **85**(1): 1-14.
- SIBLEY, C.G. & J.E. AHLQUIST, 1990. *Phylogeny and classification of birds*. Yale University Press, New Haven & London.
- SIEGEL-CAUSEY, D. 1988. Phylogeny of the Phalacrocoracidae. *Condor* **90**: 885-905.
- STRESEMANN, E. & D. AMADON 1979. Falconiformes. In: Mayr, E. & Cottrell, G.W. (ed.) *Checklist of the birds of the world*, vol. 1, 2nd ed: 271-425.
- SUSCHKIN, P. 1899. Beiträge zur Classification der Tagraubvögel mit Zugrundelegung der osteologischen Merkmale. *Zoologischer Anzeiger* **22**: 500-518.
- SUSCHKIN, P. 1900. Systematische Ergebnisse osteologischer Untersuchungen einiger Tagraubvögel. *Zoologischer Anzeiger* **23**: 269-277.
- SUSCHKIN, P. 1905. Zur Morphologie des Vögelskeletts. Vergleichende Osteologie der Normalen Tagraubvögel (Accipitres) und die Fragen der Classification. Teil II. Grundeinteilung der Accipitres. *Nouvelle mémoires Société Naturaliste, Moscou* **16**: 1-65.
- SWANN, H.K. 1924-1945. *A monograph of the birds of prey (order Accipitres)*. 16 pts. (6-16 edited by A. Wetmore). Weldon & Wesley, London.
- SWOFFORD, D.L. 1985. *PAUP: phylogenetic analysis using parsimony. Version 2.4*. Illinois Natural History Survey, Champaign. 67 p.
- TYLER, C. 1966. A study of the eggshells of the Falconiformes. *Journal of zoology, London* **150**: 413-425.
- VOOUS, K.H. & H.J.W. WIJSMAN 1964. Notes on the African Hawk-eagles. *Biologischer Jaarbucher: Dodonaea, Ghent* **32**: 151-163.
- WATTEL, J. 1973. Geographical differentiation in the genus *Accipiter*. *Publications of the Nuttall Ornithological Club*, no. 13. 231 p.
- WILEY, E.O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. Wiley-Interscience, New York.
- WILLIAMS, R.M. & R.J. BENIRSCHKE 1976. The chromosomes of four species of Falconiformes. *Experientia* **32**/3: 310-311.
- WITHERBY, H.F., F.C.R. JOURDAIN, N.F. TICEHURST & B.W. TUCKER 1939. *Handbook of British birds*, vol. III. H.G. & F. Witherby, London.

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APPENDIX 1

Material examined for phylogenetic study of the Accipitridae, listed alphabetically within families.

Institutions: BMNH, Sub-department of Ornithology, British Museum (Natural History) - now Natural History Museum - Tring, England (no prefix to specimen number); NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (all numbers prefixed USNM); NMNZ, National Museum of New Zealand, Wellington, New Zealand (numbers prefixed S).

SPECIMENS

Pandionidae

Pandion haliaetus, 1851.11.10.65, incomplete; *Pandion haliaetus carolinensis*, †, USNM 18466, Chesapeake Bay, **captivity**, 3 Jan 1969; *Pandion haliaetus carolinensis*, USNM 851, Carlisle, Pennsylvania.

Sagittariidae

Sagittarius serpentarius, S/1952.3.198, South Africa; USNM 321578, Cape of Good Hope, South Africa, Sep 1865.

Accipitridae

Accipiter nisus, †, S/1987.31.1, Witley, Surrey, England, 9 Aug 1987; ♂, immature, 1910.10.2.1, 12 Oct 1910; /, USNM 554271, Assen, Holland, 15 Feb 1979; *Aegypius monachus*, 1872.10.25.5; ♂, USNM 428040, **captivity**, 29 Aug 1949; *Aquila audax*, ♂, 1898.5.7.6, Sydney; *Aquila chrysaetos*, S/1973.66.57, **captivity**; †, adult, USNM 491476, Alaska, 1973(?); *Aviceda leuphotes*, 1845.1.12.30, Nepal; *Aviceda subcristata rufa*, ♂, Obi Besar, Moluccas, Indonesia, 29 Jul 1982; *Busarellus nigricollis*, †, 1895.3.10.7, 6 Sep 1895 [first identified as *Heterospizias meridionalis*: note by P Suschkin in box, changing identification]; USNM 345773, between Caceres and Concepcion, 6 Oct 1940; *Butastur liventer*, 1850.8.15.79, Java; *Butastur indicus*, USNM 223986, Cavite, Philippines, Feb 13 1916, skull; *Buteo buteo*, S/1952.1.173, Llwyngwair, N. Pembrokeshire, 1916; USNM 556291, Ede, Holland, 16 Apr 1981; *Hypomorphnus* [= *Buteogallus*] *urubitinga*, 1858.5.26.12; *Buteogallus urubitinga urubitinga*, †, USNM 319433, Caimancito, Argentina, Jun 1930; *Chelictinia riocourii*, 1904.4.28.3, Gambia; ♂, USNM 569279, Kelam, Ethiopia, 15 Mar 1975, leg bones removed from skin; *Chondrohierax uncinatus uncinatus*, USNM 289784, Santa Marta region, Colombia; *Circaetus gallicus*, 1930.3.24.261; ♂, USNM 430827, Essex Vale, Southern Rhodesia [Zimbabwe], 15 Sep 1958; *Circus aeruginosus aeruginosus*, 1924.5.31.234, **captivity**, Apr 1897; †, USNM 557495, Kyzyl-Agach, Azerbaijan, USSR, Jan 1977; *Elanoides forficatus*, 1902.2.2.25, Texas; †, USNM 289686, Holopaw, Florida, 27 Apr 1925; *Elanus caeruleus*, †, 1898.5.7.10, South Africa, 27 Sep 1894; *Elanus caeruleus caeruleus*, ♂, USNM 558447, 23 km north of Capetown, Cape Province, Republic of South Africa, 12 Mar 1981; *Erythrorhynchus radiatus*, 1872.10.22.9, Cape York [Australia] [= *Haliastur spheurnurus*]; *Gampsonyx swainsonii*, ♂, USNM 345789, Tres Barras, Brazil, 2 Jul 1941; *Geranoaetus melanoleucos*, ♂, S/1954.10.3, southwest South America, **captivity**, 6 May 1954; USNM 318388, Cachapoi River, Chile; *Geranospiza caerulescens*, 1903.12.20, Serra da Chapada, central Brazil, Jun 1902; *Geranospiza caerulescens nigra*, USNM 18450, Orizaba, Mexico; *Gypaetus barbatus*, 1911.2.9.2; USNM 17834, Algeria, 1842; *Gypohierax angolensis*, 1850.11.13.14; †, USNM 291316, Efulan, Cameroun, West Africa, 7 Apr 1927; *Gyps africanus*, S/1983.19.6, Karoi, 1647S, 2935E, 1983; *Gyps fulvus*, 1861.2.26.6, **captivity**, 30+ years; *Gyps ruepelli*, †, USNM 430014, **captivity**, 2 Feb 1958; *Haliaeetus albicilla*, 1851.11.10.46†; *Haliaeetus leucocephalus*, 1930.3.24.262, May 1911; †, USNM 431884, Yakutat, Alaska, Jan 1961; *Haliastur indicus*, USNM 556985, Jailolo District, Halmahera Is, Moluccas, Indonesia, 2 Apr 1981; *Haliastur spheurnurus*, S/1964.1.14, Harrow, Victoria, Australia, 24 Jan 1963; *Harpagornis moorei*, ♂†, NMNZ S 27773, Mount

Owen, Nelson, New Zealand, Jan 1990; *Harpagus dentatus*, USNM 559320, 10 miles up Cuyuni River, Guyana, 8 Jan 1984; *Harpia harpyja*, 1872.10.25.1; ♀, USNM 429223, captivity, Nov 2 1949; ♂, USNM 429223, captivity, 2 Nov 1949; *Harpophalietus solitarius*, USNM 49656, San Geronimo, Guatemala, 2 leg bones ex skin same number; *Heterospizias meridionalis*, ♂, 1903.12.20.1, Serra da Chapada, central Brazil; *Heterospizias meridionalis meridionalis*, USNM 227378, Puerto Pinasco, Paraguay, 8 Sep 1920; *Hieraaetus fasciatus*, 1847.10.21.50; *Hieraaetus fasciatus spilogaster*, ♀, USNM 430796, Mphoengs, Southern Rhodesia [Zimbabwe], 18 Aug 1958; *Ichthyophaga ichthyaetus*, 1845.1.12.20; USNM 468555, captivity, 7 Jan 1958; *Ichthyophaga humilis [=nana]*, ♀, USNM 224807, Toli Toli, Celebes [Sulawesi], Indonesia, 8 Dec 1914; *Ictinaetus malayensis*, ♂, S/1969.1.1, Gunong Benom, Malaya; *Ictiniaplumbea*, ♀, 1903.12.20.253, Serra da Chapada, Brazil, 29 Oct 1902; *Kaupifalco monogrammicus*, ♀, 1869.10.19.28, Africa; ♀, USNM 322456, Cameroun, West Africa, 10 Apr 1931; *Leptodon cayanensis*, ♂, USNM 32973, Central America, feet only; *Leucopternis (albicollis?) polionota*, 1846.4.21.18; *Leucopternis melanops*, ♂, USNM 432181, captivity, 23 Jul 1963; *Lophaelus occipitalis*, 1861.1.19.6; ♀, USNM 291451, Temkaka, Sudan, Africa, 28 Feb 1928; *Machaerhamphus alcinus*, ♂, adult, S/ 1956.20.1, Gomantong, North Borneo, 16 Apr 1956; USNM 559816, Gomantong Caves, 35 km south of Sandakan, Sabah, Malaysia, Dec 1982; *Melierax musicus (M. canorus)*, 1903.1.6.13, Deelfontein; *Melierax gabar*, ♀, USNM 290384, Africa, Oct 28 1926; *Milvus milvus milvus*, ♀, 1940.7.6.1, Wales; *Milvus migrans lineatus*, ♂, USNM 319228, Szechwan, China, 21 Jul 1930; *Morphnus guianensis*, 1851.12.2.10; ♀, USNM 432243, captivity, 4 Aug 1963, trunk skeleton; USNM 18468, skull; *Necrosyrtes monachus*, 1860.1.19.8, Natal; USNM 18894, Cunga, Angola, West Africa; *Neophron percnopterus*, 1847.10.21.25, South Africa; USNM 17835, North Africa; *Parabuteo unicinctus harrisi*, ♂, 1900.11.30.30, Brownsville, Texas, 6 May 1900; ♀, USNM 343414, Starr County, Texas, Jul 25 1936; *Pernis apivorus*, 1871.12.29.3; *Pernis apivorus gurneyi*, USNM 343983, Chiengmai, northern Siam [Thailand], 20 Jan 1937; *Pithecopha jefferyi*, S/1961.23.1, captivity, Nov 1961; ♀, captivity, 30 Jun 1970; *Polyboroides radiatus*, 1860.12.31.1, Natal; *Polyboroides typus*, ♂, USNM 291787, Efulan, Cameroun, West Africa, 4 Feb 1928; *Polemaetus bellicosus*, S/1957.9.1, Africa, captivity, 20 May 1957; ♀, USNM 430533, Syringa, Southern Rhodesia [Zimbabwe], 30 Nov 1957; *Rostrhamus sociabilis*, ♀, USNM 553612, Buenos Aires, Argentina, 4 Mar 1966, captivity; *Spilornis cheela bassus*, 1850.8.15.14, India; *Spilornis cheela*, 1845.1.12.12, Nepal; *Spilornis cheela burmanicus*, ♀, USNM 343985, San Sai Luang (near Chiengmai), northern Siam [Thailand], 27 Feb 1936; *Spizaetus ornatus*, S/1952.1.177; ♀, USNM 430495, captivity, 15 Mar 1958; *Spizastur melanoleucos*, USNM 321507, Velhas River, Brazil, 1866; *Stephanoaetus coronatus*, ♂, S/1954.30.42; ♀, USNM 346652, captivity, 15 May 1943; *Terathopius ecaudatus*, 1853.1.21.2, South Africa; ♀, USNM 431431, Norton, Southern Rhodesia [Zimbabwe], 3 Jul 1961; *Urotriorchis macrourus batesi*, ♀, USNM 292398, Efulan, Cameroun, West Africa, Aug 6 1928.

APPENDIX 2

Features evaluated for and used (bold type) in preliminary and final runs of PAUP (Swofford 1984).

No.	Code	Feature [codes for feature states and intermediates]
1	CR1	Median ridge of palatal surface of rostrum: a, obliterating median groove; b, not obliterating groove [a/0 b/1]
2	CR2	Palatal processes of premaxilla: a, fused together; b, free; c, bony septal bar; d, in contact, not fused; e, in contact anteriorly, fused posteriorly [a/0 a-b/1 b/2 c/3 d/4 e/5]
3	CR3	Tip of vomer: a, not bridging gap between palatine processes of premaxilla; b, bridging gap [a/0 b/1]
4	CR4	Maxillo-palatines and palatines: a, not widely separated or with strong rostral bar; b, widely separated, with strong rostral bar [a/0 b/1]
5	CR5	Posterolateral angle of palatine: a, square, long parallel margin; b, tapered to pterygoid

		process; c, evenly rounded; d, rounded and notched [a/0 b/1 c/2 d/3]
6	CR6	Palatine fossa: a, not excavated, no choanal ridge; b, well excavated, strong choanal ridge medially [a/0 b/0]
7	CR7	Vomer: a, absent; b, thin, laterally compressed splint; c, slender, with anterior knob; d, nearly tubular, inflated [a/0 b/1 c/2 d/3]
8	CR8	Posteropterygoids: a, clasping parasphenoid rostrum; b, not clasping rostrum [a/0 b/0]
9	CR9	Dorsal surface of maxillopalatine processes: a, fused with ventral wall of vestibule; b, free, forming lateral part of vestibule floor [a/0 b/1]
10	CR10	Prefrontal: a, free; b, in contact with frontal and with lateral ethmoid but not fused; c, fused with frontal and with lateral ethmoid [a/0 b/1 c/2]
11	CR11	Orbital process of prefrontal: a, curved posteriad; b, flat, spatulate; c, curved rostrad; d, straight [a/0 b/1 c/2 d/3]
12	CR12	Posterior margin of supraorbital process of prefrontal: a, pointed to attenuated; b, squared off or notched; c, inflated [a/0 b/1 c/2]
13	CR13	Superciliary: a, present, well-developed; b, absent or rudimentary [a/0 b/1]
14	CR14	Lateral wall of nasal vestibule: a, not, or poorly, ossified; b, ossified [a/0 b/1]
15	CR15	Zygomatic process of squamosal: a, well-developed; b, absent or rudimentary; c, present but reduced [a/0 b/1 c/2]
16	CR16	Articular process of squamosal: a, well-developed; b, absent or rudimentary [a/0 b/1]
17	CR17	Tympanic margin: a, not flared; b, flared laterally into a more or less rectangular plate; c, flared into curved plate; d, straight, rostrad [a/0 b/1 c/2 d/3]
18	CR18	Basipterygoid processes: a, usually present in adults; b, absent; c, rudimentary [a/0 a-b/1 b/2 c/3]
19	CR19	Posterior tympanic process: a, present, simple; b, absent; c, forming 'cup' around quadrate articulation [a/0 b/1 c/2]
20	CR20	Median basiparasphenoid process: a, absent; b, median tubercle at caudal end of a median ridge; c, several, separated, tubercles; d, irregular transverse ridge [a/0 b/1 c/2 d/3]
21	CR20A	Lateral basiparasphenoid process: a, absent; b, a ridge; c, a prominent swelling [a/0 b/1 c/2]
22	CR21	Interorbital septum: a, perforate; b, small perforation; c, imperforate [a/0 b/1 c/2]
23	CR22	Constriction of nasal vestibule towards middle naris: a, nil; b, slight; c, distinct [a/0 b/1 c/2]
24	CR23	Quadrate articular surface: a, 'normal'; b, smoothly rounded, blending with ventral surface; medial articular surface narrow, extending along caudal margin nearly to caudal angle [a/0 b/1]
25	CR24	Small notch in quadrate: a, absent; b, present [a/0 b/1]
25A	CR25	Postorbital process: a, broad, flat in lateral view; b, pointed, attenuated to a spike [a/0 b/1]
26	MA1	Median articular processes: a, concave ventrally; b, convex ventrally [a/0 b/1]
27	MA2	Mandibular rami: a, bent ventrad then rostrad near distal end; b, curving ventrad, then rostrad in symphysis; c, curved evenly ventrad from at least half-way to tip [a/0 b/1 b-c/2 c/3]
28	MA3	Median articular process: a, with ventrocaudal flange; b, no flange [a/0 b/1]
29	MA4	Small tubercle (continuation of linear muscle scar running dorsoventrad across internal angle of ramus at articulation): a, present; b, absent; c, ridge [a/0 b/1 c/2]
30	MA5	Tubercle on median proximal face of ramus, at dorsal edge of angular: a, absent; b, small; c, large [a/0 b/1 b-c/2 c/3]
31	MA6	Tubercle in MA5: a, so far caudal as to be on dorsal edge, giving extra tubercle there; b, in line with coronoid process; c, between coronoid and surarticular processes; d, caudal to coronoid process [a/0 b/1 c/2 d/3]
32	MA7	Mandibular symphysis: a, very short; b, not short [a/0 b/1]
33	MA8	Rami, in dorsal view: a, bowed laterad, then sharply mediad rostrally; b, straight; c, with definite angle [a/0 b/1 c/2]
34	MA9	Retroarticular process: a, absent; b, small; c, large [a/0 b/1 c/2]
35	MA10	Dorsal edge of rami: a, turned over laterally to form a flange; b, no flange [a/0 b/1]
36	MA11	Tip: a, pointed; b, blunt or rounded [a/0 b/1]
37	MA12	Symphysis: a, excavated into U-shape; b, filled to a flat surface [a/0 b/1]
38	FU1	Head of clavicle: a, attenuated, pointed caudally; b, terminating more or less acutely, but not

		pointed [a/0 b/1]
39	FU2	Coracoid articular surface: a, raised from blade dorsally and ventrally; b, not raised; c, raised ventrally; d, raised dorsally
40	FU3	Hypocleidium: a, present; b, absent [a/0 b/1]
41	FU4	Axis of coracoidal articulation: a, in line with caudal margin of furcula at ventral end of articulation; b, at angle of less than 90°; c, at c.90° [a/0 b/1 c/2]
42	FU5	Length of coracoid articular facet: a, about equal to ramal width; b, up to two-thirds ramal width [a/0 b/1]
43	FU6	Rami bent: a, once, near dorsal end; b, once, near the centre; c, twice, dorsally and ventrally [a/0 b/1 c/2]
44	FU7	Pneumatic foramina in lateral fossa with: a, absent; b, present [a/0 b/1]
45	FU8	Dorsocaudal tip of furcula: a, in contact with acromion; b, not in contact [a/0 b/1]
46	ST1	Coracoidal sulci: a, separated at manubrial spine; b, closely adjacent; c, overlapping [a/0 b/1 c/2]
47	ST2	Number of rib articulations on costal margin: a, 4; b, 5; c, 6; d, 7 [a/0 b/1 c/2 d/3]
48	ST3	Sternocoracoidal impression: a, with pneumatic foramen; b, without foramen [a/0 b/1]
49	ST4	Tubercle for brace ligament: a, present; b, absent [a/0 b/1]
50	ST5	Caudal margin: a, thickened, triangular in outline; b, bluntly pointed; c, almost square, slightly indented, or notched; d, deeply square-notched, leaving acute triangle medially [a/0 b/1 c/2 d/3]
51	ST6	Sternocoracoidal fossa extending caudally to: a, 2nd costal articulation; b, 3rd articulation; c, 4th articulation; d, 5th articulation; e, 6th or 7th [a/0 b/1 c/2 d/3 e/4]
52	ST7	Sternocoracoidal process: a, with anteromedial projection; b, with no projection [a/0 b/1]
53	ST8	Lateral processes: a, present; b, rudimentary; c, absent [a/0 b/1 c/2]
54	ST9	Ventral margin of sternocoracoidal fossa: a, adjacent to <i>M. supracoracoideus</i> scar; b, well separated from scar [a/0 b/1]
55	ST10	Manubrial spine: a, short, blunt; b, long, thin [a/0 b/1]
56	ST11	Scar of <i>M. supracoracoideus</i> : a, lobed; b, with smoothly curved outline [a/0 b/1]
57	ST12	Cranial end of sternal carina: below base of manubrial spine; b, caudal to base of manubrial spine; c, well cranial to base of spine (below spine tip) [a/0 b/1 c/2]
58	ST12A	Deepest point of sternal carina: a, at cranial end; b, displaced caudad [a/0 b/1]
59	CO1	Clavicular facet in medial view: a, divided into cranial and caudal sections by shallow depression; b, a single, well-defined facet ending ventrally in sharp, projecting line; c, a separate facet on the ventrolateral surface [a/0 b/1 c/2]
60	CO2	Distinct facet on dorsal surface between lateral margin and sternocoracoidal impression: a, present; b, absent [a/0 b/1]
61	CO3	Sternocoracoidal tuberosity (posterior ligament scar): a, prominent; b, obscure; c, absent [a/0 b/1 c/2]
62	CO4	Oval or circular impression on dorsolateral surface opposite coracoidal fenestra: a, distinct; b, obscure; c, absent; d, present, proximal to coracoidal fenestra [a/0 b/1 c/2 d/3]
63	CO4A	(CO20) Coracoidal fenestra: a, always present; b, variable; c, absent [a/0 b/1 c/2]
64	CO5	Dorsolateral surface of head: a, with distinct fossa; b, without fossa [a/0 b/1]
65	CO6	Subclavicular fossa: a, with pneumatic foramen (-ina); without foramen (-ina) [a/0 b/1]
66	CO7	Tip of procoracoid: a, deflected ventrad; b, not deflected [a/0 b/1]
67	CO8	Sternocoracoidal process: a, short, with parallel sides [a/0 b/1 c/2 d/3]
68	CO9	Insertion of posterior ligament: a, lateral; b, near sternocoracoidal impression; c, medial; d, on coracoid shaft [a/0 b/1 c/2 d/3]
69	CO10	Sternocoracoidal impression: a, without pneumatic foramina; b, without foramina [a/0 b/1]
70	HU1	Brachial impression: a, extending as deep pit between proximal edges of internal and external condyles; b, not extending between condyles as pit [a/0 b/1]
71	HU2	Outline of proximal margin of deltoid crest: a, concave; b, straight; c, convex [a/0 b/1 c/2]
72	HU2A	Distal end of deltoid crest: a, running smoothly into line of shaft (except for pectoral attachment tubercle); b, with a distinct step to shaft [a/0 b/1]
73	HU2B	Apical 'crestlet' on deltoid crest: a, present; b, absent [a/0 b/1]

74	HU2C	External tuberosity: a, on line between deltoid crest and head; b, cranial to axis of head [a/0 b/1]
75	HU2D	Proportions of deltoid crest: a, proximal section shorter than distal; b, proximal section longer than distal; c, sections of equal length [a/0 b/1 c/2]
76	HU2E	Outline of distal margin of deltoid crest: a, concave; b, straight; c, convex [a/0 b/1 c/2]
77	HU3	Position of nutrient foramen with respect to distal end of bicapital crest: a, opposite; b, distal to; c, well distal to; d, at c. 50 % of shaft [a/0 b/1 c/2 d/3]
78	HU4	Position of nutrient foramen with respect to distal end of deltoid crest: a, opposite; b, proximal to; c, distal to crest [a/0 b/1 c/2]
79	HU5	Ligamental groove: a, entire, deep, cutting off bicapital surface; b, shallow, rectangular [a/0 b/1]
80	HU6	Bicapital furrow: a, deep, narrow; b, broad; c, obscure to obsolete [a/0 b/1 c/2]
81	HU7	Shape of bicapital surface in internal view: a, convex, evenly rounded from bicapital crest; b, flat, with small radius curve from bicapital crest; c, concave [a/0 b/1 c/2]
82	HU8	Orientation of proximal margin of internal tuberosity: a, proximad; b, distad [a/0 b/1]
83	HU9	Distal extension of median crest: a, running into margo caudalis (caudal margin); b, parallel to caudal margin; c, parallel to caudal margin, but with deep fossa between [a/0 b/1 c/2]
84	HU10	Orientation of bicapital crest to shaft, at distal end of crest: a, meeting shaft at $\pm 90^\circ$; b, at acute angle; c, running into line of shaft [a/0 b/1 c/2]
85	HU11A	Outline of internal margin of bicapital crest viewed normal to shaft: a, with definite angle proximally and distally, $\pm$ parallel to shaft between; b, $\pm$ evenly curved; c, with definite proximal and distal angles and internal margin diverging internally proximally; d, with angle to shaft distally, parallel to shaft on to internal tuberosity proximally; e, as in d but angled towards shaft proximally; f, a single angle [a/0 b/1 c/2 d/3 e/4 f/5]
86	HU12	Proportion of pneumatic fossa occupied by pneumatic foramen: a, most ($>2/3$); b, part ($<2/3$) [a/0 b/1]
87	HU13	Internal tricapital groove: a, deep, with sharp external ridge; b, shallow to obscure [a/0 b/1]
88	HU13A	Distal anconal fossa: a, triangular section, with internal side deepest; b, rectangular section; c, divided by strong external margin to inner tricapital groove [a/0 b/1 c/2]
89	HU14	Distal end of bicapital crest: a, a wide shelf; b, narrow shelf; c, no shelf [a/0 b/1 c/2]
90	HU15	Attachment of <i>M. infraspinatus</i> on proximal bicapital crest: a, elongate; b, short, rounded [a/0 b/1]
91	HU16	Attachment of <i>M. supraspinatus</i> : a, clear, raised; b, inconspicuous [a/0 b/1]
92	HU17	Extent of external tuberosity in palmar view: a, prominent; b, in line from head to deltoid crest [a/0 b/1]
93	HU18	Impression of <i>M. brachialis anticus</i> in brachial depression: a, an extended pit; b, a raised scar; c, extending proximally from brachial depression [a/0 b/1 c/2]
94	HU19	Brachial crest: a, thick; b, thin [a/0 b/1]
95	HU20	Shaft anconal to ectepicondylar prominence: a, with fossa; b, without fossa, shaft smoothly convex [a/0 b/1]
96	HU21	Shape of apex of deltoid crest: a, angular, 'sharp'; b, smoothly rounded [a/0 b/1]
97	HU22	Ectepicondylar prominence: a, blunt, with or without distinct pit; b, pointed [a/0 b/1]
98	HU23	Position of deltoid crest apex: a, opposite distal end of bicapital crest; b, distal to distal end of bicapital crest [a/0 b/1]
99	HU24	Bicapital crest terminating as: a, sharp ridge along internal margin; b, ridge cranial to internal margin; c, very short ridge [a/0 b/1 c/2]
100	HU25	Distal end of median crest: a, proximal to distal end of bicapital crest; b, opposite distal end of bicapital crest [a/0 b/1]
101	HU26	Brachial depression: a, deep; b, shallow [a/0 b/1]
102	HU27	Lateral extent of ectepicondylar prominence in anconal view: a, projecting beyond external margin as strong ridge; b, not projecting beyond margin as ridge [a/0 b/1]
103	HU28	Impressions of <i>Mm. latissimus dorsi</i> : a, in shallow groove; b, not in groove [a/0 b/1]
104	HU29	Distal margin of bicapital surface delimited by: a, wide notch; b, faint groove, no notch; c, definite groove, but no notch; d, step [a/0 b/1 c/2 d/3]
105	HU30	'Swelling' below head, at distal end of capital groove: a, present to well-developed; b, absent;

- c, pit, not a swelling [a/0 b/1 c/2]
- 106 **HU31** Shape of external tricipital groove: a, shallow or indistinct; b, deep, with raised internal border [a/0 b/1]
- 107 **HU32** Caudal margin: a, rounded; b, an angle defined by planes above and below; c, as in b, but sharp angle of c. 90° [a/0 b/1 c/2]
- 108 **UL1** Shape of distal end of brachialis anticus impression: a, acute; b, rounded [a/0 b/1]
- 109 **UL2** Shaft proximal to trochlea: a, trochlea undercut by fossa; b, deep fossa, but not undercutting trochlea; c, fossa shallow or obscure [a/0 b/1 c/2]
- 110 **UL3** Intermuscular line past nutrient foramen: a, sharp; b, obscure or absent [a/0 b/1]
- 111 **UL3A** 'Double' intermuscular line: a, reaching, or nearly so, nutrient foramen; b, merging well proximal to foramen; c, merging distal to foramen; d, single throughout length [a/0 b/1 c/2 d/3]
- 112 **UL4** Proximal end of *M. brachialis anticus* impression: a, with pneumatic foramina; b, not pneumatic [a/0 b/1]
- 113 **UL5** Junction between internal margin of shaft and external condyle: a, smooth; b, with pronounced step [a/0 b/1]
- 114 **UL6** Carpal tuberosity: a, bluntly pointed; b, 'squared off' [a/0 b/1]
- 115 **UL7** Proximal end of *M. brachialis anticus* impression: a, broad, shallow; b, deep groove, with internal border extended as thin shelf; c, narrow; prominence for anterior articular ligament broad [a/0 b/1 c/2]
- 116 **UL8** Olecranon: a, acutely pointed; b, blunt [a/0 b/1]
- 117 **UL9** Outline of external condyle: a, evenly rounded; b, with distal angle = 'squared' [a/0 b/1]
- 118 **UL10** Process beside distal tendinal pit: a, prominent; b, obscure [a/0 b/1]
- 119 **UL11** Position of nutrient foramen relative to brachialis anticus impression: a, less than length of impression distal to impression; b, about length of impression distal to impression; c, further distal to impression than length of impression [a/0 b/1 c/2]
- 120 **UL12** Proximal surface of carpal tuberosity: a, undercut by fossa; b, not undercut [a/0 b/1]
- 121 **UL13** Proximal margin of trochlea: a, angular, with sharp internal angle at junction with internal condyle; b, smooth curve [a/0 b/1]
- 122 **UL14** Orientation of axis of carpal tuberosity: a, proximad; b, distad [a/0 b/1]
- 123 **CM1** Proximal internal edge of minor metacarpal: a, with prominent, flat-ended tubercle; b, no tubercle, perhaps a rounded swelling [a/0 b/1]
- 124 **CM2** Pisiform process: a, thin, rounded in section; b, long, oval or rectangular in section; c, robust, round [a/0 b/1 c/2]
- 125 **CM3** Pollical facet: a, rounded; b, proximal and distal notches dividing surface into two segments; c, surfaces separated; d, notched, internal surface reduced [a/0 b/1 c/2 d/3]
- 126 **CM4** Depressio metacarpi interna: a, shallow; b, deep [a/0 b/1]
- 127 **CM5** Sulcus internus: a, deep, internal surface of major metacarpal rounded, distal symphysis projecting internally; b, broad and shallow, internal surface of major metacarpal flattened, symphysis not projecting [a/0 b/1]
- 128 **CM6** Depressio metacarpi externa: a, deep; b, shallow [a/0 b/1]
- 129 **CM7** Shape of carpal trochlea in proximal view: a, internal condyle concave internally; b, concave externally [a/0 b/1]
- 130 **CM7A** Shape of carpal trochlea in proximal view: a, external condyle concave internally; b, external condyle concave externally; c, straight [a/0 b/1 c/2]
- 131 **CM7B** Junction of proximal end of external margin of minor metacarpal: a, in line with external condyle; b, in line with internal condyle; c, between condyles [a/0 b/1 c/2]
- 132 **CM7C** Proximal end of minor metacarpal: a, with deep fossa; b, with no fossa; c, with shallow groove [a/0 b/1 c/2]
- 133 **CM8** Posterior carpal fossa: a, deep; b, shallow [a/0 b/1]
- 134 **CM9** Ligament attachment of pisiform process: a, prominent swelling, with or without pit; b, small or obscure [a/0 b/1]
- 135 **CM10** Position of pollical facet: a, less than or equal to 50% of distance from internal condyle to distal end of proximal symphysis; b, more than 50% to distal end of proximal symphysis [a/0 b/1]
- 136 **CM11** Length of distal symphysis: a, less than or equal to distal width of major metacarpal; b, greater

- than width of major metacarpal [a/0 b/1]
- 137 **CM12** Anterior carpal fossa: a, shallow; b, deep pit; c, pit, with pneumatic foramen or foramina [a/0 b/1 c/2]
- 138 **CM13** Internal ligamental fossa: a, shallow; b, deep [a/0 b/1]
- 139 **CM14** Junction of distal end of internal of condyle with shaft: a, smooth; b, stepped [a/0 b/1]
- 140 **CM15** Shape of end of major metacarpal in distal view: a, approximately rectangular; b, more or less triangular, anteroexternal side convex [a/0 b/1]
- 141 **CM16** Facet for digit of minor metacarpal: a, set off from major metacarpal by deep pit; b, no deep pit [a/0 b/1]
- 142 **PE1** Dorsal fenestrae: a, large, conspicuous; b, absent or small [a/0 b/1]
- 143 **PE2** Postacetabular ilium and synsacral plate: a, fused, with no obvious suture; b, not fused [a/0 b/1]
- 144 **PE3** Cranial ends of iliac plates: a, rounded in dorsal view; b, straight or inclined anterolaterally [a/0 b/1]
- 145 **PE4** Posterior iliac crests: a, more or less straight and parallel; b, bowed outward [a/0 b/1]
- 146 **PE5** Width across posterior iliac crests in dorsal view: a, about equal to pelvis length; b, less than two-thirds pelvis length [a/0 b/1]
- 147 **PE6** Anterior iliac crests: a, separated from synsacral plate by large fenestrae; b, not separated [a/0 b/1]
- 148 **PE7** Posterior iliac crests: a, produced as square process above acetabulum; b, produced above acetabulum, but not forming square process; c, not produced above acetabulum [a/0 b/1 c/2]
- 149 **PE8** Shape of posterior end of ilioischadic plate: a, tapering to rounded point; b, notched; c, abruptly arrowing before posterior extremity; d, knickpoint in posterior iliac crest [a/0 b/1 c/2 d/3]
- 150 **PE9** Pubis: a, rodlike, not expanded; b, slight expansion; c, with broad expansion [a/0 b/1 c/2]
- 151 **PE10** Shape and direction of anterior synsacral caudal vertebrae: a, long, slender, parallel, or diverging towards acetabulum; b, relatively short, broadly converging [a/0 b/1]
- 152 **PE11** Posterior synsacral caudal vertebrae: coalescing with broad, medially projecting plate; b, free, articulating with mesial iliac edge (Note: In *Sagittarius* there is a broad plate enclosing the posterior ilioischadic space ventrally) [a/0 b/1]
- 153 **PE12** Number and arrangement of caudal synsacral vertebrae (anterior, posterior): a, 2+2; b, 2+3; c, 2+2+1; d, 3+3; e, 2+3+1 [a/0 b/1 c/2 d/3 e/4]
- 154 **PE13** Posterior iliac crests above ilioischadic fossa: a, shelf-like; b, not produced as a shelf [a/0 b/1]
- 155 **PE14** Mesial protuberance at posterior ilio-ischiatic suture: present, forming 'constriction' of caudal space; b, absent [a/0 b/1]
- 156 **FE1** Rotular groove: a, in line with shaft; b, at angle to shaft [a/0 b/1]
- 157 **FE2** Rotular groove: a, short; b, long [a/0 b/1]
- 158 **FE3** Pneumatic foramen: a, absent; b, present [a/0 b/1]
- 159 **FE4** Cranial outline of shaft: a, straight in lateral view; b, curved in lateral view; b, bent caudad near distal end; c, bent caudad near midpoint of shaft [a/0 b/1 b-c/2 c/3 c-a/4]
- 160 **FE5** Trochanteral ridge: a, short cranially, but extending proximoplantad as strong ridge; b, not so [a/0 b/1]
- 161 **FE6** Cranial intermuscular line(s): a, medial; b, lateral; c, along centre-line [a/0 a-b/1 b/2 c/3 c-a/4]
- 162 **FE7** Number of cranial intermuscular lines: a, 1; b, 2 [a/0 b/1]
- 163 **FE8** Medial condyle: a, projecting in line with shaft; b, projecting cranially [a/0 b/1]
- 164 **FE9** Popliteal fossa: a, deep; b, shallow and broad; c, shallow, with deep pit; d, narrow, aligned with shaft; e, undercutting condyles [a/0 b/1 c/2 d/3 e/4]
- 165 **FE10** Popliteal fossa: a, with pneumatic foramen; b, without [a/0 b/1]
- 166 **FE11** Caudal intermuscular line: a, single, weakly defined; b, forked; c, strongly defined, central on shaft; d, multiple [a/0 b/1 c/2 d/3]
- 167 **FE12** Rotular groove section: a, rectangular; b, U-shaped; c, approximately V-shaped [a/0 a-b/1 b/2 b-c/3 c/4]

- 168 **FE13** Large muscle scar proximal to popliteal fossa: a, a line; b, more or less oval; c, divided into 2 separate scars [a/0 a-b/1 b/2 c/3]
- 169 **FE13A** Large muscle scar proximal to popliteal fossa: a, central on caudal surface; b, lateral; c, medial [a/0 a-b/1 b/2 b-c/3 c/4]
- 170 **FE13B** Large muscle scar proximal to popliteal fossa: a, a pit; b, a tubercle [a/0 b/1]
- 171 **FE14** Caudal intercondylar notch: a, V-shaped; b, deep U-section completely separating surfaces so that inner face of condyle is equal to outer face height; c, shallow U-section [a/0 b/1 c/2]
- 172 **FE15** Proximal caudal fossa: a, deep; b, shallow; c, shaft convex [a/0 a-b/1 b/2 c/3]
- 173 **FE16** Caudal edge of iliac surface: a, smoothly curved; b, with distinct angle [a/0 a-b/1 b/2]
- 174 **FE17** Shallow secondary fossa proximal to popliteal fossa: a, present; b, absent [a/0 b/1]
- 175 **FE18** Median face of median condyle: a, with fossa; b, without fossa (perhaps small pit); c, with large tubercle [a/0 b/1 c/2 a-c/3]
- 176 **FE19** Transition of proximal cranial end of median condyle with shaft: a, stepped; b, smooth; c, a high step [a/0 a-b/1 b/2 b-c/3 c/4 a-c/5]
- 177 **FE20** Cranial ridge of median condyle: a, extending further proximally than lateral ridge; b, equal; c, lateral extending further proximally [a/0 b/1 c/2]
- 178 **FE21** Fibular condyle: a, narrow; b, shelf-like; c, with deep pit proximally [a/0 b/1 c/2]
- 179 **FE22** Proximal edge of fibular condyle: a, with muscle insertion pit running distally as large notch, so that outline of condyle is a blunt projection; b, partly notched; c, square; d, not notched, rounded; e, not notched, but with a large pit; f, not notched, with the proximal outline square [a/0 b/1 c/2 d/3 e/4 f/5]
- 180 **FE23** Prominent tubercle on medial margin distal to femur head: a, present; b, absent; c, a raised linear scar [a/0 b/1 c/2]
- 181 **FE24** Trochanteral ridge: a, high, so that proximal outline of bone nearly triangular; b, low, outline of bone $\pm$ rectangular [a/0 b/1]
- 182 **FE25** Median condyle: a, $\pm$ flat in distal view, from intercondylar notch to median margin; b, curved; c, with definite angle; d, concave [a/0 a-b/1 b/2 b-c/3 c/4 d/5 a-d/6]
- 183 **FE26** Proximo-lateral extension of fibular condyle: a, absent; b, pointed; c, $\pm$ square; d, rounded; e, double [a/0 a-b/1 b/2 b-c/3 c/4 a-c/5 d/6 e/7]
- 184 **FE25** Median condyle: a, square; d, rounded; e, double [a/0 a-b/1 b/2 b-c/3 c/4 a-c/5 d/6 e/7]
- 184 **FE27** Prominent tubercle medial to popliteal fossa: a, present; b, absent [a/0 b/1]
- 185 **FE28** Proximal trochanteral ridge turned medially to overhang and form fossa on and above iliac surface: a, present; b, absent; c, with second fossa [a/0 b/1 a-c/2 b-c/3 c/4]
- 186 **FE29** Cranial intermuscular line: a, nearly straight; b, directed toward lateral margin, then straight down shaft, forming clear angle [a/0 b/1]
- 187 **FE30** Caudal junction of medial condyle with shaft: a, with tubercle; b, tubercle extending laterally as ridge (forming pit); c, tubercle small to absent; d, tubercle extending proximo-laterally as line towards scar of FE13 [a/0 b/1 c/2 d/3]
- 188 **FE31** Proximal outline of trochanteral ridge in lateral view: a, angular, with distal limb returned; b, rounded; c, angular [a/0 b/1 c/2]
- 189 **FE32** Cranial edge of iliac facet: a, a slight crest; b, not a crest [a/0 a-b/1 b/2]
- 190 **FE33** Proximal end of lateral condyle; muscle insertion at proximal end of ridge: a, at junction with shaft (termination coincides with shaft margin); b, displaced laterally [a/0 b/1]
- 191 **FE34** Bone proportions: a, long and slender; b, of 'normal' proportions [a/0 b/1]
- 192 **FE35** Prominent muscle attachment across popliteal fossa: a, a line; b, absent [a/0 b/1]
- 193 **FE36** Muscle scar of 13A and B: a, distal to or $\pm$ in popliteal fossa; proximal to fossa [a/0 b/1]
- 194 **FE37** Depth of rotular groove: a, equal to depth; b, less than width; c, much less than width [a/0 a-b/1 b/2 b-c/3 c/4]
- 195 **FE38** Trochanteral ridge: a, $\pm$ smoothly curved over pneumatic foramen in lateral view; b, arched over foramen; c, with a large swelling distal to foramen; d, with a very large muscle scar distally [a/0 a-b/1 b/2 b-c/3 a-c/4 c/5 d/6]
- 196 **FE39** Area proximal to pneumatic foramen: a, with no ridge; b, with strong transverse ridge; c, with trochanter medial enough for intermuscular line to run distad down medial side of foramen directly from it [a/0 b/1 c/2]
- 197 **FE40** Distal part of external face of fibular condyle: a, impressed so that proximo-lateral process stands proud of lateral surface; b, not impressed [a/0 b/1]

- 198 **FE41** Proximo-caudal median protuberance: a, absent; b, present [a/0 b/1]
- 199 **FE42** Trochanteral ridge and lateral margin of iliac facet: a, merged cranially; b, separated [a/0 b/1]
- 200 **FE43** Proximal cranial end of lateral condyle: a, with no step; with obvious step [a/0 b/1]
- 201 **TI1** Distal condyles: a, extending as far caudally as cranially; b, $\pm$ in line with posterior surface of shaft [a/0 b/1]
- 202 **TI2** Trochlear groove and sulcus: a, very deep; b, shallow [a/0 b/1]
- 203 **TI3** Sulcus: a, caudal to line of shaft; b, running into caudal surface [a/0 b/1]
- 204 **TI4** Fibula insertion: a, near distal end of shaft; b, 0.5-0.67 distance down shaft [a/0 a-c/1 b/2 b-c/3 c/4]
- 205 **TI5** Lateral cnemial crest: a, long ($>$ width); b, short ($=$ width) [a/0 b/1]
- 206 **TI6** Medial proximal ligaments: a, inserting on shaft midline; b, inserting at distal end of medial crest [a/0 a-b/1 b/2]
- 207 **TI7** Lateral proximal articular surface: a, deeply excavated; b, not deeply excavated, or pit laterally [a/0 b/1]
- 208 **TI8** Proximal plantar surface: a, strongly keeled (with lateral and/or medial fossae); b, rounded; c, low keel or ridge, not defined by fossae [a/0 a-c/1 b/2 b-c/3 c/4]
- 209 **TI9** Lateral cranial fossa: a, open to head; b, filled to distal edge of ridge running from lateral crest [a/0 b/1]
- 210 **TI10** Median cnemial crest: a, notched; b, smoothly convex; c, short, lateral length, with sharp angle separating proximal from distal sections; d, stepped at distal end [a/0 a-b/1 a-c/3 b/4 b-d/5 c/6 d/7]
- 211 **TI11** Sulcus extending: a, $\pm$ equally up cranial and caudal surfaces; b, 50% higher up caudal surface [a/0 b/1]
- 212 **TI12** Condyles: a, equal in width; b, medial condyle wider; c, lateral wider [a/0 b/1 c/2]
- 213 **TI13** Lateral condyle caudal limb: a, entire; b, notched [a/0 b/1]
- 214 **TI14** Distal margins of shaft: a, diverging abruptly to width over condyles; b, subparallel near condyles [a/0 b/1]
- 215 **TI15** Supratendinal bridge: a, 30-60° to shaft axis; b, $\pm$ at right angles to axis; c, $\pm$ parallel to axis [a/0 a-b/1 a-c/2 b/3 c/4]
- 216 **TI16** Muscle scar: a, at proximal end of supratendinal bridge; b, proximal to proximal end; c, well proximal to end; d, on medial margin [a/0 a-b/1 b/2 b-c/3 c/4 d/5]
- 217 **TI17** Muscle scar: a, a surface roughening; b, a prominent tubercle; c, a pit [a/0 b/1 c/2]
- 218 **TI18** Intercondylar groove: a, narrow; b, broad; c, shallow or obscure [a/0 b/1 c/2]
- 219 **TI19** Tibial cartilage sulcus: a, tapering; b, $\pm$ parallel-sided [a/0 b/1]
- 220 **TI20** Caudal arm of medial condyle: a, entire; b, notched [a/0 b/1]
- 221 **TI21** Cranial proximal sulcus: a, excavated; b, obscure [a/0 b/1]
- 222 **TI22** Medial shaft margin opposite supratendinal bridge: a, convex; b, concave; c, straight [a/0 b/1 c/2]
- 223 **TI23** Supratendinal bridge: a, narrow (length $>$ width); b, broad (length width); c, length $\gg$ width [a/0 b/1 c/2]
- 224 **TI24** Supratendinal bridge: a, flat; b, twisted; c, round; d, bent [a/0 b/1 d/2]
- 225 **TI25** Supratendinal bridge: a, narrowing distally; b, parallel-sided; c, narrowing proximally; d, narrowing proximally and distally; e, narrowing centrally, pinched [a/0 a-c/1 b/2 c/3 d/4 e/5]
- 226 **TI26** Supratendinal bridge arising: a, away from medial margin; b, from medial margin [a/0 a-b/1 b/2]
- 227 **TI27** Distal tendinal bridge orifice: a, circular; b, subtriangular [a/0 a-b/1 b/2]
- 228 **TI28** Lateral condyle: a, squared off proximally; b, tapering proximally [a/0 b/1]
- 229 **TI29** Proximal cranial end of medial condyle: a, squared off; b, extending laterally to partly obscure distal orifice of tendinal canal; c, tapering proximally [a/0 a-b/1 b/2 c/3]
- 230 **TI30** Nutrient foramen: a, proximal to distal end of fibular crest; b, opposite end of crest; c, distal to end of crest [a/0 b/1 c/2]
- 231 **TI31** Entepicondylar prominence: a, very small to absent; b, small; c, large [a/0 a-b/1 b/2 b-c/3 c/4]

- 232 **TI32** External ligamental attachment: a, very small to absent; b, triangular; c, shelf-like; d, on lateral condyle; e, a lateral tubercle; f, a ridge [a/0 a-b/1 b/2 c/3 c-f/4 d/5 e/6 f/7]
- 233 **TI33** Surface distolateral to tendinal canal: a, broad; b, narrow [a/0 b/1]
- 234 **TI34** Surface distolateral to tendinal canal: a, without prominence or pit; b, with prominence; c, with pit; d, with deep, narrow pit [a/0 b/1 b-c/2 c/3]
- 235 **TI35** Tendinal canal: a, central on shaft; b, confined to medial side of centre line; c, extending across most of shaft, deep and sunken [a/0 a-b/1 a-c/2 b/3 c/4]
- 236 **TI36** Medial margin at tendinal canal: a, broad; b, a thin plate [a/0 a-b/1 b/2]
- 237 **TI37** Median condyle: a, recurved proximo-cranially; b, not recurved; c, with no sharp angle, running smoothly from shaft [a/0 b/1 c/2]
- 238 **TI38** Medial distal caudal groove: a, convex or flat, edge not extending medially; b, deeply concave, edge extending medially [a/0 b/1]
- 239 **TI39** Medial distal caudal groove: a, without proximal pit; b, with proximal pit [a/0 b/1]
- 240 **TI40** Cranial surface of median condyle: a, not inflated; b, inflated [a/0 b/1]
- 241 **TI41** Proximal cranial sulcus: a, narrow (50% of cranial surface); b, wide [a/0 b/1] (refers to position of lateral crest)
- 242 **TI42** Ectepicondylar prominence: a, absent; b, small; c, large; d, linear [a/0 a-b/1 b/2 b-c/3 b-d/4 c/5 d/6]
- 243 **TI43** Medial condyle: a, entire in distal view; b, notched [a/0 a-b/1 b/2]
- 244 **TI44** Intercondylar space: a, narrow (< condyle width); b, wide (> condyle width); c, equal to condyle width [a/0 a-c/1 b/2 b-c/3 c/4]
- 245 **TM1** Calcaneal processes: a, widely separated; b, close-set
- 246 **TM2** Tendinal canal: a, open; b, almost closed; c, closed [a/0 b/1 c/2]
- 247 **TM3** Outer calcaneal process: a, produced, almost as large as inner; b, displaced laterally and flattened; c, otherwise
- 248 **TM4** Notch for *N. peroneus*: a, absent; b, indistinct; c, wide-mouthed; d, almost closed (270° closure) [a/0 b/1 c/2 d/3]
- 249 **TM5** Lateral calcaneal ridge: a, extending distally, fading into lateral posterior margin; b, delineated medially by fossa of *M. abductor digiti IV*; c, lateral ridge displaced medially and fused with medial ridge; d, displaced medially but not fused; e, lacking, posterior aspect ± flat, ridge a line marking margins of *M. abductor digiti IV* and *M. adductor digiti II* impressions [a/3 b/4 c/0 d/1 e/2]
- 250 **TM6** Median calcaneal process: a, pillar-like; b, an elongated plate; c, otherwise [a/0 b/1]
- 251 **TM7** Proximal and posterior margins of median calcaneal process: a, bent medially; b, not bent medially
- 252 **TM8** Medial calcaneal process: a, separated from medial margin by fossa of *M. flexor hallucis brevis*; b, lacking distinct fossa medial to process, which arises almost from margin of bone
- 253 **TM9** Medial proximal vascular foramen: a, medial and proximal to distal margin of medial process; b, medial to distal margin or on ridge below distal margin; c, lateral to ridge; d, on ridge below distal margin to just lateral to margin [a/0 a-b/1 b/2 b-c/3]
- 254 **TM10** Tubercle for *M. tibialis anticus*: a, lateral to midline; b, just medial to midline
- 255 **TM11** Lateral proximal vascular foramen: a, on medial side of lateral ridge; b, on lateral side or on lateral slope of hypotarsal ridge
- 256 **TM12** Lateral condylar surface: a, higher than medial; b, surfaces at equal level, or medial higher
- 257 **TM13** *M. tibialis anticus* tubercle: a, near proximal foramina; b, not near foramina
- 258 **TM14** Lateral metatarsal prominence: a, hardly discernible; b, well-defined
- 259 **TM15** Frenula: a, completely ossified; b, present; c, absent [It should be possible to sub-divide b: scars project, narrowly separated, near medial margin; broad lateral scar nearly on mid-line; scars at different levels, medial higher than lateral; lateral higher than medial; at same level]
- 260 **TM16** Posterior flexor groove: a, hollowed out and unmarked; b, relatively flat, with a series of shallow impressions for 3 posterior muscles
- 261 **TM17** Scar of first metatarsal: a, directed ± medially; b, directed posteriorly
- 262 **TM18** Proximal edge of metatarsal facet: a, raised, separated from projecting line of medial tarsal edge by notch; b, not separated by notch
- 263 **TM19** Openings at distal end end of tendinal groove: a, two; b, one

264	TM20	<i>M. extensor digiti III</i> origin's upper and medial margins: a, indicated by scar; b, not indicated by scar
265	TM21	Cranial surface proximal to middle trochlea: a, with pit; b, no pit; c, indistinct pit
266	TM22	Origin of <i>M. abductor digiti II</i> : a, fairly distinct, roughened, extending from tibialis anticus to upper and lateral margins of first metatarsal articulation; b, not so
267	TM23	Inner trochlea (digit II) posteromedial process: a, bent toward tarsal midline; b, not bent
268	TM24	Posterolateral process of digit II trochlea: a, short, thick, separated from articular surface by groove; b, not so
269	TM25	Digit IV trochlea posterolateral projection margin: a, truncated, pointed at ventroposterior angle; b, rounded posteriorly
270	TM26	Groove for <i>M. abductor digiti IV</i> tendon on posterolateral margin of shaft: a, wide, clearly marked; b, narrow, shallow
270	TM27	Proximal anterior fossa: a, deep; b, shallow
271	PH1	Phalanges 1 and 2 on pedal digit 2: a, free; b, fused in most or all specimens [a/0 b/1]
272	PX1	Number of cervical vertebrae: a, 13; b, 14; c, 15; d, 17 [a/0 b/1 c/2 d/3]
273	PX2	Number of cervical ribs: a, 1; b, 2; c, 3 [a/0 b/1 c/2]

APPENDIX 3

Number of species in each genus of Accipitridae in each of 18 geographical areas (Fig. 16).

Node																	
	P	E	E	T	R	O	A	A	I	NG	AI		G	IMU	E		
	AALCPH	GLMLRI	PHPMLL	CGNEYG	ERTSDE	EPRERM	RK										
	NVEHEE	AAAAON	AAHIII	HYECPY	GCEPRU	ROCLOE	YAA										
	DIPORN	MNCNSI	GMOLAA	TPORAP	YARIYT	ALUITG	TCU										
	ICTNNI	POHUTA	UIIVSA	HOPOES	PEALOR	NYSERA	HCP										
1	NORTHAM	1 0 0 0 0 0	0 1 0 1 1 1	0 0 0 0 0 1	0 0 0 0 0 0	0 0 0 0 0 0	0 0 1 0 0 0	0 3 0									
2	CENTRAM	0 0 1 1 0 0	1 1 0 1 1 1	1 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0	1 0 0 0 0 0	0 4 0									
3	WINDIES	1 0 1 0 0 0	0 0 0 0 1 0	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0	0 2 0									
4	SOUTHAM	0 0 1 1 0 0	1 1 0 1 2 1	2 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0	1 0 2 0 0 0	0 5 0									
5	SOUTHAF	1 1 0 0 0 0	0 0 1 1 0 0	0 0 0 1 0 1	0 1 1 1 1 3	2 4 1 0 1 0	0 1 2 3 1 0	0 8 1									
6	NORTHAF	1 0 0 0 0 0	0 0 0 1 0 0	0 0 0 2 0 0	0 0 1 0 1 2	1 1 0 0 0 0	0 0 2 1 0 0	0 1 0									
7	MADAGAS	0 0 0 0 0 0	0 0 1 1 0 0	0 0 0 1 0 1	0 0 0 0 0 0	0 0 0 0 0 1	0 1 2 0 0 0	0 1 0									
8	EUROPE	1 0 0 0 1 0	0 0 0 1 0 0	0 0 0 2 0 1	0 0 1 0 1 1	1 1 0 0 0 0	0 0 4 0 0 0	0 3 0									
9	MIDEAST	1 0 0 0 0 0	0 0 0 1 0 0	0 0 0 2 0 1	0 0 1 0 1 1	2 1 0 0 0 0	0 0 4 1 0 0	0 4 0									
10	NORTHAS	1 0 0 0 1 0	0 0 0 0 0 0	0 0 0 1 0 3	0 0 0 0 1 2	1 1 0 0 0 0	0 0 5 0 0 0	0 5 0									
11	SEASIA	1 2 0 0 1 0	0 0 0 1 0 0	0 0 0 1 1 2	2 0 1 0 0 3	1 1 0 3 0 0	0 0 0 0 0 0	0 4 0									
12	INDOPHI	1 1 0 0 2 0	0 0 1 1 0 0	0 0 0 1 1 1	2 0 0 0 0 2	1 0 0 3 0 0	0 0 0 0 0 0	0 6 0									
13	NEWGUIN	1 1 0 0 0 1	0 0 1 1 0 0	0 0 0 1 2 1	0 0 0 0 0 0	0 0 0 0 0 0	0 0 1 0 0 1	0 9 0									
14	MELANES	1 1 0 0 0 1	0 0 0 0 0 0	0 0 0 1 2 2	0 0 0 0 0 0	0 0 0 0 0 0	0 0 1 0 0 0	0 A 0									
15	AUSTRAL	1 1 0 0 0 0	0 0 0 2 0 0	0 1 1 1 2 1	0 0 0 0 0 0	0 0 0 0 0 0	0 0 2 0 0 0	1 3 0									
16	NEWZEAL	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 1	0 0 0 0 0 0	0 0 0 0 0 0	0 0 1 0 0 0	0 1 0									
17	OCEANIA	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 1	0 0 0 0 0 0	0 0 0 0 0 0	0 0 1 0 0 0	0 0 0									
18	GREENLA	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 1	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0									

Node	B	H	G	HI	H	HASS	L	C	
	BLUHAB		EBMAC		APIQPP		OOPS	H	H
	UETERU		PRUORT		RIEUII		PROT	A	E
	TUETPS		AATRPI		PTRIZZ		HOLESR		L
	ACOEYA		RNEPIN		YHALAA		AAEPAP		I
	SOGRRH		AOOHAA		OEAASE		EEMHGA		C
1 NORTHAM	001000		107000		000100		000000		0
2 CENTRAM	023111		106110		000112		000000		0
3 WINDIES	000000		004000		000000		000000		0
4 SOUTHAM	083121		118110		000012		010000		0
5 SOUTHAF	100000		003000		002301		101110		0
6 NORTHAF	000000		001000		001300		000000		1
7 MADAGAS	000000		001000		000000		000000		0
8 EUROPE	000000		003000		002500		000000		0
9 MIDEAST	000000		002000		002300		000000		0
10 NORTHAS	100000		004000		002401		000000		0
11 SEASIA	200000		000001		002202		000000		0
12 INDOPHI	200000		000001		012003		000000		0
13 NEWGUIN	000000		000001		101100		000000		0
14 MELANES	000000		000000		000000		000000		0
15 AUSTRAL	000000		000000		001100		000000		0
16 NEWZEAL	000000		000000		000000		000001		0
17 OCEANIA	000000		002000		000000		000000		0
18 GREENLA	000000		000000		000000		000000		0



Saw-whet Owl *Aegolius a. acadicus*