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Notice 1

The Fossil History of the Family Accipitridae in Australia

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Immature Wedge-tail Eagle (*Aquila audax*) with rabbit prey
Watercolour and gouache on paper

Abstract

The aims of this study are the description of the fossil accipitrid material and the stratigraphic placement of the fossil material. This has led to an understanding of the evolutionary change and biogeographic relationships of the Australian accipitrids compared to those from the rest of the world through Tertiary and Quaternary times.

The oldest described accipitrid in Australia, *Pengana robertbolesi*, dates from the Late Oligocene–Early Miocene deposits, at the Sticky Beak Site, Riversleigh Station, Queensland (Boles, 1993). Fossil remains of accipitrids are relatively rare and poorly preserved in Australian Tertiary deposits, and consists of three claws, which are not diagnostic to genus; a distal humerus from the Mid-Miocene deposits at Bullock Creek, Northern Territory, named *Aquila bullockensis*; a proximal carpometacarpus from a Pliocene locality, which shows most similarity to *Hamirostra*; and a distal femur of unknown affinities. A tarsometatarsus from Steve' Site, South Australia, shows most relationship to the family Falconidae and is the oldest record for the family within Australia, and is named *Palaeofalco richorum*.

The Quaternary avian carnivore guild in Australia was quite different compared to that of the present day. Fossil bones of accipitrids from various sites exhibit closer affinities with the Old World vultures suggesting accipitrid vultures inhabited in Australia. The fossilised femur, QM F1118, described by de Vis (1891b) as an eagle, in fact, shows more relationship to the Old World vultures. The humerus assigned to *Uroaetus brachialis*, can has been reassigned to *Aquila audax*. *Aviceda gracilis* (de Vis, 1905) was found to be an *Accipiter*. There was a greater diversity of large-sized accipitrids in Australia during the Pleistocene. *Woltsha australensis*, the type specimen a giant sternum, was a unique

accipitrid possessing characters from both the Old World vultures and the eagles. Two distal tibiotarsi from different localities are equal in size to the smaller members of *Harpagornis moorei*, the extinct giant eagle of New Zealand, but differ significantly in morphology to be considered a separate genus. The only associated material, named *Robustopternis marywaltersae*, was a large accipitrid showing greatest similarities to the Old World vultures and *Hamirostra melanosternon*. *Elanus scriptus*, found from Cooper Creek, Pleistocene deposits, is the oldest record for the genus in the world. *Aquila audax* extends back into the Pleistocene. No significant biogeographic changes have occurred for all extant taxa found as either fossils or subfossils during the Pleistocene or Holocene.

Abbreviations

Abbreviations used in this thesis are as follows:

Full title	Abbreviation
The Australian Museum, Sydney	AM
Field number, The Australian Museum, Sydney	AM F
The Australian Wildlife Collections, (C.S.I.R.O.), Canberra	ANWC
Flinders University, Adelaide	FU
Museum Victoria, Melbourne	MV
Ornithology, Museum Victoria, Melbourne	MV B
Ornithology (working), Museum Victoria, Melbourne	MV W
Museum of Vertebrate Zoology, University of California	MVZ
The Queensland Museum, Brisbane	QM F
The South Australian Museum, Adelaide	SAM
Palaeontology, The South Australian Museum, Adelaide	SAM P
Ornithology, The South Australian Museum, Adelaide	SAM B
The Western Australian Museum, Perth	WAM
Smithsonian Institution, National Museum of Natural History	USNM
Queen Victoria Museum, Launceston, Tasmanian	QVM
Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand	AV
Canterbury Museum, Christchurch, New Zealand	DM
Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, Programme and Abstracts (1997).	C.A.V.E.P.S.
Years before present	ybp
Millions of years before present	Ma

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Chapter 1: Introduction

Birds of prey are commonly referred to as raptors, from the Latin *raptor,* a robber, and *rapere*, to seize, which refers to the manner in which they capture their prey (Olsen, 1995). The Family Accipitridae is usually placed in the Order Falconiformes, although it has been placed by some in a separate Order, Accipitriformes. The taxonomic position of the Family Accipitridae itself and the members of the family are the subject of ongoing debate, which will be discussed further in this thesis.

The fossil record of the Family Accipitridae in Australia has not been studied comprehensively. Boles (1993) described a new species of hawk from the Riversleigh deposits. Prior to Boles (1993), de Vis contributed several papers on fossil accipitrids pre-1900. Since de Vis's time, more fossil material has been collected, but most has remained unstudied.

Aims of the study

Approximately 300 raptor species exist worldwide (Olsen, 1995). Brown and Amadon (1968) accepted 220 species and 60 genera in the Family Accipitridae, of which Australia supports 19 species (Christidis and Boles, 1994). Rich and van Tets (1982) and Baird (1996) briefly surveyed the described fossil taxa, but a detailed study of the fossil history has not been undertaken for Australia. In this study, I will examine the fossil history of the Family Accipitridae in Australia through Tertiary and Quaternary.

The aims of the study are to ascertain the taxonomic position of each fossil and to diagnose and describe in detail any fossils that represent species new to science. The systematic review will provide a basis for future studies of the stratigraphic order of the Accipitridae within Australia, to better understand their evolution and biogeography. An outline of the fossil history of the Family Accipitridae itself is included, to provide a context for the Australian accipitrid record.

More generally, this study contributes to the knowledge of the fossil record of birds, which in turn will aid in defining the phylogenetic relationships of birds (Brodkorb, 1971). Further, classification of the diversity of the Australian accipitrids in the past should lead to a better understanding of the origin and evolution of Australia's unique avifauna. It may also aid in understanding the biotic interchange between Australia and other parts of the world and changes in avifaunal distribution through time.

Contrary to Carl Sagan's (1995) opinion in *The Demon-Haunted World* that "Not every branch of science can foretell the future – paleontology can't – but many can with stunning accuracy", palaeontological research has significant potential to aid in conservation, as future predictions can be made based on understanding of the past. To determine the current conservation status of a species, knowledge of both the history and modern conditions of lineages is required (Archer *et al.,*1991). Archer (1991) noted that the Crown-of-Thorns starfish is an excellent example of the value of palaeontology to current conservation problems. Initially, the increased abundance of this predatory echinoderm was thought to result from human interference. It was not until Walbran *et al.* (1986) discovered a record of 4000 years of natural blooms of this predator in a core drilled from the reef that the pre-European population cycles of this animal were brought to light. What had been seen as a novel event was shown by palaeontological research to be part of a long-term phenomenon, something that standard ecological research cannot deal with.

The populations of many birds of prey have been affected by changes resulting from European settlement. Species such as the *Eyrthrotriorchis radiatus* (Red Goshawk) and *Lophoictinia isura* (Square-Tailed Kite) have decreased in numbers as a result of land clearance, while *Milvus migrans* (Black Kite) has increased its population in response to new food resources such as slaughterhouse waste and rabbits (Olsen, 1998). Increased knowledge of the past, evaluation of their history before the arrival of humans on the Australian continent, and, therefore, life cycles and the manner in which these species deal with change, could provide information useful to the conservation of birds of prey.

The Accipitridae

In this introductory Chapter, I discuss the taxonomy of the family Accipitridae, its worldwide fossil history, and describe previous work carried out on the Australian fossil accipitrids. I also highlight potential difficulties with this study.

The Accipitridae is the largest family of diurnal birds of prey, with a wide variety of diets and habitats being exploited. They use their talons for capturing prey and the hooked beak for tearing their prey apart (Olsen, 1995). Accipitrids' diets include fish, snakes, small and large mammals, and carrion. They may also rob conspecifics. They have acute vision, which aids in hunting; they are visual predators. The osteology of the Accipitridae is unique, and is diagnosed in Chapter Two.

Sexual dimorphism is common within the family, with the female being larger than the male. Baker-Gabb (1984) used wing length, exposed culmen, and weight of 20 of Australia's diurnal raptors, to determine degrees of sexual dimorphism. He found that all 20 species exhibited sexual dimorphism, but it was more marked in some than in others. The dimorphism, often referred to as reversed sexual dimorphism, is an important consideration when assessing the fossils of this family and determining species, as the extent of the dimorphism in some taxa is equivalent to species differences in other taxa. It may aid in identifying some of the fossils to sex, but where few bones of a new species exist, it is important to recognise this variation, as not all of the individuals of the species may be in the size range of the type specimen.

Taxonomy of the Family Accipitridae

Both the higher taxonomy of the Family Accipitridae and its infrafamilial taxonomy have been frequently revised by workers using different methods of analysis. There has been much disagreement between workers regarding the taxonomy of the Accipitridae. Such is the complexity of the relationships of the Accipitridae that researchers have even revised their own work by changing the placement of the family groups (Sibley and Ahlquist, 1972, 1990). The history of classification of the Old World raptors has been summarized by Sibley and Ahlquist (1972, 1990). Kemp and Crowe (1990) listed recent works containing information on the relationships between the birds of prey, and this will therefore not be repeated in such detail here.

In his much-cited classification of birds of the world, Wetmore (1960) placed all the diurnal birds of prey in the Order Falconiformes, including the following families:

Order Falconiformes
    Suborder Cathartae
        Superfamily Cathartoidea
            Family Cathartidae, (New World Vultures)
            Family Teratornithidae, (*Teratornis*, *Cathartornis* (fossils))
    Suborder Falcones
        Superfamily Sagittarioidea
            Family Sagittariidae, (Secretarybirds)
        Superfamily Falconoidea
            Family Accipitridae, (Hawks, Old World Vultures, Harriers and Eagles)
            Family Pandionidae, (Ospreys)
            Family Falconidae, (Falcons, Caracaras)

Sibley and Ahlquist (1972) studied the egg white protein patterns within the Falconiformes, within their larger study, and suggested the following higher classification:

Order Falconiformes
  Family Cathartidae
  Family Pandionidae
  Family Accipitridae
  Family Sagittariidae
  Family Falconidae

Later studies by Sibley and Ahlquist (1990), using data from many DNA-DNA hybridization experiments, again produced a classification of raptors that also differed from that of Wetmore (1960) and their earlier work (Sibley and Ahlquist, 1972). DNA-DNA hybridization assesses the degree of similarity between the genomic DNA of species, the rate and extent of the formation of artificial "hybrids" between DNA strands from a series of different taxa. Sibley and Ahlquist (1990) placed the osprey in a separate subfamily rather than a separate family, the Pandioninae in the Family Accipitridae. The New World Vultures, including the condors, were placed in a different infraorder, Infraorder Ciconiides, associated with the stork lineage rather than the accipitrids. The Sibley and Ahlquist (1990) classification is as follows:

Order Ciconiiformes
  Suborder Ciconii
    Infraorder Falconides
      Parvorder Accipitrida
        Family Accipitridae
          Subfamily Pandioninae (osprey)
          Subfamily Accipitrinae (hawks, eagles and kites)
        Family Sagittariidae (Secretarybirds)
      Parvorder Falconida
        Family Falconidae (falcons)
    Infraorder Ciconiides (storks, pelicans)
      Parvorder Ciconiida
        Superfamily Ciconioidea
          Family Ciconiidae
            Subfamily Cathartinae (New World vultures)

Osteology has been used as a tool to determine the relationships of the birds of prey. In England, Pycraft (1902) was one of the first to study the osteology of birds now included in the Order Falconiformes. Much later, Jollie (1976) carried out a detailed but idiosyncratic analysis of the osteology for the Order Falconiformes. He described distinct characters on particular bones for each of the families as a way of separating the families Cathartidae, Falconidae, Sagittariidae, and Accipitridae. Holdaway (1994) based an exploratory phylogenetic analysis of the genera of the Accipitridae on osteological characters, which placed the osprey in a separate family to the Accipitridae and explicitly separated the Falconidae (falcons) and the Sagittaridae (Secretarybird) from the Accipitridae. Holdaway's (1994) analysis is:

Order Ciconiiformes
    Family Pandionidae
    Family Accipitridae

Mourer-Chauviré (1991) described a unique taxon of fossil accipitrid, which she placed into a new family based on the unique articulation of the tibiotarsus and tarsometatarsus that allowed the leg to flex backwards as well as laterally and medially. Her classification also varies from most other classifications at the level of Order. The new family name is derived from the Egyptian falcon-headed god, Horus.

Her classification is:

Order Accipitriformes (Vieillot, 1816)
    Famille Horusornithidae

The taxonomic position of the Osprey, *Pandion haliaetus*, has been a source of disagreement between workers. Christidis and Boles (1994) in the most recent summary of the taxonomic literature of the Australian Family Accipitridae, included *Pandion haliaetus* in the Accipitridae. Others (Wetmore, 1960, Sibley and Ahlquist 1972) placed it in the monotypic family Pandionidae.

Taxonomy of the Australian accipitrids

Christidis and Boles (1994) give the most recent review of the taxonomy of the Australian accipitrids and this will not be repeated here in such detail. Amadon (1978) discussed the genera of Australian accipitrids, and suggested that the genera *Milvus* and *Haliastur* are doubtfully separable, as their separation is based only on the differences in tail shape and differences in the nostril. Christidis and Boles (1994), however, kept these two taxa separate, pending more detailed revision.

Amadon (1978) considered that the names *Circus approximans* and *C. spilonotus* refer to a single species within one superspecies of marsh harriers, whose name should be *Circus aeruginosus*. The superspecies included three other species of harriers. Christidis and Boles (1994) retained *C. approximans,* and *C. spilonotus* separately, and not as part of *C. aeruginosus*.

Amadon (1978) suggested that *Erythrotriorchis radiatus*, the Red Goshawk, possibly properly belonged in the genus *Accipiter*, rather than remaining a monotypic genus. He suggested this because of its similarity in proportions to accipiters, and further suggested that *Erythrotriorchis* may be more closely related to the Indonesian-Papuan radiation of *Accipiter*. Christidis and Boles (1994) maintained *Erythrotriorchis* as a distinct genus, but suggested *Erythrotriorchis*, *Hamirostra* and *Lophoictinia* should be a component of a larger revision of the Accipitridae.

Both the higher taxonomy of the Family Accipitridae and its infrafamilial taxonomy create ongoing debate and disagreement, and warrant further research in both understanding the higher relationships and the intrafamilial relationships. Biochemical studies help resolve debate regarding relationships within genera and the separation of taxa to either separate species or subspecies. Seibold *et al.* (1996) found that the Spanish Imperial Eagle, *Aquila* (*heliaca*) *adalberti*, differed enough, genetically, from *A. adalberti*, to be regarded as a separate species rather than remain a subspecies. This study has significant implications concerning the conservation status of the Spanish Imperial Eagle. Further osteological research would aid in identifying fossil taxa more readily and accurately, but, biochemical research can aid in differentiating between species and subspecies status, which may not be possible to determine through osteological research. However, due to the plastic nature of the members of the Accipitridae, with convergent evolution and parallel evolution apparent, understanding the taxonomy of the group will prove to be a challenging and perhaps ongoing task.

The Fossil Record of Accipitridae

To provide a basis for the discussion of the relationships of the Australian fossil accipitrids, the following is a brief review of the fossil record for the family Accipitridae first describing the oldest records, then outlining the record geographically. The record is obviously richer and more extensive than described in this review, not only because many important papers were unobtainable, but additionally because, as mentioned by Olson (1985), many significant collections of fossil raptors have not been examined, such as those in the American Museum of Natural History.

Earliest Accipitrids

Amongst the oldest members of the Family Accipitridae is the fossil of a small hawk found at the Messel fossil locality, western Germany, which is Eocene in age (49 Ma) (Peters, 1992). The species was described and named *Messelastur gratulator,* on the basis of two skulls and several vertebrae (Peters, 1994). A species of accipitrid recovered from the Early Eocene London Clay, Isle of Sheppey, Kent, was described by Harrison and Walker (1977) as a new species, *Parvigyps praecox.* The holotype is similar to the Old World vultures. At least three different species of accipitrids from Late Eocene to Early Oligocene deposits are known from France. *Palaeocircus cuvieri* is known from a metacarpus and four phalanges of the middle toe, *Aquilavus hypogaeus* is known from a femur, and *Aquilavus corroyi* was based on a right tarsometatarsus (Brodkorb, 1964). All of these birds were buzzard-like creatures, although they differed from the modern buzzards of the genus *Buteo* (Olsen, 1995). Shufeldt (1913) described three new American species of *Aquila*, one of which, *Aquila lydekkeri*, is said to have come from Eocene deposits (Lambrecht, 1933). However, *Aquila lydekkeri* was later studied by Wetmore (1933b), who found that the fossil tibiotarsus of *A. lydekkeri* was not from an eagle, but an owl and assigned it to a new species, *Protostrix lydekkeri.* Furthermore, Wetmore (1933b) suggested that the material described as *Aquila antiqua* and *Aquila ferox* by Shufeldt (1913) are more likely to be claws of edentate mammals. A single bone of a hawk is known from Late Eocene deposits in Mongolia, but the bone is too poorly preserved for a definite assignment to the family Accipitridae (Howard, 1950).

The fossil record for the Accipitridae was outlined by Brodkorb (1964), where he listed 64 palaeospecies for this family. Since 1964, additional species of accipitrids have been described, and established species have been discovered, in new sites of various ages and from several regions. Olson (1985) reviewed Brodkorb's (1964) list as part of a wider appraisal of the avian fossil record and its implications for systematics. Two taxa can be removed from Brodkorb (1964): *Foetopterus ambiguus* (based on the humerus of the extant goose *Chloephaga picta*) and *Lagopterus minutus*, which Olson stated shows a close resemblance to species in the genus *Polyborus*. Olson (1985) proposed that *Palaehierax gervaisii,* from Early Miocene deposits of France, shows more similarity to the extant *Gypohierax angolensis*, the Palm Nut Vulture, than to the Buteoninae, as was initially suggested.

North America

As a result of both suitable deposition and an increase in researchers in the field, the published fossil record for Accipitridae in North America is notably rich, and hence the North American record will be described in chronological order using the geological time periods.

Eocene 55 – 34 Mya

A nearly complete left carpometacarpus from Early Eocene and Late Oligocene deposits in North America has been suggested to be the oldest record for the family Accipitridae. However, this bone remains unnamed, as it is too damaged to identify to generic level (Cracraft, 1969).

Oligocene 34 – 24 Mya

An eagle, *Palaeoplancus sternbergi*, was found in Oligocene deposits in Niobrara County, Wyoming (Wetmore, 1933a). This eagle had a relatively small head, moderately developed wings, strong legs, and very long powerful toes capable of subduing active prey.

Miocene 24 –5 Mya

Wetmore and Case (1934) described a Miocene hawk, *Buteo grangeri*, which represents the oldest record of that genus in North America. Brodkorb (1956) described a new species of kite, *Proictinia floridana*, from Miocene deposits in Florida. It is known only from the distal portion of a left tarsometatarsus. Wetmore (1923, 1928, 1943) described at least nine new species of accipitrids from Nebraska, United States of America. Wetmore (1923) described seven new species of hawks from the Snake Creek beds, as follows:

Lower Pliocene	*Geranoaetus conterminus*
Upper Miocene	Buteoninae (indeterminate)
	Aquila species
	Buteo typhoius
	Geranoaetus contortus
Middle Miocene	*Urubitinga enecta*
Lower Miocene	*Proictinia effera*

Wetmore (1926) described a hawk, *Geranoaetus ales,* from Miocene beds in Nebraska, based on a complete right tarsometatarsus. Later, Wetmore (1936) described a new species of Old World Vulture, *Palaeoborus howardae*, from a distal end of a tarsometatarsus, found in the Nebraskan Miocene deposits. *Neophrontops vetustus*, an Old World Vulture from Stonehouse Draw Quarry, Sioux County, Nebraska, is based on a distal humerus (Wetmore, 1943). *Palaestur atavus*, a hawk from the Stenomylus Quarry, Nebraska, described by Wetmore (1943) from the distal end of a tarsometatarsus.

Two species of osprey (Family Pandionidae) have been described from Miocene deposits from North America, for this presently monotypic family. *Pandion lovensis* (Becker, 1985) from late Miocene deposit of Florida, appears to be the most primitive member of the genus. *Pandion homalopteron,* from Miocene deposits in California, is based on two nearly complete humeri and two partial ulnae and appear to have been larger than the average-sized extant Osprey (Warter, 1976).

Feduccia and Voorhies (1989) described a new species of hawk, convergent on the Secretarybird, *Sagittarius serpentarius,* from the Miocene in North America. *Apatosagittarius terrenus* is represented by a complete tarsometatarsus with associated phalanges. During the Miocene, the landscape of North America was dominated by savannas and grasslands, the typical habitat of today's living Secretarybird. Feduccia and Voorhies (1989) suggested that the similarity between the Secretarybird and *A. terrenus* was due to convergent evolution as *A. terrenus* was under strong selection pressures in ancient North American grassland communities.

Pliocene 5 – 1.8 Mya

Two large eagles have been described from the North American Pliocene (Emslie and Czaplewski, 1999). *Aquila bivia* was a large eagle, about 10-15% larger than the extant *A. chrysaetos*. *A. bivia* represents the first valid fossil species of this genus in North America (Emslie and Czaplewski, 1999). *Amplibuteo concordatus*, found in Florida, represents the earliest occurrence of *Amplibuteo* (Emslie and Czaplewski, 1999).

Pleistocene 1.8 Mya to 10,000 ybp

Many fossil eagles have been recovered from Rancho La Brea, a rich fossil deposit of Pleistocene age in the Los Angeles Basin. Not only have members of the family Accipitridae been recovered from there but also members of the families Cathartidae and Falconidae. Fossils have been collected from several tar pits in the area. The excellent preservation qualities of the tar have preserved fossils of this assemblage of birds in great abundance (Howard, 1962). A significant percentage of the avian assemblage is made up of the Order Falconiformes; the predatory birds were attracted to the pits to feed on dying animals, and carcasses already entrapped in the tar seeps. Fortunately for palaeontologists (but unfortunately for these birds!) they were only to perish themselves. Howard (1932) described eight species of eagles and eagle-like birds from these deposits, all from various genera including accipitrid vultures. The most spectacular birds of prey from this deposit were not accipitrids, but from the family Cathartidae, the giant vultures *Teratornis incredibilis* (Howard, 1952) and *T. merriami*. *T. merriami* was found to have a wingspan approximately four metres across (Howard, 1962), and amazingly *T. incredibilis* was about 41-43% larger than *T. merriami* (Howard, 1972).

Many accipitrids have been found in other Pleistocene deposits in North America (Brodkorb, 1964; Olson and James, 1991). Howard (1935) described a new species of eagle from a Quaternary cave in Nevada, *Spizaetus willetti*, known from only the distal end of a tarsometatarsus. Olson and James (1991) described 32 new species of non-passeriform birds from the Hawaiian Islands, including *Circus dossenus,* from Late Pleistocene sites on Molokai and Oahu. The specific name, *dossenus*, is Latin for a clown or a jester, without which "one cannot have a circus" (Olson and James, 1991). The authors thought that the name was particularly applicable because the species "initially fooled (them) as to its generic placement," being initially placed in *Accipiter*.

Old World vultures in North America

Several species of vultures with close relationships to the Old World vultures (Family Accipitridae) have been recorded from deposits in the New World (Feduccia, 1974; Rich, 1980). These birds are quite distinct from the New World vultures, family Cathartidae, which inhabit North America at present (Rich, 1980). The record of Old World vultures in North America extends from the Middle Miocene to the Pleistocene, with three genera of the subfamily Aegypiinae being represented. Compton (1935) described a new species of accipitrid vulture found in Early Pliocene deposits from the distal end of a humerus as *Neophrontops dakotensis*, placing the species in a genus described by Miller (1916) but with close affinities to the African genus *Neophron*. Howard (1932) also indicated this relationship between the genera and later (1966) thought it was markedly like *Neophron*. Feduccia (1974) described a new species of Old World Vulture, *Neophrontops slaughteri*, from Late Pliocene deposits in Idaho. Rich (1980) described a new species of "New World Vulture with Old World affinities", *Neophrontops ricardoensis*. Rich (1980) concluded that the North American gypaetines are polyphyletic, being derived independently from different accipitrid lineages and converging on a "vulture" body plan and not closely allied at the subfamily level to the Old World gypaetines.

The Caribbean

Many avian fossils have been reported from caves in the Bahamas. *Accipiter striatus velox* and *Titanohierax gloveralleni* (a giant hawk) have been found in Pleistocene deposits of the Bahamas (Olson and Hilgartner, 1982). Wetmore (1937) named *Calohierax quadratus*, from Quaternary deposits in Little Exuma Island in the Bahamas, based on a fragmentary tarsometatarsus. This species has now been referred to *Buteo lineatus* in light of new fossil material (Olson, 2000).

Great predatory birds inhabited Cuba in the Pleistocene. An exploration in July 1954 revealed fossil eagle bones larger than any living species of eagle (Arredondo, 1976). The species was named *Aquila borrasi* (Arredondo, 1970). However, Olson and Hilgartner (1982) state that the tarsometatarsus of *A. borrasi* is more gracile than in typical members of the genus *Aquila*. They suggest that this species is not referable to *Aquila*, and that it is more suitably placed within the genus *Titanohierax,* which includes the giant extinct hawk *T. gloveralleni*, described by Wetmore (1937).

South America

Tonni (1980) noted two accipitrids - *Cruschedula revola*, and *Climacarthrus incompletus* - from Early Oligocene deposits in Argentina. Members of the Accipitridae have been reported from Miocene deposits in Argentina: *Thegornis musculosus*, *T. debilis*, and *Badiostes patagonicus* (Tonni, 1980). Campbell (1979) described a new genus and species of accipitrid, *Miraquila terrestris*, from the Pleistocene Talara Tar Seep in northwestern Peru.

Africa

The Varswater Formation (Late Miocene - Early Pliocene, 3.5 - 7 million ybp) at Langebaanweg (Cape Provence), South Africa, yielded an extremely rich deposit of avian fossils with greater than 10,000 bird bones, from at least 61 different taxa being represented (Rich, 1980). Included in this deposit are the remains of a small and a medium-sized hawk, a large eagle, and a possible vulture (Rich, 1980). In addition to this fossil site, a Miocene site near the mouth of Orange River (Arrisdrift) in Nambia has yielded bones of a large eagle (Rich, 1980).

Various Pleistocene localities in Africa have produced accipitrid fossils (Vickers-Rich, 1974). The extant *Haliaeetus vociferoides* has been recovered from deposits in Ambolisatra, Madagascar, and Broken Hill, Zambia. *Aquila rapax* has been noted from Olduvai Gorge, Tanzania, and *Accipiter henstii* has been identified from the deposits of Antsirable, Madagascar (Vickers-Rich, 1974).

Arabia

Accipitrids including *Accipiter* cf. *gentilis*, *Aquila chrysaetos* and *Aquila* spp. (slightly larger than *Aquila pomarina*) have been discovered in the Middle Pleistocene Ubeidiya formation in the Jordan Rift Valley, Israel (Tchernov, 1980). Tchernov (1980) described a new species, *Milvus pygmaeus*, from an incomplete tarsometatarsus. *Accipiter nisus* is known from a Late Pleistocene deposit of Kebara Cave, Mount Carmel, Israel (Tchernov, 1962 as cited by Tchernov, 1980).

Europe

Fossils of falconiform have been noted from the Messel fossil locality, West Germany, which is of Middle Eocene (49 million ybp) age. One of the fossils represents a small hawk, and the other has been referred to the Polyborinae. However, the fossil is from an immature individual and is therefore difficult to classify (Peters, 1992). As previously mentioned, *Messelastur gradulator* was found at the Messel locality (Peters, 1994).

Middle Eocene beds in Hampshire, England, have yielded fossils of a new genus of kite, *Milvoides kempi* (Harrison and Walker, 1979). Mourer-Chauviré (1991) described a new family of accipitriforms, the Horusornithidae, based on the new species *Horusornis vianeyliaudae* from the Late Eocene of the locality La Bouffie, in the so-called "Phosphorites du Quercy". A similar form has been found in lower Oligocene deposits in the United States. The main characteristic of the family is the shape of the articulation of the tibiotarsus and tarsometatarsus, which may have allowed the leg to flex posteriorly as well as laterally and medially (Mourer-Chauviré, 1991).

The Early Miocene fossil locality of Saint-Gérand-le-Puy in central France has produced a rich diversity of avian fossils (Mourer-Chauviré, 1995). Five different taxa of accipitrids have been recognised from this site: *Aquilavus depredator*, *A. priscus*, *Milvus deperditus*, *Promilio incertus,* and *Palaeohierax gervaisii* (Mourer-Chauviré, 1995). Claws from the family Accipitridae have been found in Miocene deposits from Burdigalian fissure-fillings of Wintershof (West) in Bavaria (Ballmann, 1969). Ballmann (1969) suggested that this accipitrid would have been similar in size to the extant *Haliaeetus albicilla*, but its systematic position was difficult to determine. Species of *Buteo* (buzzards) have been described from Miocene beds in Europe. *B. pusillus* from Middle Miocene beds in Southern France was described on the basis of a right carpometacarpus (Ballmann, 1969a), and *B. spassovi* from an almost complete tibiotarsus found in Upper Miocene beds (about 7 Mya) from Southwest Bulgaria (Boev and Kovachev, 1999).

Accipitrids are known from the Pliocene deposits in Poland (Bochenski, 1989). The Rebielice Królewskie locality has yielded avian remains that were referred to the genus *Aquila* (Bochenski, 1989).

Various Pleistocene deposits in Europe have produced fossil accipitrids. *Accipiter gentilis* and *Aquila chrysaetos* have been identified from deposits in Poland (Bochenski, 1989). Mourer-Chauviré (1975) described a new subspecies of *Buteo rufinus,* (*B. rufinus jansoni*) from the Middle Pleistocene site of Saint-Estèven; it differs mostly in having a smaller tarsometatarsus. From Pleistocene beds in the Carpathian Basin, Jánossy (1980) listed 19 species of accipitrids among the avian species recorded. Accipitrids have also been found in Pleistocene cave-fillings of Mallorca, one of the Balearic Islands in the Mediterranean Sea (Mourer-Chauviré *et al.*, 1977). The species from the Mallorca caves include *Aquila chrysaetos*, *Accipiter nisus*, and *Aegypius monachus* (Mourer-Chauviré *et al.*, 1977).

Asia

Several species of accipitrids have been found in widespread Paleogene deposits of Asia. Wetmore (1934) assigned a coracoid that was deposited in Late Eocene deposits of Irdin Manha, China to the Falconiformes. Fossil accipitrids found in Early Oligocene deposits of Khoer Dzan (Kurochkin, 1976) included a small accipitrid and rather large femora similar to those of Aegypiinae but differing significantly from femora of the genera *Gyps*, *Aegypius,* and *Gypaetus*.

Accipitrids have been found in Middle Oligocene deposits from the sites at Kur Sai and Min Sai in Tchelkar Nura, north of Tengiz. In particular, *Aquilavus* sp. was found in the Middle Oligocene deposit of Kyzyl Kak, on the northern slope of the basin in Central Kazankhan, Southern Siberia (Kurochkin, 1976). However, Kurochkin (1976) suggested that this site is possibly older than Middle Oligocene judging from the mammalian fossils. Small birds of prey were collected from the Middle Oligocene deposit in Tatal Gol, Mongolia, which are suggested to belong to the genera *Gobihierax*, *Venerator*, and *Buteo* (Kurochkin, 1976).

In a review of the fossil birds of China, Japan, and Southeast Asia, Rich *et al.* (1986) noted that members of the family Accipitridae have been found from numerous sites of various ages in China. Conversely, the fossil record for the Accipitridae in Japan has only been discovered from Pleistocene localities. The fossil record for the Accipitridae in eastern Asia is significantly richer in species within the Pleistocene deposits than in earlier Tertiary deposits (Rich *et al.*, 1986). In China, birds of prey have been noted from Miocene deposits, Xiacaowan Formation, Sihong district, in Jiangsu Province. These fossils include a talon which has been placed in the genus *Aquila*, a cervical vertebra referred to the subfamily Accipitrinae and a tarsometatarsus which was stated to be similar in morphology to the genus *Aegypius* but slightly more primitive (Li *et al*., 1985). Li *et al.* (1985) suggested that the talon represents the earliest record of the genus *Aquila* in China. Hou (1984) described an accipitrid vulture, *Mioaegypius qui*, also from the Xiancaowan Formation.

Pacific Islands

Balouet and Olson (1989) described two new species of accipitrids: *Accipiter efficax* and *Accipiter quartus*. Both species were discovered from Holocene deposits in Pindai Cave, Nepoui Peninsula, on the western coast of New Caledonia. However, both of these species are questionable, as the proximal femoral foramen doubling varies individually and the "differences" in length are within the ranges of the living species (Holdaway, pers. comm.).

Accipiter has been recorded from deposits on Norfolk Island (Holdaway and Anderson, 2001). This will be discussed in this thesis in chapter nine.

New Zealand

The giant eagle of the Quaternary of New Zealand, *Harpagornis moorei*, was described by Haast (1872) based only on a femur, a rib and two ungual phalanges. Since then, many more bones and at least one complete skeleton of this species have been collected. Haast (1874) described a new species of eagle, *Harpagornis assimilis*. He suspected that *H. assimilis* was the smaller sex of a sexually dimorphic species and is a junior synonym of *H. moorei*. Holdaway (1990) later confirmed Haast's suspicion. The New Zealand species is much larger than the extant Wedge-tailed Eagle, *Aquila audax*, and would have been the main predator in New Zealand. Baird (1996) suggested that this species should be transformed to the genus *Aquila*, but Holdaway (1991) maintained *Harpagornis* on the basis of its osteological specializations for catching and manipulating large prey.

At least two other species of Accipitridae have been described from the New Zealand

Quaternary, *Circus eylesi* (Fordyce, 1996) (which may include more than two taxa) and *Haliaeetus australis* (Olson, 1984). However, *H. australis* is actually *H. chimaera* based on bones of Northern Hemisphere taxa mistakenly given a Chatham Island origin (Holdaway, pers. comm., Worthy and Holdaway, 2002).

Australia

The oldest accipitrids in Australia are recorded from Lake Palankarinna, South Australia, and Riversleigh, Queensland (Vickers-Rich, 1996). A large eagle is known from Alcoota, Northern Territory of Late Miocene age (Vickers-Rich, 1996); the tarsometatarsus is similar in size to that of a Wedge-tailed Eagle. The Pleistocene, however, is richer in accipitrids with many of the fossils recovered from cave deposits.

Much of the early work on the Australian fossil accipitrids was undertaken by de Vis in the late nineteenth and early twentieth century. In total, de Vis named a cuckoo-falcon (1905), two hawks (1905, 1911), and three eagles (1890, 1891b, 1905). De Vis completed significant initial work, for his time, in assessing the fossil birds. His resources were considerably limited in comparison to those available today. However, when his work was revised by van Tets and Vickers-Rich (1990), the cuckoo-falcon was suggested to be a goshawk. *Asturaetus furcillatus* named by de Vis as a hawk is actually a falcon, *Falco berigora* (Rich *et al.*, 1982). The material of *Palaeolestes gorei* (de Vis, 1911) was found not to have been a bird bone. *Taphaetus brachialis* and *Necrastur alacer*, both described by de Vis, need further study to determine their taxonomic significance. These two species are reviewed and discussed in Chapter Three.

More recently, Boles (1993) described a new Tertiary bird of prey from Riversleigh, northwestern Queensland. *Pengana robertbolesi* (Boles, 1993) is of Late Oligocene to Early Miocene age and is known at present from a distal end of a tibiotarsus, which differs from living species with similar features (*Geranospiza caerulescens* and *Polyboroides radiatus*) by being much larger. The distinct morphology would have allowed great flexibility between the tibiotarsus and the tarsometatarsus, as seen in the extant species *G. caerulescens* and *P. radiatus* to which it was compared (Boles, 1993). Very few accipitrid fossils of Tertiary age have been discovered from deposits in Australia. Those few fossils that have been discovered are discussed and described in Chapter Four.

A new undescribed species of accipitrid has been found in Green Waterhole cave, south-eastern South Australia which contains deposits between 125,000 and 15,000 years old (Baird, 1986). The material includes left and right ulnae, complete left and right radii, complete left and right carpometacarpi and a thoracic vertebra. These fossils are analyzed and discussed in detail in Chapter Seven. Further fossil material from Pleistocene localities include two giant tibiotarsi and a giant sternum, which are described and discussed in Chapters Five and Six respectively.

The fossil history of modern Australian accipitrids

Extant Australian genera have a varied fossil history. Some of the extant Australian genera with a cosmopolitan distribution extend back to the Miocene. *Milvus* extends back to the Early Miocene in Europe, *Hieraaetus,* and *Haliaeetus* have fossil records extending back into the Late Miocene in Europe. The fossil record of *Milvus*, *Haliaeetus* and *Hieraaetus* is relatively short in Australia extending back to the Holocene, and, therefore, they possibly arrived from the north, via Asia, relatively recently. *Aquila* had dispersed widely by the end of the Miocene, with fossils found in Late Miocene deposits in Europe, and is recorded from Miocene deposits in Asia. The fossil history of *Aquila* will be discussed further in Chapter Four.

The extant Australian avifauna lacks gypaetines, yet these managed to reach as far as India, and have a long history in Europe, Asia and North America. The gypaetines may have had a long history in Africa, as today Africa supports a high diversity of gypaetines. However, the African accipitrid fossil material is as yet relatively unstudied.

Table 1.1: Summary of the distribution in space and time of the Family Accipitridae. (note: there is no fossil record for SE Asia)

	Europe and Arabia	**Africa**	**North America**	**South America**	**Asia**	**Australia and the Pacific**
Lower Eocene	*Parvigyps praecox*					
Eocene	*Messelastur gratulator* *Milvoides kempi*					
Upper Eocene	*Palaeocircus cuvieri* *Aquilavus hypogaeus* *Aquilavus corroyi* *Horusornis vianeyliaudae*					
Lower Oligocene	*Palaeocircus cuveri* *Aquilavus hypogaeus* *Aquilavus corroyi*			*Climacarthrus incompletus* *Cruschedula revola*		
Oligocene			*Buteo grangeri* *Buteo fluviaticus* *Palaeoplancus sternbergi*		Aeqypiinae, *Aquilavus* sp. *Gobihierax* sp. *Venerator* sp. *Buteo* sp.	
Upper Oligocene			*Buteo antecursor*			
Lower Miocene	*Aquilavus depredator* *Aquilavus priscus* *Aquilavus bilinicus* *Milvus deperditus* *Promillo incertus* *Palaeohierax gervaisii*		*Buteo ales* *Palaeastur* *Miohierax stocki* *Promillio efferus* *Promillio floridanus* *Promillio epileus* *Promillio brodkorbi*			*Pengana robertbolesi*
Miocene		Large eagle	*Hypomorphnus enectus* *Palaeoborus rosatus* *Palaeoborus howardae* *Neophrontops vetustus*	*Thegornis musculosus* *Theogornis debilis* *Badiostes patagonicus*	*Aquila* sp. *Mioaegypius qui*	*Aquila* sp.
Upper Miocene	*Hieraaetus edwardsi* *Haliaeetus piscator* *Aquila delphinensis* *Aquila pennatoides* *Buteo spassovi*	Small hawk, medium hawk, large eagle, vulture	*Buteo typhoius* *Buteo contortus* *Palaeoborus umbrosus*			
Lower Pliocene			*Buteo dananus* *Buteo conterminus,* *Proictinia gilmorei,* *Neophrontops dakotensis*			
Pliocene	*Aquila* sp.		*Neophrontops dakotensis* *Neophrontops slaughteri* *Aquila bivia* *Amplibuteo concordatus*			*Hamirostra* sp.
Pleistocene	*Gyps melitensis* *Aquila chrysaetos* *Accipiter gentilis* *Milvus pygmaeus* *Accipiter nisu* *Buteo rufinus jansoni* *Aegypius monachus*	*Haliaeetus vociferoides* *Aquila rapax* *Accipiter henstii*	*Hypomorphnus sodalis* *Spizaetus pliogryps* *Neophrontops vallectoensis*	*Miraquila terrestris*		
Upper Pleistocene			*Spizaetus grinnelli* *Spizaetus willetti* *Buteogallus fragilis* *Buteogallus milleri* *Buteo lineatus* *Titanohierax gloveralleni* *Morphnus woodwardi* *Wetmoregyps daggetti* *Neophrontops americanus* *Neogyps errans* *Circus dossenus* *Accipiter striatus velox*	*Lagopterus minutus*,- Olson (1986) suggests this species is more closely related to *Polyborus.*		*Harpagornis moorei* *Circus eylesi* *Circus teauteensis* *Aquila audax* *Aquila brachialis* *Icthyophaga lacertosus* *Necrastus alacer*
Holocene						*Accipiter alphonsi* *Accipiter efficax* *Accipiter quartus*

Methods and Materials

There are many accipitrid fossils in museum collections throughout Australia. Fossils examined in this study were obtained on loan from the major museums in Australia. Collections in the following institutions were examined: Australian Museum (Sydney), Queensland Museum (Brisbane), Western Australian Museum (Perth), Museum Victoria, South Australian Museum, Department of Palaeontology Flinders University, and Division of Wildlife and Ecology C.S.I.R.O. (Canberra). At each institution, I searched the relevant palaeontology collections for fossils of Accipitridae. The specimens were then graciously loaned to me for study in Melbourne. Information such as field notes were compiled from each collection pertaining to the relevant sites. Additional material from Mair's Cave, in the Flinders Ranges was provided by Professor Pat Vickers-Rich of Monash University.

The fossils were then compared with material of living species from ornithological skeletal collections in the following institutions: Museum Victoria; South Australian Museum; Smithsonian Institution, Washington, DC; University of California, USA; Canterbury Museum, Christchurch, New Zealand; Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand. Each specimen of Australian fossil material attributed to the Accipitridae was compared to the corresponding element from a representative of each avian family (where a representative avian skeleton was available) to confirm its attribution to the Accipitridae. If its attribution was valid, it was then compared to appropriate material from various genera within the Accipitridae to ascertain its position within the family. The Australian fossil material was compared to relevant fossil material in the literature because a direct comparison was not possible for most palaeospecies.

In describing the bones, the terminology of Howard (1929) was used. Occasionally Baumel *et al.* (1979) terminology was used when the need for more detailed terminology of the avian skeleton was necessary, but, for the most part the Howard (1929) terminology was clear and allowed accurate descriptions. Fossil material, which has been described and measured with size comparisons of fossil accipitrids to extant accipitrids, were graphically presented using the program Microsoft Excel or Cricket. Bones were measured with Mitutoyo calipers. Measurements of the bones follows those of von den Dreisch (1976).

Photographs of the bones were taken by Steven Morton and Adrian Dyer at Monash

University. Adobe Photoshop was used to cut and paste the photographs into one plate. Adobe Canvas was used to draw locality maps.

Difficulties with the Study

Difficulties associated with this study include biases in the fossil record that usually result in fewer fossils of predators than prey being preserved. Furthermore, the fossil record of birds in Australia is poor when compared to that of other continents (Vickers-Rich and Baird, 1986). However, assembling all available material has provided a significant quantity of fossil accipitrid material, from a diverse range of localities of a range of geological ages.

Not all elements of avian bones have diagnostic features, so while it may be possible to identify a bone to family level, confident referral to generic level might not be possible. Amadon (1963) suggested that one difficulty with avian palaeontology is that most avian taxonomy has been based on traits of plumage, colour pattern, external anatomy, type of nest, eggs, and habits. Holdaway (1994) also cited this problem, noting that most classifications are primarily based on external morphology or biochemical characters (Sibley and Ahlquist, 1972, 1990). Amadon (1963) suggested that for fossils it would be more useful if genera were defined on the basis of their osteology. For the purpose of this study, osteological characters are used to distinguish variation between the genera of accipitrids.

Many specimens have been donated to the museums by enthusiastic amateur collectors, or are parts of old collections that were accompanied by limited data regarding collection locality and the stratigraphic position of the fossil. For specimens whose stratigraphic position was not available, an age range of the deposit from oldest to youngest is given. Dating the occurrence of a fossil at a site is difficult without knowledge of the stratigraphic position of the fossil. As many of the fossils are quite small and fragile, it is not possible to date the fossils themselves, even if it were likely that they were within the range of ^{14}C dating (less than 40,000 years).

An even greater difficulty was that locality information was not recorded for some specimens at the time of collection. Such material might not even be from Australia.

Where possible, a locality has been suggested based on the state of preservation and colour of the bone. However, such determination must remain subjective and suspect in the absence of other information.

There are severe problems in describing a new species on fragmentary fossil material. It has proven difficult to relate some of the palaeospecies to extant species, with such limited fossil material with which to work. The fossil material was not compared with all genera within the Accipitridae. Not all genera were available for comparison; some species are not housed in any collection, such as *Erythrotriorchis radiatus*, the Red Goshawk. Relevant skeletal specimens were borrowed for comparison from overseas collections, such as those of accipitrid vultures and forest eagles, but due to time and financial constraints it was not possible to visit these collections. Moreover, only one specimen was available for study of some of the extant species, which did not allow the examination of intraspecific variation. Intraspecific variation is particularly important in the Accipitridae, as reversed sexual dimorphism is exhibited in many species within the family, and could potentially affect the outcomes of graphs based on quantitative characters.

Cladistic computer analysis was not undertaken, as information from such fragmentary fossils and with only one third of the genera (and in most cases only one specimen per genera) within the Accipitridae for comparison, the results would have been highly questionable. Additionally, Wiley (1981) stated that at least a 3:1 feature:taxon ratio should be used. This ratio is not feasible for this study, as the fossil material, for the most part, is represented by isolated elements. Obtaining a ratio of 3:1 feature:taxon would not be possible from one bone if it was compared against the 60 genera within the Accipitridae. Further complicating the analysis is the varying usefulness of different elements as diagnostic tools.

Statistical analysis was not undertaken, except to provide the mean, as sample sizes were too small to provide a meaningful result. Often only one specimen of a genus was available; thus, statistical analysis was not possible.

Rich and van Tets (1982) noted the presence of birds of prey at Mammalon Hill and Lake Kanunka, and Vickers-Rich (1996) noted an accipitrid tarsometatarsus from Alcoota. Despite searching the collections mentioned in the Methods section, and examining the loan forms at Monash University, these specimens were never found.

Chapter 2: Diagnosis of the Accipitridae skeleton

Introduction

The following chapter is concerned with the diagnosis of the family Accipitridae skeletal elements described in this study. Only those elements that have been described as a new species in this thesis are diagnosed in this chapter. This study assesses numerous fossil specimens, so to avoid repetition, the diagnosis of the Accipitridae skeleton is separate from the descriptions. The terminology in English follows Howard (1929), and the Latin follows Baumel (1979). Osteological measurements follow von den Driesch (1976).

The Sternum

Diagnosis:

The accipitrid sternum can be distinguished from those of all other families in possessing the following suite of characteristics. The sternum has a rounded to sometimes slightly pointed carinal apex, which does not protrude proximally of the ventral manubrial spine. The manubrial spine is simple to modified (Jollie, 1976), with the ventral and dorsal manubrial spine always separate from one another. The ventral manubrial spine is often triangular in cross-section. The costal margin extends between 40% to 60% along the length of the sternum. The ventral and the dorsal lip of the coracoidal sulcus are separate, with a deep groove between the two. The coracoid pads are well developed (Jollie, 1976). The keel extends between 80% to 95% of the length of the sternal plate. The distal margin of the sternum is square, and may have none to one pair of fenestrae in the posterior margin of the sternum. The sternocoracoidal processes are rectangular to triangular, with the tip of each process forming a rounded point (Jollie, 1976). The sternal plate, as a whole, is very concave.

Comments on the distinction of the Accipitridae sternum from the sternum of other avian families

The accipitrid sternum can be distinguished from those of many families in which the carinal apex is hooked, such as Diomedeidae (albatross), Procellariidae (petrels), and Oceanitidae (diving petrels); the accipitrid carinal apex is rounded. The carinal apex does not project proximal to the ventral manubrial spine, unlike those in the families Anhingidae (snake birds), and the Phalacrocoracidae (cormorants), whose carinal apex protrudes proximal to the ventral manubrial spine.

The accipitrid sternum differ from the falconids (falcons), as the accipitrid dorsal manubrial spine is greatly reduced, whereas the falcon dorsal manubrial spine protrudes proximally. The ventral manubrial spine is separate from the dorsal manubrial spine in the Accipitridae, whereas birds in the families Megapodiidae (megapodes), Cracidae (curassows), Phasianidae (quails), Numididae (guineafowls), Meleagridiae (turkeys) and Turniecidae (bustard quails) whose ventral and dorsal manubrial spine are fused. The dorsal margin of the accipitrid sternum is square either lacking or with one pair of fenestrae, unlike birds whose sternal plate is greatly reduced by the presence of sternal notches, such as those in the families Pedionomidae (plain wanders), Rallidae (rails), Recurvirostridae (stilts), and the Strigidae (owls).

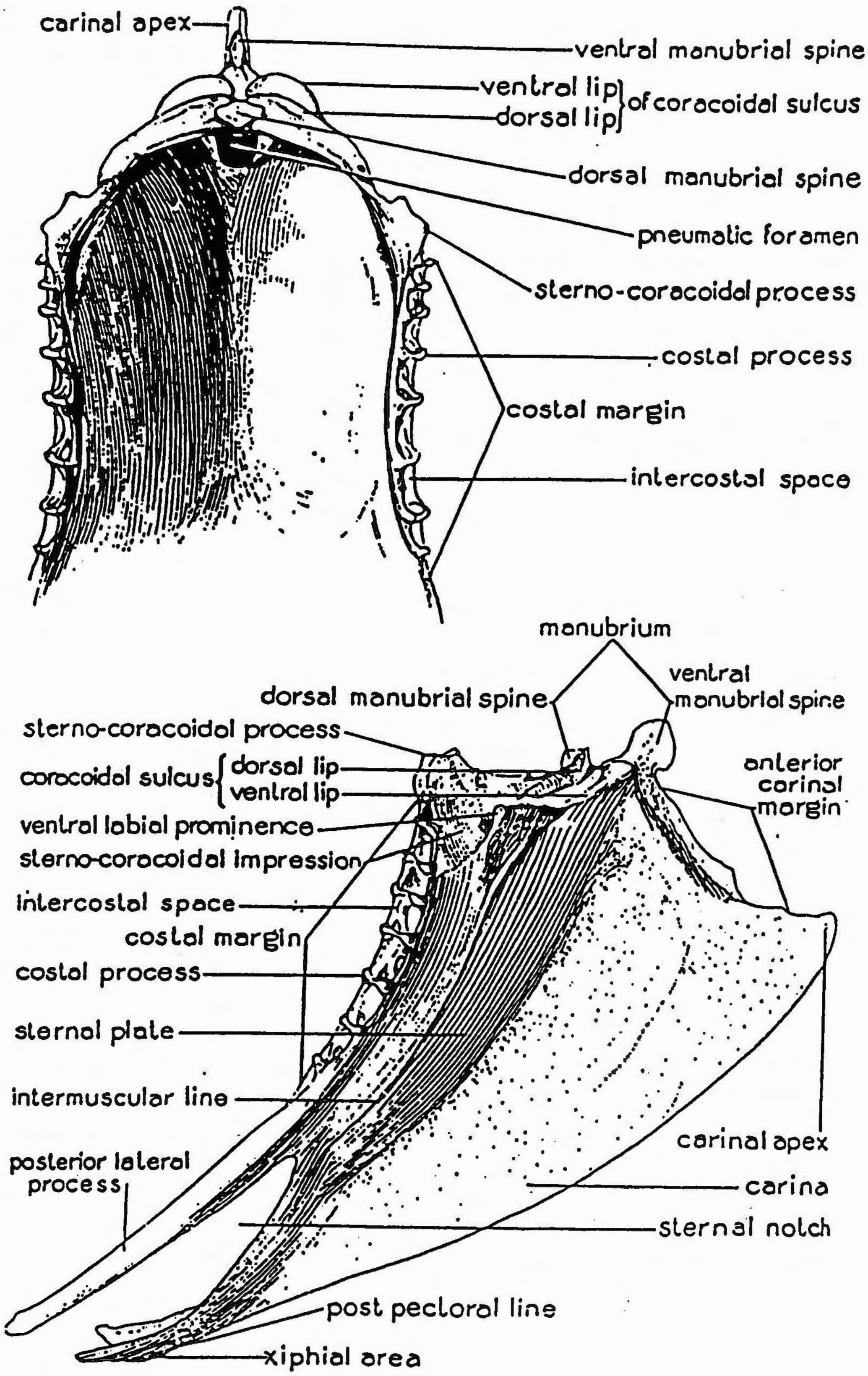


Figure 2.1: The sternum of *Chen hyperboreus*. Top: dorsal view. Bottom: lateral view (Howard, 1929)

The Humerus

Diagnosis:

The Accipitridae humerus can be distinguished from those of all other families in possessing the following suite of characteristics: the shaft is long, slender and cylindrical and is bent in a characteristic S-shape (in palmar view); the pneumatic foramen is deep (in anconal view); the deltoid crest is large, protrudes far laterally from the shaft, and forms a half diamond-shape; the ligamental furrow is shallow, the bicipitial surface is circular to oval and is marginally raised; the entepicondyle protrudes distally; and the impression of *brachialis anticus* is shallow and triangular to teardrop shaped.

Comments on the distinction of the Accipitridae humerus from the humerus of other avian families

The shaft of the humerus of accipitrids is bent in a rather characteristic S-shape. Dorso-ventral flexion as well as lateral flexion in the shaft of the humerus is common in many families of Aves, such as in the Meleagridiae (turkeys), Burhinidae (thick knees), Strigidae (owls) and the Tytonidae (barn owls). Numerous bird families posses a straight shaft, such as the Procellaridae (petrels) and the Scolopacidae (sandpipers).

In anconal view, the pneumatic foramen is deep compared with those in the Phoenicopteridae (flamingoes) and the Ardeidae (herons), and narrow when compared with members of the Falconidae (falcons). The deltoid crest is large, and projects far laterally from the shaft, unlike in many other families whose deltoid crest projects in a posterior direction, such as in the Burhinidae (thick knees) and Meropidae (bee eaters). The deltoid crest is shaped like a half diamond, with its edges more rounded than the pointed deltoid crest typical of the family Falconidae. In palmar view, the ligamental furrow is shallow compared with that in the family Cacatuidae (cockatoos); the Strigidae and the Tytonidae have slightly deeper ligamental furrows. The bicipital furrow is noticeably shallower in the Accipitridae than it is in the Falconidae

In palmar view, the entepicondyle protrudes distally; this feature is less pronounced in the Falconidae, Strigidae or the Tytonidae. In anconal view, the impression of *M. brachialis anticus* is triangular to teardrop in shape and shallow when compared with that in the Tytonidae and the Procellaridae.

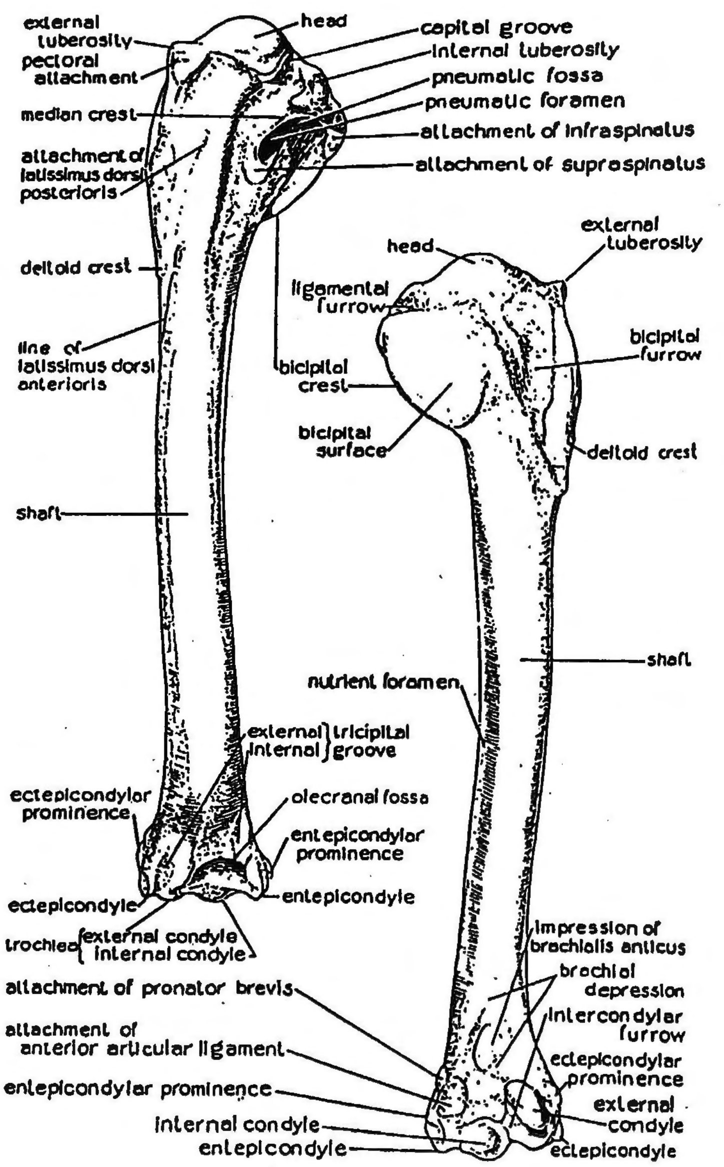


Figure 2.2: The humerus of *Chen hypoboreus*. Left: anconal view. Right: palmar view (Howard, 1929).

The Ulna

Diagnosis:

The accipitrid ulna can be distinguished from those of all other families in possessing the following combination of characters. The shaft is cylindrical and curved. At the proximal end, in palmar view, the internal cotyla is more deeply grooved and larger than the external cotyla. The internal cotyla is circular, slightly tapering and pointed to the palmar side. The external cotyla protrudes distally and forms a shelf over the proximal radial depression. The olecranon is highly raised, and square shaped in proximal view. The impression of *brachialis anticus* is of medium depth. The external condyle is circular. The internal condyle is small and rectangular. The ligamental attachment of carpal tuberosity is relatively small. Papillae are oval to square shape and are noticeably protruding, but not notches.

Comments on distinction of the Accipitridae ulna from the ulna of other avian families

The olecranon of the accipitrid ulna greatly protrudes proximally, which distinguishes it from other families whose olecranon is considerably less protruding, such as the Diomedeidae (albatrosses), Procellaridae (petrels), Podicipedidae (grebes), Spheniscidae (penguins), Pelecanidae (pelicans), Sulidae (boobies), Anhingidae (darters), and the Falconidae (falcons).

The internal cotyla is much larger and more deeply grooved than the external cotyla, unlike those in families whose internal cotyla and external cotyla are of similar size such as in families Rostratulidae (painted snipes), Charadriidae (plovers), Recurvirostridae (stilts), Scolopacidae (sandpipers), Glareolidae (plovers), and Chionididae (sheathbills).

The external cotyla protrudes distally, towards the palmar side, and thus forms an inverted L-shape, this distinguishes the accipitrid ulna from that of Strigidae (typical owls), and the

Tytonidae (barn owls) ulna, whose external cotyla does not protrude distally.The external condyle is circular, unlike that in the Alcedinidae (kingfishers), and the Momotidae (motmots), whose external condyle is more square-shaped. The ligamental attachment is rectangular and very reduced when compared with those in the families Cuculidae (cuckoos), Cacatuidae (cockatoos), Columbidae (pigeons), Lariidae (gulls), and Stercoraridae (skuas). The papillae are oval to circular and raised, but not as well raised as those in the families Ramphastidae (toucans), Picidae (woodpeckers), and Corvidae (crows), whose papillae are very prominent.

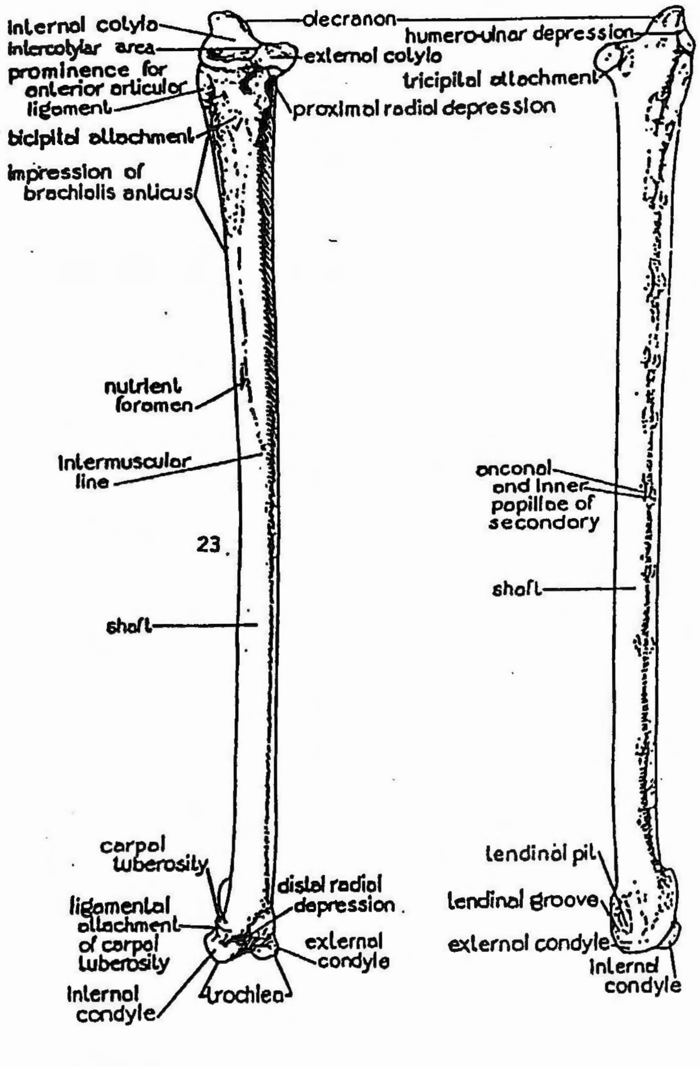


Figure 2.3: The ulna of *Aquila chrysaetos*. Left: palmar view. Right: anconal view (Howard, 1929)

The Radius

Diagnosis:

The accipitrid radius can be distinguished from those of all other bird families by the following combination of characteristics. The humeral cotyla is deep and oval to circular in proximal view. The shaft is curved, and has a relatively sharp ridge along the shaft in palmar view. The bicipital tubercle is oval to circular and is more distally located than in other bird families. The ligamental papillae are located on the external side of the bicipital tubercle. The scapho-lunar facet is pointed in anconal view. The ligamental prominence is highly raised. The ulnar depression is relatively deep, and the tendinal groove is deep.

Comparison of the Accipitridae radius to that of other bird families

The Accipitridae radius can be distinguished from many other bird families whose humeral cotyla is square, such as those in the families Pelecanidae (Pelicans), Ardeidae (herons), Phaethontidae (tropic birds), Phoenicopteridae (flamingoes), Anatidae (ducks), whereas the accipitrids have an oval to circular shaped humeral cotyla.

The ulnar depression is relatively deep in the Accipitridae, but in the Strigidae (owls), and the Tytonidae (barn owls) the ulnar depression is relatively shallow.

The ligamental prominence in the Accipitridae is highly raised as opposed to those in the families Cacatuidae (cockatoos), Podargidae (frogmouths), Aegothelidae (owlet-nightjars), Alcedinidae (kingfishers), Meropidae (bee-eaters), Capitonidae (barbets) and the Ramphastidae (toucans), whose ligamental prominence is reduced in comparison.

The tendinal groove is deep in the Accipitridae, whereas in the families Phasianidae (quails), Megapodiidae (megapodes), Numididae (guineafowls), Turnicidae (buttonquails), Burhinidae (thick knees), Rostratulidae (painted snipes), and the Recurvirostridae (stilts), the tendinal groove is relatively shallow.

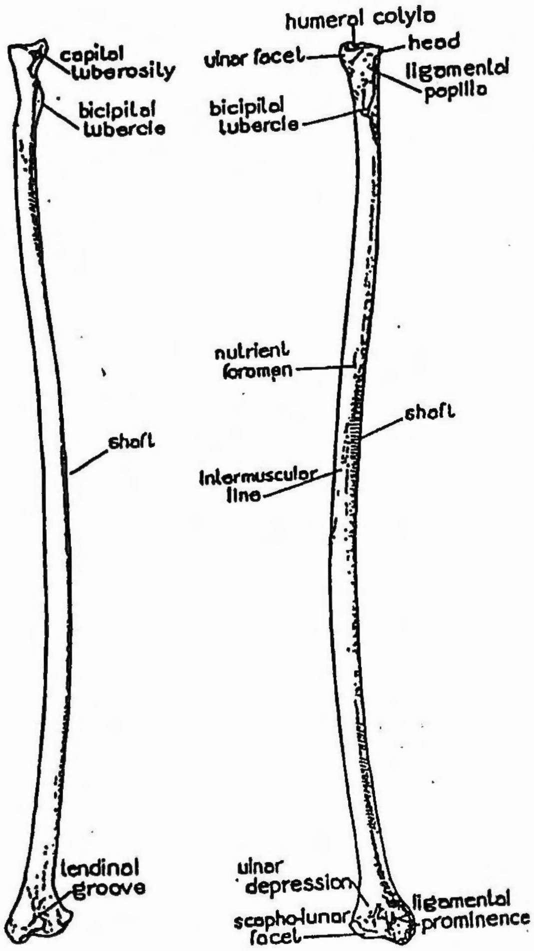


Figure 2.4: The radius of *Aquila chrysaetos*. Left: anconal view. Right: palmar view (Howard, 1929)

The Carpometacarpus

Diagnosis:

The accipitrid carpometacarpus can be distinguished from those of all other avian families in possessing the following suite of characteristics. The pisiform process is well raised and circular to oval in shape. The internal ligamental fossa is deep. The process of metacarpal I is large and at an angle of about 45° to the carpal trochlea. The extensor attachment is oval. The metacarpal II and III are relatively straight. Metacarpal III is flattened and is widest proximally, decreasing in width distally. The tendinal groove is deep, and curves around metacarpal II. The facet for digit III protrudes distally. The distal metacarpal symphysis is relatively short. The internal carpal trochlea does not merge with the external edge of metacarpal III. The intermetacarpal space is large.

Comments on the Accipitridae carpometacarpus from the carpometacarpus of other avian families

The accipitrid pisiform process is well raised and can be distinguished from those in the families Podicipedidae (grebes) and Pelecanoididae (diving petrels), whose pisiform process is relatively flat. Furthermore, the accipitrid pisiform process is circular to oval, whereas those in the families Sulidae (gannets) and Anhingidae (darters) are square to rectangular.

The facet for digit III does not protrude as far distally for those in the families Phaethontidae (tropicbirds), Ardeidae (herons), Phalacrocoracidae (comorants), Plataleidae (ibises), Phoenicopteridae (flamingoes) and Anatidae (ducks) as for those in the family Accipitridae. However the facet for digit III protrudes further distally for those in the family Corvidae (crows).

In the Accipitridae, the internal ligamental fossa is deep when compared to those in the families Cathartidae (New World vultures), Sagittaridae (Secretarybirds), Pandionidae (ospreys), Falconidae (falcons) and Megapodiidae (megapodes) whose internal ligamental fossa is shallow. The metacarpal III is relatively straight for those in the Accipitridae, whereas those in the families Meleagridiae (turkeys), Phasianidae (quails), and Turnicidae (button-quails) possess a very curved metacarpal III.

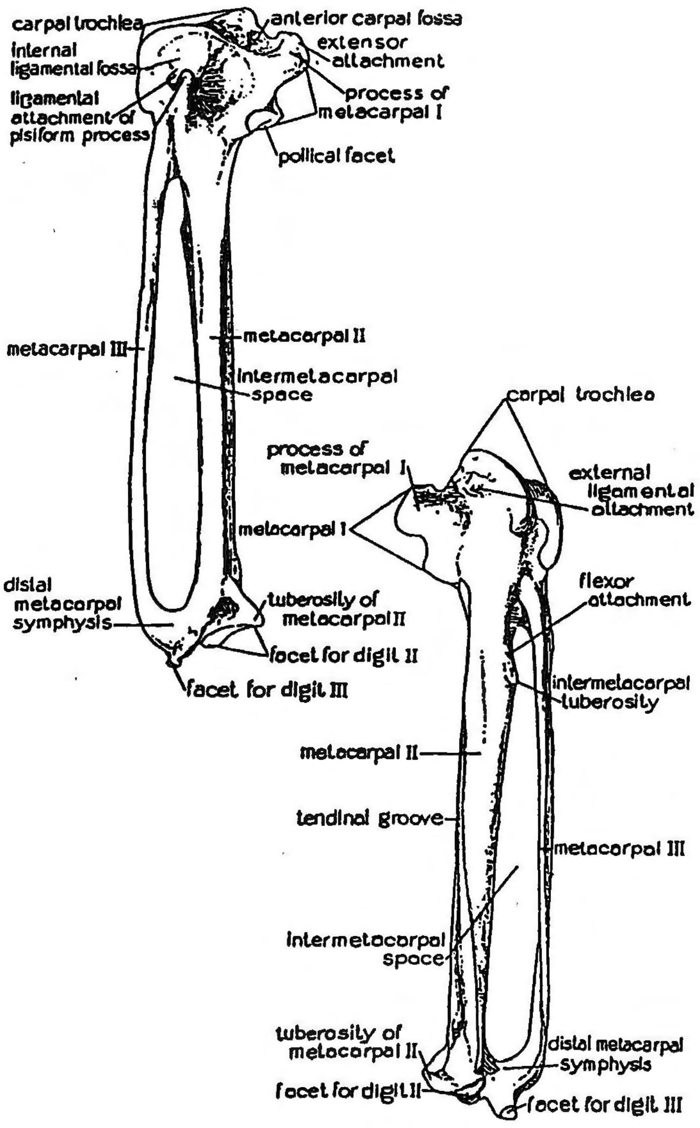


Figure 2.5: Carpometacarpus of *Aquila chrysaetos*. Top left: internal view. Bottom right: external view (Howard, 1929).

The Femur

Diagnosis:

The accipitrid femur can be distinguished from those of all other families in possessing the following combination of characters: the pit for *tibialis anticus* is deep, the popliteal area is of medium depth, the fibular groove is deep, the distal end of the fibular condyle extends proximally and externally to form a protruding notch which varies in size between the genera, the rotular groove is deep, the trochanter is slightly raised proximally and anteriorly, the head is circular and the attachment for the round ligament is relatively deep.

Comments on the distinction of the Accipitridae femur from other avian families

The trochanter of the Accipitridae femur is only slightly raised proximally and anteriorly, when compared with those in the families Megapodidae (megapodes), Phasianidae (quails), Numididae (guineafowls), and Meleagridiae (turkeys), whose trochanter is well raised proximally and anteriorly.

The distal end of the accipitrid femur has the most diagnostic features. It can be distinguished from those in the families Podicipedidae (grebes), Spheniscidae (penguins), Diomedeidae (albatrosses), Procellariidae (petrels), and Sulidae (boobies), whose pits for *tibilis anticus* are very shallow, whereas the accipitrids possess a relatively deep pit for *tibialis anticus*. The accipitrid femur has a relatively deep popliteal area compared with those in the families Anhingidae (darters), Phalacrocoracidae (cormorants), and the Phoenicopteridae (flamingoes), but it is not as deep as those in the families Sagittariidae (Secretarybirds), Falconidae (falcons) or the Pandionidae (ospreys). The fibular condyle has a unique feature not present in other avian families; the distal end of the fibular condyle extends proximally and externally to form a protruding notch, which can vary in size between the genera of the Accipitridae.

Anteriorly, the rotular groove is relatively deep when compared with those in the families Burhinidae (thick knees), Corvidae (crows), and the Ramphastidae (toucans).

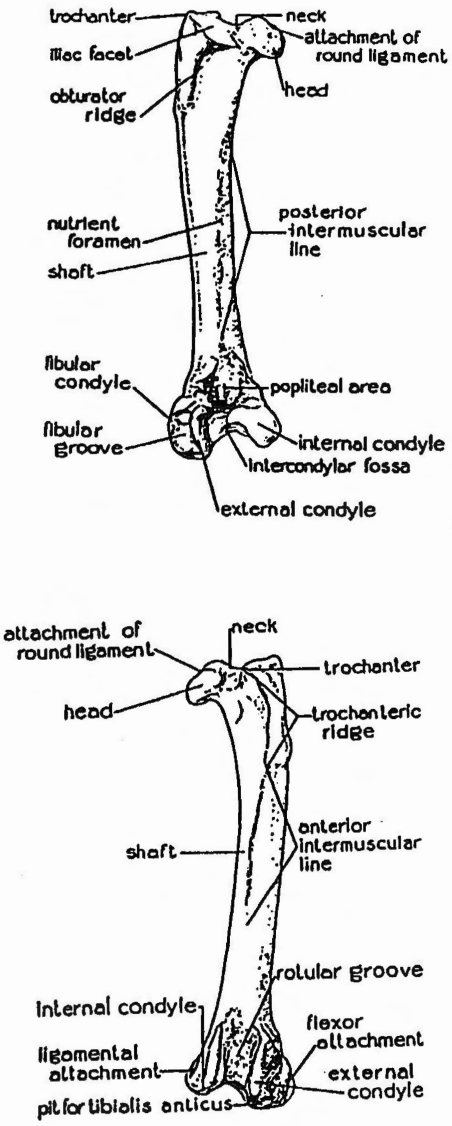


Figure 2.6: The femur of *Chen hyperboreus*. Top: posterior view. Bottom: anterior view (Howard, 1929).

The Tibiotarsus

Diagnosis:

The accipitrid tibiotarsus can be distinguished from those of all other families in possessing the following suite of characteristics: centrally, the shaft is cylindrical; distally, the shaft is anteroposteriorly flattened; the condyles protrude anteriorly at approximately equal distance; the tendinal groove is deep and begins medially along the shaft proximal of the supratendinal bridge; the supratendinal bridge forms an angle of about 40 degrees with the shaft (but can vary depending on the genus); the anterior intercondylar fossa is deep; the inner cnemial crest and the outer cnemial crest lie roughly at right angles to each other.

Comments on distinction of the Accipitridae tibiotarsus from the tibiotarsus of other avian families

The inner cnemial crest is relatively small compared with those in other families, such as the Podicipedidae (grebes) and the Diomedeidae (albatrosses), and protrudes anteriorly.

The internal ligamental prominance is circular and very prominent when compared to those in such families as the Rallidae (rails), the Pelicanidae (pelicans) and the Psittacidae (parrots). In the Accipitridae, the supratendinal bridge forms an angle of about 40 degrees with the shaft, but can vary depending on the genera. The supratendinal bridge is perpendicular to the shaft in families such as Diomedeidae and Pelecanidae. The condition of the supratendinal bridge being at an angle, rather than perpendicular, to the shaft is shared with those in the Anhingidae (darters), the Phalacrocoracidae (cormorants), the Columbidae (pigeons), the Pandionidae (Osprey), the Cathartidae (New World Vultures), and the Sagittaridae (Secretarybirds).

The anterior intercondylar fossa is relatively deep when compared with the families Megapodiidae (megapodes) and the Otididae (bustards). The posterior intercondylar sulcus is of medium depth when compared with the Pandionidae, whose posterior intercondylar sulcus is deeper, or the Diomedidae, whose members possess a relatively shallow posterior intercondylar sulcus.

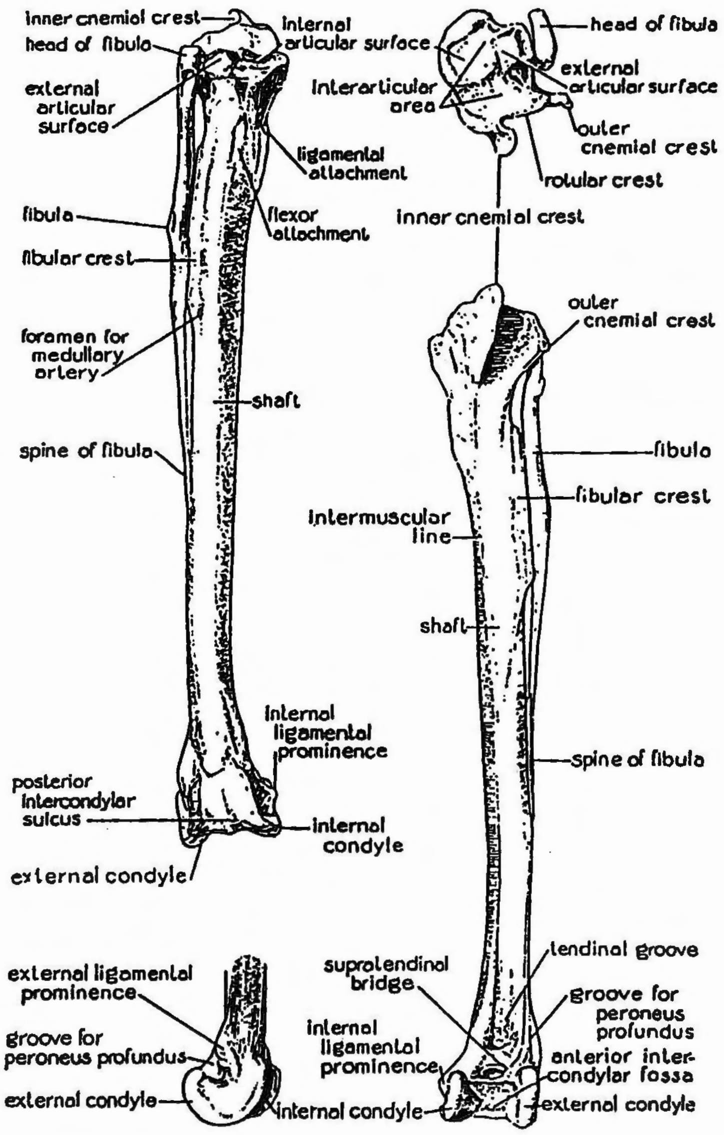


Figure 2.7: The tibiotarsus and fibula of *Chen hyperboreus*. Top left: posterior view. Top right: proximal end. Bottom left: distal end. Bottom right: anterior view (Howard, 1929).

The Tarsometatarsus

Diagnosis:

The tarsometatarsus of accipitrids can be distinguished from that of all other avian families in possessing the following suite of characters: trochleae II, III and IV all protrude at equal lengths distally (in anterior view); trochleae II and IV curve caudally so that in distal view they are arranged in a semicircle; the distal foramen is of medium size; the internal cotyla is slightly deeper than the outer cotyla; there are two distinct calcaneal ridges on the hypotarsus, that border and define a broad, open tendinal canal; there is no shelf between the two hypotarsal ridges; the inner hypotarsal ridge is longer than the outer (except in accipitrid vultures, where the ridges are of equal to subequal length); and the posterior metatarsal groove is deep and broad, so that the shaft of the bone has a V to U shaped cross-section with the posterior surface excavated.

Comments on the comparison of the Accipitridae tarsometatarsus to the tarasometatarsus of other avian families

The tarsometatarsus of the family Accipitridae can vary from being a long slender bone, for example *Circus* sp., to a more thickset bone like those of the genera *Aquila*, *Pithecophaga*, or *Gyps* to name a few. The shaft is often triangular in cross section, as it has a deep posterior metatarsal groove.

At the distal end of the tarsometatarsus, trochleae II, III, and IV all protrude at equal lengths distally (in anterior view), unlike those in families such as the Diomedeidae (albatrosses), Phoenicopteridae (flamingoes), and the Anatidae (ducks and swans), whose trochlea II is much shorter than trochleae III and IV. In the distal view, of the distal end, trochleae II and IV curve caudally so that in distal view they are arranged in a semicircle, unlike those in the family Ardeidae (herons) whose trochleae do not curve at all. The wings of trochleae II and

IV extend posteriorly in the family Strigidae (typical owls) and the Tytonidae (barn owls), to form a semi circle, like the Accipitridae, but the two owl families form more complete circles than in the Accipitridae. The distal foramen is of medium size when compared to those in the family Pandionidae (osprey), whose distal foramen is large, or the family Falconidae (falcons), whose distal foramen is small and often possess two distal foramen. The inner calcaneal ridge of hypotarsus is longer than the outer calcaneal ridge of hypotarsus, with the exception of the accipitrid vultures, in which the ridges are of equal to subequal length. This differs significantly from the condition in the Falconidae, whose internal calcaneal ridge of hypotarsus extends 3/4 of the length of the posterior side of the shaft of the tarsometatarsus.

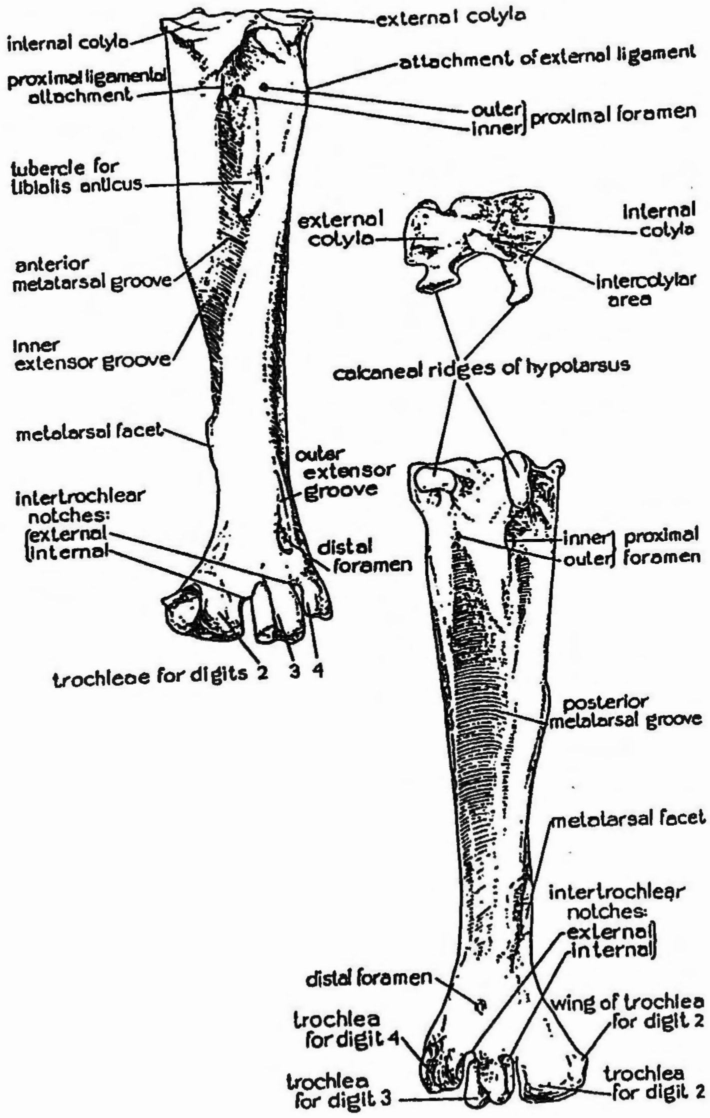


Figure 2.8: The tarsometatarsus of *Aquila chrysaetos*. Top left: anterior view. Top right: proximal end, proximal view. Bottom right: posterior view (Howard, 1929).

Ungual phalanx I

Diagnosis:

The ungual phalanx I of accipitrids can be distinguished from that of all other avian families in possessing the following suite of characters: curved (vultures) to highly curved (eagles); top surface rounded (*corpus phalanges*); flat underneath (*sulcus neurovascular*); highly pointed apex; fossa on both sides of the *tuberculum flexorium*; *tuberculum flexorium* bulbous, greatly protruding, and posteriorly pinched; and deep *cotyla articularis* which tends to be narrower proximally than distally.

Chapter 3: Revision of de Vis's work

Introduction

C.W. de Vis completed substantial work identifying and naming many of the fossil birds of Australia. His work was undertaken in the late 1800s and early 1900s when the comparative skeletal collection of extant birds was not as extensive or as easily available as today. For many species, only one specimen was available for comparison (van Tets and Vickers-Rich, 1990). With such a collection, it would have been impossible to realistically assess for intraspecific variation. Within the Family Accipitridae it is particularly important to assess this variation, as reverse sexual dimorphism is displayed in many species, and it has been the cause of misidentification of fossil taxa in the past. This was the case for *Harpagornis assimilis,* originally thought to be a separate species from *H. moorei* owing to its smaller size, but now classified as smaller members of *H. moorei* (Holdaway, 1990). De Vis's work on the fossil birds has since been reexamined by van Tets and Vickers-Rich (1990), who found that many of the fossil birds identified by de Vis are referable to modern species. They assessed the accipitrid material and found one of the hawks, *Asturaetus furcillatus* (QM F5509) to be, in fact, a falcon, *Falco berigora* (Rich *et al*, 1982). They suggested that a cuckoo-falcon described by de Vis (1905), *Baza gracilis*, is an *Accipiter* sp. Other accipitrids are mentioned, but the authors noted that the two specimens are currently under study. Van Tets has since died and Vickers-Rich is no longer working on this material, thus these specimens are examined and discussed below.

Specimen no.	Element	Species name as given by de Vis
QM F5510	humerus	*Aviceda gracilis*
QM F1117	distal humerus	*Taphaetus brachialis* (originally *Aquila brachialis*)
QM F1118	femur	*Taphaetus brachialis* (reassigned to *T. lacertosus* (de Vis, 1905) and then to *Icthyophaga lacertosus* (van Tets, 1974))
QM F1136	proximal humerus	*Necraster alacer*
QM F5552	distal ulna	*Necraster alacer*

Review of *Aviceda gracilis*

De Vis (1905) described a cuckoo-falcon, *Baza gracilis*, from a distal humerus (QM F5510). Van Tets and Vickers-Rich (1990) suggested this specimen is more likely an *Accipiter* sp. *Baza* (Hodgson, 1837) is a junior synonym of *Aviceda* (Swainson, 1837). *Baza gracilis* (De Vis, 1905) is not a member of the genus *Aviceda*, as *Aviceda subcristatus* possess the following characters which are not seen in QM F5510:

1) a deeper brachial depression
2) slightly more robust shaft
3) the deltoid crest extends straight out palmarly from the shaft (rather than pointing out to the side as is the case for QM F5510)
4) entepicondyle protrudes no further distally than the internal condyle.

I agree with van Tets and Vickers-Rich (1990) that QM F5510 is an *Accipiter* sp. as both the fossil and *Accipiter* share the following characters:

1) a shallow brachial depression,
2) the entepicondyle protrudes further distally than the internal condyle,
3) the shaft is gracile and curved,
4) direction of the initial protrusion of the deltoid crest.

QM F5510 is not likely *A. cirrhocephalus* as QM F5510 is significantly larger. QM F5510 is similar in size and morphology to *A. fasciatus* or *A. novaehollandiae*, but there is no significant difference between the humerus of these two species that would allow the fossil to be assigned to either species (Table 3.1), particularly as the distal end of the fossil is not entirely complete.

Table 3.1: Measurements (in millimeters) of the humerus of *Accipiter novaehollandiae*, *A. fasciatus*, and QM F5510.

Species	No.	Distal width	Breadth of shaft	Length to distal end of deltoid creast
Fossil	QM F5510	12.9	5.7	43.1
A. novaehollandiae	MV W 6123	13.1	5.3	44.1
A. novaehollandiae	MV B 12804	16.3	7.1	52.4
A. novaehollandiae	MV W 5988	15.8	6.5	53.4
A. novaehollandiae	MV B 20155	16.2	6.8	55.0
A. fasciatus	MV W 6657	12.5	5.6	42.3
A. fasciatus	MV W 6647	15.2	6.6	51.7
A. fasciatus	MV W 6872	14.5	6.2	45.7
A. fasciatus	MV W 9967	14.1	5.9	46.8

Review of *Taphaetus brachialis*

Introduction

De Vis (1890) first noted and named a new palaeospecies of eagle from Queensland based on a distal humerus, QM F1117 which he placed in a new species *Uroaetus brachialis. Uroaetus* is a junior synonym of *Aquila*. Later, de Vis (1891) described QM F1118, a fossilized femur, as an eagle, he noted that the femur was quite distinct from recent genera. De Vis assigned the femur to a new genus, *Taphaetus*, "in allusion to its appearance among the disentombed remains of its contemporaries" (de Vis, 1891). Additionally, he referred QM F1117 to *Taphaetus*, removing it from *Uroaetus brachialis,* on the basis that it was doubtful that two "species of eagles existed in practically the same habitat" (de Vis, 1891). De Vis retained the species name *brachialis*, and assigned QM F1117 and QM F1118 to *Taphaetus brachialis*. Later, de Vis (1905) restored the humerus (QM F1117) *brachialis* to *Uroaetus*, and created a new species, *Taphaetus lacertosus*, based on a second humerus and quadrate and included the femur, QM F1118, to this new species. In a review of de Vis's work, van Tets (1974) noted that the type species of *Taphaetus* is *brachialis* and that de Vis was incorrect in retaining it only for his new species, *lacertosus*. Van Tets (1974) suggested that *lacertosus* should be placed in the genus *Icthyophaga*, and he selected the humerus (QM F5507) of '*Taphaetus*' *lacertosus* de Vis 1905 as the lectotype. The material assigned to *lacertosus*, the second humerus and quadrate were not available for study. However, QM F1117 and QM F1118 were available for study. After examination and comparison of the fossils, QM F1117 and QM F1118, to various accipitrids, it is apparent that these two specimens are not members of the same species or even genus.

QM F1118: femur

While collecting specimens for this project at C.S.I.R.O., Department of Wildlife and Ecology, in Canberra, I was fortunately allowed to dig through boxes of notes belonging to the late Gerry van Tets. There I found unpublished notes regarding QM F1118 written by Gerry van Tets and Pat Vickers-Rich. They suggest that QM F1118 resembles the femora of Old World Vultures, and differs from those of eagles by having:

Point 1) an anterior-dorsally expanded trochanter,

Point 2) a transversely more extensive "flat saddle" between the trochanter and the head,

Point 3) a more horizontally oriented proximal articular surface that forms a right angle where it meets the trochanter,

Point 4) a very small pnuematic foramen on the anterior surface of the trochanter,

Point 5) a more anteriorly placed and more highly curved long ligamental depression on the anterior part of the trochanter,

Point 6) an oblique scar, at the distal end of the shaft in posterior view, running towards the internal condyle.

Method

QM F1118 was compared to the following femoral casts of Old World Vultures that were available for this study: *Gyps fulvus*, *Gypaetus barbatus*, *Torgos tracheliotus*, *Sarcogyps calvus*, *Gypohierax angolensis* and *Neophron percnopterus*. All other specimens used for comparison are real bones from extant taxa. The description points for the Old World Vulture by van Tets and Vickers-Rich are considered and examined. However, as multiple specimens of Old World Vultures were not available, assessing for intraspecific variation was not possible.

Discussion

Point 1

Van Tets and Vickers-Rich suggested that the Old World vultures and QM F1118 share an anterior-dorsally expanded trochanter. Howard (1932) noted a similar character, stating the vulturid character of the femur is the presence of a short, flaring trochanteric ridge. In eagles, the trochanter is long and less flared. The ratio of the length of the femur to the width of the trochanter were obtained by measuring the length of the femur from the proximal point of the trochanter to the fibular condyle and dividing this number by the width of the trochanter (Table 3.2). It was found that there is considerable variation within *Aquila audax* as to the degree of flaring of the trochanter (Table 3.2). While *Aquila* and *Haliaeetus* possess a less flared trochanter when compared to the Old World Vultures, QM F1118 could easily fit within the range of variation of *A. audax* and *H. leucogaster*. However, the trochanter of QM F1118 is slightly abraded, which affects the results and makes accurate description difficult. To assess the variation in the degree of flaring, a larger sample size of Old World vultures is needed. While there seems to be a general pattern for the Old World Vultures to possess a more anterior-dorsally expanded trochanter, point one is a not useful character for diagnosis in this case. The ratio of the length of the femur to the width of the trochanter in the fossil fits within the range of *A. audax* and it fits within the ratio of the Palm-Nut Vulture, *Gypohierax angolensis*.

Table 3.2: Analysis of point one, used to describe QM F1118 as a member of the Old World Vultures by van Tets and Vickers-Rich.

Species	**Length of the femur : width of the trochanter**
Fossil QM F1118	**5.08**
Gyps fulvus	4.11
Gypaetus barbatus	4.51
Torgos tracheliotus	3.90
Sarcogyps calvus	3.88
Gypohierax angolensis	5.22
Neophron percnopterus	4.25
Aquila audax (n=27)	**6.23 (max)** **4.42 (min)** **5.13 (mean)**
Aquila chrysaetos	5.21 5.28
Aquila bonnelli	6.19 5.92
Haliaeetus leugocaster	5.66 5.07 5.12 5.94 5.63
H. leucocephalus	4.91 5.25

Point 2

Van Tets and Vickers-Rich suggested that QM F1118 and the Old World vultures possess a transversely more extensive "flat saddle" between the trochanter and the head. The proximal width of the femur and the width behind the head (in proximal view) were measured, and the first measurement was divided by the second to give a ratio of the two measurements to determine the validity of this point (Table 3.3). The ratio of the proximal width of the femur to the width behind the head in the fossil QM F1118 was 2.23. The Old World Vultures had a lower ratio compared to the eagles. The highest ratio of the proximal width of the femur to the width behind the head for the Old World Vultures was 2.35 for *Gypohierax angolensis*, and the lowest eagle ratio of the proximal width of the femur to the width behind the head was 2.39 for *Haliaeetus leucogaster*. In regards to this character, QM F1118 corresponds with the Old World vultures.

Table 3.3: Ratio of the proximal width of the femur to the width behind the head to the femur

Species	*n*=	Ratio of proximal width to width behind head
Fossil QM F1118	1	2.23
Gyps fulvus	2	Minimum = 2.05 mean =2.21 maximum = 2.36
Gypaetus barbatus	1	2.30
Torgos tracheliotus	1	2.26
Sarcogyps calvus	1	2.15
Gypohierax angolensis	1	2.35
Neophron percnopterus	1	2.16
Aquila audax	15	Minimum = 2.48 mean = 2.63 maximum = 2.80
Aquila chrysaetos	1	2.45
Aquila bonnelli	1	2.53
Haliaeetus leugocaster	3	Minimum = 2.39 mean = 2.46 maximum = 2.53
Haliaeetus leucocephalus	1	2.54

Point 3

The Old World Vultures and QM F1118 possess a more horizontally oriented proximal articular surface that forms a right angle when it meets the trochanter, while the eagles possess a more angular surface.

Point 4

The Old World vultures and QM F1118 possess a small pneumatic foramen, while *Aquila* and *Haliaeetus* possess a large pneumatic foramen.

Point 5

In regards to point five, QM F1118 possesses a more anteriorly placed and more highly curved long ligamental depression on the anterior part of the trochanter compared to *Aquila audax* and *Haliaeetus leucogaster*, but this feature is not as obvious in the Old World vultures examined in this study. Therefore, this character does not appear to be diagnostic for the Old World vultures.

Point 6

All *Aquila audax*, *A. chrysaetos* and *A. bonnelli* specimens examined possess a scar that runs towards the external condyle. *Haliaeetus leucogaster* possess a circular scar. Only QM F1118 and Old World Vultures possess a scar that runs towards the internal condyle.

In addition to the above points, the head of the femur appears wider in the Old World Vultures when compared to that of the eagles. QM F1118 possesses a wide head, and fits in with the Old World Vultures (Table 3.4).

Table 3.4: Ratio of length of femur (proximal end of trochanter to proximal end of internal fibular condyle)/width of head for large accipitrids.

Species	**Ratio**
Fossil QM F1118	8.20
Gyps fulvus	8.07
Gypaetus barbatus	8.87
Torgos tracheliotus	7.92
Sarcogyps calvus	8.01
Gypohierax angolensis	8.93
Neophron percnopterus	7.48
Aquila audax (n=27)	**Minimum:** 8.87, **mean:** 9.62, **maximum:** 10.42
Aquila chrysaetos	9.79 9.58
Aquila bonnelli	10.39 10.24
Haliaeetus leucocephalus	9.39 9.52
Haliaeetus leucogaster	**minimum:** 8.97, **maximum:** 9.50

QM F1117: humerus

Van Tets and Vickers-Rich evaluated QM F1117, a fossil humerus de Vis (1890) originally identified as an eagle and named *Uroaetus brachialis*, which he later placed in a new genera *Taphaetus* (de Vis, 1891) and then back into *Uroaetus* (1905). Van Tets and Vickers-Rich examined a large sample of *Aquila audax*, and found that the characters de Vis (1890) used to distinguish QM F1117 as a separate species occurred in members of *A. audax,* if variation was taken into account. Therefore, de Vis's characters are not useful in diagnosing a new species. Additionally, van Tets and Vickers-Rich noted the following: "QM F1117 clearly differs from the humeri of Old World vultures and resembles those of eagles, by the ectepicondylar prominence being flattened and not rounded, and by the distal end being relatively not as deep."

After examination of a large sample of *Aquila audax*, I agree with the findings of van Tets and Vickers-Rich. Additionally, QM F1117 is more likely to be a member of *A. audax* and not *Haliaeetus leucogaster*. QM F1117 is similar in size and shape to both eagles, but the following character states are shared by *A. audax* and QM F1117 and not seen in *H. leucogaster*:

1) In palmar view, there is a greater degree of excavation at the distal end of the intercondylar furrow.
2) *A. audax* has a shallow olecranal fossa, whereas *H. leucogaster* has a deeper olecranal fossa.

Conclusion

QM F1117 should be re-assigned to *A. audax*. QM F1117 is probably not associated with the femur QM F1118, as QM F1117 clearly differs from the Old World vultures and agrees with *A. audax*. Therefore, the name *Uroaetus brachialis* becomes a junior synonmy of *A.*

audax. Van Tets (1974) pointed out that the type-species of *Taphaetus* is *brachialis*, therefore this genus also becomes a junior synonmy of *A. audax*.

Van Tets (1974) reassigned *Taphaetus lacertosus* to *Icthyophaga lacertosus*, to which the femur QM F1118 was assigned, but is not part of the type material for the species. Therefore, *Icthyophaga lacertosus* remains a valid species, with QM F5507 as the lectotype, and QM F1118 can be removed from *I. lacertosus* as it can be distinguished from the eagles it was compared to and allied with the Old World vultures. As a consequence, QM F1118 should be placed in a new genus and species. This will be the subject of further research and a new genus and species will be established when the work is published.

Review of *Necraster alacer*

De Vis (1892) assigned two specimens to *Necraster alacer*, QM F1136 and QM F5552, a proximal humerus and a distal ulna respectively. De Vis designated the proximal humerus as the type specimen of *N. alacer*, assigning it to the family Accipitridae owing to the shape of the ligamental furrow having "a certain crude resemblance to the footstep of a horse trotting on soft clay". De Vis stated the generic traits as the sub-tuberous pneumatic foramen being small, round, and thick walled, the tunnel into which it opens proceeds uninterrupted into the substance of the bone. He suggested the strong differences in characters compared with modern genera did not allow for "any decided opinions as to the bird's relationships with recent genera", but that it may be most like *Hieraaetus morphnoides* (Little Eagle).

Necraster alacer differs significantly in size and morphology from modern Australian accipitrids. Both the humerus and ulna of *Necraster alacer* are considerably smaller than those of *Aquila audax* and *Haliaeetus leucogaster*, but larger than those of *Hieraaetus morphnoides* and *Hamirostra melanosternon*. De Vis described the pneumatic foramen as considerably thick walled and proceeding uninterrupted; this feature was not seen in other accipitrids in this study. Additionally the external tuberosity is smooth and does not project like a flat oval surface as is the case for *Aquila audax*, *Haliaeetus leucogaster*, *Hamirostra melanosternon*, and *Hieraaetus morphnoides*. I suggest that *Necraster alacer* differs enough from extant Australian accipitrids to represent a distinct taxon, and that the diagnosis and name as proposed by de Vis (1892) remain valid. For a more detailed study, *Necraster alacer* could be compared to other members of the Accipitridae. However, the fossil material is very fragmentary, the proximal end of the humerus and distal end of an ulna, and have limited value for diagnosis, which restricts the interpretation and understanding of its relationships.

Chapter 4: Tertiary Accipitrid Fossil Material in Australia

Introduction

The Tertiary fossil record for the Family Accipitridae in Australia is extremely poor, with *Pengana robertbolesi* (Boles, 1993) the only named species from the Australian Tertiary. Vickers-Rich (1996) noted a large eagle tarsometatarsus (UCMP 70089) from Alcoota, Late Miocene in age, but, unfortunately, it could not be located in the collections visited for this study. The following accipitrid fossils from Australian Tertiary localities are discussed in this chapter:

Locality	Epoch	Age	Element
Bullock Creek, NT	Miocene	5-11mya	distal humerus
Alcoota, NT	Late Miocene	5-11mya	claw, distal ulna
Ringtail Site, Riversleigh, Qld	Mid to E. Late Miocene	9-12mya	two claws
White Hunter Site, Riversleigh, Qld	L.Oligo		distal femur
Chinchilla, SE Qld	Pliocene	1.5-3mya	carpometacarpus

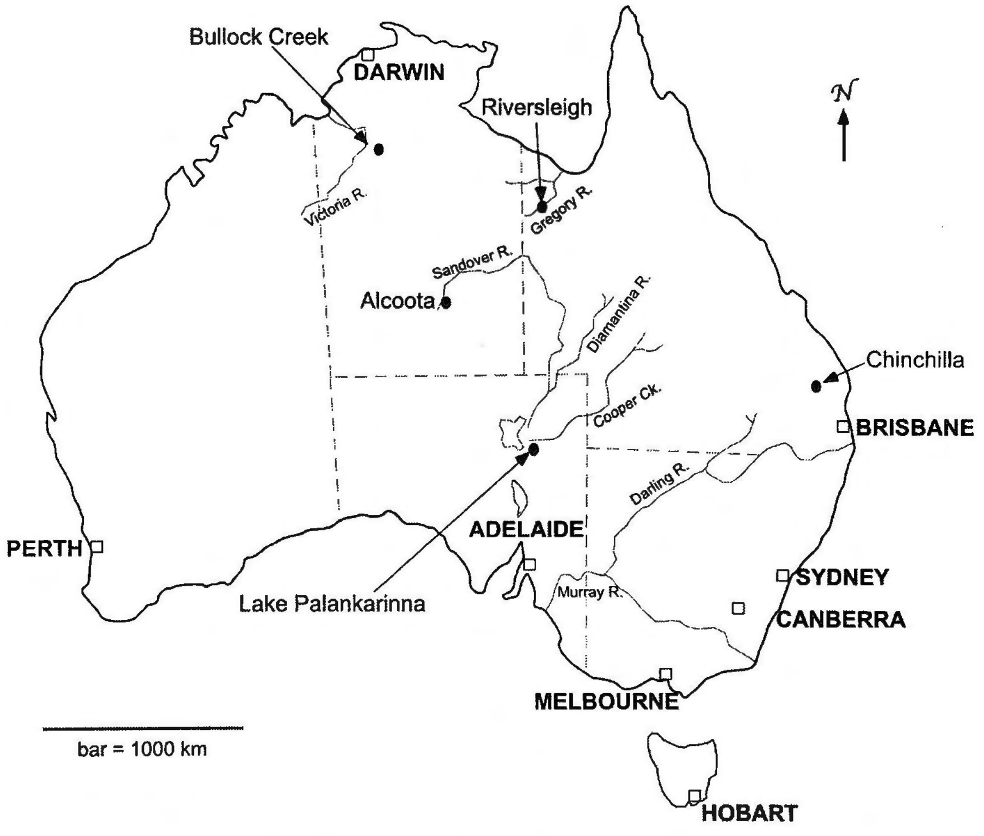


Figure 4.1: Tertiary localities producing fossil accipitrids (Accipitridae) and falconids (Falconidae) in Australia

A distal tarsometatarsus from Steve's Site, Lake Palankarinna, South Australia, originally thought to be an accipitrid, has been found to represent a falconid. Although the fossil is not a member of the family Accipitridae, it will be briefly discussed due to its palaeobiogeographical significance in representing the oldest record of the family Falconidae in Australia.

Bullock Creek, NT

Family Accipitridae (Vieillot 1816)

Aquila bullockensis **sp. nov.**

Etymology: Bullock Creek is the type locality, and 'ensis' (Latin) means 'belonging to'.

Holotype: distal end of humerus (right), QVM:2000:GFV:154. The holotype is held in the palaeontology collections in the Queen Victoria Museum, Launceston, Tasmanian.

Locality and stratigraphy: Bin 23, Bullock Creek (Figure 4.1)

Age: Mid-Miocene, 5-11mya

Diagnosis to *Aquila*: The Bullock Creek humerus has a closer resemblance to *Aquila* than to *Haliaeetus* due to the following characters:

1) The olecranal fossa is shallower in the Bullock Creek accipitrid and *A. audax, A. chrysaetos* and *A. bonnellii* compared to *H. leucogaster* and *H. leucocephalus,* which have a deeper and a more defined fossa (Plate 4.1).
2) A deep circular pit is present proximal of the attachment of anterior articular ligament in the fossil and *A. audax*, *A. chrysaetos* and *A. bonnellii.* The pit is slightly shallower and a less defined circle in *H. leucogaster* and *H. leucocephalus.*
3) In palmar view, the distal area of the intercondylar furrow is excavated in the fossil and *A. audax*, *A. chrysaetos*, (not visible in the specimen of *A. bonnellii*) but not in *H. leucogaster* and *H. leucocephalus* (Plate 4.2).

4) The entepicondyle, in lateral view, is round and protruding in *A. audax, A. chrysaetos, A. bonnellii* and the fossil. In *Haliaeetus,* the entepcondyle has a less rounded base and does not project as far.
5) *Haliaeetus* has a wider shaft to distal width ratio compared to *Aquila* and the Bullock Creek fossil (Figure 4.2).

Diagnosis: Compared to other members of *Aquila, Aquila bullockensis* is characterised by the combination of the following characters: attachment of anterior articular ligament is flat, the scar proximal of the ectepicondylar prominence has a rugose surface, the external tricipital groove is narrower and deep, one pit is present along with a second scar on the ectepicondyle, and the ectepicondylar prominence is less projecting.

Description

The distal end of the humerus remains, with the shaft broken above the impression of *brachialis anticus*. In lateral view, the shaft is antero-posteriorly curved. The impression of *brachialis anticus* is round and deep distally, and pointed proximally. The attachment of anterior articular ligament is flat compared to *Aquila audax,* in which it appears like a protruding shelf. The intercondylar furrow is deep, narrow, and distally excavated in palmar view. The ectepicondylar prominence protrudes only slightly compared to *Aquila audax* and *Haliaeetus leucogaster*. Two pits are present on the entepicondyle, one is deeper and circular. A single pit is present on the ectepicondyle. A round, deep pit lies proximal to the entepicondylar prominence in palmar view. In anconal view, the internal tricipital groove is shallow and wide. The external tricipital groove is narrow, with both sides of the groove at equal height in distal view. The olecranal fossa is shallow. In anconal view, the entepicondyle is bulbous, extending laterally from the shaft (Plate 4.1 and 4.2).

Measurements

Distal width 27.7 mm; width of shaft proximal to ectepicondylar prominence 18.5 mm; greatest width of brachial depression 9.4 mm; distal depth 14.1 mm.

Comparative material

Not all members of the Accipitridae were available for comparison, but, future studies could incorporate comparison of the fossil humerus to other accipitrids, in particular other eagles. The following species were used for comparison in this study: *Gyps fulvus, Neophron percnopterus, Aquila audax, Aquila chrysaetos, Aquila bonnelli, Haliaeetus leucogaster, Haliaeetus leucocephalus, Hieraaetus morphnoides,* and *Pandion haliaetus.*

Discussion

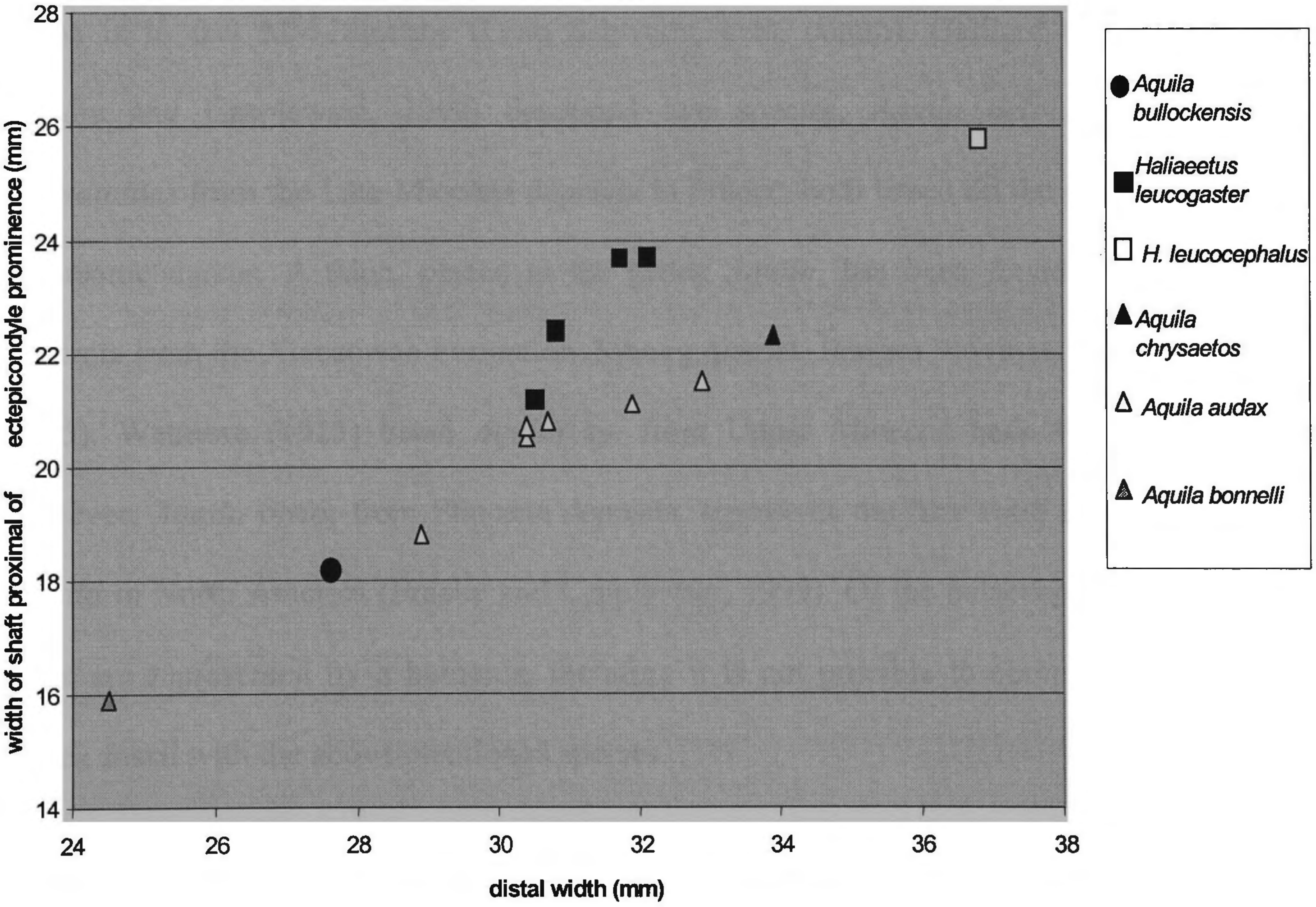
The Bullock Creek humerus can be distinguished from that of the Old World vultures. Old World vultures possess; a deeper brachial depression, the entepicondyle is less bulbous compared to eagles, and have a relatively more narrow external condyle than the Bullock Creek specimen.

The Bullock Creek humerus can be distinguished from *Aquila audax, A. chrysaetos* and *A. bonnellii* by the following features:

1) Attachment of anterior articular ligament is flat in the fossil, but a raised shelf in *A. audax, A. chrysaetos* and *A. bonnellii.*
2) In *A. audax* and *A. chrysaetos* the scar proximal of the ectepicondylar prominence is a linear scar nearly perpendicular to the long axis of the shaft. A rugose surface is present in the fossil.

3) The external tricipital groove is narrower and deeper than in *A. audax* and *A. chrysaetos*. The condition in *A. bonnellii* is similar to the fossil, however, this may be size related.
4) Double pit present on the ectepicondyle in *A. audax*, and *A. chrysaetos.* In the fossil and *A. bonnellii* only one pit is present and a second scar is observed.
5) The ectepicondylar prominence is less projecting in the fossil than in *A. audax, A. chrysaetos* and *A. bonnellii.*
6) The fossil is smaller than *A. audax* and *A. chrysaetos* specimens, but larger than *A. bonnellii* (Figure 4.2). However, as the Accipitridae display sexual dimorphism, size is not useful in distinguishing between taxa, and the fossil is only slightly smaller than the smallest individuals of *A. audax*.

Figure 4.2: Width of the shaft of the Bullock Creek humerus compared to extant eagles



Fossil History of *Aquila*

The genus *Aquila* was originally suggested to extend back into the Late Eocene to Early Oligocene in France by Milne-Edwards (1892, 1871, cited by Lambrecht, 1933), who described numerous palaeospecies, *Aquila hypogaea*, *A. depredator*, and *A. priscus*. Lambrecht (1933) assigned these species to a new genus, *Aquilavus*, and diagnosed the genus by stating that this group comprises all of the (so far) described Palaeogene vulture-like birds of prey remains of the European Palaeogene. Lambrecht (1933), however, did not provide a diagnosis based on the morphology of the bones, nor did he outline how these fossils differ significantly enough from *Aquila* to be assigned to a new genus. Regardless of this, a direct comparison with the fossil from Bullock Creek is not possible, as *Aquilavus* is not represented by a humerus.

A. bullockensis, if appropriately placed within *Aquila*, would represent the oldest record of the genus *Aquila* in Australia, and possibly the oldest in the world if the Bullock Creek fauna is in fact Mid-Miocene (Leah Schwarts, pers. comm). Gaillard (1938, cited by Emslie and Czaplewski, 1999) described two species, *Aquila delphinensis* and *A. pennatoides* from the Late Miocene deposits in France, both based on the proximal end of a tarsometatarsus. A talon, placed in the genus *Aquila*, has been found from Miocene deposits from the Xiacaowan Formation, Sihong district, Jiangsu Province, China (Li *et al.* 1985). Wetmore (1923) listed *Aquila* sp. from Upper Miocene beds from Snake Pit, however, *Aquila bivia*, from Pliocene deposits, represents the first valid fossil species of *Aquila* in North America (Emslie and Czaplewski, 1999). Of the palaeospecies of *Aquila*, none are represented by a humerus, therefore it is not possible to compare the Bullock Creek fossil with the above mentioned species.

Aquila bullockensis can be distinguished from the extant species *A. audax, A. chrysaetos* and *A. bonnellii* on the basis of morphological and size differences relevant to all three, and therefore is assigned to a new species. Not all species of *Aquila* or all genera of eagles have been available for this study, however, the fossil seems most appropriately placed within the genus *Aquila*, rather than assigning the fossil to a new genus. Future studies could involve comparisons with other members of *Aquila* and other accipitrids. Whether *A. bullockensis* represents an ancestor to *A. audax* is a matter for speculation with such limited fossil material.

Alcoota, Northern Territory

Material: ungual phalanx QMF 39556 (Plate 4.3), distal ulna QMF 7047.

Locality and stratigraphy: Alcoota (Figure 4.1)

Age: Miocene, 7-9 million years old

Diagnosis (ungual phalanx): see Chapter Two.

Description

Gracile, highly curved, typical of large active predators within the Accipitridae. *Tuberculum flexorium* deep, circular in lateral view and highly laterally compressed; *cotyla articularis* is triangular and is considerably wider distally than proximally, fossa not visible on either side of the tubercle, and the apex is missing (Plate 4.3).

Measurements: Ungual phalanx QMF 39556: length 30.4 mm; flexor depth 15.4 mm; depth of cotyla articularis 9.7 mm.

Discussion

The distal ulna is poorly preserved, with the external and internal condyle abraded. This specimen is similar in size to both *Aquila audax* and *Haliaeetus leugocaster*, but diagnosis of the fossil to generic level is not possible due to its poor state of preservation. It does, however, provide evidence that large accipitrids were present during the Miocene period in Australia.

The fossil claw is most likely from an actively hunting accipitrid, rather than a vulturine accipitrid, due to the high degree of curvature and the depth of the tubercle compared with the length of the claw. The claw may be from digit I or II, indicated by the shape of the *cotyla articularis* being significantly broader distally as compared to the condition in phalanges III and IV. If this claw is, indeed, from digit I or II, this bird may have been significantly smaller than *Aquila audax* or *Haliaeetus leucogaster,* assuming the claw to body-size ratio remains the same. The claw is slightly larger than those of *Hieraaetus morphnoides*. No other accipitrid examined in this study possesses a highly laterally compressed tubercle. The claw could belong to a unique species of accipitrid, but without more fossil material, diagnosis to genus is not possible.

Ringtail Site, Riversleigh, Queensland

Material: two claws; QMF 30311, QMF 31600 (Plate 4.3)

Locality and stratigraphy: Ringtail site, Riversleigh, Qld (Figure 4.1)

Age: Middle to Early Late Miocene, 9-12 million years ago

Diagnosis (ungual phalanx I): as above for the Alcoota specimen.

Description

QM F30311: The claw is curved as is typical of large active predators within the Accipitridae; the *tuberculum flexorium* is deep, wide and robust; the *cotyla articularis* is triangular; deep fossa are present on both sides of the *tuberculum flexorium*; and the apex is missing.

QM F31600: The claw is highly curved as is typical of large active predators within the Accipitridae; the *tuberculum flexorium* is deep, wide and robust; the *cotyla articularis* is triangular and is considerably wider distally than proximally; fossa are present on both sides of the *tuberculum flexorium*; small fossa are present on both sides of the *cotyla articularis*, and the apex is missing.

Measurements:

Specimen	Length (apex missing)	Flexor depth	Depth of cotyla articularis	Degrees of arch angle (tip missing, measurement should be larger if the claw is complete)
QM F30311	29.5 mm	17.1 mm	9.2 mm	89°
QM F31600	32.0 mm	16.8 mm	9.9 mm	95°

Discussion:

The claws are likely members of the Family Accipitridae. These claws can be distinguished from those of Strigiformes, as they possess a square *cotyla articularis*, not triangular as for accipitrids (Walter Boles pers. comm.).

These claws are likely to belong to the same taxon because they are very similar in size and morphology. The main difference between the claws is due to them being from different positions on the foot of the bird. Determining which number claw they are proves difficult with only isolated claws. However, in *Aquila audax*, and to a lesser degree in *Haliaeetus leucogaster*, the ungual phalanx of digit I has a broader distal base of the *cotyla articularis* compared to that of ungual phalanx of digit II. The ungual phalanx of digit III is square. Based on these differences, QM F31600 may represent an ungual phalanx from digit I as it has a broader *cotyla articularis* distally when compared to QM F30311, which may be from digit II.

The claws differ from *Haliaeetus,* as these fossil claws have a proximal projection on the *cotyla articularis*, which is not present in *Haliaeetus leucogaster*. In *H. leucogaster*, a shelf is present under the *cotyla articularis*, which is not present in the fossil.

The claws are unlikely to be related to *Aquila audax*, although they both possess a proximal projection on the *cotyla articularis*, the angle of projection of the tubercle varies between them. In distal view, the tubercle appears more pinched in *Aquila audax* with a ridge present running towards the *cotyla articularis*. Although the fossils differ substantially from extant Australian accipitrids claws as described above, a diagnosis to genus or species was not possible with such fragmentary fossil material.

Riversleigh, Queensland

Material: distal femur, AR16794 (Plate 4.4)

Locality and stratigraphy: White Hunter, Riversleigh, Queensland (Figure 4.1)

Age: Late Oligocene

Diagnosis: See Chapter Two, osteology chapter

Description

The femur is broken through the shaft proximal of the external condyle and internal condyle; the external condyle and internal condyle are abraded posteriorly. The rotular groove is deep and narrow compared to those of *Aquila* and *Haliaeetus*. The pit for *tibialis anticus* cuts across the external condyle ridge. The popliteal area is deep, but not as deep as in *Pandion haliaetus*. The protrusion, termed "fibular process" by Vickers-Rich (1980), is narrow and square. A pit for ligament attachment is present on the internal condyle. A rectangular protrusion at an angle of about 45° to the shaft is proximal of the internal condyle. A circular pit is proximal of the fibular condyle.

Measurements: Distal width 20.9 mm; depth of external condyle 17.5 mm; width of rotular groove 7.2 mm.

Discussion and conclusion

AR 16794 can be assigned to the Family Accipitridae due to the presence of the fibular process. The fossil can be excluded from the Old World vultures, as the Old World vultures possess a less curved margin of the external condyle in external view and a less developed fibular process.

The fossil possesses a unique character, the raised rectangular protrusion above the internal condyle. This feature is not present in Australian accipitrid genera, but may be present in other members of the Accipitridae. To ascertain the correct generic placement it would be necessary to compare the fossil to all genera of the Accipitridae. This fossil could potentially be referable to *Pengana robertbolesi* (Boles, 1993) due to its similar size, age and that it possesses features which are unique compared with modern Australian accipitrids, although as they are different elements, this cannot be assessed. Future work could involve comparing AR 16794 to the genera *Pengana* has been suggested to share a close resemblance, *Geranospiza* and *Polyboroides*.

Chinchilla, South-East Queensland

Material: QM F37014 proximal carpometacarpus (Plate 4.5)

Locality and stratigraphy: Chinchilla, Rifle Range, Queensland (Figure 4.1)

Age: Pliocene, 1.5 to 3 Mya, dated by presence of diprotodontid marsupial

Diagnosis: See Chapter Two, osteology chapter

Description

The fossil is broken through metacarpal II and III. In internal view, the internal ligamental fossa is very deep, approaching the process of metacarpal I, proximal of the pisiform process the fossa is shallow. In internal view, there is a high degree of ossification between the proximal end of metacarpal II and metacarpal III. The anterior carpal fossa is of medium depth compared to that of *Aquila audax*. The pisiform process and pollical facet are missing. The extensor attachment is oval. The carpal trochlea appears to be half-circular terminating distally of the pisiform process. In external view, the rims of the carpal trochlea terminate in line with one another, unlike in *Aquila* and *Haliaeetus*. In external view, a ridge runs from metacarpal III to meet with the proximal carpal trochlea. Metacarpal II is robust.

Measurements (mm)

Species	number	proximal width	proximal depth	depth of metacarpal II	width of metacarpal II
Fossil	QM F37014	21.0	8.5	7.2	6.2
Hamirostra melanosternon	SAM B36200	19.1	7.5	6.1	5.1
Hamirostra melanosternon (juvenille)	SAM B39289	17.1	7.0	5.1	4.7

Discussion

QM F37014 can be distinguished from extant Australian eagles, *Aquila*, *Haliaeetus* and *Hieraaetus* in the following characters:

1) The carpal trochlea appear more circular in internal view in the extant genera
2) The internal carpal trochlea ends distally nearly at a right angle, this is not the case for the fossil.
3) The carpal trochlea extend to different lengths in *Aquila*, *Haliaeetus* and *Hieraaetus*. This is not the case for the fossil.

QM F37014 shares most similarity to *Hamirostra melanosternon*. The following characters are shared by the fossil and *H. melanosternon*:

1) The rims of the carpal trochlea extend to the same length in external view
2) The rims of the carpal trochlea, in internal view, are shaped like a half circle and extend to terminate in line with the pisiform process.
3) metacarpal II is robust
4) the process of metacarpal I is oval

QM F37014 differs from *H. melanosternon* by being considerably larger and possessing a deeper internal ligamental fossa, a highly raised margin from the pisiform process to the carpal trochlea, a more highly raised ligamental attachment of the pisiform process. QM

F37014 is most similar to the genus *Hamirostra,* but due to the unique morphology of the carpometacarpus as described above, it probably represents a separate species from *Hamirostra*. Due to the fossil material being extremely fragmented it is not possible to establish if QM F37014 is a new species belonging in the (currently) monotypic genus *Hamirostra*, or if it is more appropriately placed in a new genus. Therefore, until further fossil material comes to light, it is most appropriately to list this fossil as *aff. Hamirostra* (affinity to *Hamirostra*).

Steve's Site, Lake Palankarinna, South Australia

Introduction

SAM P27975 examined as part of this study was originally thought to be an accipitrid. It actually represents a falconid. Although not a member of the Family Accipitridae, it will be discussed because the fossil is the oldest record of the Falconidae in Australia, and extends the record of the family back into the Tertiary. All previous records comprise Pleistocene fossils.

Diagnosis of the falconid tarsometatarsus

The falconid distal tarsometatarsus can be distinguished from that of other families by the following characters: in distal view, trochlea III protrudes farther anteriorly than the other two trochlea, trochlea II is box-like with a tapering flange, in internal view trochlea III extends farther anteriorly than trochlea II, presence of small groove on distal end of trochlea II and the shaft proximal of the trochleae is flat in accipitrids but curved and raised in falconids. The fossil specimen, SAM P27975, possess these combination of characters, and can be included in the Family Falconidae.

Systematics

Family Falconidae (Vigors 1824)

Palaeofalco **gen. nov.**

Etymology: 'Palaeo' is from the Greek word ‘palaios’ meaning ‘ancient’. Falco is from the Latin word ‘falx’ meaning ‘sickle’. The gender is feminine.

Type species: *Palaeofalco richorum* **sp. nov.**

Diagnosis of *Palaeofalco richorum* **(tarsometatarsus)**

Palaeofalco richorum is characterised by the combination of the following characters: (in distal view) the flange on trochlea II points posteriorly and is short, (in external view) trochlea III does not project as far distally and anteriorly when compared with trochlea IV, (in distal view) it is less curved across the trochleae compared with other falcons and trochlea IV tapers less posteriorly.

Palaeofalco richorum **sp. nov.**

Etymology: *richorum*, is dedicated to my supervisor, Pat Vickers-Rich, and to Richard Holdaway, who have both supported, encouraged and inspired me throughout my project.

Holotype: distal tarsometatarsus, SAM P27975 (Plate 4.6). The holotype is held in The South Australian Museum, Department of Palaeontology.

Locality and stratigraphy: Steve’s Site, Lake Palankarinna, SA. Geological horizon: Etadunna Fauna (Figure 4.1)

Age: Late Oligocene to Mid Miocene

Diagnosis: As for the genus.

Description: Only a distal fragment of left tarsometatarsus remains, trochleae curved in distal view but not as highly curved as in other falconids. Gracile and small. Trochlea III is the deepest of the three trochlea in distal view. The groove on trochlea III is medially aligned and relatively shallow. In posterior view, trochlea III narrows proximally and becomes wider distally. Trochlea II is robust and tapers posteriorly in distal view, and a slight groove is located distally on trochlea II. In internal view, trochlea III projects farther anteriorly than trochlea II. In external view, trochlea III protrudes farther anteriorly than trochlea IV. Trochlea IV possesses a groove. Trochlea IV tapers slightly posteriorly in distal view. One distal foramen is present approximately the size of a pinhole. The metatarsal facet is shallow, and the shaft is broken off approximately 0.5mm proximal of the metatarsal facet. The proximal surface of the shaft is relatively flat. Cross-section of the shaft is square.

Measurements: Distal width 7.8 mm; distal depth 4.8 mm; depth of trochlea III 3.3 mm; width of trochlea II 3.0 mm

Discussion

SAM P27975 represents a separate genus of falconid compared to *Falco*, *Milvago*, and *Polyborus*. SAM P27975 has greater affiliation with *Falco*, and differs from *Milvago* and *Polyborus*, by the following characters:

1) trochlea III is narrow proximally in posterior view
2) external intertrochlear notch is wider than internal
3) in external view, there is a ridge present along trochlea IV
4) trochlea III is the deepest of three trochleae in distal view.

SAM P27975 was compared to *Falco cenchroides*, *F. sparverius*, *F. berigora*, *F. longipennis*, *F. subniger* and *F. peregrinus*, and can be considered a separate genus to

Falco, as the distal end of the tarsometatarsus of *Falco* possess the following suite of characters:

1) trochlea III projects further distally and anteriorly than trochlea IV in lateral view. This feature appears to a lesser degree in the fossil.
2) Trochlea IV is narrow anteriorly and slanted in distal view. In the fossil, trochlea IV is wider anteriorly and box-like.
3) The flange on trochlea II tapers posterio-laterally. In SAM P27975 the flange tapers posteriorly.
4) In lateral view, trochlea III protrudes anteriorly and juts out from the shaft. This feature is present in SAM P27975.
5) *Fovea lig. collateralis* on trochlea II is deep and wide. *Fovea lig. collateralis* is not as deep or wide in SAM P27975.

SAM P27975 shares some characters with the Polyborines. Jollie (1976) considered the Polyborines tarsometatarsus, best typified by *Milvago*, to be the most primitive. SAM P27975, *Milvago* and *Polyborus* possess a wider trochlea IV, which could be a shared primitive character. *Milvago* and the fossil possess a posteriorly pointing flange on trochlea II, however, the shape of the flange in the fossil is more like that of *Falco*. Overall, SAM P27975 shares a number of characters with *Falco* that align the fossil closer to this genus, such as a shorter trochlea III that juts out from the shaft anteriorly. Unfortunately, the proximal region of the tarsometatarsus, which is missing from the fossil, is diagnostic for the falconid genera. In light of this and without comparison to other genera within the Falconidae, it is important not to over interpret from such fragmented fossil material. This fossil is tentatively assigned to a new genus, *Palaeofalco*, based on the variation of the fossil compared to other members of the Falconidae as stated above. The assignment is tentative as the fossil needs to be compared to the tarsometatarsus of all genera within the family Falconidae to warrant erecting a new genus. This will comprise the basis of future work on the family Falconidae, and is not within the scope of this project.

Palaeofalco richorum, the oldest record of the Family Falconidae from Australia, is the only novel species of falconid in the Australian fossil record. *P. richorum* represents a separate taxon from the genus *Falco*, which is the only falconid genus present in the extant Australian avifauna. Previously, the fossil record of the Family Falconidae in Australia has been restricted to the Pleistocene and all fossils have been represented by extant species; *Falco berigora*, *F. cenchroides* and *F. peregrinus* (Vickers-Rich, 1996).

Fossil history of the family Falconidae

The Etadunna Formation has been dated Late Oligocene to Mid-Miocene (Woodburne *et al.*, 1993 and Vickers-Rich *et al.*, 1996), which places this fossil among the oldest members of the Falconidae. The oldest record of the family is listed from Eo-Oligocene deposits at Quercy, France (Mourer-Chauviré, 1982). In South America, the family extends back into the Early Miocene; *Badiostes patagonicus*, which was originally recognized as an owl (Ameghino, 1894), but later Wetmore (1922) and Olson (1976) noted its affinities with the Falconidae. *Falco ramenta*, described by Wetmore (1936) from Middle Miocene deposits in Nebraska, was thought to be the oldest record of this genus, but as more complete fossil material was discovered, Becker (1987) redescribed *F. ramenta*, and changed its generic position to a new genus, *Pediohierax ramenta*. The oldest record of the genus *Falco* is represented by ?*Falco* from the Late Miocene of Idaho, and *Falco medius* from the Late Miocene deposits in the Ukraine (Becker, 1987).

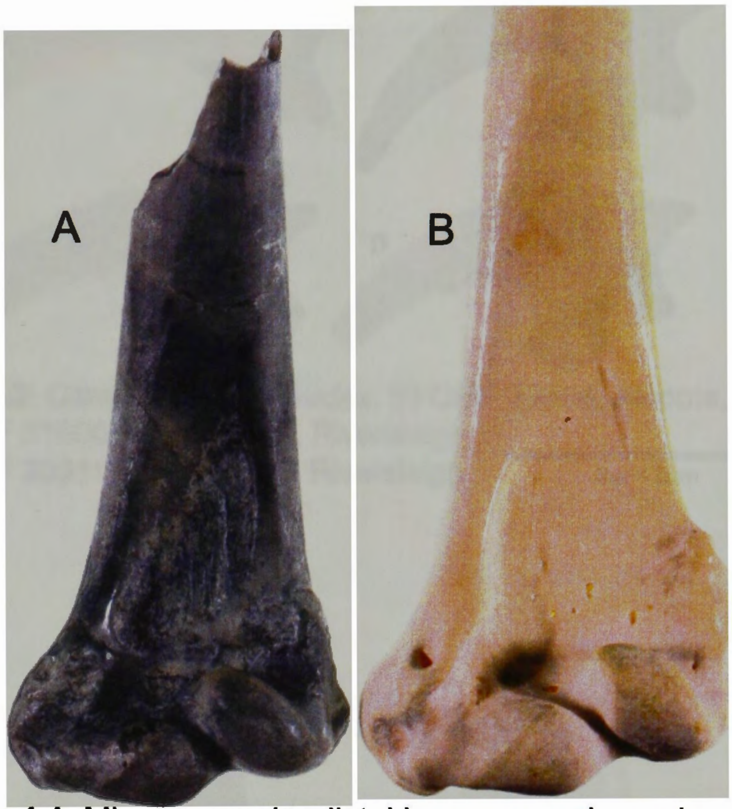


Plate 4.1: Miocene eagle, distal humerus, palmar view:
A) *Aquila bullockensis*
B) *Aquila audax*

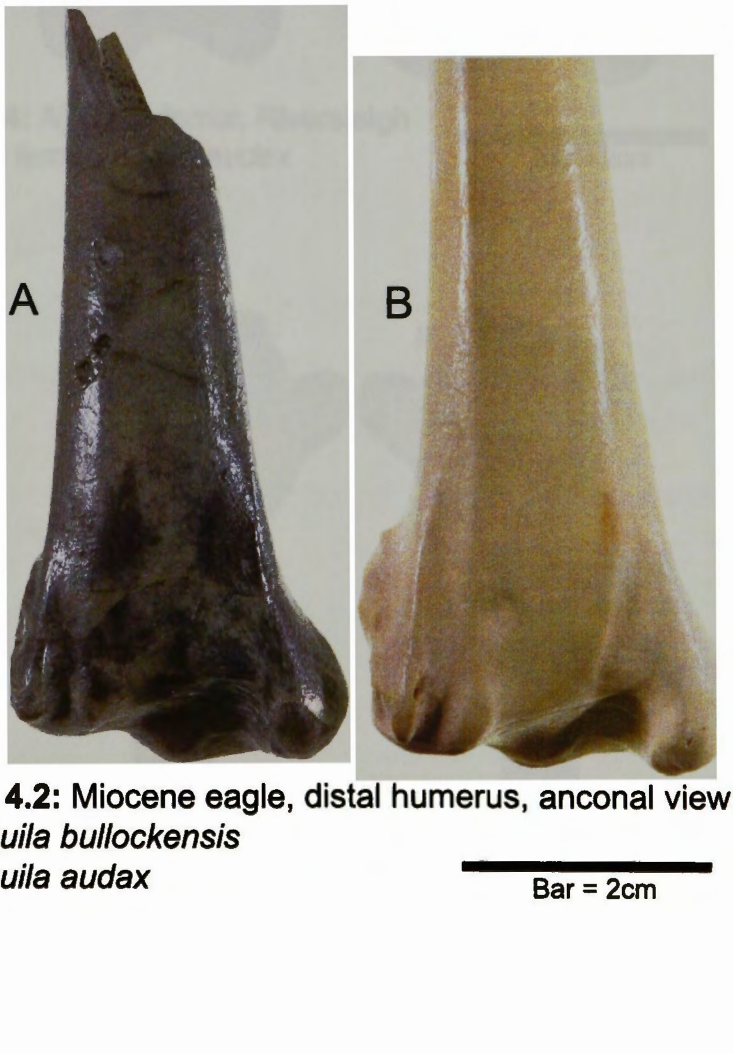


Plate 4.2: Miocene eagle, distal humerus, anconal view:
A) *Aquila bullockensis*
B) *Aquila audax*

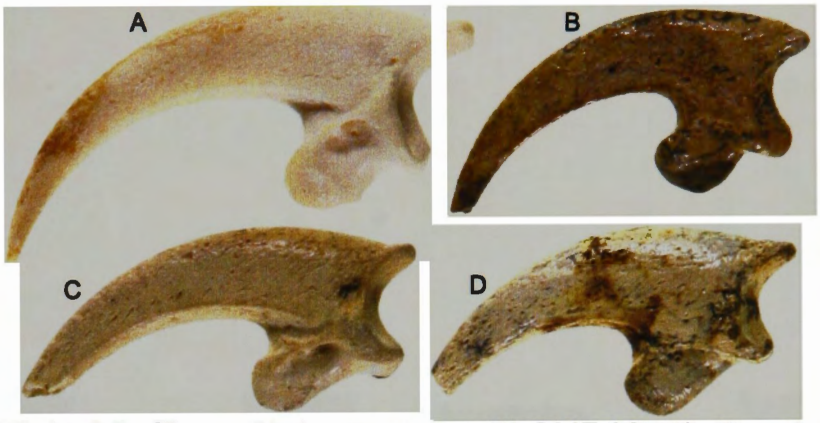


Plate 4.3: Claws: A) *Aquila audax*, B) QMF 39556, Alcoota, C) QMF 31600, Ringtail Site, Riversleigh, D) QMF 30311, Ringtail Site, Riversleigh

Bar = 2cm

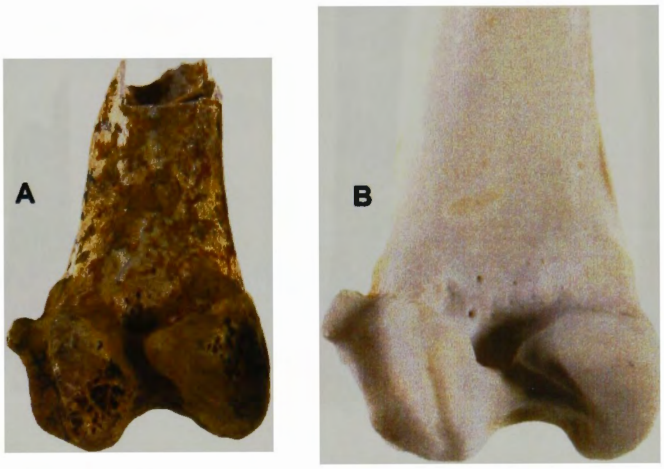


Plate 4.4: A) distal femur, Riversleigh
B) distal femur, *Aquila audax*

Bar = 2cm

Plate 4.5: Carpometacarpus QM F37014, from Chinchilla, Queensland: A) external view, B) internal view

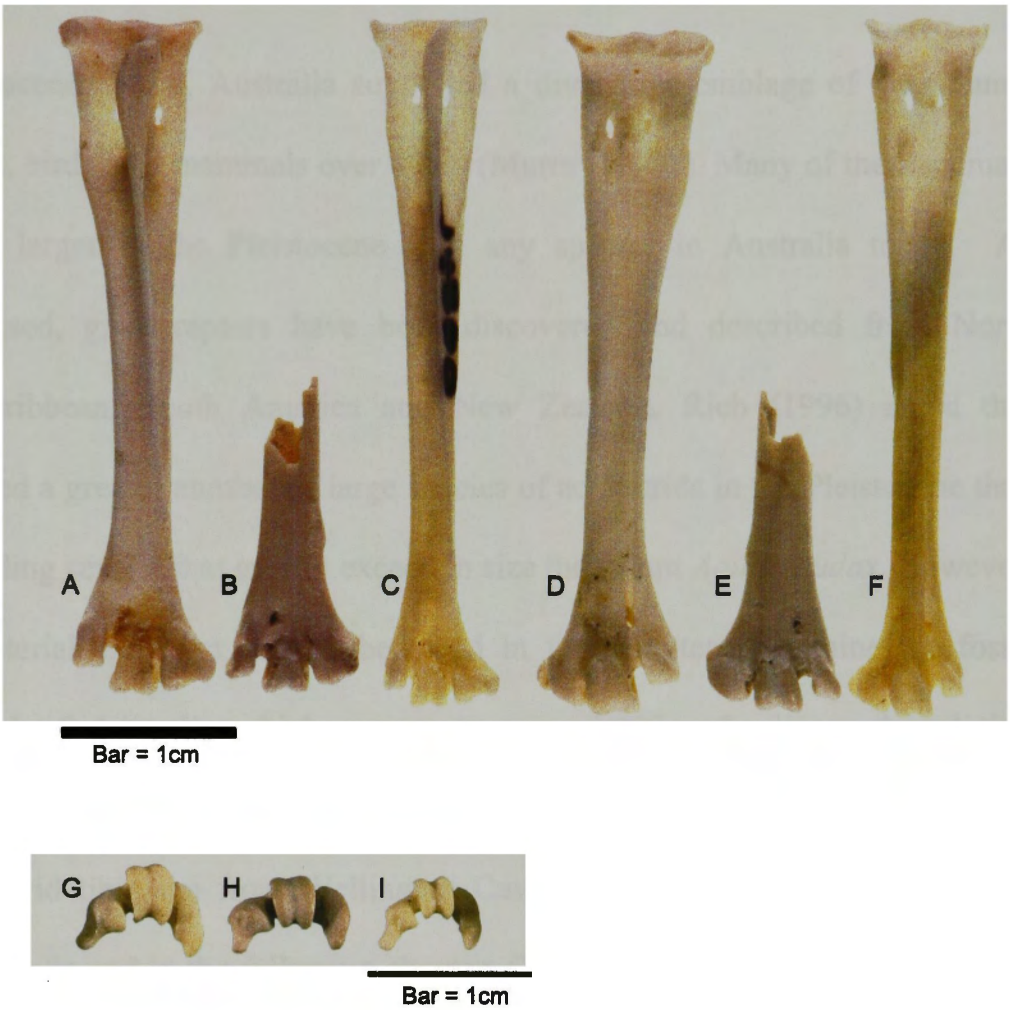


Plate 4.6: Miocene Australian falcon: Posterior view of the tarsometatarsus; A) *Falco longipennis*, B) Miocene falconid, C) *Falco cenchroides,* Anterior view of the tarsometatarsus; D) *Falco longipennis*, E) Miocene falconid, F) *Falco cenchroides,*Distal view of the tarsmetatarsus; G) *Falco longipennis*, H) Miocene falconid, I) *Falco cenchroides*

Chapter 5: Material of giant fossil accipitrids from Pleistocene deposits in Australia

Introduction

During the Pleistocene period, Australia supported a diverse assemblage of megafauna, defined as reptiles, birds, and mammals over 40 kg (Murray, 1991). Many of these animals were remarkably larger in the Pleistocene than any species in Australia today. As previously discussed, giant raptors have been discovered and described from North America, the Caribbean, South America and New Zealand. Rich (1996) noted that Australia supported a greater number of large species of accipitrids in the Pleistocene than exist today, including several that greatly exceed in size the extant *Aquila audax*. However, much of this material is as yet undescribed, and in this chapter I examine the fossil accipitrid material of Australia which represents taxa significantly larger than living species on this continent. In this chapter, Chapter Five, I compare and contrast two Pleistocene accipitrid tibiotarsi from Wellington Caves, New South Wales and Cooper Creek, South Australia and in the following chapter, Chapter Six, I discuss material found in Mair's Cave, Flinders Ranges, South Australia.

A comparison of two giant accipitrid tibiotarsi from Pleistocene deposits in Eastern Australia

Evidence for the existence of a giant eagle in the Australian Pleistocene is provided by two accipitrid tibiotarsi, preserved in separate Pleistocene deposits in eastern Australia. Although initial inspection suggests that the two specimens are very similar to one another, there are several significant morphological differences. In this section, I examine the differences between the two fossils, and assess whether the differences are significant enough to place the two in separate taxa or if the degree of variation is similar to that expected in a single species of large accipitrid today. For these comparisons, the two fossils are first described separately. In addition, the comparisons focus on whether the fossils represent a new taxon, or are simply giant precursors of the present eagles in Australia, exhibiting a phenomenon parallel to that identified in large macropods such as the red kangaroo, *Megaleia rufa* (Murray, 1991). Finally, a comparison of the Australian specimens to the giant *Harpagornis moorei* of New Zealand is made.

Family Accipitridae

Species indet.

Material: SAM P25218, distal end of right tibiotarsus (Cooper Creek, South Australia); AM F106562, distal end of right tibiotarsus (Wellington Caves, New South Wales).

Locality and stratigraphy: SAM P25218 was collected at Waralamanka Waterhole, Cooper Creek, South Australia (Figure 5.1). Deposits in the site are older than 15,000 years as dated by the avian fauna (Baird, 1996). Rich (1979) stated that all the vertebrate-producing localities along Cooper Creek prospected by the University of California and South Australia Museum are probably of Late Pleistocene age, as the fauna includes

Diprotodon, amongst other material, hence likely to be older than 40,000 ybp (Roberts *et al*, 2001). The depositional environment is fluviatile (Baird, 1996).

AM F106562 is from Wellington Caves area in New South Wales (Figure 5.1), but no other site information is available. The caves are of Pleistocene age (Dawson and Augee, 1997), however, some of the uppermost layers, in Cathedral Cave, Wellington Caves are dated to the Holocene. The sediments in Cathedral Cave are mostly heavy red clays. The cave contains the remains of megafauna in some of the layers. Dawson and Augee (1997) suggested that most animals would have entered the cave by falling in, as the cave acts as a natural pit trap, and that occasional scavengers, enticed by the chance of an easy meal, suffered the same fate.

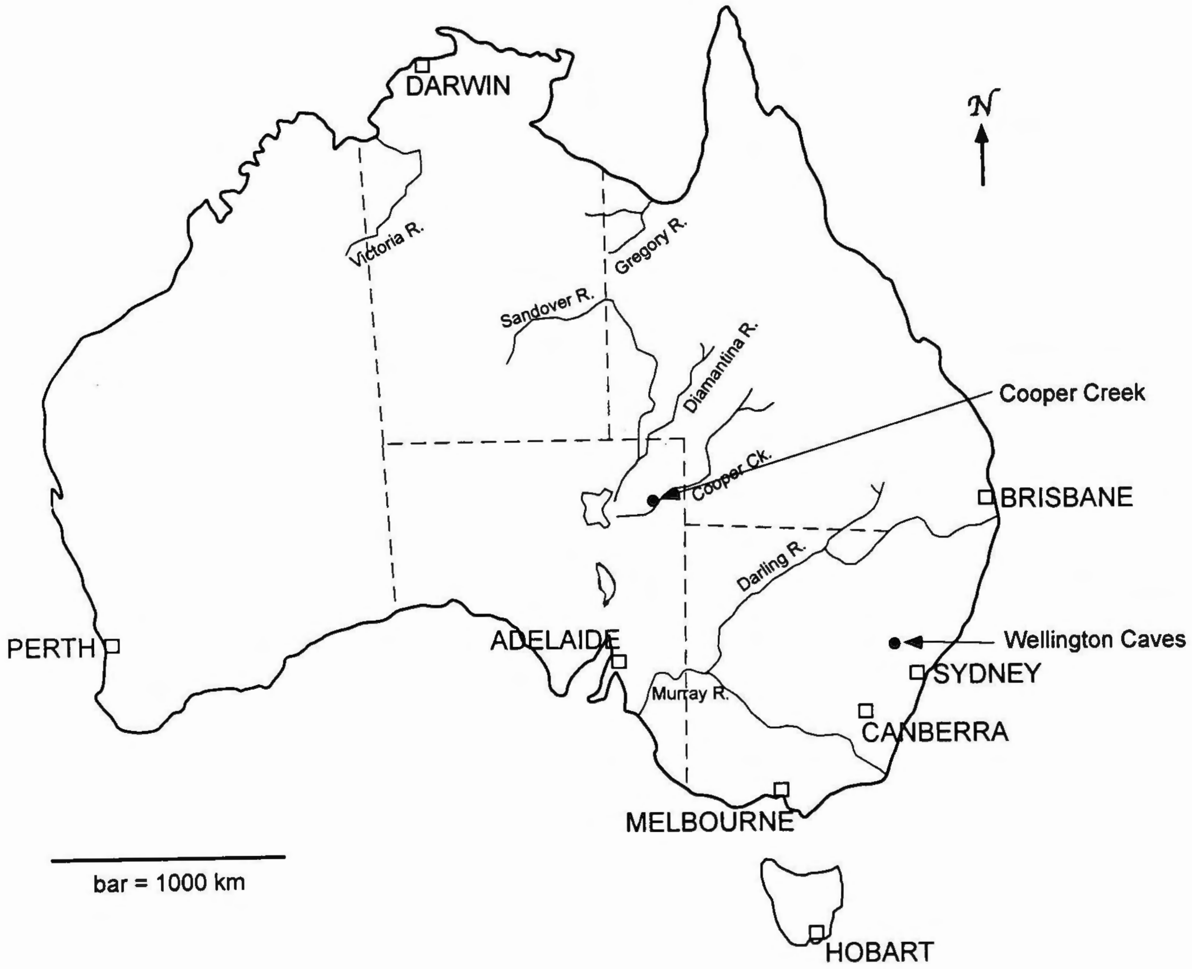


Figure 5.1: Quaternary localities producing giant fossil accipitrid tibiotarsi (Family Accipitridae)

Diagnosis: see Chapter Two.

SAM P25218 (Cooper Creek):

Measurements: Maximum distal width 27.1 mm; depth of internal condyle 19.8 mm (slightly abraded); depth of external condyle 16.2 mm (abraded posteriorly). The shaft was broken off between 10-15 mm proximal to the supratendinal bridge and the proximal end is missing.

Description: The shaft is anterioposteriorly compressed, straight in lateral view, slightly wider anterioposteriorly distally than proximally. The tendinal groove is relatively broad (about 25% of shaft width), medially located proximally of the supratendinal bridge; after passing very deeply beneath the supratendinal bridge, the tendinal groove is proximal to the lateral half of the internal condyle and medial half of the intercondylar fossa. The supratendinal bridge is slightly wider proximally than distally, raised above the shaft so that it protrudes anteriorly from the shaft and is at an angle of c. 40° to the shaft. The anterior intercondylar fossa is deep, increasing in depth from the lateral side of the internal condyle to the medial side of the external condyle. The anterior intercondylar fossa is wide, but is narrower than either condyle. There are two slightly raised ridges between the proximodistal midpoints of the condyles. The internal ligamental prominence is high, large and oval, and is distal to the anterior margin of the shaft. The posterior intercondylar sulcus is shallow. The external and internal condyles project further anteriorly than posteriorly (however, this might be an artefact of the abrasion to the posterior margins of the condyles). The internal condyle extends further anteriorly than the external condyle. The internal condyle is oval (medial view), with its long axis c. 90° to the shaft axis. In anterior view, the internal condyle is oval, with its long axis parallel to the shaft.

AM F106562 (Wellington Caves):

Measurements: maximum distal width 28.1 mm; depth of internal condyle 16.5 mm (abraded posteriorly); depth of external condyle 17.1 mm (abraded posteriorly). The internal and external condyles are abraded around their margins; only the distal end of the tibiotarsus remains (total length: 97.8 mm).

Description: The shaft is anterioposteriorly compressed, becoming slightly less compressed proximally than distally, and straight in lateral view. The tendinal groove is relatively broad (c. 25% of shaft width), medial proximal to the supratendinal bridge, very deep beneath the supratendinal bridge, and terminates above the medial half of the intercondylar fossa. The supratendinal bridge is at an angle of c. 45° to the long axis of the shaft, and is considerably wider proximally than distally. The anterior intercondylar fossa is deep, increasing in depth from the lateral side of the internal condyle to the medial side of the external condyle. The anterior intercondylar fossa is wide, but slightly less so than the width of the internal condyle, and possibly of the external condyle but the latter is abraded. In anterior view, a low ridge lies between the midpoints of the condyles. The internal ligamental prominence is highly raised, oval and directly distal to the anterior margin of the shaft. The posterior intercondylar sulcus is shallow, but its exact depth is difficult to determine because the posterior margins of the condyles are abraded. The internal and external condyles project further anteriorly than posteriorly. The internal condyle projects further anteriorly than does the external condyle.

Table 5.1: Measurements (mm) of the distal end of the tibiotarsus of the fossils SAM P25218, AM F106562, *Aquila audax*, *Haliaeetus leucogaster* and *Harpagornis moorei*.

Species	Breadth of distal end	Depth of distal end	Depth of internal condyle	Depth of external condyle	Width of proximal end of supratendinal bridge	Width of distal end of supratendinal bridge	Width of anterior intercondylar fossa
Giant eagle SAM P25218	27.1	19.3	19.2	16.3	5.2	4.5	8.5
Giant eagle AM F106562	27.5	18.3	16.2	16.7	6.7	3.8	7.8
Aquila audax	17.7 – 21.3	12.6 – 15.0	12.6 – 15.0	11.9 – 14.8	4.2 – 5.6	3.2 – 4.3	5.3 –6.8
Haliaeetus leucogaster	17.7 – 19.7	11.9 – 13.9	12.0 – 13.7	11.8 – 13.7	4.2 – 6.1	3.1 – 3.9	6.4 – 7.0
Harpagornis moorei	27.0 – 38.9	18.5 – 26.1	18.4 – 26.3	16.9 – 25.4	7.1 – 9.9	2.8 – 7.6	8.4 – 12.3

Comparison of two large tibiotarsi from Pleistocene deposits in Australia

The two fossil tibiotarsi are very similar in size (Table 7.1) and morphology, are both referable to the Accipitridae, and are both of Pleistocene age. However, there are several differences between the specimens as follows:

1) The ratio of distances between the width of proximal end of the supratendinal bridge and the width of the distal end differs (Table 7.2).
2) The number of ridges between the condyles situated in the anterior intercondylar fossa, one in AM F106562, two in SAM P25218.
3) The location of the tendinal groove distad to the supratendinal bridge; either proximal to the lateral half of the internal condyle and medial half of the intercondyle fossa, or located wholly above the medial half of the intercondylar fossa.
4) The location and distance of the proximo-medial end of the supratendinal bridge with respect to the medial margin of the shaft.
5) The projection of the supratendinal bridge anteriorly from the shaft.
6) The shape and size of the rugose surface proximad of the supratendinal bridge.

However, there is often considerable variation in bone morphology within a single species in modern taxa. The difference in width of the proximal end versus the distal end of the supratendinal bridge can vary greatly within a single species of large eagle (Table 5.2), so this feature in the two fossils does not support their separation as different species.

Table 5.2: Range of difference between the proximal width (mm) of the supratendinal bridge versus the distal width in some large species of accipitrid.

Species	minimum	Maximum
Giant Pleistocene eagles (*n*=2)	0.7 (SAM P25218)	2.9 (AM F 106562)
Aquila audax (*n*=21)	0.5	2.0
Haliaeetus leucogaster (*n*=10)	0.9	2.2
Aquila chrysaetos (*n*=2)	1.4	2.4
Harpagornis moorei (*n*=5)	1.8	5.2

The second point of difference between the two fossils is in the number of ridges between the condyles in the anterior intercondylar fossa, *impressio ligamentalis intercondylaris*. SAM P25218 has two ridges running from the proximodistal midpoints of the condyles, whereas AM F106562 has one that is more prominent. In the sample of *Aquila audax* and *Haliaeetus leucogaster* the number of ridges varied between no ridge to one highly raised ridge (Appendix 1). Therefore, this feature does not allow the separation of the two fossils into different species.

The third point of variation is in the location of the tendinal groove distad of the supratendinal bridge. In SAM P25218 the tendinal groove distad of the supratendinal bridge is proximal to the lateral half of the internal condyle and medial half of the intercondylar fossa, whereas in AM F 106562 it is located wholly above the medial half of the intercondylar fossa (Plate 5.1). The location of the tendinal groove distad of the supratendinal bridge varies in *Aquila audax*. Although, its location varies between either predominately over the internal condyle, or proximal of the lateral half of the internal condyle and medial half of the intercondylar fossa, in only one specimen was it entirely proximal to the intercondylar fossa in that species (Appendix 1). Again, the range of variation possible in one species does not allow separation of the two fossils on that character. Yet this point of variation was observed in *A. audax* and not in *H. leucogaster*, with the provision that the number of *A. audax* skeletons available for study was greater than that of *H. leucogaster* skeletons. Hence, the apparent difference in variation between the two species may be an artefact of sample size.

The location and distance of the proximomedial end of the supratendinal bridge from the medial margin of the shaft varied between the two fossils, but again this degree of variation was apparent in both *A. audax* and *H. leucogaster* (Appendix 1).

Finally, the projection of the supratendinal bridge anteriorly from the shaft, which varied between the fossil tibiotarsi, can also vary within a species (Appendix 1), so again the level of variation is too great for the character to be a valid point of separation.

Altogether, the data suggests that the two fossils can be assigned to the same species, as they are subject to the same level of variation as exists in extant species of accipitrids.

Comparison of the large fossil tibiotarsi to recent Australian eagles

The fossil tibiotarsi represent an accipitrid of significantly larger size than any species of eagle living in Australia today (Table 5.1). A comparison of SAM P25218 and AM F 106562 with tibiotarsi of *Aquila audax* and *Haliaeetus leucogaster* revealed no clear relationship to either genus (Table 5.3). However, the fossils have a closer resemblance to *Aquila* than to other genera in the Accipitridae that they were compared to in the following points:

1) In the fossil specimens the internal condyle, in anterior view, is oval, as it is in *A. audax*; in *H. leucogaster* it is squarer, in *Pithecophaga* and *Stephanoaetus* the internal condyle appears to be bulbous and square (Plate 5.1).

2) The anterior intercondylar fossa is very deep in the fossils and in *A. audax, Pithecophaga,* and *Stephanoaetus*; in *H. leucogaster* it is of medium depth (Table 5.3).

3) The internal ligamental prominence of the fossil resembles that in *A. audax* rather than *H. leucogaster*. In the fossils and *A. audax, Pithecophaga,* and *Stephanoaetus,* this feature is large and oval with the long axis aligned at right angles to the margin of the shaft; in *H. leucogaster* this feature is slightly less bulbous and oval, and has the long axis aligned at an angle to the margin of the shaft.

4) The tendinal groove proximal of the supratendinal bridge is centred along the shaft, as in *A. audax*, *Pithecophaga*, and *Stephanoaetus*; the tendinal groove is closer to the external margin of the shaft in *H. leucogaster* (Plate 5.1).

5) The internal condyle is deeper than the external condyle; it is shallower in *A. audax*, *H. leucogaster*, *Pithecophaga,* and *Stephanoaetus*.

6) Anterior intercondylar fossa width is considerably wider in the fossils; in *Aquila* and *Haliaeetus* the fossa is comparatively as wide as in the fossils, in *Pithecophaga* and *Stephanoaetus,* the fossa is comparatively narrow.

Emslie and Czaplewski (1999) stated that the tibiotarsus in *Aquila* differed from that in *Haliaeetus* in having: the tendinal bridge angled less medially and in the tendinal groove being placed more internally. On account of features 1-6 and the characters given by Emslie and Czaplewski (1999), SAM P25218 and AM F106562 can be excluded from the genus *Haliaeetus*. Both SAM P25218 and AM F106562 are osteologically most similar to *Aquila*, to which genus I tentatively refer the fossils.

Comparison of SAM P25218 and AM F106562 with the distal tibiotarsi of the giant *Harpagornis moorei* (Haast, 1872) of New Zealand

Despite the much greater size of these specimens in comparison to the tibiotarsi of recent Australian eagles, they are still considerably smaller than the largest specimens of *Harpagornis moorei* of New Zealand (Table 5.1) yet, similar in size to the smaller (assumed male) specimens of *H. moorei* (Plate 5.2). There are, however, some morphological differences as follows:

1) The intercondylar fossa is wide in *H. moorei*, but comparatively not as wide as in SAM P25218 and AM F106562.
2) Internal view of the internal condyle is oval in *H. moorei*, in both SAM P25218 and AM F106562 it is circular.
3) The scar for muscle attachment proximal of the supratendinal bridge is located further proximally from the supratendinal bridge in *H. moorei* than in the Australian fossils.
4) The supratendinal bridge protrudes anteriorly in all *H. moorei* examined.

Comparison of SAM P25218 and AM F106562 with tibiotarsi of Old World vultures

SAM P25218 and AM F106562 do not show any affinities to the Old World vultures. The Old World vultures differ from SAM P25218 and AM F106562 in the following features:

1) The internal condyle in internal view is semicircular in the Old World vultures, whereas it is well rounded in the fossils.
2) The shaft appears to become wider distally, proximal to the internal condyle in the Old World vultures, but this is not apparent in the fossils (Plate 5.1).
3) The distal end, in distal view, is deeper compared to the width in the Old World vultures than is observed in the eagles and in SAM P25218 and AM F106562.

Conclusions

Both SAM P25218 and AM F106562 can be assigned with confidence to the family Accipitridae. Although they are similar in size to one another and both are from Pleistocene deposits, they differ substantially in their morphology. However, the same degree of variation can be seen within extant taxa of eagles in Australia, consequently, SAM P25218 and AM F106562 could be referable to the same taxon.

SAM P25218 and AM F106562 represent a species or species of eagle larger than any of the extant Australian eagles. After comparison of the fossils with comparable material of several accipitrid genera, the generic position within the Accipitridae of the fossils remains as yet undetermined, but the material shows more affinity to specimens from the genus *Aquila* rather than those in *Haliaeetus* and the Old World vultures. Further fossil material is required before determining the correct generic placement, and could be the subject for further investigation.

SAM P25218 and AM F106562 differ considerably to the *H. moorei*, morphologically, and in size from the larger *H. moorei*, but are comparable in size with the smaller specimens of *H. moorei.* SAM P25218 and AM F106562 are not likely those of a vagrant *Harpagornis moorei*, and more probably represent a new taxon or taxa of formidably-sized eagle from the Australian Pleistocene.

In the Pleistocene, Australia supported many species of large and medium-sized mammals, including carnivores such as dasyurids, the thylacines *Thylacinus cynocephalus*, a "marsupial leopard" *Thylacoleo carnifex*, and the giant monitor *Megalania prisca* (Rich, 1996). These carnivores could have competed for food with a large eagle, which perhaps limited the size of Australian accipitrids. In New Zealand, in the absence of competition from mammalian and reptilian carnivores, there was no such constraint. There, *H. moorei* could evolve the large size necessary to kill the large herbivores (moas, Dinornithiformes).

Table 5.3: A comparison of the two fossil distal ends of the tibiotarsus to modern accipitrids

Feature	**SAM P25218** Cooper Creek	**AM F106562** Wellington Caves tibiotarsus	***Aquila audax*** Wedge-tailed Eagle	***Haliaeetus leucogaster*** White-bellied Sea-eagle	***Harpagornis moorei*** Haast's Eagle
Tendinal groove depth	Deep	Deep	Deep	Deep	Very deep
Tendinal groove width	Wide	Wide	Wide	Wide	Wide
Tendinal groove location proximal of supratendinal bridge	Medial	Medial	medial	Medially to external side of shaft	Medial
Tendinal groove location distal of supratendinal bridge	Lateral along shaft	Lateral	Lateral	?	Half over the condyle and half over the fossa
Supratendinal bridge	Wider proximally than distally, protrudes anteriorly to the edge of the shaft.	Much wider proximally than distally, located deeper within the edges of the shaft	Slightly wider proximally than distally	Varies, equal distance proximally as distally or wider proximally than distally	Very wide proximally, very narrow distally, located deep within the shaft, protrudes anteriorly
Internal condyle (internal view)	Oval, protrudes further anteriorly than the external condyle	Internal condyle protrudes further anteriorly than external condyle	Oval to circular	Oval to square	Oval, with the long axis horizontal
External condyle (anterior view)	Abraded posteriorly and anteriorly	Abraded posteriorly and anteriorly	Oval	Oval	Rectangular
External condyle (external view)	Abraded	Abraded	Circular	Circular	Circular
Anterior intercondylar fossa width	Wide	Wide	Wide	Wide	Wide
Anterior intercondylar fossa depth	Deep, deeper to the external side	Deep, deeper to the external side	Deep, deeper to the external side	Medium depth, deeper to the external side	Deep, deeper to the external side
Ridges between the internal condyle and external condyle	2	1	1, not always present	1 to none	1 to 2
Internal ligamental prominence	Oval, large, highly raised, with the long axis aligned vertically	Oval, large, highly raised, located proximo-medially	Oval to circular, medial on the internal condyle (internal view), directly distad of margin of the shaft, long axis vertical	Oval, touches proximal anterior margin of internal condyle, the long axis at an angle to the medial margin of the shaft	Oval, well raised, directly distal to the margin of the shaft and central on the condyle

Table 5.3: A comparison of the two fossil distal ends of the tibiotarsus to modern accipitrids

Feature	*Gyps fulvus* Griffon vulture	*Aegypius monachus* Cinereous vulture	*Trigonoceps occipitalis* White headed Vulture	*Gypaetus barbatus* Bearded Vulture	*Gypohierax angolensis* Palm Nut Vulture	*Terathopius ecaudatus* Bateleur
Tendinal groove depth	Deep	Deep	Deep	Deep	Medium depth	Deep
Tendinal groove width	Narrow	Narrow	Wide	Narrow	Medium width	Wide
Tendinal groove location proximal of supratendinal bridge			Medially	Medial	Internal side of the shaft	Medial
Tendinal groove location distal of supratendinal bridge	proximal to the intercondylar fossa	proximal to the intercondylar fossa	Half over condyle, half over anterior intercondylar fossa	Terminates proximal to the intercondyle fossa	Over the fossa	Above the intercondylar fossa
Supratendinal bridge	Proximal and distal width equal, thick bridge at an angle, protrudes anteriorly	Slightly wider proximally than distally, at an angle to the shaft	Length > width	Wide proximally and distally, thick bridge, at an angle to shaft	Length = width	Narrow, raised Length>width
Internal condyle (internal view)	Semicircular	Semicircular	Semicircular	Semicircular	Circular	Oval
External condyle (anterior view)	Triangular	Oval	Oval	Oval	Oval	Oval to rectangular
External condyle (external view)	Oval	Circular	Circular, raised margin	Circular	Circular	Oval
Anterior intercondylar fossa width	Narrow	Narrow	Narrow	Wide	Wide	Wide
Anterior intercondylar fossa depth	Medium depth	Medium depth	Very deep	Medium depth	Medium depth	Shallow
Ridges between the internal condyle and external condyle	1	2	1	Not visible	N/A	1
Internal ligamental prominence	Circular, well raised, raised margin of shaft merging with the prominence, proximo-medially on condyle	Circular, raised; margin of the shaft raised and merging with prominence, proximo-medially on condyle	Oval, raised, margin of the shaft merges with the prominence	Circular, raised; raised margin from margin of the shaft merging with prominence, proximal on condyle	Oval raised, slight margin between it and shaft margin, more anterior on internal condyle	Circular, anterior, in line with margin of shaft

Table 5.3: A comparison of the two fossil distal ends of the tibiotarsus to modern accipitrids

Feature	***Spilornis cheela*** Crested Serpent Eagle	***Pithecophaga jefferyi*** Monkey-eating Eagle	***Stephanoaetus cornatus*** Crowned Hawk-Eagle	***Oroaetus isidori*** Black and Chestnut Eagle	***Spizaetus ornatus*** Ornate Hawk-Eagle
Tendinal groove depth	Medium depth	Very deep	Deep	Deep	Very deep
Tendinal groove width	Narrow	Wide	Wide	Wide	Very wide
Tendinal groove location proximal of supratendinal bridge	Internal side of shaft	Medial	Medial	Medial	Medial
Tendinal groove location distal of supratendinal bridge	Above internal condyle and above intercondylar fossa	Located ½ over intercondylar fossa and ½ over internal condyle	Located ½ over intercondylar fossa and ½ over internal condyle	Located ¼ over intercondylar fossa and ¾ over internal condyle	Located ½ over intercondylar fossa and ½ over internal condyle
Supratendinal bridge	Narrow Length > width	Length > width	Wider proximally Length > width	Length > width. Proximal and distal ends nearly equal	Length > width Wider proximally than distally
Internal condyle (internal view)	Circular	Circular	Circular	Circular	Circular
External condyle (anterior view)	Rectangular	Square	Square	Rectangular	Oval
External condyle (external view)	Oval	Circular	Oval	Circular.	Circular
Anterior intercondylar fossa width	Wide	Slightly narrower than condyles	Narrower than the width of either condyle	Slightly narrower than the width of either condyle	Width equal to width of condyles
Anterior intercondylar fossa depth	Shallow to medium	Deep	Very deep	Very deep	Very deep
Ridges between the internal condyle and external condyle	1	2 to none	1	1	1
Internal ligamental prominence	Circular, central, in line with the margin of the shaft	Oval, central	Oval, central	Slightly raised, oval, central	Central on condyle, oval, slight ridge between shaft margin and prominence

Plate 5.1: Anterior view of the tibiotarsus of various accipitrids

Species	Common name
A) *Elanus axillaris*	Black-shouldered kite
B) *Aviceda subcristata*	Pacific baza
C) *Ictinia misisippiensis*	Mississippi kite
D) *Milvus migrans*	Black kite
E) *Lophoictinia isura*	Square-tailed kite
F) *Hamirostra melanosternon*	Black-breasted buzzard
G) *Haliastur sphenurus*	Whistling kite
H) *Accipiter fasciatus*	Brown goshawk
I) *Buteo buteo*	Common buzzard
J) *Pithecophaga jefferyi*	Monkey-eating eagle
K) *Spizaetus ornatus*	Ornate hawk-eagle
L) *Aquila audax*	Wedge-tailed eagle
M) *Haliaeetus leucogaster*	White-bellied sea-eagle
N) *Hieraaetus morphinoides*	Little eagle
O) Cooper Creek accipitrid fossil	
P) Wellington Cave accipitrid fossil	
Q) *Trigonoceps occipitalis*	White-headed vulture
R) *Gyps fulvus*	Griffon vulture
S) *Gypaetus barbatus*	Lammergeier, or Bearded vulture
T) *Gypohierax angolensis*	Palm-nut vulture
U) *Circus approximans*	Swamp harrier
V) *Terathopius ecaudatus*	Bateleur
W) *Spilornis cheela*	Crested Serpent eagle

Plate 5.1

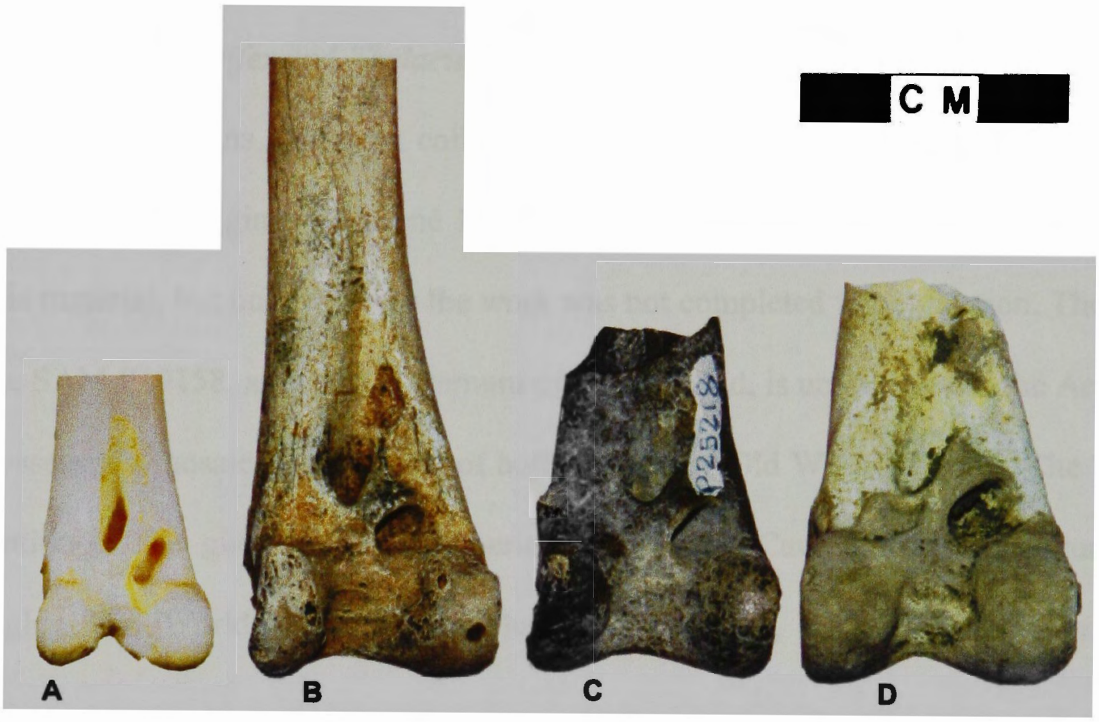


Plate 5.2: Distal tibiotarsi; A) *Aquila audax*, B) Wellington Cave fossil, C) Cooper Creek fossil, D) *Harpagornis moorei*.

Chapter 6: A giant accipitrid from Mair's Cave, Flinders Ranges, South Australia

Introduction

Mair's Cave, Buckalowie, is located in the Flinders Ranges, South Australia. This well known cave was mined for guano in the 1930's. Since the 1950's the South Australian Museum has kept records of fossil material collected from this cave. Included in the collections are extinct species, including *Thylacoleo carnifex* and *Thylacinus cyanocephalus*, but more relevant to this study, in 1969 Brian Daily and Hans Mincham collected fossilized accipitrid material similar in size to *Harpagornis moorei*, the giant Holocene Eagle in New Zealand. The late Gerry van Tets was studying this material, but unfortunately the work was not completed to publication. The material under study, SAM P19158, a fossilized sternum of an accipitrid, is unique within the Accipitridae in that it possesses a mosaic of characters of both eagles and Old World vultures. The following is a description of this giant accipitrid material from Mair's Cave and a comparison of it to modern eagles, Old World vultures, kites, harriers, goshawks, and the extinct *Harpagornis moorei*.

Systematics

Family Accipitridae Vieillot 1816

Diagnosis of the family Accipitridae: see Chapter II, page

Woltsha **gen. nov.**

Etymology: From the Australian Aboriginal (within South Australia) 'woltsha' meaning 'eagle'. The gender is feminine. Coincidentally, this word sounds rather like the English word "vulture". I thought it was a very appropriate name for an accipitrid possessing a mosaic of characters between the accipitrid vultures and eagles.

Type species: *Woltsha australensis* **sp. nov.**

Diagnosis of ***Woltsha*****:**

Members of the genus *Woltsha* are characterized by possessing the following suite of character states of the sternum: very large, triangular shaped lateral processes; narrow ventral manubrial spine; thick carinal apex in proximal view; carinal apex appears "pushed back", aligned distally of the ventral labial prominences, in lateral view; and the carina is deepest proximally, in lateral view.

Woltsha australiensis **sp. nov.**

Etymology: From the Latin word 'ensis' meaning 'belonging to', combined with the word Australia, to mean 'belonging to Australia'.

Holotype: Sternum (SAM P19158), lacking the ventral manubrial spine, and the posterior section (about 30-40%) (Plate 6.1 and 6.2), held in the South Australian Museum Palaeontology collection.

Paratypes: Two large ungual phalanges (SAM P19157, SAM P17139) (Plate 6.2).

Locality and stratigraphic position: SAM P17139 was found on the surface under loose rocks, 54.8 metres from the entrance, Mair's Cave, Buckalowie, South Australia, Latitude 32° 10' 34.2'S, Longitude 138°52'18.9'E. Most fossils found in this cave were located in this area (Rod Wells, pers. comm). As the two other specimens, ungual phalanges, do not have details of their location, they may have come from this section of the cave. It is suggested that much of the fossil material was brought into the cave by owls, due to the bias in the size of the bones found in the cave, and the breakage pattern of the bones (Rod Wells, pers. comm). The deposit is autochthonous (Rod Wells, pers. comm), but larger species, which could not have been carried in by an owl, have also been found. These include *Thylacoleo carnifex* (field notes of Neville Pledge) and the fossilized sternum and claws of a very large accipitrid. The cave consists of a shale wall with a silt floor where the fossils were collected. The cave was formed by autogenic processes (Rod Wells, pers. comm).

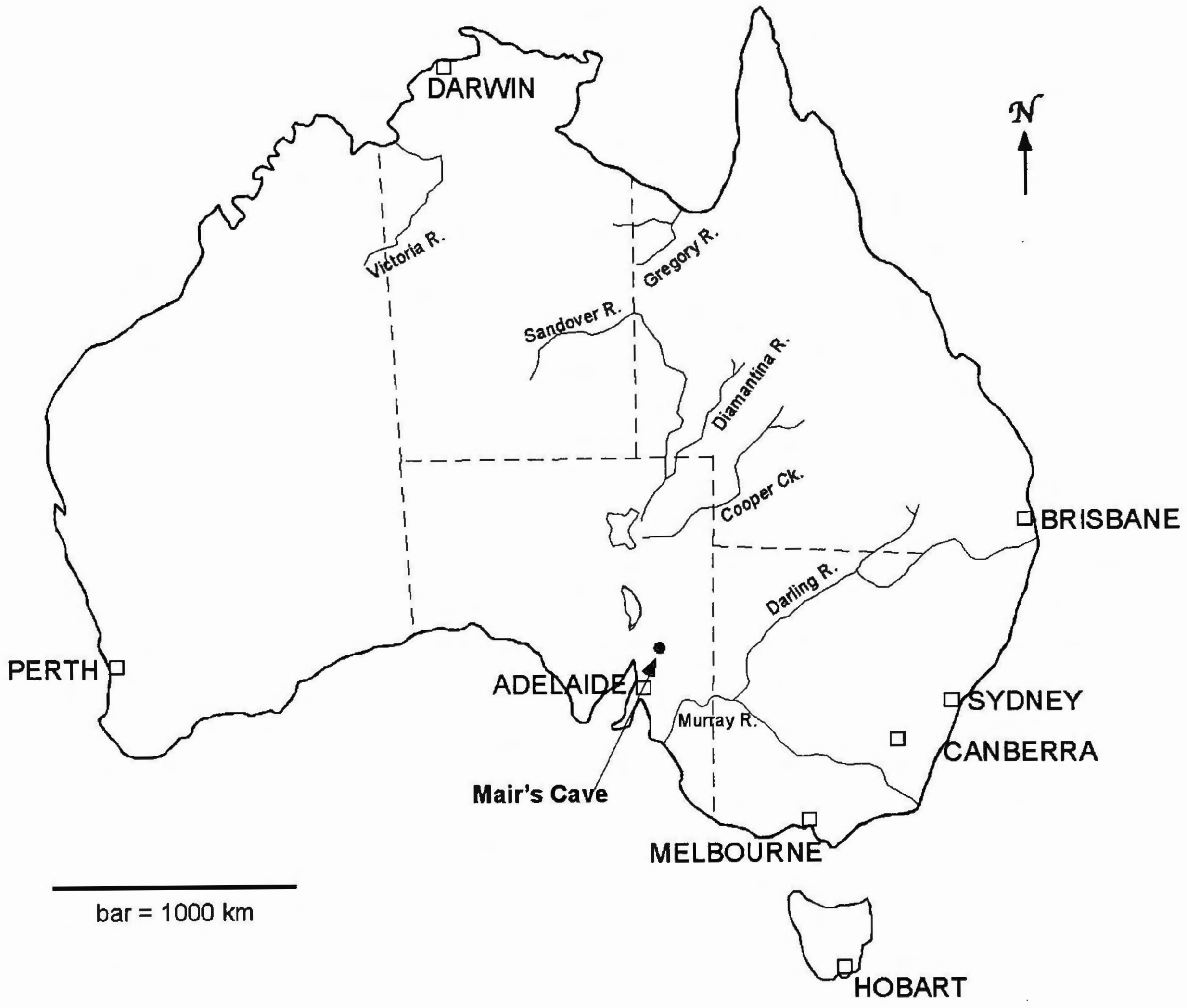


Figure 6.1: Mair's Cave, South Australia

Age: suggested to be Pleistocene in age due to the presence of *Gallinula mortierii*, the Tasmanian Native Hen, which became extinct on the continent between 12,000 to 20,000 ybp due to an increase in aridity (Baird, 1984).

Diagnosis of ***W. australiensis*****:** as for the genus.

Description: (sternum) SAM P19158: the distal 30% of the sternum is missing along with the majority of the left-hand side of the sternum, the sterno-coracoidal processes, and most of the ventral manubrial spine. The sternum is approximately 75-100% larger than living eagle species in Australia. The sternal plate is concave; an open bowl shape. In lateral view, the anterior carinal margin is slightly curved to almost straight, with a thick, raised and well defined border along the anterior carinal margin. The carinal apex is thick, rounded, bulbous and does not protrude proximally of the anterior carinal margin. In lateral view, the carinal apex is in line with the ventral labial prominences; this feature gives the look of the carina being "pushed backed" when compared to those of other eagles. The carinal apex is wider than the distal margin of the carina, but overall the width remains constant along the length of the carina (ventral view). In lateral view, the carina is deepest proximally and becomes considerably shallower distally. In ventral view, the ventral labial prominences have very smooth and rounded edges, and appear more like an extension of the ventral lip of the coracoidal sulcus than a definite prominence. The groove between the ventral lip and dorsal lip of the coracoidal sulcus is very shallow, but it is slightly deeper where the ventral labial prominence overhangs the sterno-coracoidal impression. The ventral manubrial spine has the distal-most end preserved, which protrudes distally; the cross-section of the ventral manubrial spine is relatively narrow, triangular and slanted to the left-hand side of the sternum. Five costal processes remain, with wide intercostal spaces, although the sternum may have possessed seven costal processes or more. In proximal view, the anterior lateral processes are very large and triangular with rounded edges. The lateral processes extend more than 5.0 mm from the edge of the sternal plate.

Measurements:

SAM P19158: Maximum depth from the dorsal manubrial spine to the carinal apex 68.4 mm; length from the ventral manubrial spine to the keel at the distal end of the sternum (does not represent the total length of sternum as SAM P19158 is broken posteriorly) 125.5 mm; estimated length of sternum 199.1 mm (if P19158 is equal to 63% of the initial length of the sternum based on the length from the manubrial spine to the distal end of the costal margin, in extant eagles this section represents between 62 to 65% of the length of the sternum).

Comparison of SAM P19158 to various extant Old World vultures

There are a number of similarities and differences between the Old World vultures and the fossil sternum SAM P19158. When using the term Old World vultures or accipitrid vultures, this group includes the following genera (unless otherwise stated): *Gypohierax, Neophron, Gypaetus, Necrosytes, Aegypius, Gyps, Trigonoceps, Sarcogyps, Torgos,* and *Pseudogyps*. Comparing SAM P19158 to the Old World vultures poses some problems because of the significant variation within the Old World vultures in regards to the morphology of the sternum. This may be a result of the polyphyly of the group (as inferred from nucleotide sequences of their mitochondrial cytochrome *b* gene (Siebold and Helbig, 1995)). Siebold and Helbig (1995) suggested that *Gyps*, *Pseudogyps*, *Aegypius*, *Torgos*, *Trigonoceps* and *Sarcogyps* form a monophyletic subfamily that share a more recent common ancestor with *Buteo*, *Aquila*, *Haliaeetus* and *Circaetus* than with *Gypaetus barbatus* and *Neophron percnopterus*. *Gypaetus* and *Neophron* are suggested to be more primitive forms than the *Aegypius-Gyps* clade. Siebold and Helbig (1995) propose that the *Aegypius-Gyps* clade evolved convergently to the more ancient *Gypaetus* and *Neophron* vultures, suggesting that the similarities of the Old World vultures as a whole may be due to convergent evolution within the family Accipitridae rather than a close relationship. Additionally, determining whether shared character states are due to convergent evolution or derived from a shared ancestor is particularly difficult with such limited fossil material from a family in which convergent evolution has occurred frequently. All of this makes it really impossible to assign a fossil with such intermediate features as seen in SAM P19158 and with such fragmentary material to its closest relative within the family. Therefore, the characters are discussed, and the fossil is assigned to a new species based on its variation to all other accipitrids to which it was compared, but it is not aligned with any genera.

The fossil sternum SAM P19158 shares the following character states with the Old World vultures:

1. 'Pushed back' carina. In lateral view, the carinal apex is either in line or posterior of the ventral labial prominence. Except in *Neophron percnopterus,* the carina is not pushed back.
2. The shape of the sternal plate is more open and U-shaped, when compared to the eagles.

The fossil sternum SAM P19158 differs from Old World vultures in the following states:

1. SAM P19158 has a very deep carina, Old World vultures tend to have a low carina with the exception of *Neophron* (Plate 6.1)
2. The carina is deepest proximally in SAM P19158, and not in Old World vultures, except in *Neophron* and *Gypohierax* (Plate 6.1)
3. The carinal apex is thick and well rounded in SAM P19158, and not so in most Old World vultures except in *Neophron*, *Gypohierax*, *Gypaetus* and *Necrosyrtes* and possibly *Neogyps errans* (Howard, 1932).
4. The ventral spine is narrow in SAM P19158. In Old World vultures it is broad with the exception of *Gypohierax. Neophronotops ricardoensis,* an accipitrid vulture from North America, has a small manubrial spine (Rich, 1980a)

Comparison of SAM P19158 to *Harpagornis moorei*

SAM P19158 is similar in size to *Harpagornis moorei*, yet it represents a separate taxon due to a significant number of morphological differences. SAM P19158 differs from *H. moorei* as follows:

1. The ventral manubrial spine does not extend as far anteriorly and distally and is smaller in *H. moorei* compared to that in SAM P19158;
2. The anterior carinal margin is more curved in *H. moorei*;
3. In ventral view, the carinal apex is situated further proximally in *H. moorei* and in line with the ventral manubrial spine. In SAM P19158, in ventral view, the carinal apex is located in line with the ventral labial prominence;
4. Lateral processes are not present in *H. moorei*, but are very large in SAM P19158;
5. The ventral labial prominences are square-shaped in anterior view in *H. moorei*, whereas they are rounded in SAM P19158.

Despite the similarity in size of SAM P19158 to *Harpagornis moorei*, it differs significantly enough that it represents quite a separate taxon. Furthermore, SAM P19158 would have most likely employed a different style of locomotion to *H. moorei* due to the depth of the carina and the slant of the carinal margin.

Comparison of SAM P19158 to modern eagle species

There are a number of points of difference between SAM P19158 and modern eagles:

1. SAM P19158 has very large, triangular-shaped lateral processes. *Aquila*, *Harpia*, *Pithecophaga*, *Stephanoaetus*, *Oroaetus*, *Geranoaetus*, *Haliaeetus*, *Accipiter*, *Hieratus*, and *Elanus*, have only slight to medium-sized lateral processes (Table 6.5). *Hamirostra* possesses very large lateral processes.

2. The carinal apex does not lie proximal to the anterior carinal margin in SAM P19158. In *Aquila, Pithecophaga, Stephanoaetus, Geranoaetus, Oroaetus, Haliaeetus, Accipiter, Hieratus, Elanus, Harpia, Terathopius, Hamirostra* and *Lophoictina* the carinal apex is located proximally to the anterior carinal margin (Table 6.5). This feature is suggested to be related to the flying style of the bird. In flapping birds, such as eagles, the carinal apex is located proximal to the anterior carinal margin (Dr Richard Holdaway, pers. comm.). In gliding birds such as Old World vultures, the carinal apex is distal of the carinal margin, with the exception of *Gypohierax*.
3. Shape of the sternum in cross section is V-shaped in eagles, whereas it is more half-circular in SAM P19158 (Table 6.5).

SAM P19158 shares some conditions with the eagles as follows:

1. Rounded and thick carinal apex;
2. The carina in SAM P19158 is relatively deep;
3. The carina is deepest proximally;
4. Ventral manubrial spine appears from the cross section as though it would be relatively narrow.

These features are present in the eagles, however, a few of these features are seen in some members of the Old World vultures.

Discussion

The following table lists features seen in Old World vultures, eagles and the fossil SAM P19158, so as to give a clearer overview of the differences. However, these features are very general, and there are some exceptions within the vultures, which is to be expected in light of the suggested polyphyletic status of the group. Whilst every effort was made to obtain numerous specimens for comparison, not every genus within the Accipitridae was obtained for comparison.

Table 6.1: Comparison of the fossil sternum to eagles and Old World vultures

Feature	**Eagles**	**Old World vultures**	**SAM P19158**
Carina depth	Very deep	Medium to shallow depth (***except** deep in *Gypohierax* and *Neophron*)	Deep
Deepest point of carina	Deepest proximally	Depth relatively even along the sternum (***except** in *Gypohierax* and *Neophron*)	Deepest proximally
Carinal apex shape	Thick and rounded apex	Thin apex (***except** in *Neophron* and *Gypohierax*)	Thick well rounded apex
Carinal apex position (in lateral view)	Aligned proximally of the ventral labial prominence	Aligned with or distally of the ventral labial prominence (except in *Gypaetus*)	Aligned distally of the ventral labial prominence
Shape of sternal plate	V – shaped in cross section	Wide U – shaped in cross section (except *Gypohierax*)	Wide U – shaped in cross section
Lateral processes	None to slight	Notch present	Enormous notches
Ventral manubrial spine	Narrow	broad, (***except** in *Neophron* and *Gypohierax*.)	Narrow (as seen from the scar)

Howard (1932) outlined the characters of the sternum of the Old World vultures as distinguished from the eagles as follows: low carina; broad ventral manubrial spine; and a short and broad sternocoracoidal impression. Contrary to Howard (1932), Jollie (1976) stated that "a type of sternum, limited to the subfamily Aegypiinae, cannot be characterized by any single feature or combination of features, unless the species content of that subfamily is altered." For example, the carina depth in *Gypohierax*, *Neophron*, and *Gypaetus* is not "low" when compared with *Necrosyrtes*, *Gyps* and *Aegypius*. The ventral manubrial spine is narrow in *Gypohierax*. These character states of the sternum of Old World vultures do not distinguish all modern genera of the group, and consequently cannot be used as a strict rule to distinguish all palaeospecies of Old World vultures. SAM P19158 does not have a low carina like those of the *Aegypius*-*Gyps* clade, nor a broad ventral manubrial spine, but as mentioned, these features are present in members of the Old World vultures. Furthermore, SAM P19158 does have a "pushed back" keel, which is only seen in members of the Old World vultures, and not in any of the eagles studied.

The absence of a broad ventral manubrial spine and low carina would suggest that SAM P19158 is not derived from the *Gyps-Aegypius* clade of vultures. Howard (1932) suggests these two features to be fairly constant within the accipitrid vulture subfamily and she suggests that these features are not simply related to vulturine habits. This supports the idea that the *Gyps-Aegypuis* clade seems an unlikely ancestor of SAM P19158, in light of the morphological differences between the two.

Hamirostra and SAM P19158 both possess very large ventral lateral processes, the apex of *Hamirostra* is relatively pushed back with the keel arising farther distally along the sternum as compared to the eagles, the apex is not pointed as with the eagles. Whether these two genera share a common ancestor, with the ancestors of SAM P19158 converging on the vulturine habits is a matter for contemplation, as with such little material it is not possible to distinguish the ancestor.

Whilst the eagles share a suite of character states, some of these character states are present in members of the Old World vultures as previously discussed. The pushed back keel, and a wide and open sternal plate are not observed in any of the eagles in this study, these features are only present in some members of the Old World vultures, and *Hamirostra* which possess a 'pushed back' keel. In particular, SAM P19158 shows more affinities to the *Neophron* and *Gypohierax* vultures than to the *Aegypius-Gyps* clade. *Neophron* and *Gypohierax* vultures and SAM P19158 are clearly not eagles yet they possess features that are seen in eagles and not in other members of the Old World vultures as discussed above. SAM P19158 could, however, be an independent vulturine accipitrid, unique to Australia, its similarities to accipitrid vultures being due to convergent evolution rather than sharing a common ancestor with the *Gyps-Aegypius* clade. This is not an unlikely scenario, as convergent evolution has been noted in other members of the Accipitridae. For example Feduccia and Voorhies (1989) described a species of hawk, *Apatosagittarius terrenus*, which converged on a secretary bird, and the similarities between *Ictinia* and *Elanus* kites is apparently due to convergent evolution (Shufeldt, 1896, as cited by Holdaway, 1994).

Palaeobiology

It has been suggested that the condition of the low and "pushed back" carina exhibited in the Old World vulture is an adaptation to their gliding flight (Richard Holdaway pers. comm). The *Aegypius* and *Gyps* appear to be relatively similar to one another in morphology of the sternum. *Neophron* shows quite different conditions (plate 8.1) of the sternum that could relate to its flight patterns. *Neophron* has been noted to use flapping flight more frequently when compared to *Aegypius* and *Gyps,* whose main mode of locomotion is gliding flight. *Neophron* has a deeper and less pushed back carina than that observed in *Gyps*, *Aegypius* and *Trigonoceps*. SAM P19158 could have used gliding as opposed to flapping as the main form of locomotion, which would help to conserve energy in such a large bird. Holdaway (1991) investigated the variation in skeletal element ratios to determine the flight patterns of palaeospecies; unfortunately, the measurements used are not applicable to this study due to the lack of fossil material.

Giant ungual phalanges from Mair's Cave

In addition to the sternum SAM P19158, two large ungual phalanges (SAM P19157, SAM P17139) typical of large accipitrids (refer to Plate 6) were collected from Mair's Cave, Buckalowie, South Australia. These ungual phalanges may be associated with the sternum due to their size and shape. Despite this, it cannot be assumed that the claws and sternum are positively associated.

Diagnosis of the Accipitridae ungual phalanx I: see Chapter Two.

Description:

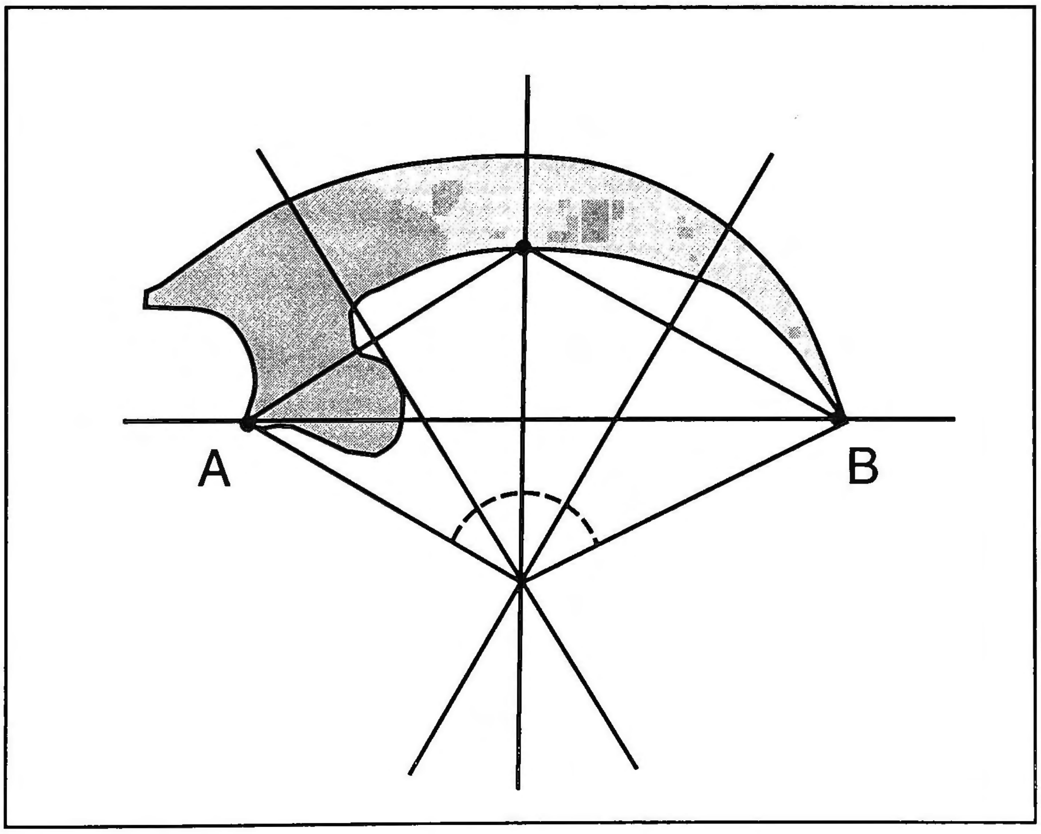
SAM P19157: typical of large active predators within the Accipitridae, in particular *Pithecophaga jefferyi*, but more robust; larger than those of extant Australian eagles *Aquila audax* and *Haliaeetus leucogaster*, highly curved; apophysis flexoris (Ballmann, 1976) or tuberculum flexorium deep, wide and robust; deep fossa present on both sides of the tuberculum flexorium; and the apex is missing (Plate 6.2).

SAM P17139: typical of large active predators within the Accipitridae, in particular *Pithecophaga jefferyi*, but more robust; larger than those of extant Australian eagles *Aquila audax* and *Haliaeetus leucogaster*, highly curved; slightly less robust than SAM P19157; apophysis flexoris (Ballmann, 1976) or tuberculum flexorium deep, wide and robust; and the apex is missing (Plate 6.2).

Method

The length, depth of the flexor tubercle and the depth of the cotyla of the fossil claws and those of other large species of accipitrids were measured. The claw curvature was measured using a similar method as per Feduccia (1993). However, a photocopier was used to take an image of each claw, rather than photographing the claws. A and B points used in this experiment were the distal most point of the *facies glenoidalis* and the claw apex respectively. Digit I of other accipitrids was used for comparison against the fossil claws. Claws were measured with and without a sheath covering where possible, however, most claws lacked a sheath. Only measurements from those claws lacking sheaths were used in the graphs unless otherwise stated. Claw curvature was graphed against claw length using Cricket.

Figure 6.2 Method for measuring the claw curvature (After Feduccia, 1993).



Measurements:

Table 6.2: Measurements of claw I of fossil birds compared to other accipitrids. All measurements in (mm).

Species	Claw no:	Number	Length	Flexor depth (A)	Depth of cotyla articularis (B)	Ratio of length to (A)	Ratio A/B
Mair's Cave		SAM P19157	43.6	22.5	15.8	1.94	1.42
Mair's Cave		SAM P17139	43.8	22.3	15.5	1.96	1.44
Aquila audax	I	MV B 19993	40.6	15.6	11.4	2.6	1.37
		MV W 3612	39.6	18.3	12.1	2.16	1.51
		MV W 5047	36.5	17.3	11.6	2.11	1.49
Pithecophaga jefferyi	I	MVZ 136481	44.8	20.8	14.1	2.15	1.48
		MVZ 136481	46.1	20.7	14.0	2.22	1.48
		MVZ 134059	44.2	20.2	14.0	2.19	1.44
		MVZ 134059	43.4	20.6	14.4	2.11	1.43
Spizaetus ornatus	I	MVZ 85551	40.2	16.5	11.0	2.43	1.50
		MVZ 85554	33.0	14.1	9.2	2.34	1.53
Haliaeetus leucogaster	I	MV B 13631	35.9	16.7	12.0	2.15	1.39
		MV B 13631	36.2	16.9	12.3	2.14	1.37
		MV B 12814	37.5	17.3	12.3	2.16	1.41
		MV B 12814	37.0	17.4	11.6	2.13	1.50
Harpagornis moorei	I	AV 10,472	57.7	31.7	21.3	1.82	1.49
		AV 12,354	57.2	33.0	22.7	1.73	1.45
Gyps fulvus	I	AV 21.207	33.1	13.8	10.2	2.39	1.35
		DM 15886	31.0	12	9.3	2.58	1.29
		MV W 6708	28.9	13.4	9.8	2.16	1.36
Aegypius monachus	I	AV 21,206	36.7	18.9	13.2	1.94	1.43
Trigonoceps occipitalis	I	USNM 347358	31.9	14.9	10.4	2.14	1.43
			31.9	14.8	10.2	2.16	1.45
Gypohierax angolensis	I	USNM 226143	26.4	13	8.5	2.03	1.53
			25.9	12.7	8.4	2.04	1.51
Gypaetus barbatus	I	AV 7139	35.5	16.8	10.9	2.11	1.54
		USNM 17834	34.8	17.1	11.4	2.04	1.50
		USNM 17834	34.9	16.2	10.7	2.15	1.51

Claw Curvature Results

SAM P19157 and SAM P17139 were found to have a curvature measured at 128.5° and (117.7°/127°) respectively. The results may be affected as SAM P17139 is missing considerably more of the apex than SAM P 19157 (Plate 6.2). Claw curvature was plotted against the claw length to compare the ratio of the two values to other large accipitrids, with particular emphasis on the difference between the Old World vultures and eagles. As the graphs, figure 6.3 and 6.4, do not take into account the overall size of the animal, only large accipitrids were used.

Table 6.3: Claw curvature (in degrees) of claw I in various species of large accipitrids

Species	*n*=	Min value	Mean	Max value
SAM P 19157	1		128.5	
SAM P 17139	1	117.7		127.0
Aquila audax		118.5	125.7	131.0
Haliaeetus leucogaster		110.5	125.3	130.0
Pithecophaga jefferyi	1		119.5	
Spizaetus ornatus	1		125.0	
Trigonoceps occipitalis	2	104.5	112.0	119.5
Gypohierax angolensis	2	115.0	118.0	121.0
Gyps fulvus	2	103.0	104.5	106.0
Neophron percnopterus	1		128.5	
Terathopius ecaudatus	1		147.0	
Spilornis cheela	1		121.0	

Claw Curvature Discussion

The claw curvature to length of SAM P19157 and SAM P17139 are relatively high and grouped with the eagles *Aquila audax, Haliaeetus leucogaster, Pithecophaga jefferyi* (Figure 6.3). Old World Vultures claw curvature tended to be lower than those of the eagles (Table 6.3), with the exception of *Gypoheirax* (claw curvature 118°). As eagles kill their prey with their talons they need a higher claw curvature to pierce their prey, whereas vultures diet consists of carrion and therefore highly curved claws for killing are not needed and less curved claws are more beneficial for walking on the ground. A high claw curvature to length suggests that the fossil claws belonged to an actively hunting predator rather than a carrion feeder, such as a vulture.

Flexor depth versus claw length

The flexor depth was plotted against the claw length in order to compare the fossil claws to other large accipitrids to assess if there is a significant difference between eagles and vultures. SAM P 19157 and SAM P 17139 measured to be similar to each other (Figure 6.4) suggesting that these claws came from the same taxon, and grouped with the eagles rather than the vultures suggesting that the claws belong to an active predator rather than a carrion feeder.

Claw Length versus sternum size

Old World vultures tend to have smaller claws in comparison to their body size when compared to the size of eagle claws versus body size. If the fossilized claws were, indeed, related to the sternum SAM P19158, which is as large as the *Harpagornis moorei* and those of the larger accipitrid vultures, the claws would be considered relatively small compared to the animal's body size for an active predator. The claws are considerably smaller than those of *H. moorei*, but slightly larger than those of the larger vultures with similar sternum size. The fossil claws are slightly larger than those of *Aquila* and *Haliaeetus*, but not to the degree expected if they were associated with the fossil sternum and represented an actively hunting accipitrid. The small fossil claws relative to large sternum suggests that the accipitrid had a more vulturine lifestyle. However, without a precise measurement of the fossilized sternum and the uncertainty of the relationship between the claws and the sternum, it is not possible to make an accurate assessment.

Table 6.4: Length of claw I and length of sternum of various accipitrids.

Species	**Number:**	**Claw Length (mm)**	**Sternum Length (mm)**	**Ratio of SL/CL**
Mair's Cave	SAM P 19157	43.6	Estimated length = 175 +/- 20	4.01
Mair's Cave	SAM P 17139	43.1	Estimated length = 175 +/- 20	4.06
Aquila audax	3571	37.4 36.6	105.4 105.4	2.82 2.88
Haliaeetus leucogaster	B12814	37.5 37.0	84.5 84.5	2.25 2.28
Pithecophaga jefferyi	MVZ 134059	44.2 43.4	117.9 117.9	2.66 2.72
Pithecophaga jefferyi	MVZ 136481	44.8 46.1	115.5 115.5	2.58 2.51
Harpagornis moorei	Mt Owen specimen	56.5	154.0	2.73
Trigonoceps occipitalis	USNM 347358	31.9 31.9	133.7 133.7	4.19 4.19
Gypaetus barbatus	AV 7139 USNM 17834	34.8 34.9	181.0 181.0	5.20 5.19
Gypohierax angolensis	USNM 226143	25.9 26.4	124.7 124.7	4.81 4.72
Aegypius monachus	AV 21,206	37.8 36.7	133.7 133.7	3.54 3.64
Gyps fulvus	AV 21,207	33.1 32.8	169.3 169.3	5.11 5.16
	MV W 6708	28.9 26.6	166.0 166.0	5.74 6.24

Figure 6.3: Arc angle versus the length of claw 1 in large accipitrids

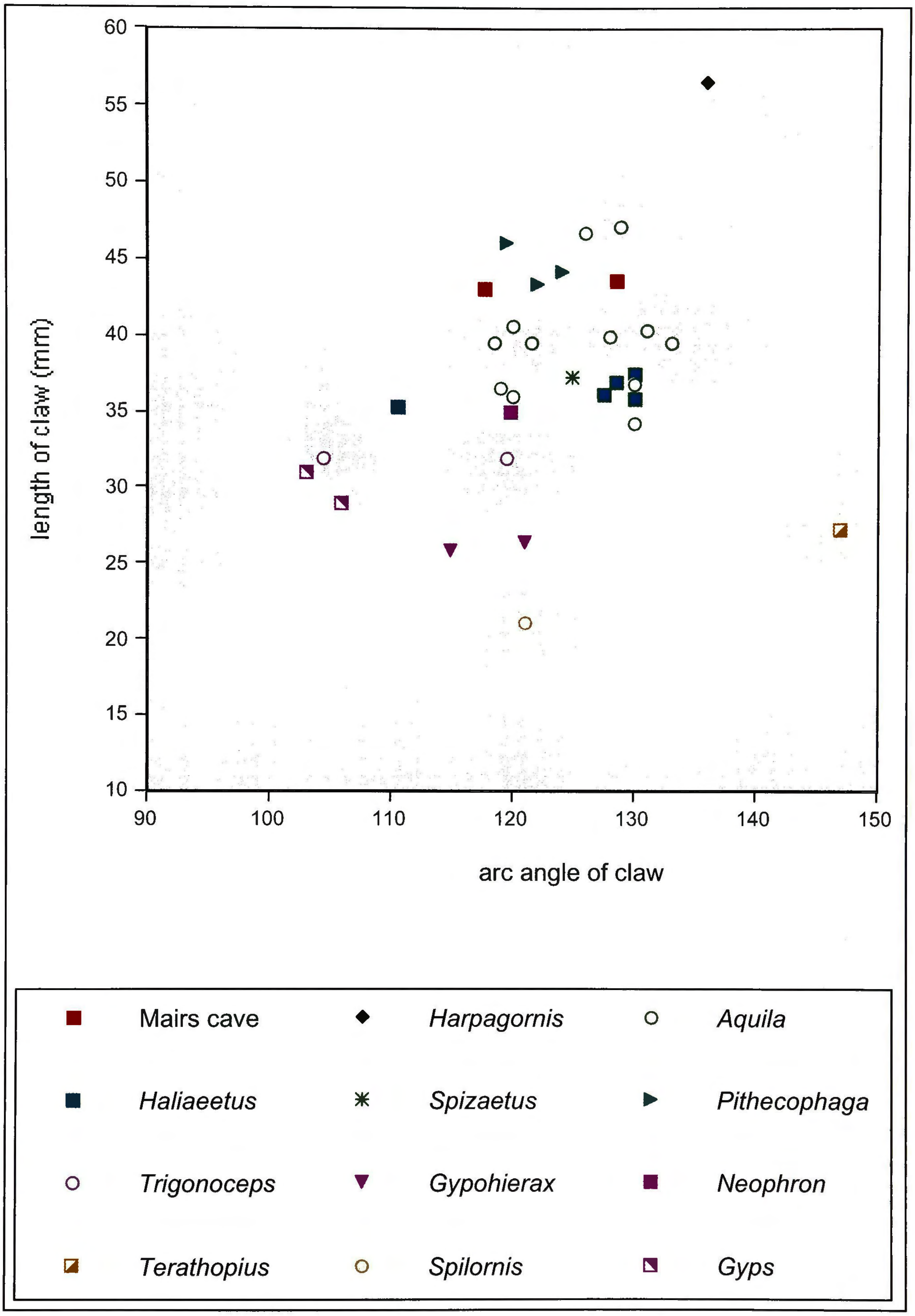
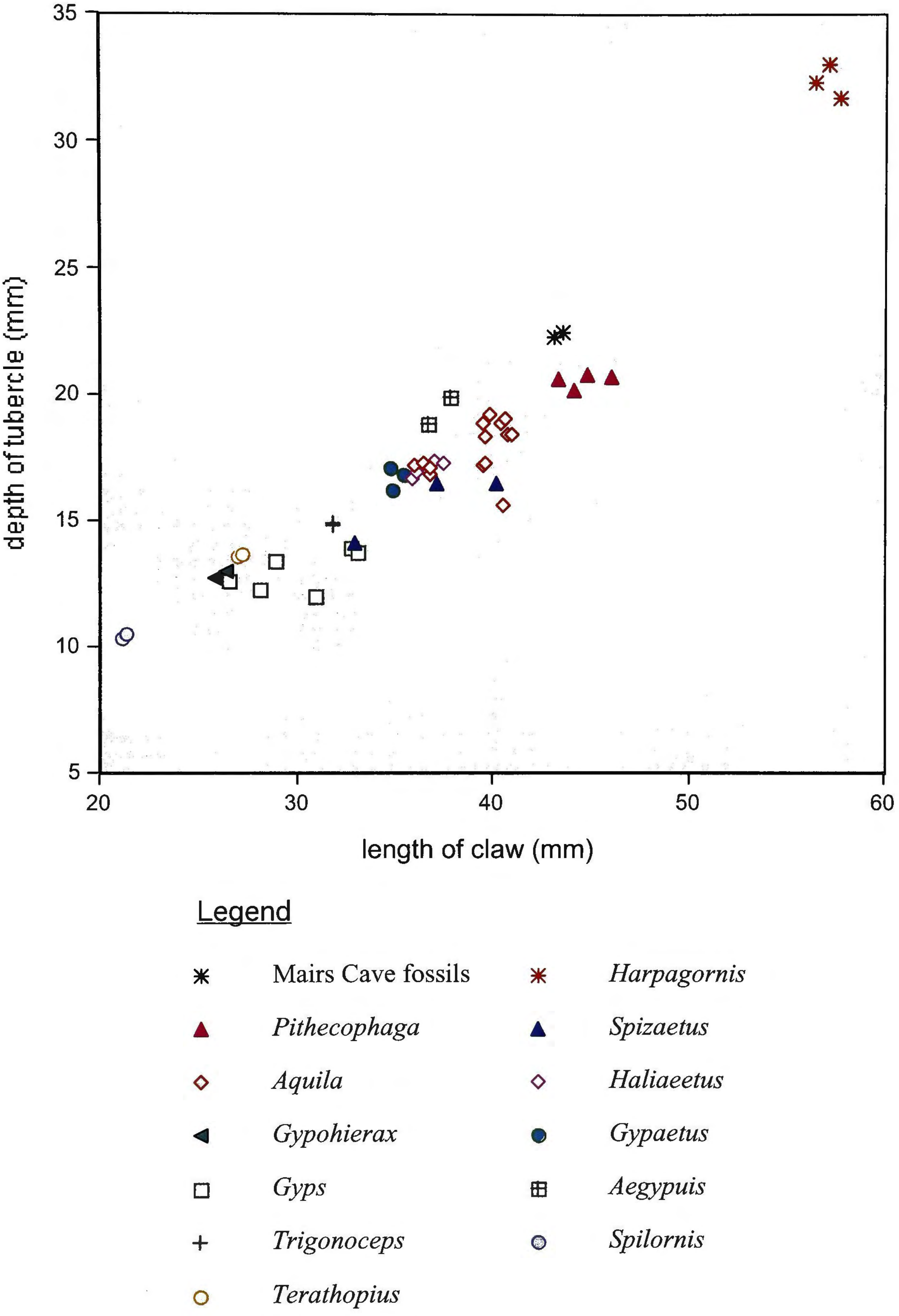


Figure 6.4: The length of the claw versus the depth of the tubercle of various large accipitrids



Conclusions

The sternum SAM P19158 represents a giant accipitrid, which is not a member of any extant species within Australia. Due to the degree of morphological variation in SAM P19158 when compared to modern accipitrid genera, the fossil material was assigned to a new genus and species; *Woltsha australensis*. Not all members of the Accipitridae were used for comparison, so identification may be subject to review at a later date when it is possible to study a representative from each genus within the family Accipitridae. SAM P19158 may be more closely affiliated with *Neophron* and *Gypohierax* vultures than any other members of the family Accipitridae, although whether this apparent affiliation is due to convergent evolution or a true relationship with either *Neophron* or *Gypohierax*, is a matter for further study in light of new fossil material. *W. australensis* shares many characters with *Hamirostra*, such as the pushed back keel and large lateral processes, but, again, with such little fossil material available it is important not to over interpret. *W. australensis* represents an accipitrid with vulturine adaptations but could have been derived independently of the extant accipitrid vultures in particular the *Gyps-Aegypius* clade. This would explain the significant variation *W. australensis* shows from both the accipitrid vultures and the eagles. Without more complete fossil material, it is not possible to determine the most probable phyletic position of *W. australensis*, and for this reason the fossil material is not aligned to any particular genus within the Accipitridae.

The fossil material, SAM P19158 (sternum), SAM P17139 (ungual phalange), SAM P19157 (ungual phalange) can be confidently assigned to the family Accipitridae. Due to the size and morphology of the claws, the fossils could be assigned to *W. australensis*, with SAM P19158 as the type specimen, as it is unlikely that Australia supported two separate taxa of giant accipitrids during the Pleistocene which happened to be fossilized in the same cave. However, there is danger in suggesting this, as has been the cause of misidentification in the past. I suggest that *W. australensis* was an accipitrid that used gliding, as the vultures do, more frequently, as a mode of locomotion as reflected in the relatively small and pushed back keel in SAM P19158. The claws (if associated) would further suggest a vulturine lifestyle based on the length of the claws compared to the size of the sternum; conversely, the highly curved claws suggest a more rapacious habit. *W. australensis* was truly unique compared to extant accipitrids, possessing a mosaic of features between the eagles and Old World vultures.

Table 6.5: Comparison of SAM P19158, sternum from Mair's Cave, to modern species of accipitrids

Species	No. of costal processes	Ventral manubrial spine	Anterior carinal margin	Carinal apex	Lateral processes	Carina	Shape of sternal plate
Fossil sternum, SAM P19158. Mair's Cave	5+	Broken, protrudes anteriorly	Slightly curved, margin well defined	Not protruding proximally over the anterior carinal margin	Very large, triangular	Deepest proximally, becoming shallow distally	Open bowl, U-shaped
Aquila audax B8524 Wedged-tailed Eagle	6 to 7	Flat proximally	Margin curved, well defined	Protrudes proximally of the margin. Slightly pointed.	Slight notches	Very deep proximally, becoming shallow distally	Deep, open, V-shaped
Stephanoaetus coronatus Crowned Eagle	7	Narrow	Curved, thick with a raised margin	Thick, bulbous, apex proximal of ventral labial prominence	Rudimentary	Deepest proximally, very deep, extends 90% of the sternum.	Deep, V-shaped
Pithecophaga jefferyi Monkey eating Eagle	6	Blunt, short, narrow triangular in cross section	Curved, with raised margin	In line with ventral labial prominence	Absent	Deepest proximally	Deep bowl
Harpagornis moorei Haast's Eagle	6	Not extending as far anteriorly and distally as P15198	Slightly more curved than P19158	Apex broken	Not present	Very deep	Concave and slightly narrower than P19158
Harpia harpyja Harpy Eagle	6	Elongate, triangular and rounded in lateral view	Curved and thick with a raised margin, Notch present	Rounded and wide. Keel thick in anterior view. Apex in line with the ventral labial prominence.	Very small triangles	Rounded, very deep, large	Highly concave
Haliaeetus leucogaster White-bellied Sea-eagle	6	Pointed proximally, arrow head shaped in side view	Margin curved, well raised	square and protrudes from margin	Medium sized notches	Very deep proximally, becoming shallow distally.	Very deep, V-shaped
Spizaetus ornatus Ornate Hawk Eagle	6	Blunt, short, triangular in cross section	Curved, with raised margin	In line with ventral manubrial spine	Rudimentary	Very deep proximally	Deep bowl
Geranoaetus melanoleucus astralia Buzzard Eagle	7	Very narrow	Straight, thick, raised margin	Thick, bulbous, located proximal of the ventral labial prominence	Rudimentary	Deepest proximally, very deep, extends along 90% of sternum	Deep, V-shaped

Table 6.5: Comparison of SAM P19158, sternum from Mair's Cave, to modern species of accipitrids

Feature/ Species	No. of costal processes	Ventral manubrial spine	Anterior carinal margin	Carinal apex	Lateral processes	Carina	Shape of sternal plate
Oroaetus isidori Black-&-chestnut Eagle	7	Very narrow	Diseased in specimen	Diseased	Rudimentary	Very deep, deepest proximally, extends 90% of the sternum	Deep, V-shaped
Hieraaetus morphinoides Little Eagle	7	Protrudes proximally, flat proximally, triangular in proximal view	Margin is slightly curved	protrudes slightly proximally over margin. Square to rounded	Slight notches	Deep, deepest proximally	Deep, V-shaped
Hamirostra melanosternon Black-breasted Buzzard	6	Blunt, almost square	Curved, notched anteriorly. Thick raised margin	Thick, bulbous, further proximally of the ventral labial prominence	Massive, pointed	Rounded, deeper proximally than distally	Open bowl shaped
Lophoictina isura Square-tail Kite	6	Triangular	Curved, with narrow raised margin	Narrow, rounded, proximal of ventral labial prominence	Large, pointed	Rounded, deeper proximally than distally	Concave, bowl shaped
Accipiter fasciatus Brown Goshawk	7	Very pointed, greatly protruding proximally	Well curved to half square margin	Protrudes proximally over margin and is pointed	Slight notches	Very deep proximally. Becoming shallow distally	Deep, narrow, V-shaped
Elanus notatus Black-shouldered Kite	6	Small, slightly protrudes proximally, square in side view	Notch in the centre of the margin	Does not protrude and is rounded	Slight to medium sized notches	Very deep proximally, becoming shallow distally	Open, deep bowl shaped
Aegypius monachus Cinereous vulture	5	Blunt, 3-leaf clover shape in cross section projecting distally	Highly curved, short, arises far posteriorly	Protruding proximal of carinal margin, squared, in line with posterior point of ventral labial prominence	Small notches	Rounded, and shallow	Highly concave
Gyps fulvus Griffon Vulture	5	Blunt, broad	Highly curved, Shorter than P19158. Keel arises more posteriorly than P19158	Rounded, protrudes slightly over the carinal margin	Wide and small notches	Rounded and shallow	Highly concave, open bowl shape
Trigonoceps occipitalis White-headed Vulture	5	Blunt, large, triangular	Short, curved, notch present, slight/short margin	Thin and pointed. In line with the ventral labial prominence	Small wide notches	Medium depth. Arises in line with the ventral labial prominence, shallower posterioly	Open bowl shaped

Table 6.5: Comparison of SAM P19158, sternum from Mair's Cave, to modern species of accipitrids

Feature/ Species	**Number of costal processes**	**Ventral manubrial spine**	**Anterior carinal margin**	**Carinal Apex**	**Lateral processes**	**Carina**	**Shape of sternal plate**
Neophron percnopterus Egyptian Vulture	6	Triangular, not extending far, broad.	Thick, with raised margin. Notch present. Curved margin, but not "pushed back" as in other vultures and fossil.	Rounded, thicker at apex than along margin. In anterior view, the apex is in line with the ventral labial prominence	Small notches	Very deep, deepest proximally	Highly concave
Gypaetus barbatus Bearded Vulture	6	Blunt, triangular in cross section, broad	Straight to curved, short with a raised margin.	Narrow, pointed. Posterior of ventral labial prominence	Pointed, large	Thick, shallow, and round	Wide, deep bowl/
Terathopius ecaudatus Bateleur	6	Large, triangular and well protruding	Straight, thick with well raised margin along it	Rounded, thick and bulbous	Large rounded bumps	Deeper proximally, arises just dorsal of the ventral manubrial spine	Concave, deep
Spilornis cheela Creasted Serpent Eagle	6	Blunt, and triangular in cross section	Curved, thick with raised margin.	Thick, divides into two, proximal of ventral labial prominence	triangular	Very deep proximally	Deep, open
Gypohierax angolensis Palm Nut Vulture	6	Blunt, triangular in cross section	Straight, notched, raised margin present	Thick and square	Pointed , triangular	Deepest proximally. Arises in line with the ventral labial prominence	Very deep
Necrosyrtes monachus Hooded Vulture	4 (5)	Triangular and well protruding	Curved and narrow	Narrow and almost at right angle	Slightly raised and wide bumps	Shallow, arises in line with distal point of ventral labial prominence	Concave, shallow bowl

Plate 6.1: Lateral view of the sternum of various accipitrids

Species	Common name
A) *Elanus axillaris*	Black-shouldered kite
B) *Aviceda subcristata*	Pacific baza
C) *Ictinia misisippiensis*	Mississippi kite
D) *Milvus migrans*	Black kite
E) *Haliastur sphenurus*	Whistling kite
F) *Hamirostra melanosternon*	Black breasted buzzard
G) *Hieraaetus morphnoides*	Little eagle
H) *Spizaetus ornatus*	Ornate hawk-eagle
I) *Accipiter fasciatus*	Brown goshawk
J) *Aquila audax*	Wedge-tailed eagle
K) *Circus approximans*	Swamp harrier
L) *Spilornis ecaudatus*	Serpent eagle
M) *Haliaeetus leucogaster*	White-bellied sea-eagle
N) *Pithecophaga jefferyi*	Monkey-eating eagle
O) *Gypohierax angolensis*	Palm-nut vulture
P) *Neophron percnopterus*	Egyptian vulture
Q) *Trigonoceps occipitalis*	White-headed vulture
R) *Gypaetus barbatus*	Lammergeier, or Bearded vulture
S) *Gyps fulvus*	Griffon vulture
T) *Necrosyrtes monachus*	Hooded vulture
U) *Terathopius ecaudatus*	Bateleur
V) ***Woltsha australensis***	**Mairs Cave accipitrid**

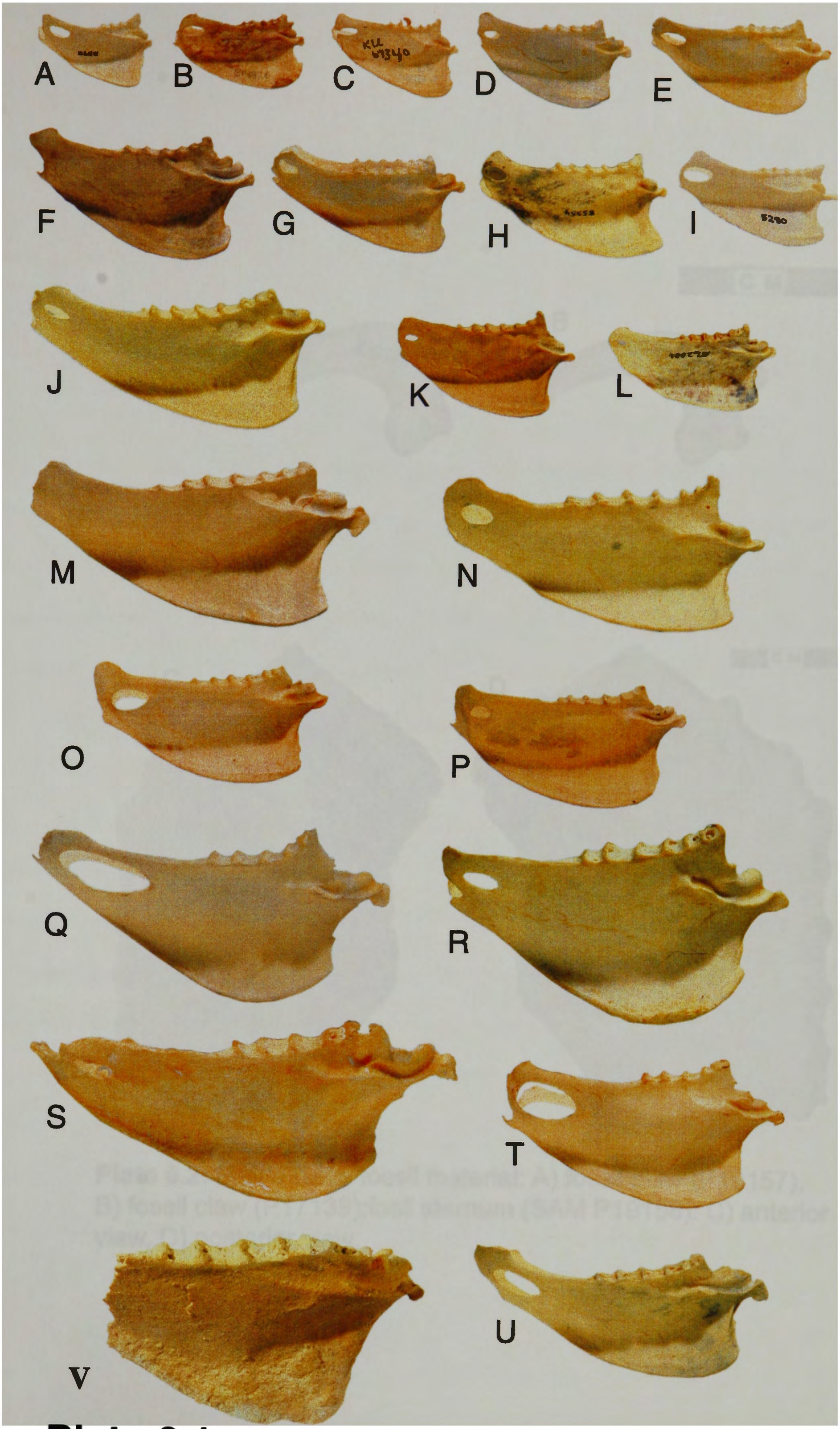


Plate 6.1

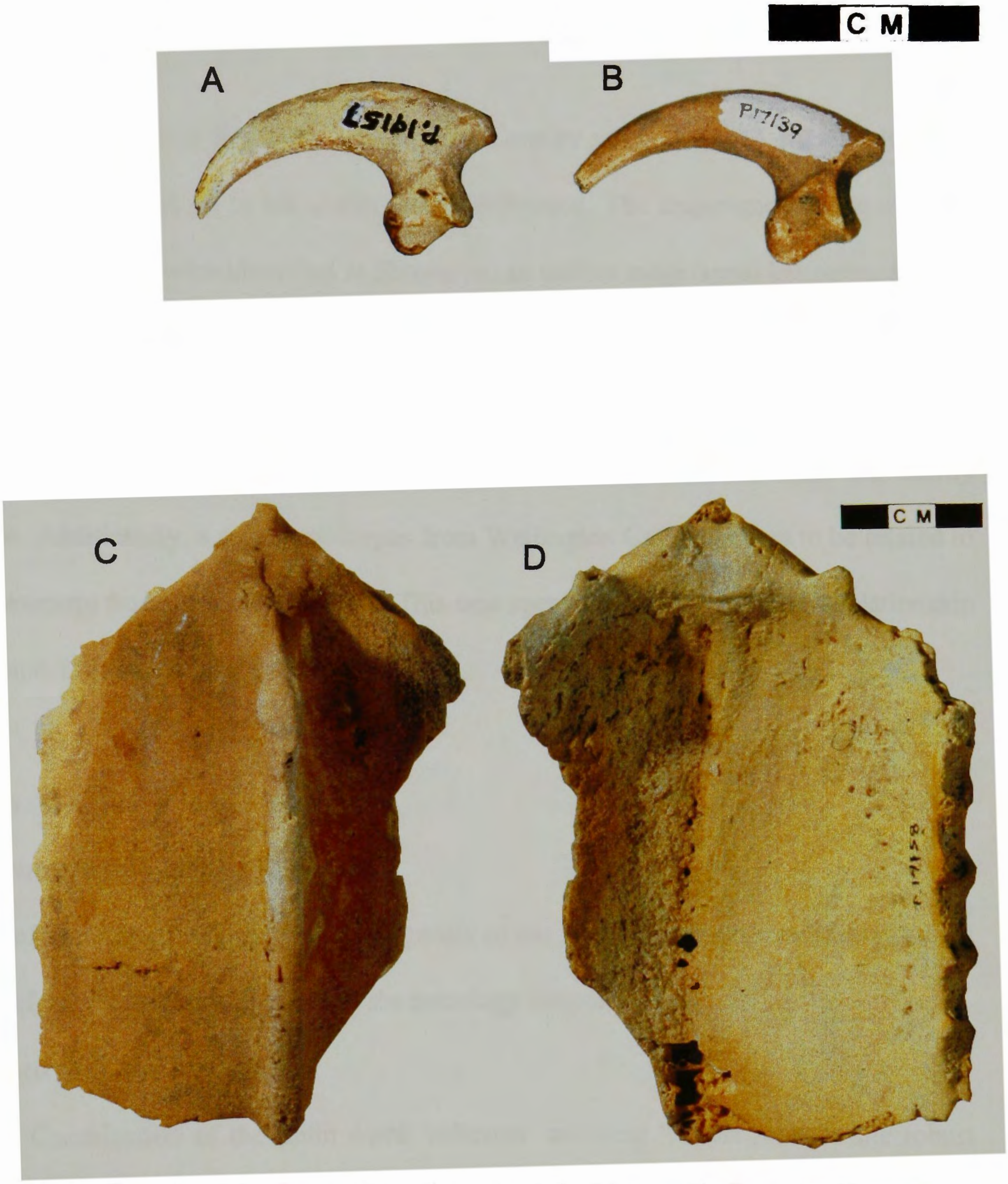


Plate 6.2: Mair's Cave fossil material: A) fossil claw (P19157), B) fossil claw (P17139);fosil sternum (SAM P19158): C) anterior view, D) posterior view.

Chapter 7: A new species of accipitrid from Green Waterhole Cave, South Australia

Introduction

Bones were first discovered from Green Waterhole Cave by scuba diver, G. McKenzie. They were subsequently passed on to Mr. Aslin for identification. The importance of the site was realized when the bones were identified as *Sthenurus*, an extinct megafaunal kangaroo. Further diving expeditions revealed semi-articulated specimens (Pledge, 1980). Among the specimens retrieved from the cave, sixteen species of birds have been identified. All but three of these are referable to modern species (Baird, 1985). Of the new species, one is from the family Accipitridae. Additionally, a carpometacarpus from Wellington Caves appears to be related to the carpometacarpi from Green Water Hole. This new species is described, and its relationship to other accipitrids discussed in this chapter.

Systematics

Family Accipitridae (Vieillot, 1816)

Diagnosis (of the Accipitridae): For the diagnosis of the Accipitridae carpometacarpus, ulna and radius refer to the relevant sections in the osteology chapter.

Robustopternis **gen. nov.**

Etymology: Combination of the Latin word ‘robustus’ meaning ‘robust’, due to the robust size of the wing bones, and 'pternis' (Greek) meaning 'bird of prey'. The gender is feminine.

Type species: *Robustopternis marywaltersae* **sp. nov.**

Diagnosis:

The genus *Robustopternis* can be distinguished by possessing the following character states: the carpometacarpus is robust; the internal and external margins of the carpal trochlea extend equal lengths distally; metacarpal II is very robust, with a deep and curved tendinal groove extending 90% of the length; the intermetacarpal space is wide, narrowest proximally, and increasing in width distally; and the distal metacarpal symphysis is thick and wide. The ulna is very robust and slightly curved; the papillae are closely spaced along the shaft; and the impression of *brachialis anticus* extends about 25% of the length of the shaft and is relatively shallow and wide. The radius is robust, and slightly curved; the intermuscular line runs along 70% of the shaft length; the humeral cotyla is oval; and the ligamental papilla is prominent, rectangular and connected to the head of the radius.

Robustopternis marywaltersae **sp. nov.**

Etymology: dedicated to Mary Walters for all her help reading manuscripts, introducing me to the avian osteological collection and accompanying me to South Australia to collect this specimen. The gender is feminine.

Holotypes: complete left and right ulnae (SAM P24323, and SAM P24324), complete left and right radii (SAM P24325 and SAM P24326), complete left and right carpometacarpi (SAM P24327 and SAM P24328). All holotype material is held in the South Australian Museum, Department of Palaeontology.

Referred specimen: a thoracic vertebra (SAM P.24329)

Locality and stratigraphy: Green Waterhole Cave is a drowned cave in the Tantanoola district of south-east South Australia, L-81 of the Cave Exploration Group of the South Australia cave classification (Figure 7.1).

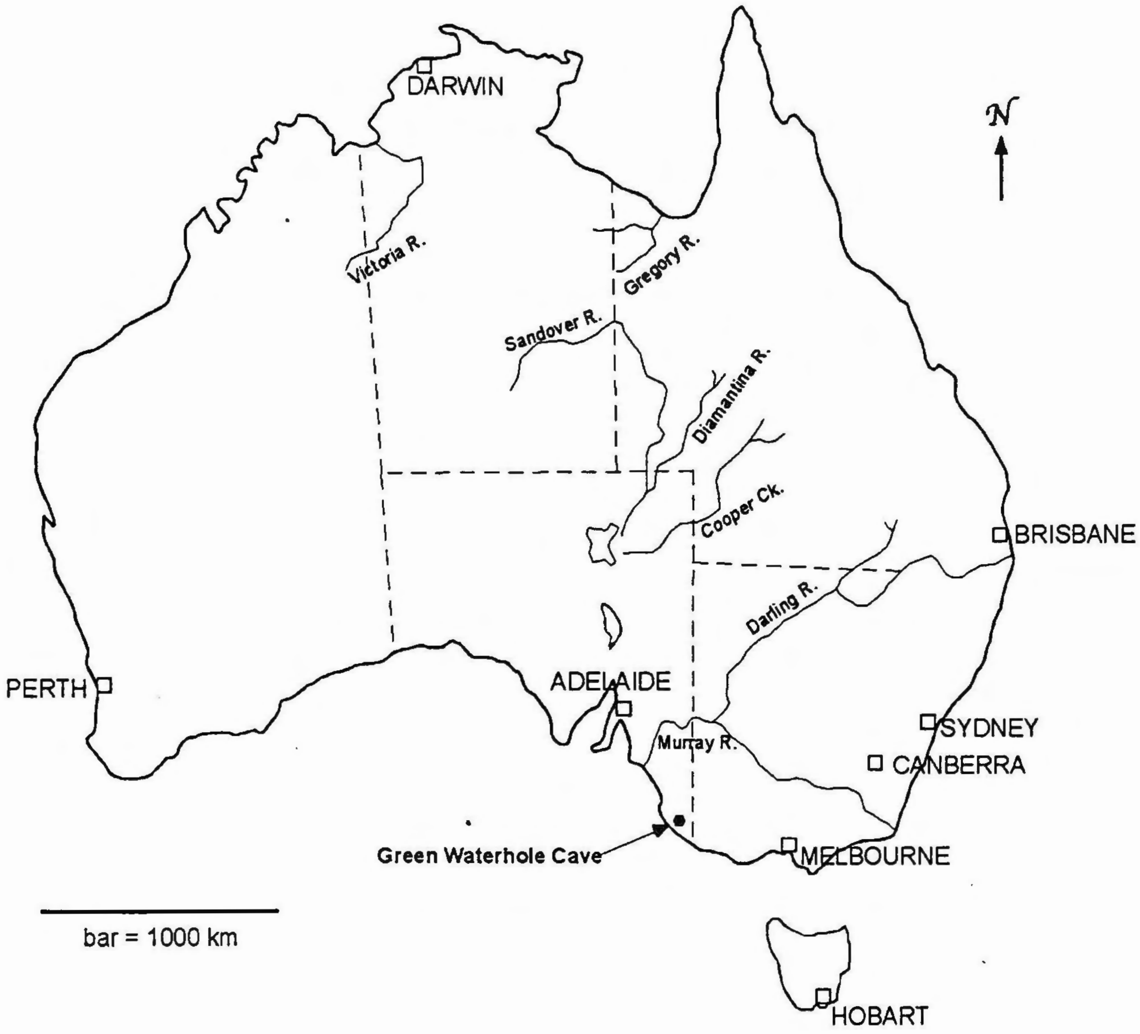


Figure 7.1: Quaternary locality, Green Waterhole Cave, South Australia

Age: Late Pleistocene: between 124,000 to 15,000 ybp is suggested because the last marine incursion in the area was 124,000 years ago, and the cave shows no marine influence (Baird, 1985). The minimum age for the cave is suggested as such due to this being the last date of mammalian megafauna survival in Australia, and this age is suggested to be the same for large extinct avian species (Baird, 1985). However, the minimum age for megafauna in Australia is now suggested to be greater than 40,000 years before present (Roberts *et al.*, 2001), based on this the age of the cave is between 124,000 to 40,000 ybp.

Diagnosis of *R. marywaltersae*: As for the genus.

Measurements:

Table 7.1: Carpometacarpus measurements (mm)

Number	Length	Prox width	Distal width	Metacarpal II width	Metacarpal II depth	Proximal depth	Distal depth	Proximal width of intermetacarpal space	Distal width of intermetacarpal space
P 24327	108.6	26.0	22.3	7.5	10.3	11.3	12.4	4.7	7.9
P 24328	108.5	26.0	21.6	7.7	10.0	11.6	12.4	5.0	7.5
Proximal carpo, Wellington	N/A	25.6	N/A	7.4	10.2	11.4	N/A	N/A	N/A

Table 7.2: Ulna measurements (mm)

P. number	Length	Pdv	d	Wd	Pap
P 24323	208.0	22.7	16.0	16.9	19.1
P 24324	207.0	22.7	16.0	16.4	18.8

Table 7.3: Radius measurements (mm)

P. number	Length	Distal width	Proximal width
P 24325	197.0	15.4	10.5
P 24326	195.0	15.5	9.8

Description:

Carpometacarpi SAM P24327 and SAM P24328: Overall, the carpometacarpus is robust. In external view, the internal and external margins of the carpal trochleae extend equal lengths distally. The internal ligamental fossa is deep, and a high ridge runs between the pisiform process and the carpal trochleae, which separates the posterior and anterior sections of the fossa. The pisiform process is well raised, oval and broad. The ligamental attachment of pisiform process is long and oval. The anterior carpal fossa is deep. The extensor attachment is oval, smooth. The process of metacarpal I is long and wide, with the proximal margin at an angle greater than 90° in external view. The pollical facet consists of two flat oval facets, with the external pollical facet slightly larger than the internal. The distal margin is entirely in contact with the shaft of metacarpal II. Metacarpal II is very robust, with a deep and curved tendinal groove extending 90% of the length. The intermetacarpal space is wide, narrowest proximally, and increasing in width distally. Metacarpal III is flat and broad proximally, narrower distally, and contains a deep groove on the surface facing the intermetacarpal space. The distal metacarpal symphysis is thick and wide. The facet for digit III is rectangular and projects distally.

Ulnae, SAM P24323-4: The shaft of the ulna is very robust and slightly curved, the papillae along the shaft are closely spaced. The olecranon is highly raised, smooth and square in proximal view. The internal cotyla is deep, wide, with the margin most highly raised proximally and distally, and less raised to the internal and external sides. The intercotylar area is rectangular, extending proximally as far as the external cotyla. The external cotyla is deep, square and projects distally to the palmar and external sides. The prominence for anterior articular ligament is slightly raised. The bicipital attachment is small, circular and slightly raised. The impression of *brachialis anticus* extends about 25% of the length of the shaft and is relatively shallow and wide. The margin of the external condyle is rounded but flat distally (in anconal view). In distal view, the internal condyle appears like a figure 8. A deep, circular groove runs between the internal condyle and the carpal tuberosity.

Radii SAM P24235-6: The shaft is robust, slightly curved, and the intermuscular line runs along 70% of the shaft length. The humeral cotyla is oval (proximal view), and of medium depth. The ligamental papilla is prominant, rectangular and connected to the head of the radius. The bicipital tubercle is raised, oval and convex. The ligamental prominence is a large, triangular and highly raised prominence. The ulnar depression is of medium depth. In anconal view, the scapho-lunar facet is pointed at the most external margin. The tendinal groove is of medium depth and width. (Medium depth pertains to comparisons with other accipitrids used in this study, Table 7.8).

Results and discussion

Comparison of the fossil material to the Family Accipitridae

There are many points of difference between the set of accipitrid fossils from Green Waterhole Cave and the modern and fossil counterparts with which they were compared. The fossil material was compared to the following species: *Aquila audax, Haliaeetus leucogaster, Harpagornis moorei, Terathopius ecaudatus, Hieraaetus morphnoides, Milvus migrans, Hamirostra melanosternon, Neophron percnopterus, Aegypius monachus, Gyps fulvus, Trigonoceps occipitalis, Gypaetus barbatus, Gypohierax angolensis, Spizaetus ornatus, Pithecophaga jefferyi* and *Spilornis cheela.*

Comparison of the carpometacarpi (SAM P24327-8) to modern accipitrids

The carpometacarpi, SAM P24327-8, exhibits similarity to the Old World Vultures. However, it is difficult to compile a list of characters to define the Old World Vulture carpometacarpus due to the polyphyletic evolution of the group as suggested by Sielbold and Helbig (1995). The fossil carpometacarpi SAM P24327-8 can be distinguished from the eagles, and show more affinity to the Old World Vultures and *Hamirostra melanosternon* for the following reasons:

1) In external view, the carpal trochlea extend distad equally in SAM P24327-8, this condition also is seen in *Terathopius ecaudatus, Milvus migrans, Hamirostra melanosternon, Neophron percnopterus, Aegypius monachus, Trigonoceps occipitalis* and *Gypaetus barbatus*. Whereas in *Aquila audax*, *Haliaeetus leucogaster, Harpagornis moorei, Hieraaetus morphnoides, Pithecophaga jefferyi, Spizaetus ornatus* and *Spilornis cheela,* the carpal trochleae extend to different lengths. The carpal trochleae extend to slightly different lengths in *Gypohierax angolensis* (Plate 7.2)

2) Metacarpal II of SAM P24327-8 is considerably wider and more robust when compared to *A. audax* and *H. leucogaster*. Metacarpal II is robust in *Gyps fulvus, Aegypius monachus, Gypaetus barbatus, Gypohierax angolensis* and *Hamirostra melanosternon* (Plate 7.1 and 7.2).

3) The distal metacarpal symphysis is considerably wide and deep in SAM P24327-8 (Plate 7.1). This condition is seen in the Old World vultures *Aegypius*, *Gyps*, *Gypaetus*, *Gypohierax*, *Neophron* and to a lesser degree *Trigonoceps* and *Hamirostra*. The distal

metacarpal symphysis is narrow and shorter in *Aquila, Pithecophaga, Spizaetus, Hieraaetus,* and *Haliaeetus*.

4) The carpal trochlea in internal view in SAM P24327-8 is semicircular (Plate 7.1). This condition is seen in *Gyps, Trigonoceps, Gypaetus*, *Gypohierax* and *Hamirostra*. The carpal trochlea extends more distally, producing a more complete, in *Aquila, Pithecophaga, Haliaeetus, Spizaetus* and *Hieraaetus*.

5) The carpal trochlea, in internal view, extends to terminate in line with the base of the pisiform process in SAM P24327-8 (Plate 7.1). This condition is seen in *Gyps*, *Gypaetus*, *Trigonoceps*, *Gypohierax*, *Neophron* and *Hamirostra*. The carpal trochlea, in internal view, extends further distally to terminate nearly in line with the pollical facet in the eagles such as *Aquila*, *Pithecophaga*, and *Harpagornis moorei*.

6) SAM P24327-8 exhibit a high degree of ossification proximally between metacarpal II and III, this condition is seen in *Trigonoceps*, *Gyps*, *Aegypius Gypaetus*, *Gypohierax* and *Hamirostra* (Plate 7.1). In the eagles, *Aquila*, *Pithecophaga*, *Hieraaetus*, *Spizaetus* and to a lesser extent *Haliaeetus*, the carpometcarpus is less ossified proximally between metacarpal II and III.

Summarizing the features which distinguish the eagles from the Old World vultures are as follows:

Table 7.4: Summary of the characters defining the carpometacarpus for eagles and accipitrid vultures.

Feature	**Eagles**	**Accipitrid Vultures**
Distal metacarpal symphysis	Medium length	Considerably deeper and wider
Degree of ossification proximally between metacarpal II and III	Ossified to a lesser extent	Greater degree of ossification
Shape of carpal trochlea in internal view	Circular Distal end of carpal trochlea in line with the pollical facet	Half circular shape Distal end in line with the pisiform process
Carpal trochlea in external view	Either (*H. moorei*) external margin of metacarpal III completely separate from carpal trochlea **OR** (*Aquila*) separate, not in line but with a faint margin between the two	External margin of metacarpal III lines up and merges with external distal margin of carpal trochlea.

Rich (1980a) noted that with regards to the ulna, no single set of characters could be used to set the Gypaetinae apart from the remainder of the accipitrids. The fossil ulnae (SAM P24323-4) can be distinguished from the modern Australian eagle genera, *Aquila* and *Haliaeetus*, and show more affinity to the Old World vultures than to the eagles due to the following conditions:

1) SAM P24323-4 ulnae are more robust in appearance than those of *Aquila audax* and *Haliaeetus leucogaster* (Plate 7.3) The following genera posses a robust shaft; *Gypaetus, Trigonoceps, Gypohierax, Aegypius, Gyps, Stephanoaetus cornatus* and *Harpagornis.*

2) The papillae are spaced closer together in SAM P24323-4 as compared to *Aquila audax, Haliaeetus leucogaster, A. chryaetos, Pithecophaga jefferyi, Stephanoaetus cornatus, Spilornis ornatus* and *Harpagornis moorei.* The papillae are closely spaced

in *Gyps*, *Aegypius*, *Gypoheirax*, *Gypaetus*, *Trigonoceps, Spizaetus ornatus* and *Hamirostra* (Plate 7.4)

3) SAM P24323-4 differ from all genera compared with as the prominence for the anterior articular ligament is only slightly raised in SAM P24323-4, but highly raised in *Aquila audax*, *A. chryaetos, Haliaeetus leucogaster*, *Pithecophaga jefferyi, Stephanoaetus cornatus, Terathopius ecaudatus, Harpagornis moorei, Aegypius monachus, Gyps fulvus, Trigonoceps occipitalis,* and *Gypaetus barbatus*.

Contrary to the accipitrid vultures, the fossil ulnae are short and robust, whereas modern genera of accipitrid vultures tend to have elongate and robust ulna. The condition of the increased number of papillae along the shaft was only observed in a smaller member of the eagles, *Spizaetus ornatus*, and not observed in the larger eagles.

Radii SAM P24325-6 represent a separate species compared to large members of Australian accipitrids. However, the value of the radius for diagnosis is limited, Howard (1932) stated that the radius proves to be an unsatisfactory bone for classification. It was not possible to find a suite of characters to distinguish between the eagles and the Old World vultures. For example; some of the larger members of the accipitrid vultures, *Gyps fulvus* and *Trigonoceps occipitalis,* posses pneumatic fossa on the ulnar depression, but this was not the case for all accipitrid vultures or SAM P24325-6. *T. occipitalis* and *Gypaetus barbatus* posses robust radii, whereas *Aegypius monachus*, *Gyps fulvus*, and *Gypoheirax angloensis* posses slender radii.

Nevertheless, SAM P24235-6 can be distinguished from extant large Australian accipitrids, *Aquila audax* and *Haliaeetus leucogaster,* by the following characters:

1) SAM P24325-6 are more robust than *A. audax*, and *H. leucogaster*.

2) In proximal view, the humeral cotyla is circular to oval-shaped, whereas in *A. audax*, and *H. leucogaster* the humeral cotyla is a definite oval. Rich (1980a) stated that *Aegypius*, *Gyps*, *Pseudogyps*, *Trigonoceps* and *Torgos* all possess a humeral cotyla that is nearly circular.

3) The bicipital tubercle is concave in SAM P24325-6, but convex in *A. audax*, and *H. leucogaster*.

Size comparison to modern analogues

Table 7.5: Ratio of the ulna length (mm) to carpometacarpus length (mm) in the Green Waterhole accipitrid compared to other accipitrids

Species	Number	Length ulna (a)	length carpometacarpus (b)	Ratio (a/b)
Robustopternis	SAM P24327	208.0	108.6	1.92
Robustopternis	SAM P24328	207.0	108.5	1.91
Eagles				
Aquila audax	25642	211.7	98.1	2.16
Aquila audax	25643	212.2	98.8	2.15
Aquila audax	25956	214.2	98.8	2.17
Aquila chrysaetos	DM 15894	224.0	107.4	2.08
Harpagornis moorei	S 23825	244.5	121.3	2.02
Harpagornis moorei	S 23611	268.6	125.3	2.14
Harpagornis moorei	DM 2134	259.8	124.4	2.09
Harpagornis moorei	Mt Owen	252.3	124.6	2.02
Spizaetus ornatus	MVZ 85551	141.9	65.4	2.17
Spizaetus ornatus	MVZ 85554	118.8	54.1	2.19
Pithecophaga jefferyi	MVZ 136481	210.5	91.2	2.31
Pithecophaga jefferyi	MVZ 134059	213.0	92.3	2.31
Accipitrid Vultures				
Aegypius cinereus	DM 15887	338.6	143.0	2.38
Aegypius cinereus	DM 15887	339.6	142.2	2.39
Gyps fulvus	DM 15886	326.2	132.4	2.46
Gyps fulvus	DM 15886	325.5	134.9	2.41
Trigonoceps occipitalis	USNM 347358	281.0	110.6	2.54
Gypaetus barbatus	USNM 17834	260.0	123.2	2.11
Gypohierax angolensis	USNM 226143	164.0	71.0	2.31
Hamirostra melanosternon	SAM B36200	159.6	77.2	2.06
Spilornis cheela	USNM562001	119.6	55.0	2.17
Terathopius ecaudatus	USNM 17836	194.5	79.2	2.46

The ulnae of *Robustopternis* are considerably robust compared to other accipitrids. The ulnae are notably short when comparing the ratio of ulna length to carpometacarpus length with other large accipitrids. *Robustopternis* has the shortest carpometacarpus to ulna ratio of all the accipitrids measured (Table 7.5). The ulna length to carpometacarpus length ratio in *Robustopternis* is closest to both *Hamirostra melanosternon*, typically a glider, and *Harpagornis moorei*, a forest eagle where short wings were advantageous for maneuvering through thick forest. The ratio of *Robustopternis* is considerably smaller than those of the accipitrid vultures *Aegypius*, *Gyps*, *Trigonoceps* and *Gypohierax* suggesting that the mode of flight used by *Robustopternis* would have differed somewhat from these genera, therefore, it was unlikely to have used gliding as the main mode of locomotion. On the contrary, *Gypaetus* has a small ratio compared to other accipitrid vultures, but not as small as is the case for *Robustopternis*. *Pithecophaga jefferyi* has a high ratio like the vultures, however, this bird typically uses flapping flight, and has a short broad wingspan adapted for living within rain forests of the eastern Philippines. This ratio may not be useful in suggesting whether the bird was primarily either a glider or flapper, but it does differentiate this bird from the typical ratio found in the *Gyps-Aegypius* clade.

Comparison with Australian palaeospecies of large accipitrids

Comparison with other large Australian fossil accipitrids proves impossible, as all other species are based on elements other than the carpometacarpus, ulna or radius. *Robustopternis marywaltersae* can be excluded from the Mair's Cave fossil material, due to the significant size difference; it is highly doubtful that an accipitrid possessing such a large sternum would posses such short wings. It seems unlikely to be related to *Taphaetus brachialis*, represented by a femur, as *Taphaetus brachialis* shares most similarity with accipitrid vultures, and is distinct from *Hamirostra melanosternon*.

Conclusion

Robustopternis differs significantly morphologically and proportionally, having the shortest ulna to carpometacarpus ratio of any of the large accipitrids, to all accipitrid genera in this study. While the ulna length to carpometacarpus ratio was closest to that of the eagles, morphologically the fossil carpometacarpus and ulna share more characters with the Old World vultures and *Hamirostra*, not with the eagles. Brown and Amadon (1968) suggested that the accipitrid vultures evolved from kites, and, therefore, had a distant relationship. Holdaway's (1994) research on the phylogeny of the Accipitridae using osetological characters found *Neophron* (Egyptian vulture) and *Pernis* (Honey Buzzard) to be a monophyletic group. *Hamirostra* shares many osteological characters of the carpometacarpus with the Old World vultures as discussed above, so perhaps these two groups have a distant relationship.

The Green Waterhole accipitrid, *Robustopternis*, is quite unique compared with extant accipitrids, and represents a truly unique and new palaeospecies of accipitrid within the Pleistocene of Australia. The Green Waterhole accipitrid may have shared a common ancestor with *Hamirostra melanosternon*, as the fossil material shares the most characters with this genus. Whether the *Hamirostra* and the Old World vultures share a common ancestor is questionable and could be the subject of further research, as they appear to share many characters particularly between the genera *Neophron*, *Gypohierax* and *Hamirostra*. The ratio of the length of the carpometacarpus to ulna length in *Robustopternis* is closer to *Hamirostra* than to accipitrid vultures. *Robustopternis* was most likely a giant vulture-like buzzard, or accipitrid, quite distinct from modern accipitrid vultures and from large accipitrids in Australia today. This degree of difference between the fossil taxon and modern taxa warrants setting up a new genus of accipitrid.

Table 7.6: Comparison of the carpometacarpus from Green Waterhole to other accipitrids

Feature	***Robustopternis marywaltersae*** P24327-8	***Aquila audax*** Wedged-tailed Eagle	***Haliaeetus leucogaster*** White-bellied Sea-eagle
Carpal trochlea (in external view, posterior margin of the carpal trochlea)	Slightly worn, carpal trochleae same length posteriorly	Carpal trochleae not the same length posteriorly	Carpal trochleae not the same length posteriorly
Internal ligamental fossa	Anterior of pisiform process deep, posterior deep, high bridge between the two regions	Deep, high bridge between the two	Deep, no bridge between the two
Pisiform process	Oval and thick	Smaller, and oval	Oval to rectangular, smaller
Anterior carpal fossa	Deep	Medium depth	Deep
Extensor attachment	Oval, smooth, rounded	Rectangular to oval, narrow and long	Oval to rectangular, thicker, similar to fossil
Process of metacarpal I	Large, long, wide, >90° to the carpal trochlea	Square shaped, =90° to the carpal trochlea, wider and shorter.	Similar to the fossil, >90° to the carpal trochlea
Pollical facet	Two oval bulbs of equal size.	External side much larger and oval, the internal bulb flat and small, the external pollical facet not touching the shaft	The external bulb is larger than the internal side of the pollical facet, internal side is flat, the external side is raised from the shaft
Metacarpal II	Robust	Thin	Thin
Tendinal groove	Thickest, deepest, curves slightly around metacarpal II, and extends 90% of metacarpal II	Deep, curves more than fossil, extends 90% of metacarpal II	Deep, more curved, extends 80% of metacarpal II
Intermetacarpal Space	Widest distally, narrower distally, overall wide	Slightly narrower than fossil, narrower proximally, widest distally	Narrower than fossil, narrower proximally, wider distally
Metacarpal III	Flat proximally, deep groove anteriorly, thinner and rounded distally	Broad proximally, thinner distally, anterior groove shallower than fossil. Metacarpal III thinner than fossil.	Thinner than fossil, anterior groove shallow, not as wide as fossil.
Distal metacarpal symphysis	Thick, high	Thinner than fossil	Thinner than fossil
Facet for digit 3	Protrudes distally	Protrudes distally, similarly to fossil	Protrudes greatest distance distally
Ossification proximally between metacarpal II and metacarpal III in internal view	Highly ossified	Moderately ossified	Moderately ossified
Shape of carpal trochlea in internal view	Semi-circular, terminates in line with pisiform processs	Circular, terminates distally of the pisiform process	Circular, terminates distally of the pisiform process

Table 7.6: Comparison of the carpometacarpus from Green Waterhole to other accipitrids

Feature	***Harpagornis moorei*** Haast's Eagle	***Terathopius ecaudatus*** Bateleur	***Hieraaetus morphnoides*** Little Eagle
Carpal trochlea (in external view, posterior margin of the carpal trochlea)	Trochleae not the same length posteriorly. External carpal trochlea does not extend into the external margin of the metacarpal III	Extends equal lengths	Carpal trochleae extend to different lengths. Slight margin connecting external carpal to the external margin of metacarpal III
Internal ligamental fossa	Very deep. Ridge present	Medium depth	Very deep. Raised margin
Pisiform process	Highly protruding. Oval shaped	Oval, raised	Oval. Well raised
Anterior carpal fossa	Deep	Shallow	Medium depth
Extensor attachment	Large, long oval to rectangular shaped	Distorted, large, oval shaped.	Narrow, oval and rounded.
Process of metacarpal I	Very wide, large and long. Square shaped. Angle greater than 90°	Oval, very well protruding. Angle larger than 90°	Large, thick and oval. Angle less than 90°
Pollical facet	Proportionally larger. Unequal shapes and sizes. External pollical facet not touching shaft	Not visible	Oval shaped. External raised from the shaft
Metacarpal II	Robust	Robust	Robust
Tendinal groove	Wide, deep, curves, extends 70-80% of metacarpal II	Curved. Shallow. Extends 80% of the metacarpal II	Deep, curved, extends 80%
Intermetacarpal space	Long, narrow, wider distally than proximally	Narrow	Wide, widest distally
Metacarpal III	Flat and broad proximally. Thinner and rounded distally. Deep anteriorly. Relatively straight and inline with metacarpal II	Flat and broad proximally. Rounded and narrow distally	Flat and broad proximally. Rounded and narrow distally
Distal metacarpal symphysis	Thick, but indented	Thick and concave	Narrow, concave
Facet for digit 3	Protrudes distally	Protrudes distally	Protrudes far distally
Ossification proximally between metacarpal II and metacarpal III in internal view	Wide gap	Moderately ossified	Not well ossified
Shape of carpal trochlea in internal view	Circular. Complete distally. Finishes distally of pisiform process	1/2 circle. Terminates in line with the pisiform process.	Circular. Terminates distally of the pisiform process.
Margin of carpal trochlea	Rounded, but sharper margin close to the anterior carpal fossa	Rounded with sharper margin nearer to anterior carpal fossa	Well rounded but with a sharp margin near anterior carpal fossa

Table 7.6: Comparison of the carpometacarpus from Green Waterhole to other accipitrids

Feature	***Milvus migrans*** Black Kite	***Hamirostra melanosternon*** Black-breasted Buzzard	***Neophron percnopterus*** Egyptian Vulture
Carpal trochlea (in external view, posterior margin of the carpal trochlea)	Carpal trochleae same length posteriorly. External carpal trochlea does not extend into the external margin of metacarpal III	Carpal trochleae same length posteriorly. Slight connecting margin between external carpal trochlea and external margin of metacarpal II	Carpal trochleae same length posteriorly. Slight connecting margin between external carpal trochlea and external margin of metacarpal II
Internal ligamental fossa	Medium depth. Slight ridge	Medium to shallow, slight ridge	Shallow
Pisiform process	Highly protruding, oval	Oval, protruding	Oval, raised
Anterior carpal fossa	Medium depth	Medium depth	Deep, pneumatic
Extensor attachment	Oval, rounded	Large, oval and rounded.	Distorted (zoo specimen)
Process of metacarpal I	Well extended. Angle less than 90°	Well extended. Oval. Angle greater than 90°.	Distorted (zoo specimen)
Pollical facet	2 indistinct ovals. Smooth. Flat. Only internal connected to the shaft	2 indistinct ovals. Smooth. Flat. Both connecting to the shaft.	Both equal size. Flat internal connected to the shaft.
Metacarpal II	Gracile	Robust	Gracile
Tendinal groove	Curved. Extends 80%	Curved. Deep. Extends 90% of the shaft	Deep, relatively straight
Intermetacarpal space	Narrower proximally than distally	Narrower proximally, wider distally	Narrower proximally, wider distally
Metacarpal III	Flat and broad proximally. Circular and narrow distally	Flat and broad proximally. Circular and narrow distally	Flat and broad proximally. Circular and narrow distally
Distal metacarpal symphysis	Narrow	Thick	Thick. Convex
Facet for digit 3	Protrudes distally	Protrudes very far distally	Protrudes distally
Ossification proximally between metacarpal II and metacarpal III in internal view	Well ossified	Well ossified	Greatly ossified
Shape of carpal trochlea in internal view	Rounded, circular. Extends past pisiform process	1/2 circle. Extends to be in line with proximal part of the pisiform process	Rounded, extends to be in line with the base of the pisiform process
Margin of carpal trochlea	Well rounded, but sharper margin closer to the anterior carpal fossa	Well rounded and 'smoothed over'	Well rounded, 'smoothed over'

Table 7.6: Comparison of the carpometacarpus from Green Waterhole to other accipitrids

Feature	***Aegypius monachus*** Cinereous Vulture	***Gyps fulvus*** Griffon Vulture	***Trigonoceps occipitalis*** White-headed Vulture
Carpal trochlea (in external view, posterior margin of the carpal trochlea)	Carpal trochleae same length posteriorly. External carpal trochlea extends into the external margin of the metacarpal II	Carpal trochleae do not extend same length posteriorly. External carpal trochlea extends into the external margin of the metacarpal II	Extend nearly similar length. Margin present between external carpal trochlea and external side of metacarpal II
Internal ligamental fossa	Deep, high ridge	Deep, ridge present	Shallow
Pisiform process	Relatively small. Raised, but less so than *H. moorei*	Oval, well raised	Highly protruding and oval
Anterior carpal fossa	Large open fossa	Large open fossa	Deep
Extensor attachment	Oval to rectangular shaped. Highly rounded, as opposed to flat surface of *H. moorei*	Oval. Highly raised in proximal view	Distorted
Process of metacarpal I	Large, square, wide. Angle greater than 90°, Wider and less protruding proportionally to fossil	Wide, large. Square. Angle greater than 90°. Wider and larger than fossil	Oval, (distorted) angle > 90°
Pollical facet	Proportionally small. External facet touching shaft. Ridge between the two indistinct	Relatively small. External slightly larger and not touching metacarpal II	Similar to fossil
Metacarpal II	Robust	Robust	Robust
Tendinal groove	Deep, wide, curved Extends 95%	Shallow, slightly narrower. Extends 80% of metacarpal II	Deep, slight curve
Intermetacarpal space	Wide, widest distally	Wide, widest distally	Wide
Metacarpal III	Flat and broad proximally. Thin and rounded distally	Flat and broad proximally. Thin and rounded distally	Flat and wide proximally. Circular distally
Distal metacarpal symphysis	Moderately thick and high	Very thick and high	Thick (but not as thick as in fossils)
Facet for digit 3	Large. Bulbous, protrudes distally	Protrudes distally but less so than fossil	Slightly protrudes distally
Ossification proximally between metacarpal II and metacarpal III in internal view.	Greatly ossified	Well ossified	Well ossified
Shape of carpal trochlea in internal view	Oval, terminates distally of the pisiform process	1/2 circle. Circular proximally. Blunt distally. Terminates in line with the pisiform process	Circular. Terminates in line with the pisiform process
Margin of carpal trochlea	Well rounded and smoothed over	Well rounded	Rounded and smoothed over

Table 7.6: Comparison of the carpometacarpus from Green Waterhole to other accipitrids

Features	***Pandion h. carolinensis*** Osprey	***Gypaetus barbatus*** Lammergeier	***Gypohierax angolensis*** Palm nut vulture
Carpal trochlea (in external view, posterior margin of the carpal trochlea)	Extends equal lengths. Definite margin between the external carpal connecting to external margin of metacarpal III	Carpal trochlea extend similar length. Slight margin between external carpal connecting to external margin of metacarpal III	Extend slightly different length. Slight margin between external carpal and external margin of metacarpal III
Internal ligamental fossa	Shallow. Slight raised margin	Deep with raised margin	Very deep with raised margin
Pisiform process	Oval, Very well raised	Oval. Well raised	Oval and raised
Anterior carpal fossa	Shallow	Wide, medium depth	Shallow
Extensor attachment	Small, circular, rounded	Distorted on specimen	Oval and rounded over
Process of metacarpal I	Long, oval, protruding. Angle greater than 90°	Large, square. Angle greater than 90°	Rectangular. Angle greater than 90°
Pollical facet	Small, circular, external facet raised from the shaft	Different sizes, external facet not touching shaft	Different sizes, both touching shaft
Metacarpal II	Gracile	Robust, oval in cross section	Robust, square in cross section
Tendinal groove	Shallow, extends 60%	Slight curve	Deep, slightly curved
Intermetacarpal space	Narrow	Narrow, not as wide as fossil	Wide
Metacarpal III	Flat proximally, circular distally	Flat proximally, circular distally	Flat proximally, circular distally
Distal metacarpal symphysis	Thick	Thick and convex.	Thick and convex
Facet for digit 3	Not visible in specimen	Protrudes distally	Protrudes distally
Ossification proximally between metacarpal II and metacarpal III in internal view.	Moderately ossified	Greatly ossified	Greatly ossified
Shape of carpal trochlea in internal view	Circular, distally of pisiform process	Rounded carpal, terminates distal of pisiform process	Half circle. Terminates in line with the pisiform process
Margin of carpal trochlea	Well rounded	Well rounded and smoothed over	Well rounded and smoothed over

Table 7.6: Comparison of the carpometacarpus from Green Waterhole to other accipitrids

Features	***Spilornis cheela*** Crested Serpent Eagle	***Spizaetus ornatus*** Crested Hawk-Eagle	***Pithecophaga jefferyi*** Monkey-eating Eagle.
Carpal trochlea (in external view, posterior margin of the carpal trochlea)	Extends different lengths. Slight margin between external carpal trochlea to external and with the internal trochlea	Extend different lengths	Extend different lengths
Internal ligamental fossa	Deep with raised margin	Very deep, highly raised margin	Deep
Pisiform process	Highly protruding and oval	Highly raised	Oval and raised
Anterior carpal fossa	Medium depth	Deep	Shallow
Extensor attachment	Oval and round	Oval and rounded over	Large oval/rectangular, rounded over
Process of metacarpal I	Large and oval. Angle >90°	Large, rectangular, angle less than 90°	Large, wide and rectangular, angle greater than 90°
Pollical facet	One continuous facet, joint to shaft	Equal sizes. External facet not touching shaft	Not equal, external facet not touching shaft
Metacarpal II	Robust, oval in cross section	Oval in cross section	Robust
Tendinal groove	Deep, slightly curved	Very deep, slightly curved, extends 90% of metacarpal	Deep, curved and extends 80% of the metacarpal
Intermetacarpal space	Wide	Wide	Wide
Metacarpal III	Flat and wide proximally, circular distally	Flat and broad proximally, circular distally	Flat and broad proximally, circular distally
Distal metacarpal symphysis	Relatively thick	Concave and thin	Concave and thin
Facet for digit 3	Protrudes distally	Protrudes distally	Protrudes distally
Ossification proximally between metacarpal II and metacarpal III in internal view	Less ossified than fossil	Not well ossified	Not well ossified
Shape of carpal trochlea in internal view	Circular, terminates distally of pisiform process	Circular, terminates distally of pisiform process	Circular, terminates distally of pisiform process
Margin of carpal trochlea	Rounded to sharp cf. fossil	Rounded and smoothed over	Rounded and smoothed over

Table 7.7: Comparison of the Ulna P24324 from Green Waterhole Cave, SA, to that of other accipitrids

Feature	***Robustopternis marywaltersae*** **P.243224**	*Aquila audax* Wedge-tailed eagle	***Aquila chrysaetos***	***Haliaeetus leucogaster*** White-bellied sea-eagle	***Harpagornis moorei*** Haast's Eagle
Shaft	Very robust, curved, papillae closely spaced	Thin, cylindrical, papillae widely spaced	Robust, papillae widely spaced	Thin, papillae widely spaced	Very robust, curved, Papillae more widely spaced
Olecranon	Highly raised, square and smooth	Highly raised, square, and smooth	Relatively pointed	Highly raised, square	Highly raised, smooth and square
Internal cotyla	Deep, wide, circular	Deep, circular, edges most raised distally	Deep, circular, distal end raised and pointed	Shallow, circular, distal end not raised	Deep, circular, pointed and raised distally, Large
External cotyla	Deep, square, protrudes palmar side distally and to the external side	Slightly shallower and smaller than fossil, rectangular, tapers distally	Smaller, deep, square, tapers distally slightly less	Smaller, slightly shallower than fossil, square, tapering distally	Square, and rectangular.
Prominence for anterior articular ligament	Slightly raised	Well raised, triangular	Well raised, bulbous	Well raised, triangular	Well raised and bulbous
Bicipital attachment	Small, circular, slightly raised	Rectangular, highly raised, proximally located	Large circular notch	Rectangular, angular to the shaft	Raised slightly
Impression of brachialis anticus	Shallow, long, wide	Shallow, narrow, deeper proximally, similar shape to fossil	Shallow, similar shape and size to the fossil	Shallow, deeper proximally, different shape to the fossil, pointed distally	Shallow, long and wide
External condyle	Rounded, but flat distally	Rounded, but flat distally	Rounded, but flat distally	Rounded entire margin	Well rounded
Internal condyle	Rectangular to a figure 8	Rectangular to oval, protrudes slightly less distally than fossil	Rectangular to oval, slightly more raised than fossil	Rectangular, similar shape to fossil, less raised than fossil	Large, rectangular, well protruding
Carpal tuberosity	Circular	Oval to triangular	Larger rectangular to oval	Square to oval,	Oval, proportionally larger than fossil
Incisura tub.carp.	Deep	Shallow	Shallow	Shallow	Deep
Number of papillae	14	11		12	12
Proximal radial depression	Medium depth	Shallow		Medium depth	Medium depth, similar to fossil
Tendinal pit	Oval, deep	Oval, deep		Oval, deep	Oval, very deep. No notch

Table 7.7: Comparison of the Ulna P24324 from Green Waterhole Cave, SA, to that of other accipitrids

Features	***Hieraaetus morphnoides*** Little Eagle	***Milvus migrans*** Black Kite	***Pithecophaga jefferyi*** Monkey eating Eagle	***Spizaetus ornatus*** Ornate Hawk-Eagle	***Stephanoaetus cornatus*** Crowned Hawk-Eagle	***Hamirostra melanosternon*** Black-breasted Bazzard
Shaft	Curved	Curved	Slightly curved, papillae raised and spaced out	Slightly curved, papillae close together (1/2 size of fossil)	Robust, curved, papillae less densely spaced cf fossil	Slightly curved, gracile, papillae close together
Olecranon	Highly raised and pointed	Highly raised, pointed	Raised and slanted	Highly raised and slanted	Highly raised and pointed	Highly raised and pointed
Internal cotyla	Deep, circular, Distally pointed	Circular, deep, distally pointed	Circular	Deep, circular, pointed distally	Circular, medium depth	Deep, circular, pointed distally
External cotyla	Narrow square	Square, but with distal overhang	Triangular shaped, distal overhang	Squared, distal end protruding	Square, distal overhang	Square. Distal end slightly protruding
Prominence for anterior articular ligament	Well raised	Raised	Bulbous	Well raised	Bulbous	Well raised
Bicipital attachment	Raised rectangle	Indistinct, raised rectangle	Raised	Circular and raised	Oval scar	Raised, Circular
Impression of *brachialis anticus*	Short, deep proximally, shallow distally	Oval, medium depth	Deep, 20% length of shaft	Deep, 25% the length of shaft	20% length of shaft, shallow	Deep, oval
External condyle	Oval and rounded	Rounded base, flat side	Circular	Circular	Circular	Flat distally, like a rounded square
Internal condyle	Smooth, oval	Rounded, raised	Rectangular	Rectangular	Rectangular	Figure-8 shaped
Carpal tuberosity	Moderately deep	Well protruding, flat distally	Oval, reduced	Extended	Protrudes, but not as far as fossil.	Well extended, flat distally
Incisura tub.carp.	Moderately deep.	?	Medium	Shallow	Shallow	Deep
Number of papillae	11	11	10	10	10	13
Proximal radial deprssion	Wide, deep	Deep and wide	Deep	Deep	Deep	Deep
Tendinal pit	Small and shallow	Deep	Moderate	Medium depth	Moderate	Deep

Table 7.7: Comparison of the Ulna P24324 from Green Waterhole Cave, SA, to that of other accipitrids

Features	***Terathopius ecaudatus*** Bateluer	***Neophron percnopterus*** Egyptian Vulture	***Aegypius monachus*** Cinereous Vulture	***Gyps fulvus*** Griffon Vulture	***Trigonoceps occipitalis*,** White-headed Vulture	***Gypaetus barbatus*** Bearded Vulture	***Gypohierax angloensis*** Palm Nut Vulture
Shaft	Curved	Slightly curved, gracile, papillae close together	Long, robust, papillae closely spaced	Long, robust, papillae close together	Curved and robust, papillae close and raised	Curved and very robust, papillae closely spaced	Curved, robust, papillae closely spaced
Olecranon	Raised	Highly raised, pointed	Highly raised. Pointed, slanted	Highly raised, pointed, slanted	Square and raised	Raised and square	Raised, square and slanted
Internal cotyla	Circular, deep, rounded distally	Deep, circular, pointed distally	Deep, circular, pointed and raised distally	Circular, deep, pointed and raised distally	Circular	Circular	Deep and circular
External cotyla	Square, protruding distally	Square. Distal end protruding	Square, distal margin fuses with shaft	Square, distal margin protrudes but fuses with the shaft	Square, overhangs distally	Square, lacks overhang	Overhang and square
Prominence for anterior articular ligament	Bulbous	Well raised	Well raised, bulbous	Well raised, bulbous	Very bulbous	Bulbous	Raised
Bicipital attachment	Highly raised, oval	Raised, circular	Raised, proximal	Slightly raised, proximal	Oval and raised	Raised and circular	Circular
Impression of *brachialis anticus*	Deep	Medium depth, oval, Short (cf. fossil)	Deep, wide, long	Medium depth, wide and long	Very deep, pneumatic, <20% length of shaft	Shallow, wide, 18% length of shaft	Deep, oval. Extends 20% of the shaft
External condyle	Small, circular	Rounded, but flat distally	Rounded, but flat distally	Flat distally, square with rounded edge	Circular, flat distally	Circular	Circular and flat distally
Internal condyle	Raised, oval	Not visible	Large, rectangular	Large, rectangular,	Rectangular	Oval	Shaped like figure 8
Carpal tuberosity	Not visible	Not visible	Very large, circular, well protruding	Very well projecting, circular	Well protruding and circular	Well protruding and circular	Well protruding and circular
Incisura tub.carp.	Deep	Not visible	Deep	Deep	Deep	Deep	Deep
Number of papillae	16	15	16	14	18	15	11
Proximal radial depression	Deep, wide	Deep	Very deep, pneumatic	Very deep, pneumatic	Very deep	Deep and wide	Moderate
Tendinal pit	Shallow	Medium depth	Shallow, slight notch	Medium depth, notched, circular	Deep	Deep	Shallow

Table 7.8: Comparison of the radius P24325, from Green Waterhole, SA, to those of other accipitrids

Feature	***Robustopternis marywaltersae*** **SAM P.24325**	***Aquila audax*** Wedged-tailed Eagle	***Haliaeetus leucogaster*** White-bellied Sea-eagle	***Aquila chrysaetos***	***Harpagornis moorei*** Haast's Eagle	***Pithecophaga jefferyi*** Monkey-eating Eagle	***Spizaetus ornatus*** Ornate Hawk-Eagle	***Hieraaetus morphnoides*** Little Eagle
Humeral cotyla	Circular to slightly oval, medium depth	Oval, deep	Oval, shallow	Oval, medium depth	Circular and deep	Oval and shallow	Oval and deep	Oval and deep
Ligamental papilla	Raised rectangular, joins to the head	Square, groove between the head and ligamental papilla	Relatively flat, rectangular, joins to head	Small, square, separate from the bicipital tubercle, touches head	Well protruding, circular, not attached to the head	Oval, connected to head	Raised, square, separate from the head.	Oval, raised, joined to head
Bicipital tubercle	Raised, oval, convex,	Oval, concave	Oval, concave	Oval, concave	Well raised, concave Fossa present	Raised and indented	Concave	Raised, oval with fossa.
Shaft	Robust, triangular in cross section, thick and rounded distally	High and sharp ridge along the shaft,	Thinner than fossil, more rounded ridge along the shaft, rounded distally	Thinner than fossil, high ridge along the shaft	Robust. Distal end oval in cross section. Broader than fossil.	Curved, gracile (like in *Aquila*)	Robust and curved	Gracile, curved
Ligamental prominence	Highly raised, 1 large knob	2 knobs, highly raised, ridge between the two	1 large knob similar to fossil, highly raised	Wide, raised, notch, ridge between	Well raised, small groove running proximo-distally along prominence	Bulbous feature, narrow compared to fossil.	Bulbous feature	Bulbous
Ulnar depression	Medium depth	Medium depth	Slightly deeper than fossil	Deep	Medium depth, slightly deeper than fossil.	Medium depth	Shallow to medium depth	Shallow
Scapho-lunar facet	More pointed than the other species	Less pointed than fossil	Less pointed than fossil	oval	Pointed in anconal view. Well developed with raised margin	Pointed	Broad and well pointed.	Pointed, well raised margin
Tendinal groove	Medium depth	Medium depth	shallow	Medium depth	Medium depth	Deep	Deep	Medium depth

Table 7.8: Comparison of the radius P24325, from Green Waterhole, SA, to those of other accipitrids

Feature	***Hamirostra melanosternon*** Black-brested Buzzard	***Spilornis cheela*** Crested Serpent Eagle	***Terathopius ecaudatus*** Bateleur	***Milvus migrans*** Black Kite	***Gypohierax angolensis*** Palm Nut Vulture	***Trigonoceps occipitalis*** White-headed Vulture	***Gypaetus barbatus*** Bearded Vulture	***Aegypius monachus*** Cinereous Vulture	***Gyps fulvus*** Griffon Vulture
Humeral cotyla	Circular and deep	Oval, deep	Oval, medium depth	Oval, medium depth	Oval, shallow	Oval, medium depth	Oval/circualr, medium depth	Deep and circular	Oval, medium depth
Ligamental papilla	Oval, raised, not attached to head.	Oval or rectangular, raised, not connected to head	Circular, raised, not touching head.	Round, raised, not attached to head	Raised, oval or rectangular, attached to head	Raised rectangular, attached to head	Slightly raised, close to head	Slightly raised, rectangular, not joined to head	Raised, rectangular, joined to head
Bicipital tubercle	Raised, round with fossa	Raised concave feature.	Raised, indented	Raised, with concave feature	Raised and concave	Raised, slight depression	Raised, concave	Raised, circular, convex	Raised, oval, convex, fossa present
Shaft	Gracile, very curved	Slightly curved, gracile.	Very well curved, gracile	Gracile and curved	Well curved, gracile	Curved, robust	Curved, robust	Long and slender, highly curved	Long, slender., highly curved
Ligamental prominence	Bulbous, similar to fossil	Bulbous	Bulbous	Bulbous, with groove in the middle	Bulbous	Raised feature with pneumatic fossa	Bulbous	Highly raised, bulbous, groove dissecting feature, pnuematic fossa proximal	Highly raised, bulbous groove, large pneumatic fossa proximally
Ulnar depression	Shallow	Shallow	Deep	Shallow	Shallow	Pneumatic, deep	Shallow	Very deep and oval	Very deep, pneumatic fossa
Scapho-lunar facet	Pointed in anconal view, well raised margin	Pointed in anconal view	Pointed in anconal view	Pointed in anconal view	Pointed in anconal view	Well pointed, anaconal view	Pointed in anconal view	Highly raised, pointed in anconal view	Highly raised margin, square in anoconal view
Tendinal groove	Medium depth	Deep	Shallow	Medium depth	Shallow	Medium depth	Medium depth	Shallow to medium depth	Medium depth

Plate 7.1: Internal view of the carpometacarpus of various accipitrids compared to the Green Waterhole fossil carpometatcarpus

Species	Common name
A) *Haliastur sphenurus*	Whistling kite
B) *Accipiter fasciatus*	Brown goshawk
C) *Buteo buteo*	Common buzzard
D) *Elanus axillaris*	Black-shouldered kite
E) *Aviceda subcristata*	Pacific baza
F) *Ictinia mississippiensis*	Mississippi kite
G) *Milvus migrans*	Black kite
H) *Lophoictinia isura*	Square-tailed kite
I) *Hamirostra melanosternon*	Black breasted buzzard
J) *Pithecophaga jefferyi*	Monkey-eating eagle
K) *Aquila audax*	Wedge-tailed eagle
L) *Haliaeetus leucogaster*	White-bellied sea-eagle
M) *Trigonoceps occipitalis*	White-headed vulture
N) *Gyps fulvus*	Griffon vulture
O) *Gypaetus barbatus*	Lammergeier, or Bearded vulture
P) ***Robustopternis marywaltersae***	**Green Waterhole accipitrid**
Q) *Hieraaetus morphnoides*	Little eagle
R) *Spizaetus ornatus*	Ornate hawk-eagle
S) *Gypohierax angolensis*	Palm-nut vulture
T) *Circus approximans*	Swamp harrier
U) *Terathopius ecaudatus*	Bateleur
V) *Spilornis cheela*	Serpent eagle

Plate 7.1

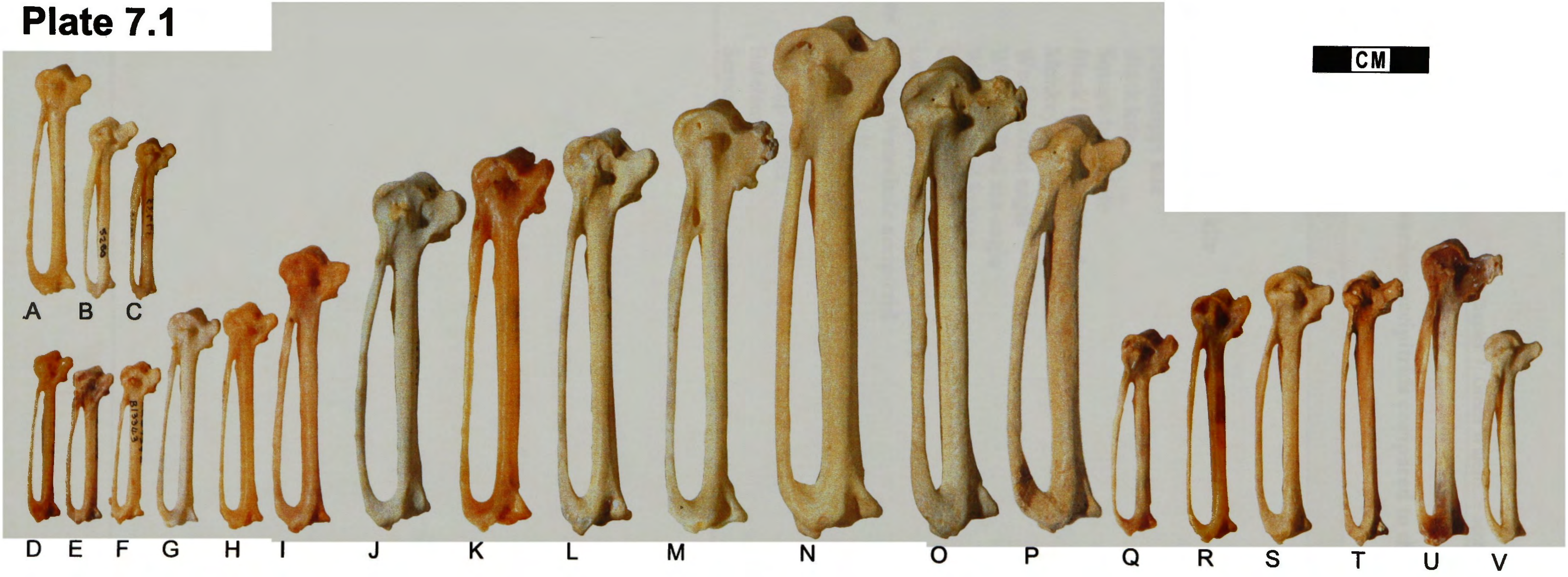


Plate 7.2: External view of the carpometacarpus of various accipitrids compared to the Green Waterhole fossil carpometatcarpus

Species	Common name
A) *Haliastur sphenurus*	Whistling kite
B) *Accipiter fasciatus*	Brown goshawk
C) *Buteo buteo*	Common buzzard
D) *Elanus axillaris*	Black-shouldered kite
E) *Aviceda subcristata*	Pacific baza
F) *Ictinia mississippiensis*	Mississippi kite
G) *Milvus migrans*	Black kite
H) *Lophoictinia isura*	Square-tailed kite
I) *Hamirostra melanosternon*	Black breasted buzzard
J) *Pithecophaga jefferyi*	Monkey-eating eagle
K) *Aquila audax*	Wedge-tailed eagle
L) *Haliaeetus leucogaster*	White-bellied sea-eagle
M) *Trigonoceps occipitalis*	White-headed vulture
N) *Gyps fulvus*	Griffon vulture
O) *Gypaetus barbatus*	Lammergeier, or Bearded vulture
P) ***Robustopternis marywaltersae***	**Green Waterhole accipitrid**
Q) *Hieraaetus morphnoides*	Little eagle
R) *Spizaetus ornatus*	Ornate hawk-eagle
S) *Gypohierax angolensis*	Palm-nut vulture
T) *Circus approximans*	Swamp harrier
U) *Terathopius ecaudatus*	Bateleur
V) *Spilornis cheela*	Serpent eagle

Plate 7.2

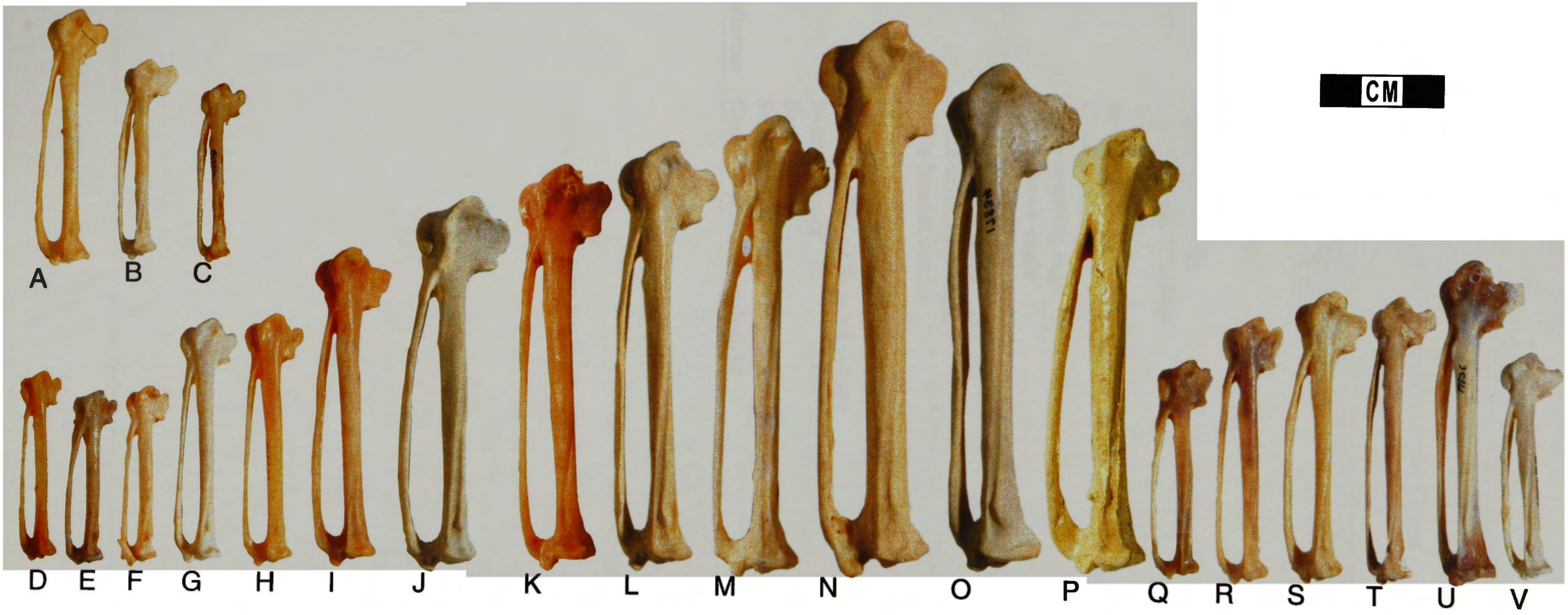


Plate 7.3: Palmar view of the ulna of various accipitrids compared to the Green Waterhole fossil ulna

Species	Common name
A) *Elanus axillaris*	Black-shouldered kite
B) *Aviceda subcristata*	Pacific baza
C) *Ictinia mississippiensis*	Mississippi kite
D) *Milvus migrans*	Black kite
E) *Lophoictinia isura*	Square-tailed kite
F) *Hamirostra melanosternon*	Black breasted buzzard
G) *Haliastur sphenurus*	Whistling kite
H) *Accipiter fasciatus*	Brown goshawk
I) *Buteo buteo*	Common buzzard
J) *Pithecophaga jefferyi*	Monkey-eating eagle
K) *Spizaetus ornatus*	Ornate hawk-eagle
L) *Hieraaetus morphnoides*	Little eagle
M) *Aquila audax*	Wedge-tailed eagle
N) *Haliaeetus leucogaster*	White-bellied sea-eagle
O) *Trigonoceps occipitalis*	White-headed vulture
P) *Gyps fulvus*	Griffon vulture
Q) *Gypohierax angolensis*	Palm-nut vulture
R) *Gypaetus barbatus*	Lammergeier, or Bearded vulture
S) *Circus approximans*	Swamp harrier
T) *Terathopius ecaudatus*	Bateleur
U) *Spilornis cheela*	Serpent eagle
V) ***Robustopternis marywaltersae***	**Green Waterhole accipitrid**

Plate 7.3

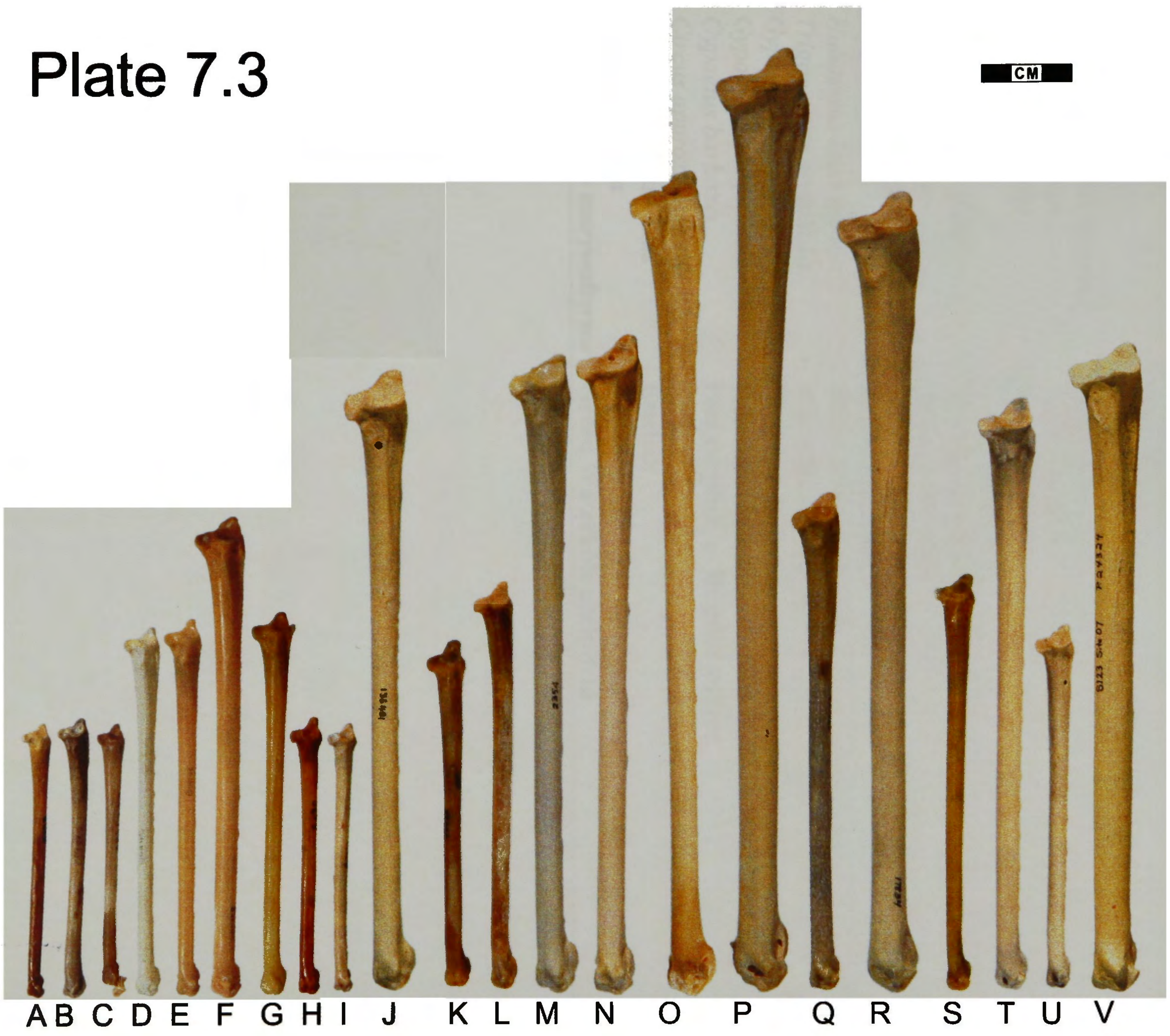
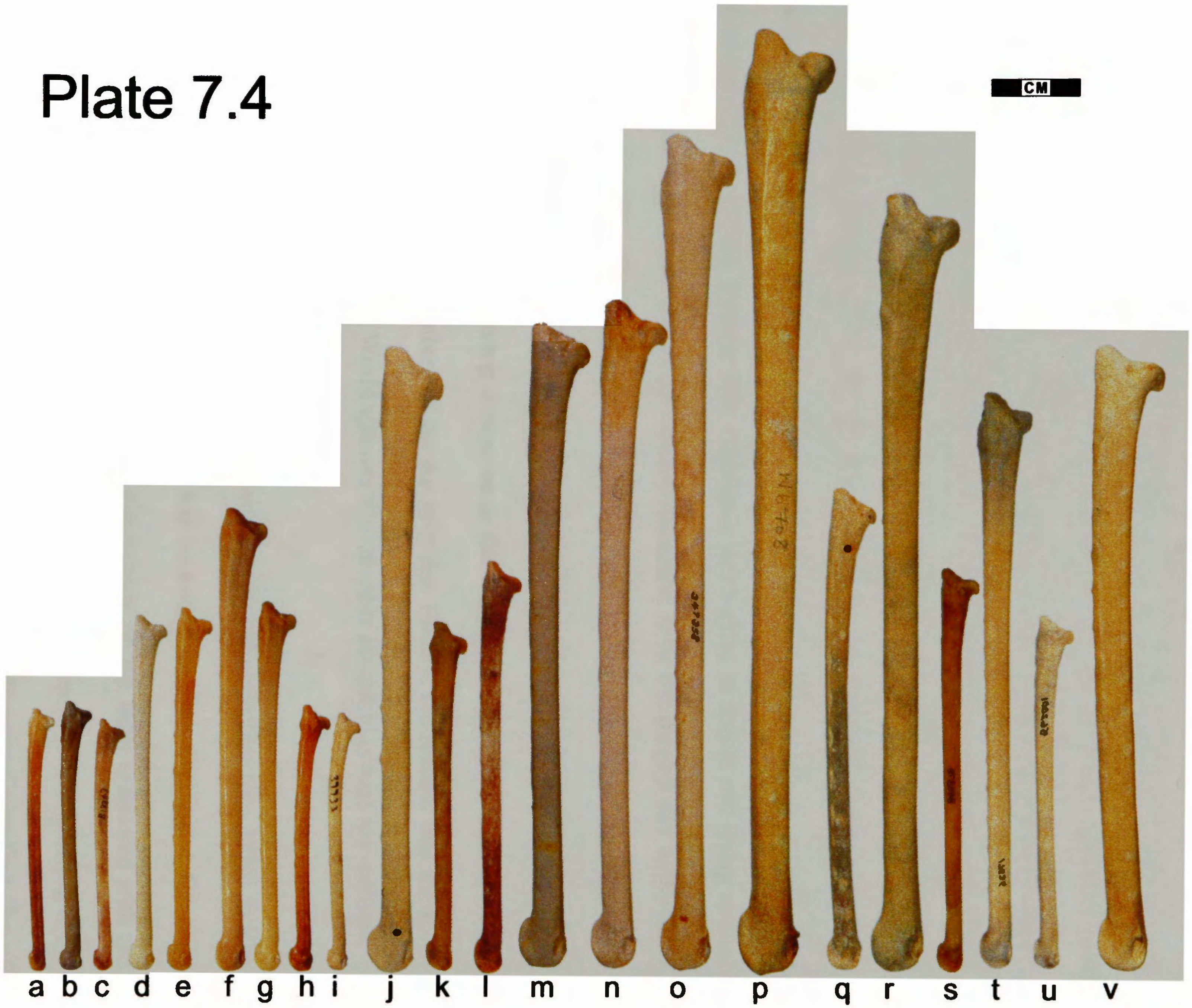


Plate 7.4: Anconal view of the ulna of various accipitrids compared to the Green Waterhole fossil ulna

Species	Common name
A) *Elanus axillaris*	Black-shouldered kite
B) *Aviceda subcristata*	Pacific baza
C) *Ictinia mississippiensis*	Mississippi kite
D) *Milvus migrans*	Black kite
E) *Lophoictinia isura*	Square-tailed kite
F) *Hamirostra melanosternon*	Black breasted buzzard
G) *Haliastur sphenurus*	Whistling kite
H) *Accipiter fasciatus*	Brown goshawk
I) *Buteo buteo*	Common buzzard
J) *Pithecophaga jefferyi*	Monkey-eating eagle
K) *Spizaetus ornatus*	Ornate hawk-eagle
L) *Hieraaetus morphnoides*	Little eagle
M) *Aquila audax*	Wedge-tailed eagle
N) *Haliaeetus leucogaster*	White-bellied sea-eagle
O) *Trigonoceps occipitalis*	White-headed vulture
P) *Gyps fulvus*	Griffon vulture
Q) *Gypohierax angolensis*	Palm-nut vulture
R) *Gypaetus barbatus*	Lammergeier, or Bearded vulture
S) *Circus approximans*	Swamp harrier
T) *Terathopius ecaudatus*	Bateleur
U) *Spilornis cheela*	Serpent eagle
V) ***Robustopternis marywaltersae***	**Green Waterhole accipitrid**

Plate 7.4



Chapter 8: A bone of an Old World vulture from eastern Australia

Introduction

The current distribution of Old World vultures (Family Accipitridae, Subfamily Aegypiinae) includes Africa, Europe, and Asia, whereas the New World vultures (Family Cathartidae) now inhabit North and South America. The modern biogeography of both groups of 'vultures' stands in stark contrast to the palaeodistribution of both the Old World and New World vultures. The Old World vultures (or accipitrid vultures) have a rich and diverse fossil record in the New World, extending back to the Early Miocene. Four distinct genera have been described from the fossil record of North America; *Arikarornis*, *Neophrontops, Neogyps* and *Palaeoborus* (Rich, 1980a). Despite their abundance and variety as fossils and living species elsewhere in the world, both groups of vultures are absent from the present day avifauna of Australia. Nevertheless, a tarsometatarsus found in the 'old' collection of the Australian Museum shows close affinities to Old World vultures and suggests that they were once present in Australia. In the following discussion of the fossil AM F58093, it is compared to and contrasted with various members of the Accipitridae. Finally, the reasons that the fossil shows more affinity with the Old World vultures than to other accipitrid groups are outlined.

Locality and stratigraphy: AM F58093 was found in an old collection (pre 1976) in The Australian Museum, Sydney, but unfortunately has no collection data. Wellington Caves in New South Wales (Figure 8.1) is suggested as the locality on the label associated with the fossil. This provenence may have been proposed based on the red earth matrix adhering to the fossil. The matrix is the same color and texture as the soil in Wellington Caves (but also of caves in many other parts of the world). Additionally, AM F58093 would fit within the taphonomic history, as suggested by Dawson and Augee (1997), of Cathedral Cave at

Wellington Caves. Dawson and Augee (1997) suggested that carcasses, of large animals that fell into the cave, would have attracted scavengers, which after entering the cave and been unable to escape, would have suffered the same fate and been incorporated into the deposits with their prey. It is, therefore, plausible that a carrion feeder such as a vulture (or even an eagle) would be preserved in the Wellington Caves deposit. Further investigation as to the origin of the fossil can be pursued using XRD (x-ray diffraction) analysis, of the adhering sediment, which could confirm the locality of the fossil, in a future investigation. The fossil, on the other hand, could have come from an overseas location, for example *Agrosaurus* was long thought to have come from Australia, only to later discover its original locality was in England (Vickers-Rich, pers. com).

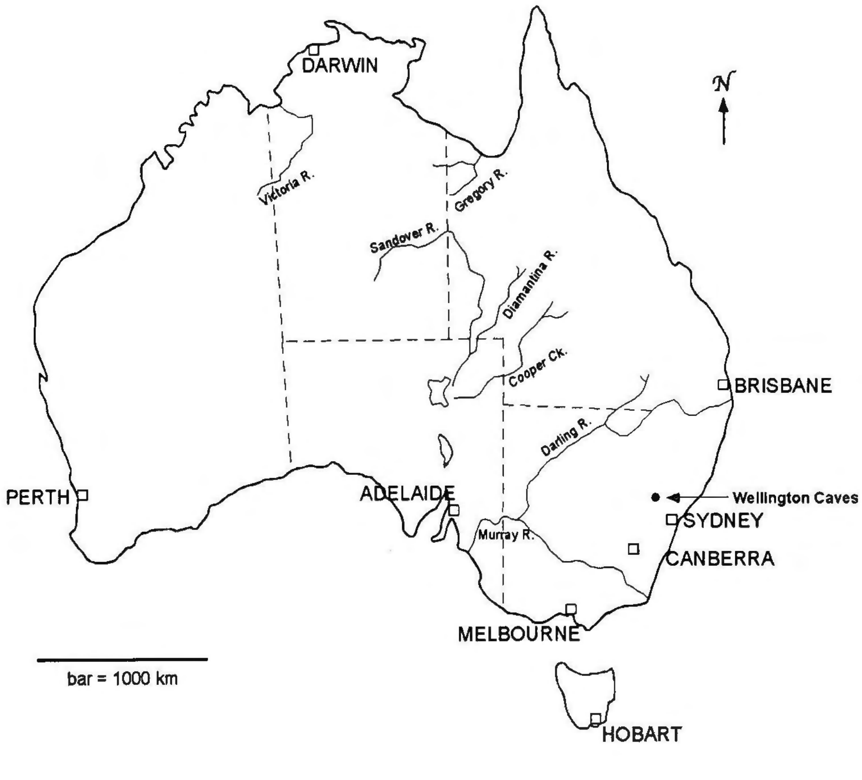


Figure 8.1: Wellington Caves, proposed locality for the vulturine tarsometatarsus (Accipitridae)

Age: Unknown (uncertain locality). If, however, the fossil is from Wellington Caves, it would be of Pleistocene age.

Material: AM F58093 tarsometatarsus (Plate 8.1, 8.2, 8.3).

Diagnosis (tarsometatarsus): See Chapter Two, diagnosis of the Accipitridae skeleton.

Description: In proximal view, the intercotylar area is highly raised and circular, projecting anterior to the cotyla; the internal cotyla is circular and deeper and larger than the square external cotyla. In posterior view, the internal calcaneal ridge of hypotarsus is missing. The external calcaneal ridge of hypotarsus is large, bulbous, and oval, it protrudes significantly from the shaft of the tarsometatarsus and is aligned with the long axis of the shaft. The hypotarsal calcaneal canal is narrow and shallow. In anterior view, the tubercle for *M. tibialis anticus* is prominent, oval, and medially located along the shaft between the lateral margins of the anterior metatarsal groove, distal to and relatively close to the proximal foramen. The anterior metatarsal groove is wide and deep, deepening further proximally, and deeply undercuts the cotyla area. The groove is displaced slightly to the internal side, not medially. The posterior metatarsal groove is deeply excavated, and is deeper on the internal side of the posterior part of the shaft than on the external side, giving it the appearance that it is located towards the internal side of the shaft. In distal view, the internal edge of trochlea II protrudes slightly laterally; it has a relatively shallow *fovea lig. collateralis.* Trochlea III is the widest and deepest trochlea. Trochlea II tapers slightly posterio-medially. Trochlea IV tapers slightly, posterio-laterally. The groove on trochlea III is deep, wide, and medial so that the internal side and the external side of trochlea III are equal. In distal view, the outline of the three trochleae is slightly curved. Overall, the bone is robust.

Measurements: (AM F58093) Greatest length 91.46 mm; proximal depth 22.1 mm; distal width 24.8 mm; distal depth 15.1 mm; smallest circumference width 12.8 mm; depth of trochlea II 8.7 mm; depth of trochlea III 11.9 mm; depth of trochlea IV 9.5 mm; width of trochlea II 6.05 mm.

Comparison of AM F 58093 with Old World Vultures and Eagles

Features on AM F 58093 that resemble those of tarsometatarsi of Old World vultures, and differ from those of most eagles are as follows:

1) In posterior view, the external calcaneal ridge of the hypotarsus is vertical to the shaft, and is a large and bulbous oval feature. This is not seen in any of the eagles, but is present in *Gyps fulvus* and *Aegypius monachus* (Plate 8.2);
2) In posterior view, the hypotarsal canal is narrow as in most gypaetines except in *Trigonoceps* where the hypotarsal canal is slightly wider than in most other Old World vultures (Plate 8.2);
3) In anterior view, the tubercle for *M. tibialis anticus* is oval, medially located and close to the proximal foramen in AM F58093, which is a vulturine feature (Jollie, 1976) (Plate 8.1);
4) In posterior view, the posterior metatarsal groove appears to be on the internal side of the shaft, a result of being deeper to its medial side and shallower to the lateral side of the shaft, thus forming a proximo-distal ridge (Plate 8.2);
5) In distal view, trochlea III is the deepest;
6) In distal view, trochlea II tapers only slightly postero-medially, in comparison to the state in the eagles;
7) In distal view, trochlea IV tapers only slightly posterio-laterally in comparison to the condition in eagles;
8) The groove on trochlea III is medial;
9) In distal view, the curvature across the trochleae is only slight.
10) Frenulum scars are absent, which Jollie (1976) noted as vulturine, with the exception of well developed scars present in *Gypohierax*, which habitually perches in trees (Plate 8.1).

Rich (1980a) pointed out that the following characters are shared by members of the Gypaetinae, with the exception of *Gypohierax* and *Neogyps*:

1) an enlarged third trochlea;
2) a shallow hypotarsal canal;
3) a hypotarsal ridge;
4) proximodistally shortened calcaneal ridges, nearly subequal in length.

AM F58093 agrees with the gypaetine states of these, except that part of the internal calcaneal ridge has been broken off, making it difficult to accurately assess character state 4. However, the external calcaneal ridge appears to be shortened in comparison to that in eagles.

AM F 58093 is similar to the tarsometatarsus of "eagles" as follows:

In anterior view, the anterior metatarsal groove is wide and deep, deepest proximally so that it undercuts the cotyla area, and it sweeps along internal side of the shaft. This condition is however, not unique to "eagles", being present in *Neophron percnopterus* among the gypaetine (Table 8.1).

Comparison of AM F58093 to the tarsometatarsus of some genera of North American Old World vultures

Comparison of AM F58093 with the tarsometatarsus of *Neogyps errans* (from plate 24 of Howard, 1933) shows that AM F58093 represents a different genus for the following reasons:

1) The external calcaneal ridge of the hypotarsus is horizontally aligned to the shaft in *Neogyps errans*.
2) The tubercle for *M. tibialis anticus* is more distal in *Neogyps errans* than in AM F58093.

3) The surface to the internal side of the inner calcaneal ridge of hypotarsus is concave in *Neogyps errans*, but not in AM F58093.

Comparison of AM F58093 with the figures of the tarsometatarsus of *Neophrontops americanus* in Howard (1932) and *N. ricardoensis* in Rich (1980a), shows that AM F58093 cannot be referred to *Neophrontops*. The tarsometatarsus of *Neophrontops* is far more gracile and elongate, and the external calcaneal ridge of hypotarsus is horizontally aligned to the shaft.

Discussion and conclusions

AM F58093 represents an Old World vulture, although, it is difficult to assess which genus AM F58093 is most closely related to from the material presently available. Whilst AM F58093 shares the feature of a vertically aligned external calcaneal ridge of hypotarsus with *Gyps* and *Aegypius*, (not present in any other accipitrids examined), other features in AM F58093 differ significantly from those genera, such as the wide and very deep anterior metatarsal groove in AM F58093. Given the similarities and differences, the taxon to which AM F58093 belongs could have derived from the *Gyps-Aegypius* clade, or it could have evolved independently from other ancestral accipitrid stock in Australia. Unfortunately, whether AM F58093 represents a vulture that evolved independently of other accipitrid vultures from ancestral stock in Australia, or was derived from a vulture from the north, cannot be determined from the limited material – a single bone – available.

AM F58093 varies enough from tarsometatarsi of all the genera to which it was compared, to be regarded a distinct genus within the Accipitridae. Erecting a new genus may not be appropriate in this case, as AM F58093 could perhaps be included in the existing taxon *Taphaetus brachialis* (de Vis, 1891b), which is based on vulturine accipitrid femur. The two specimens are, however, different elements, a femur and a tarsometatarsus, yet they are of relatively similar proportions as would be expected if they were both members of the same species. Both specimens are more closely aligned with the accipitrid vultures than any other group within the Accipitridae, for these reasons, I propose that AM F58093 is most appropriately placed as a paratype of *Taphaetus brachialis*, rather than erecting a new genus for a specimen which lacks locality data.

Table 8.1 Comparison of AM F58093 to various species of extant eagles and accipitrid vultures

Feature	**AM F 58093**	***Gyps fulvus*,** AV21,207, Griffon Vulture	***Aquila audax*** B8813 Wedge-tailed Eagle	***Haliaeetus leucogaster*** B11537, White-bellied Sea-Eagle	***Harpagornis moorei*** Haast's Eagle	***Pithecophaga jefferyi*,** 136481 Monkey-eating Eagle	***Spizaetus ornatus*,** 85554 Ornate Hawk-Eagle
Intercotylar area	Highly raised, circular, protrudes anteriorly to cotyla	Well raised, circular,	Raised, oval	Raised, rectangular	Raised, square	Slightly raised	Slightly raised
External calcaneal ridge of hypotarsus	Internal eroded, external oval, vertically aligned to the shaft large, bulbous	Long axis vertically aligned to the shaft, large, bulbous, oval	Small, oval, horizontally aligned to the shaft	Oval /rectangular, horizontal to the shaft, medium size	Long axis horizontal, rectangular/oval, internal calcaneal ridge protrudes further distally than external	Long axis horizontal, small and square	Long axis horizontal, small and square
Width of calcaneal canal	Narrow	Narrow	Wide	Medium width	Very wide	Very wide	Wide
Tubercle for *tibialis anticus*	Oval, central	Medial and close to proximal foramen, oval	Long oval, located along external margin of anterior metatarsal groove	Long oval to rectangular, located along external margin of anterior metatarsal groove	Oval, long, located far distally from proximal foramen	Located far from proximal foramen, very long	Located far distally from the proximal foramen, long
Anterior metatarsal groove	Wide, deep, deeper proximally as it undercuts the cotyla area, groove extends to the internal side	Wide proximally but shallow along the shaft	Wide, deep, groove predominately to internal side of shaft, undercuts cotyla area	Deep, narrow, groove on the internal side of shaft, slightly undercuts the cotyla area	Wide, deep, very deep proximally – undercuts the cotyla area	Deep proximally, undercuts the cotyla	Deep proximally, undercuts the cotyla
Posterior metatarsal groove	Deeply excavated to the internal side of the shaft	Deeply excavated along the internal side of the shaft	Deeply excavated, medial	Deeply excavated, medial	Deeply excavated to the internal side of the shaft	Deep and wide	Deep and wide
Trochlea 2	Internal edge slightly protruding posterio-laterally	Tapering posterio-laterally	Tapers well posterio-laterally	Internal edge tapers well posterio-laterally	tapers posterio-laterally	Highly tapered	Highly tapered
Comparison of trochleae	Trochlea 3 deepest; trochlea 4 tapers slighty posterio-medially	Trochlea 3 deepest and wides; trochlea 4 tapering posterio-medially	Trochlea 3 reduced compared with the fossil, trochlea 4 tapering well posterio-medially	Trochlea 3 reduced compared with the fossil, trochlea 4 tapering well posterio-medially	Trochlea 4 tapers posteriorly, trochlea 3 protrudes slightly further anteriorly than trochlea 2 and 4	Trochlea 2 and 4 well tapered, trochlea 3 small	Trochlea 2 and 4 well tapered, trochlea 3 small.
Groove on middle trochlea	Wide, medially located	Medially located, wide and deep	Off centre	Wide, off centre, external side larger	Wide, deep, internal side	Shallow, not medially located	Not medially located
Curvature across the trochleae in distal view	Slightly curved	Slightly curved	Highly curved	Highly curved	Highly curved	Highly curved	Highly curved
Proportions of tarsometatarsus	Robust	Robust	Elongated	Thin and long	Elongate, but robust	Very large and robust	Gracile
Notch for peronaeus nerve	Absent	Absent	Present	Absent	Very deep	Present	Present
Frenula scars	Absent	Absent	Present	Present	Well developed	Present	Present
Posterior ridge extending proximal-distally	Present	Raised and wide	Absent	Absent	Absent	Absent	Absent

Table 8.1. Comparison of AM F58093 to various species of extant eagles and accipitrid vultures

Feature	*Spilornis cheela* Crested Serpent Eagle USNM 562001	*Stephanoetus coronatus* 140190	*Trigonoceps occipitalis* USNM 347358	*Gypohierax angolensis* USNM 226143	*Gypaetus barbatus* AV7139	*Neophron percnopterus*	*Aegypius monachus* AV21,206
Intercotylar area	Slightly raised	Raised	Raised, circular	Raised, circular	Raised, square, protrudes slightly anteriorly	Rasied, circular	Raised, square, protrudes anteriorly
External calcaneal ridge of hypotarsus	Long axis vertical, pushed over	Long axis horizontal, pushed over to external side	Long axis horizontal. Pushed over to external side	Long axis horizontal, pushed over to external side	Long axis aligned vertically to shaft, small, circular	Square, pushed over to the external side, long axis horizontal	Long axis vertically, oval and bulbous
Width of calcaneal canal	Wide	Very wide	Wide	Narrow	Narrow	Narrow and shallow	Narrow
Tubercle for *tibialis anticus*	Located close to proximal foramen, raised oval	1cm distal of the proximal foramen	Medially located, oval, close to foramen	Close to foramen, long, oval	Circular, medially located 1cm from proximal foramen	Medially located close to proximal foramen, oval	Medially located close to proximal foramen, oval
Anterior metatarsal groove	Deep, undercuts the cotyla	Deep and wide, sweeping towards the external side	Shallow	Medium depth, undercuts cotyla	Wide and deep proximally, undercuts cotyla, shallow along shaft	Wide, deep, and undercuts cotyla area	Very deep and narrow proximally, shallow and wide along shaft
Posterior metatarsal groove	Very deep, wide	Very deep and wide	Deep to internal side	Wide and deep	Medium excavation, proximal on internal side	Excavated on internal side of the shaft	Deeply excavated on internal side of the shaft
Trochlea 2	Tapers posterio-laterally	Tapers posterio-laterally	Tapers posterio-laterally	Tapers posterio-laterally	Slightly tapering posterio-laterally	Tapers posterio-laterally	Tapering posterio-laterally
Comparison of trochleae	Trochlea 4 tapers well	Very curved	Trochlea 3 deepest	Trochlea 3 deepest	Trochlea 3 very deep, most distally protruding; trochlea 4 tapers posterio-medially	Trochlea 3 protrudes further anteriorly and distally; trochlea 4 small, tapers posteriorly	Trochlea 3 very wide, and deep, trochlea 4 tapers posteriorly
Groove on middle trochlea	Deep, wide, not medial	Deep, wide, not medial	Deep, medial	Not medial	Medial, wide and deep	Wide, deep, medial	Medial, wide, deep
Curvature across the trochleae in distal view	Moderately curved	Highly curved	Slightly curved	Slightly curved	Slightly curved	Moderately curved	Medium curvature
Proportions of tarsometatarsus	Elongate	Very stout	Elongated	Elongated	Stout	Elongate	Elongate but stout
Notch for peronaeus nerve	Present	Present	Present	Present	Present	Absent	Absent
Frenula scars	Present	Present	Absent	Slightly present	Absent	Absent	Absent
Posterior ridge extending proximal-distally	Absent	Absent	Raised	Slightly raised	Raised	Raised	Well raised

Plate 8.1: Anterior view of the tarsometatarsus of various accipitrids compared to a fossil vulturine tarsometatarsus from an unknown locality

Species	Common name
A) *Milvus migrans*	Black kite
B) *Lophoictinia isura*	Square-tailed kite
C) *Haliastur sphenurus*	Whistling kite
D) *Elanus axillaris*	Black-shouldered kite
E) *Aviceda subcristata*	Pacific baza
F) *Ictinia mississippiensis*	Mississippi kite
G) *Hamirostra melanosternon*	Black breasted buzzard
H) *Accipiter fasciatus*	Brown goshawk
I) *Buteo buteo*	Common buzzard
J) *Pithecophaga jefferyi*	Monkey-eating eagle
K) *Spizaetus ornatus*	Ornate hawk-eagle
L) *Hieraaetus morphnoides*	Little eagle
M) *Aquila audax*	Wedge-tailed eagle
N) *Haliaeetus leucogaster*	White-bellied sea-eagle
O) *Trigonoceps occipitalis*	White-headed vulture
P) *Gyps fulvus*	Griffon vulture
Q) *Gypaetus barbatus*	Lammergeier, or Bearded vulture
R) *Gypohierax angolensis*	Palm-nut vulture
S) *Circus approximans*	Swamp harrier
T) *Terathopius ecaudatus*	Bateleur
U) *Spilornis cheela*	Serpent eagle
V) **QM F 58093**	**vulturine tarsometatarsus**

Plate 8.1

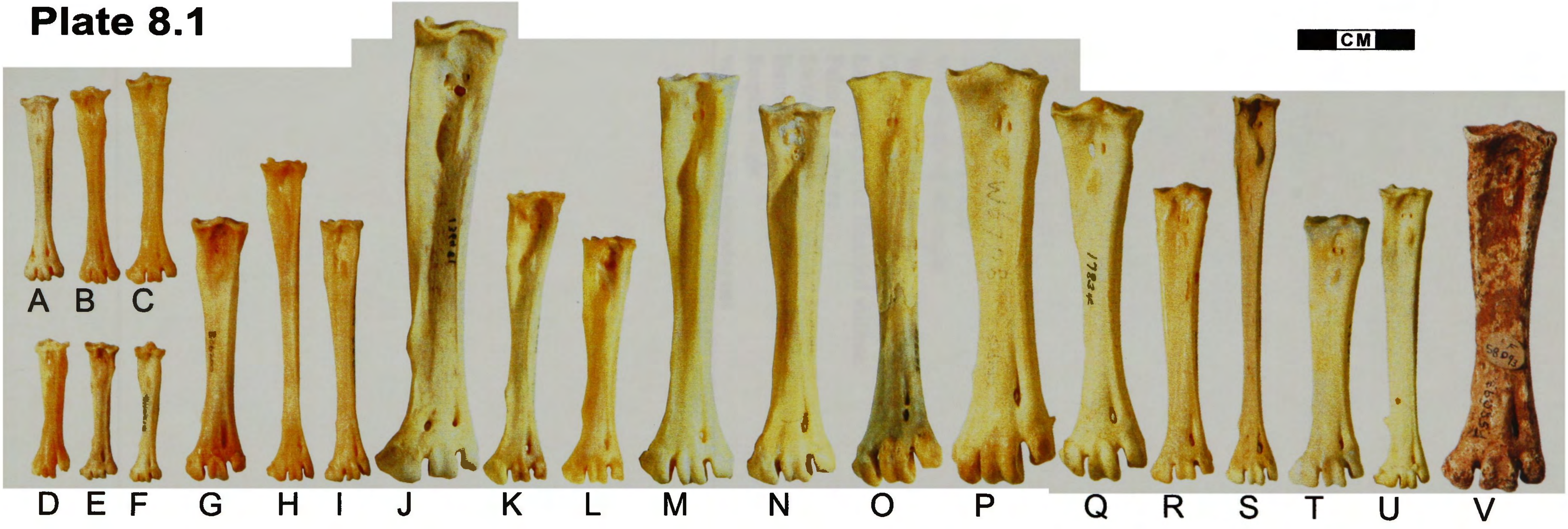
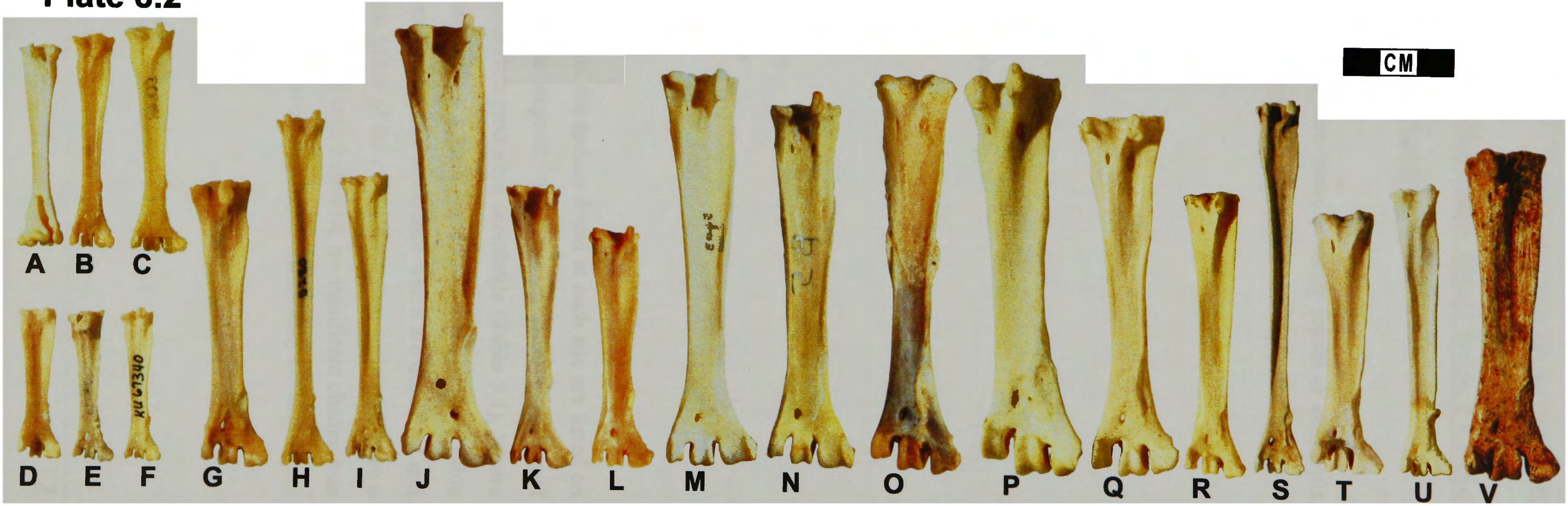


Plate 8.2: Posterior view of the tarsometatarsus of various accipitrids compared to a fossil vulturine tarsometatarsus from an unknown locality

Species	Common name
A) *Milvus migrans*	Black kite
B) *Lophoictinia isura*	Square-tailed kite
C) *Haliastur sphenurus*	Whistling kite
D) *Elanus axillaris*	Black-shouldered kite
E) *Aviceda subcristata*	Pacific baza
F) *Ictinia mississippiensis*	Mississippi kite
G) *Hamirostra melanosternon*	Black breasted buzzard
H) *Accipiter fasciatus*	Brown goshawk
I) *Buteo buteo*	Common buzzard
J) *Pithecophaga jefferyi*	Monkey-eating eagle
K) *Spizaetus ornatus*	Ornate hawk-eagle
L) *Hieraaetus morphnoides*	Little eagle
M) *Aquila audax*	Wedge-tailed eagle
N) *Haliaeetus leucogaster*	White-bellied sea-eagle
O) *Trigonoceps occipitalis*	White-headed vulture
P) *Gyps fulvus*	Griffon vulture
Q) *Gypaetus barbatus*	Lammergeier, or Bearded vulture
R) *Gypohierax angolensis*	Palm-nut vulture
S) *Circus approximans*	Swamp harrier
T) *Terathopius ecaudatus*	Bateleur
U) *Spilornis cheela*	Serpent eagle
V) **QM F 58093**	**vulturine tarsometatarsus**

Plate 8.2



Chapter 9: The Late Pleistocene to Holocene fossil record of the Accipitridae in Australia

Many of the extant Australian accipitrids have been found as either fossils or subfossils. Quaternary fossil remains of the following extant taxa have been found in Australia:

Pleistocene deposits: *Accipiter* sp.
Aquila audax
Elanus scriptus

Holocene deposits: *Accipiter fasciatus*
Accipiter cirrhocephalus
Aquila audax
Circus assimilis
Circus approximans
Lophictinia isura
Hieraaetus morphoides
Haliaeetus leucogaster
Milvus migrans
Circus sp.

The fossil localities producing accipitrids, and the species found at each site are listed on table 9.1. Data regarding the age of the deposit, method of dating, depositional environment was not available for all localities producing accipitrids (Table 9.1). Figure 9.1 shows the locality in Australia for most of the sites. Each element is diagnosed (Table 9.2), with the exception of the specimens that are new to science which are described and diagnosed in full in the previous chapters. Many of the extant Australian accipitrids have a wide distribution on the continent. Of the extant taxa fossilized, no significant change was seen in their palaeodistribution compared to their present day biogeography (Blakes *et al.*, 1984).

The only significant variation was seen in, *Accipiter fasciatus*, from Norfolk Island. The specimen from Norfolk Island was thought to be *A. cirrhocephalus*, due to its small size. However, it appears to represent a very small adult (as the bone is fully ossified) *A. fasciatus*, that is similar in size to *A. cirrhocephalus* (Figure 8.1 and 8.2). The sternum of *A. fasciatus*, the carinal apex is not protruding proximal of the ventral manubrial spine as is the condition in the sternum of *A. cirrhocephalus*. However, the northern subspecies of *A. fasciatus, A. fasciatus didimus,* is smaller than the southern subspecies *A. fasciatus fasciatus* (Condon, 1975). All measurements of the *A. fasciatus* are taken from specimens within the Museum Victoria, which could potentially all be from the larger southern sub species *A. fasciatus fasciatus*. The Norfolk Island *Accipiter* could be either a dwarf of either subspecies, as it is common for taxa that have migrated from the mainland to an island to reduce in size overtime, for example the King Island Emu is a dwarfed relative of the mainland Emu.

Figure 9.1: Comparison of the length of the sternum of three Australian *Accipiter* species to a fossil from Cave Bay Cave, Norfolk Island

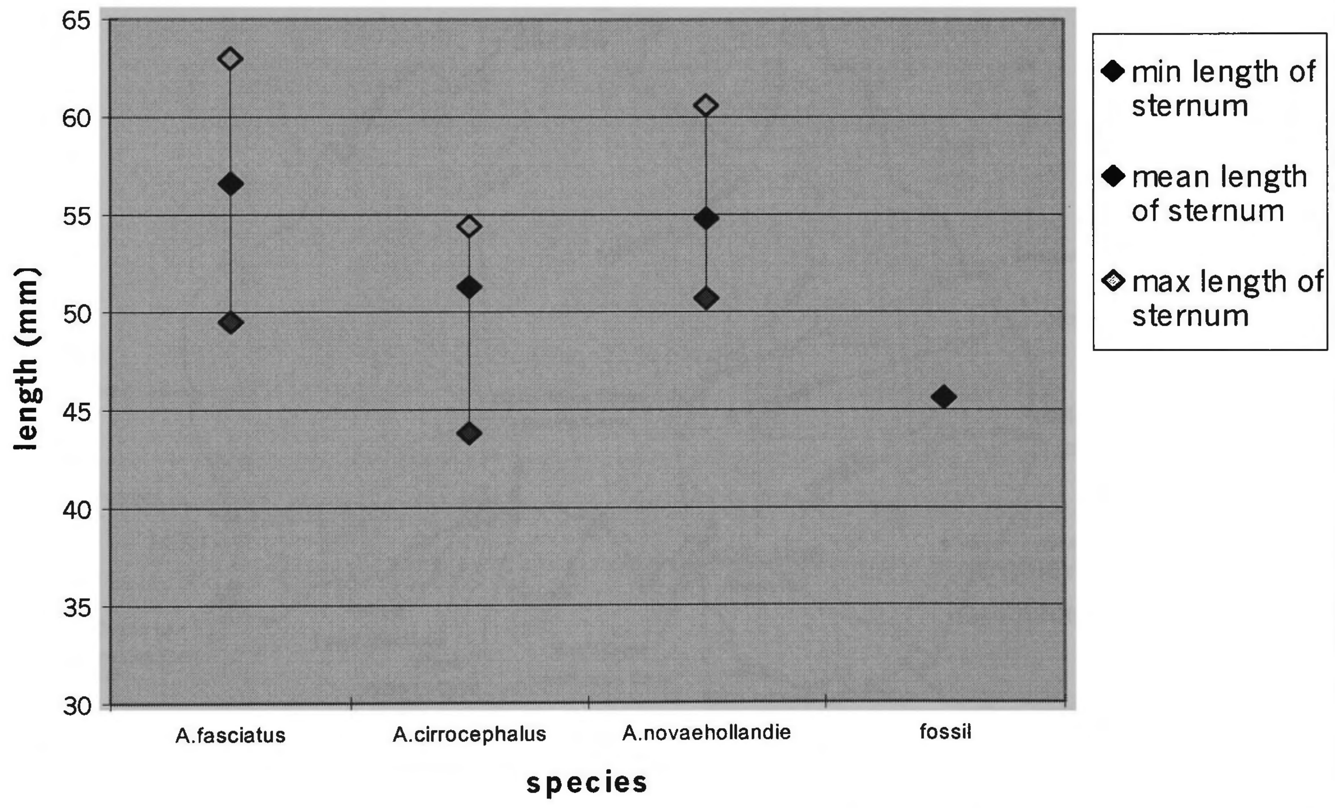
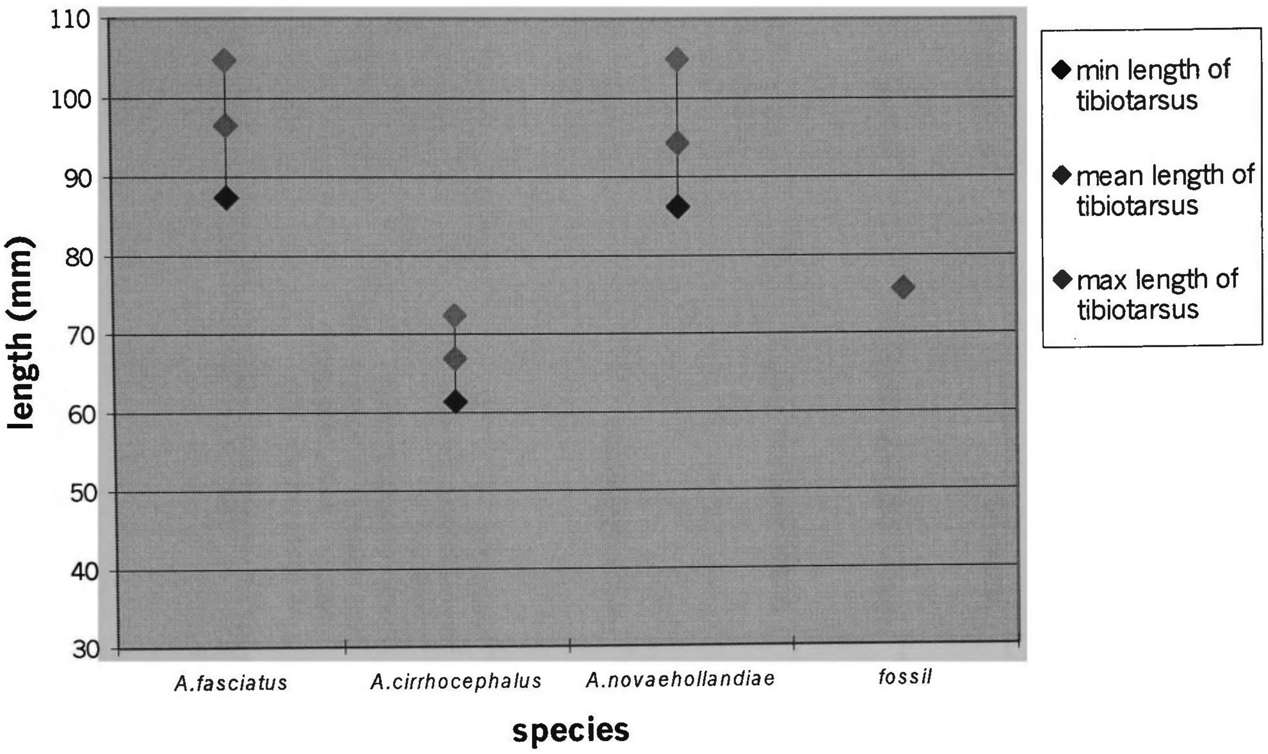


Figure 9.2: Comparison of the length of tibiotarsi in Australian *Accipiter* species to a fossil species from Cave Bay Cave, Norfolk Island.



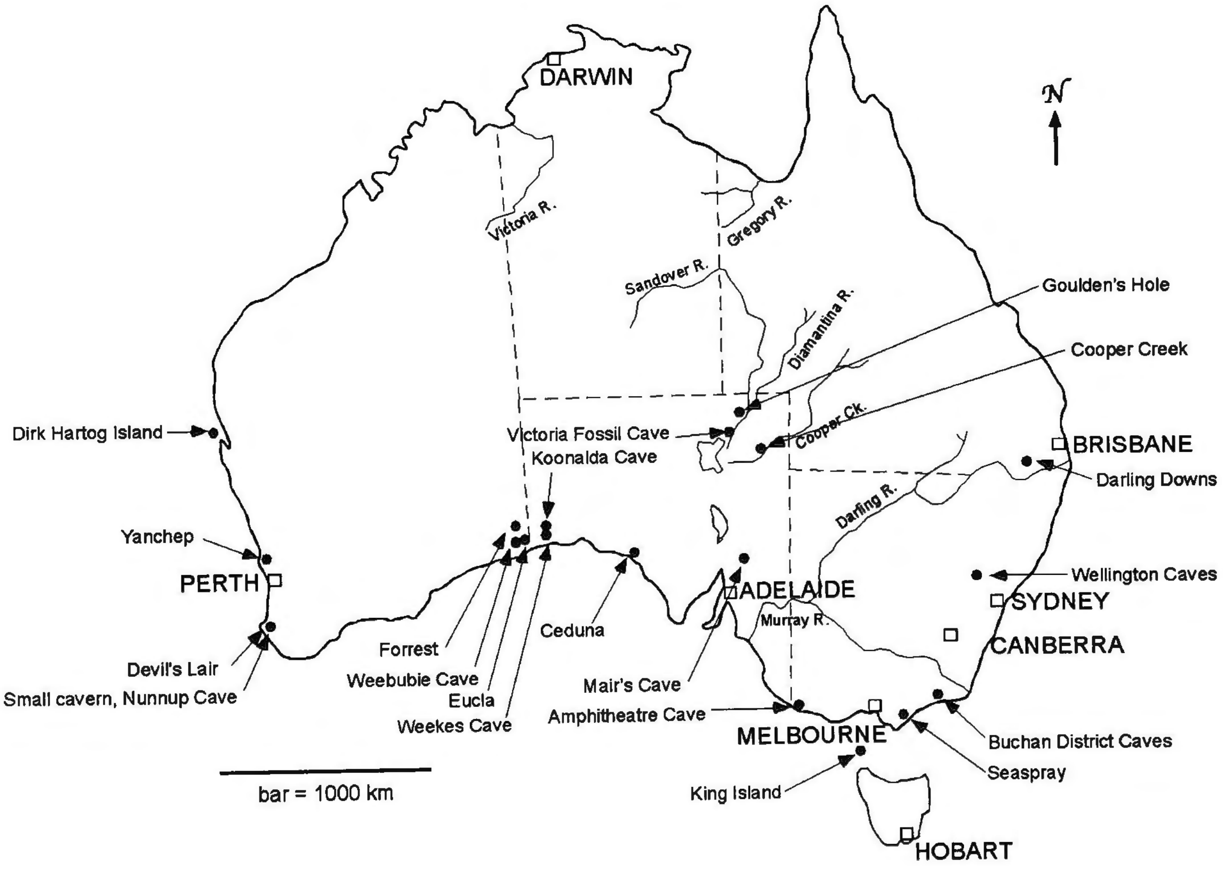


Figure 9.1: Quaternary localities producing fossil accipitrids (Accipitridae)

Table 9.1: Quaternary localities in Australia where accipitrid fossil material has been recovered

Site	State	Epoch	Age (years before present)	Method of dating	Depositional environment	Quality of preservation	Degree of association	Size of bird/s	Elements found	No. of species (minimum number)	Species name
Cathedral Cave, Wellington Caves	NSW	Late Pleistocene	BTW 20,700 to 34,600 *Roughly**	radiocarbon	natural pit trap	relatively good, red colour to fossils.	poor	giant to large	Two distal humeri (AM F58092), Tarsometatarsus (AM F58093), 3 phalanx, two distal phalanges, large tibiotarsus, a carpometacarpus and phalanges.	min=2	AM F58093 cf *Taphaetus brachialis*. Carpometacarpus = *Robustopternis marywaltersae*
Central Australia, site unknown	NSW	Quaternary				good	poor	medium	Tarsometatarsus	1	*Hieraaetus morphnoides* (male)
Amphitheatre Cave, Glenelg River, Nelson District.	Vic	Holocene	4,670+/-90	14C bone	Pit fall	good	nil	medium	1 tarsometarsus. 1 ulna	1	*Accipiter fasciatus*, *Falco cenchroides*
Alexander Cave, Buchan.	Vic	Quaternary				great	good	large	Nearly complete skeleton	1	*Aquila audax*
Kitson Cave, Buchan	Vic	Pleistocene				great	poor	Large	1 humerus	1	*Aquila audax*
Six miles east of Seaspray	Vic	Holocene			Aboriginal Midden	fair	nil	small	Tarsometatarsus	1	*Accipiter fasciatus*

Table 9.1: Quaternary localities in Australia where accipitrid fossil material has been recovered

Site	State	Epoch	Age (years before present)	Method of dating	Depositional environment	Quality of preservation	Degree of association	Size of bird/s	Elements found	No. of species	Species name
Tower Hill beach, West Victoria.	Vic	Holocene	6-10,000	14C bone	Aboriginal midden	fair	nil	medium	Humerus	1	*Circus* sp.
Victoria Fossil Cave	SA	Pleistocene	16,700 +/- 3000/2180, 19,300 +/- 1690/1390.	14C bone and charcoal	tytonid owl. Pit fall	good	nil	large	ulna	1	cf *Robustopternis marywaltersae*
Cooper Creek	SA	Pleistocene	23,000 to 25,000	^{14}C diprotodon bone, assoc with Pleist taxa	fluviatile	fair	nil	giant	distal tibiotarsus, humerus	1	Tibio unnamed, *Elanus* cf. *Elanus scriptus* (humerus)
Koonalda Cave	SA	Holocene	13700+-270 23700+-850	radiocarbon	Deposited by owls	good	good	medium	complete skeleton, partial skeleton, tarsometatarsus, 2 radii, humerus, skull and 2 claws	5	*Accipiter cirrhocephalus* (2 skeletons), *Aquila audax* (tmt), *Circus assimilis* (partial skeleton), *Lophictinia isura* (skull)
Green Water Hole	SA	Late Quaternary	Max age 125,000 to 15,000.	avian fauna	lacustrine	good	good	large	left and right ulna, left and right radii, left and right carpometacarpi and a thoracic vertebra	1	cf *Robustopternis marywaltersae*

Table 9.1: Quaternary localities in Australia where accipitrid fossil material has been recovered

Site	State	Epoch	Age (years before present)	Method of dating	Depositional environment or primary accumulator	Quality of preservation	Degree of association	Size of bird/s	Elements found	No. of species	Species name
Mair's Cave, Bucklowie, Flinders Ranges	SA	Pleistocene		biostratigraphy. *(Gallinula mortierii*)	owl	fair to good	nil	medium to giant	sternum, talons	1	*Woltsha australensis*
Goulden's Hole	SA	Pleistocene			cave	good	good	large	partial skeleton	1	*Aquila audax*
Rocky Point	SA	Quaternary				good	nil	medium	2 humeri	1	*Hieraaetus morphnoides*
Weeke's Cave	SA	Quaternary			Sink hole, Tyto or falco	good	poor	medium	skull	1	*Circus assimilis*
Cemetary Bay, Norfolk Island		Holocene	800-900	C4		poor	poor	medium	tibiotarsus, tarsometatarsus, sternum	1	*Accipiter fasciatus*
Cave Bay Cave, Hunter Island, Bass Strait	Bass Strait	Holocene	2500-900	C4	Aboriginal midden	fair	nil	medium	tarsometatarsus	1	cf *Accipter* sp.
North Blow, New Year Island, Bass Strait	Bass Strait	Quaternary			sand dune	good	good	large	2 humeri, 2 ulnae, 1 tibiotarsus	1	*Haliaeetus leucogaster*

Table 9.1: Quaternary localities in Australia where accipitrid fossil material has been recovered

Site	State	Epoch	Age (years before present)	Method of dating	Depositional environment or primary accumulator	Quality of preservation	Degree of association	Size of bird/s	Elements found	No. of species	Species name
Small cavern, Nannup Cave	WA	Quaternary				good	nil	small	tarsometatarsus	1	*Accipiter cirrhocephalus*
Weebubbie Cave, Eucla Basin	WA	Quaternary				good	nil	medium	1 skeleton, 2 skulls	2	*Milivus migrans* (skeleton), *Circus approximans* (sternum B) *Circus approximans* (skulls)
Dirk Hartog Island: blown out dune on track to Herald Heights	WA	Quaternary				good	nil	large	carpometacarpus, humerus	1	*Aquila audax*
Devil's Lair	WA	Pleistocene to Holocene	0.32+/- 0.08 35.2+/- 1.8	radiocarbon, charcoal	Tyto (owl) accumula-tor	poor to fair	nil	small to large	2 tarsometatarsi (73.7.77), and 2 distal tibiotarsi	3	*Accipiter fasciatus* (tmt), *Accipiter cirrhocephalus* (tib), *Aquila audax* (tib)
Yanchep; Youdewp Cave	WA	Quaternary				good	nil	large	humerus tibiotarsus	1	*Aquila audax*
Eucla Basin: Kestrel Cavern no.1	WA	Quaternary				good	good	large	skeleton	1	*Aquila audax*

Table 9.2: Diagnosis of the elements of the Australian fossil material from extant accipitrids

Site	Scientific no	Element	Species	Diagnosis
Yanchep: Youdeup Cave, WA	G. 9815	humerus (missing distal portion)	*Aquila audax*	Large size, pneumatic fossa oval shaped, bicipital crest not flared as in *Haliaeetus leucogaster*
Yanchep: Youdeup Cave, WA	G.9816	distal tibiotarsus	*Aquila audax*	Large size, depth of the cnemial crest
Eucla Basin: Kestrel Cavern no.1, WA	68.11.73	skeleton (except sternum, vertebra and ribs)	*Aquila audax*	Large size, (for tarsometatarsus) inner calcaneal ridge of hypotarsus extends further distally than in *Haliaeetus* sp., tubercle for *tibialis anticus* located further distally, notch for peronaeus nerve well developed.
Eucla Basin: Kestrel Cavern no.1, WA	68.11.73	skeleton (except sternum, vertebrae and ribs).	*Aquila audax*	For **humerus;** large size, pneumatic fossa oval, bicipital crest not flared as in *Haliaeetus* sp.
Dirk Hartog Island: blown out dune on track to Herald Heights	78.1.53	humerus and carpometacarpus	*Aquila audax*	Large size. **Humerus:** as for above diagnosis. **Carpometacarpus:** smaller and concave distal metacarpal symphysis, less ossification between metacarpal II and III proximally, angle between proximal surface of process of metacarpal I and carpal trochlea.
Nullarbor region: cave c. 100 miles NE of Forrest.	75.9.59	Carpometacarpus	*Aquila audax*	As above, plus; more circular carpal trochlea in internal view, wider intermetacarpal space, thinner distal metacarpal symphysis

Table 9.2: Diagnosis of the elements of the Australian fossil material from extant accipitrids

Site	**Scientific no**	**Element**	**Species**	**Diagnosis**
Small cavern, no. Nannup Cave, WA.	70.3.10	tarsometatarsus	*Accipiter cirrhocephalus*	Small and gracile and elongate, anterior fossa undercuts cotyla and the trochleae are all in line.
Weekes Cave, Nullarbor (SA?)	P36701	skull	*Circus assimilis*	Shape of tympanic wing extends further dorsally and has a dorsal process which narrows partially obscures the temporal fossa in caudal view
Devil's Lair. Trench 3. Horizon: surface to c.58cm below cave datum.	73.7.177	two tarsometatarsi	*Accipiter fasciatus*	Size, gracile, turbercle for *tibialis anticus* close to the proximal foramen, shallow metatarsal facet and shallower *fovea lig collateralis*.
Devil's Lair. Trench 8/7 Hrizon 7a. Depth from cave datum 220 - 222cm	77.2.620	distal tibiotarsus	*Aquila audax*	Diagnosed by ....(Merrilees et al)
Devil's Lair cave. Trench 6. Horizon brownish earth layer. datum 151-153cm	73.8.171.	trochleae for digits2 and 3.	*Aquila audax*	Diagnosed by Merrilees et al.
Devil's Lair. Trench 9. Horizon 2. depth 190 - 193.	77.2.885	distal end of a tibiotarsus.	*Accipiter cirrhochephalus*	Diagnosed by unknown person. My note: very gracile and small, only condyles and distal portion of the supratendinal bridge present.

Table 9.2: Diagnosis of the elements of the Australian fossil material from extant accipitrids

Site	Scientific no	Element	Species	Diagnosis
Kingsley Cave, Buchan Victoria.	P162221	Skull and sternum	*Aquila audax*	**Sternum:** large size, narrow ventral manubrial spine, deep carina, deepest proximally.
Kitson Cave, Buchan Caves area, Victoria	P162214	humerus	*Aquila audax*	As for above *Aquila audax* humeri
Alexander (Kingsley) Cave, Buchan area caves, Victoria	P162080	humerus, tibiotarsus, fermur (x2), ulna, radius, and carpometacarpus	*Aquila audax*	For humerus and carpometacarpus, as per above. Ulna: Radius: Femur: Tibiotarsus:
Weebubie Cave, Nullarbor, WA (near Eucla)	P36736	partial skeleton, sternum (A)	*Milvus migrans*	**Sternum:** triangular, blunt ventral manubrial spine, carina extends 90-95% distally, sternal plate wide, costal margin extends 50% of plate, triangular protruding lateral processes and rounded carinal apex.
Weebubie Cave, Nullarbor, WA (near Eucla)	P36736	partial skeleton, sternum (A)	*Milvus migrans*	**Tibiotarsus:** supratendinal bridge narrows distally, wide and shallow anterior intercondylar fossa, internal condyle larger than external, short inner cnemial crest.

Table 9.2: Diagnosis of the elements of the Australian fossil material from extant accipitrids

Site	Scientific no	Element	Species	Diagnosis
Weebubie Cave, Nullarbor, WA (near Eucla)	P36736	partial skeleton, sternum (A)	*Milvus migrans*	**Humerus**: pointed deltoid crest, rounded bicipital crest, slightly curved shaft, (anconal view) flange on bicipital crest.
Weebubie Cave, Nullarbor, WA (near Eucla)	P36736	partial skeleton, sternum (A)	*Milvus migrans*	**Femur:** strong posterior intermuscular line, deep popliteal area, not short like *Aviceda* or *Elanus*, medium depth rotular groove, slight anterior-dorsal curve in shaft, medium sized pneumatic fossa, rounded trochanter (cf Lophoctina)
Weebubie Cave, Nullarbor, WA (near Eucla)	P36736	partial skeleton, sternum (A)	*Milvus migrans*	**Carpometacarpus:** distal end of intermetacarpal space pointed cf. *Lophoictinia*, more gracile metacarpal and distal end of intermetacarpal space pointed cf. *Lophoictinia*.
Weebubie Cave, Nullarbor, WA (near Eucla)	P36736	partial skeleton, sternum (A)	*Milvus migrans*	**Ulna:** Olecranon highly raised and rounded over the proximal end, raised papillae, external cotyla L-shaped, bicipital attachment thin oval at an angle pointing towards internal cotyla, bulbous prominence for anterior articluar ligament.
Weebubie Cave, Nullarbor, WA (near Eucla)	P36736	partial skeleton, sternum (A)	*Milvus migrans*	**Radius:** less curved than *Hieraaetus*, pointed scapho-lunar facet, *Accipiter* shorter and less curved.
Weebubie Cave, Nullarbor, WA (near Eucla)	P36736 (B)	sternum	*Circus approximans*	fossa present on juvenile, bifurcated carinal apex

Table 9.2: Diagnosis of the elements of the Australian fossil material from extant accipitrids

Site	Scientific no	Element	Species	Diagnosis
?Lake Pinpa? Locality unknown		tarsometatarsus	*Hieraaetus morphnoides*	
Koonalda Cave (5N-4) K8. SA	P 36733	broken tarsometatarsus	*Aquila audax*	as above for tarsometatarsus
Koonalda Cave	P36702	partial skeleton	*Accipiter cirrhocephalus*	Small and gracile. **Tarsometarsus**: elongate, gracile, protrusion lateral of the outer calcaneal ridge.
Koonalda Cave, SA.	P26216	partial skeleton	*Circus* cf. *Circus assimilis*	**Tibiotarsus:** elongate, large and gracile. **Tarsometarsus:** gracile, shaft not bulbous proximally as with *C. approximans*, very elongate, size and shape of external calcaneal ridge. **Femur:** protrusion on external condyle. **Humerus:** flange on bicipital crest
Koonalda Cave, C21	P36702	skull, sternum, humerus, pelvis, and femur	*Accipiter cirrhochepalus*	**Sternum**: highly extended ventral manubrial spine, carinal apex anteriorly protruding and in line with the ventral manubrial spine. Dimensions of greatest length of the skull, humerus and sternum
Koonalda Sinkhole (N-4)	P36734	skull	*Lophoictinia isura*	Joined between maxillary and jugal, joined between nasal and frontal, shallow groove along front, large nares, shape of palatine, small size of vomer, narrower orbitals cf. *Circus* sp.
Goulden's Hole (L-8) Mt Gambier, SA.	P36732	2 humeri, femur, 2 carpometatcarpus, 2 tarsometatarsus, 3 claws, 1 phalange, 1 vertebra	*Aquila audax*	as above per for the carpometacarpus, tarsometatarsus and humeri

Table 9.2: Diagnosis of the elements of the Australian fossil material from extant accipitrids

Site	Scientific no	Element	Species	Diagnosis
Cooper Creek, SA	FU 1676	humerus	*Elanus cf. scriptus*	curved gracile shaft, medium depth brachial depression, distal width/length of shaft before deltoid crest arises is the same length (unlike short shaft length in *Accipiter*), thin ridge running beside the brachial depression attachment of anterior ligament
Aboriginal midden in dunes about 6 miles east of Sea spray, Vic	P172912	tarsometatarsus	*Accipiter fasciatus*	Size, elongate, gracile (too gracile to be *A. novaeholliandiae*),
Amphitheatre cave, Glenelg River Nelson district, Vic	P167068	tarsometatarsus	*Accipiter fasciatus*	size, gracile, larger than *A. cirrochepalus*, shallower *fovea lig. collateralis*, tubercle for *tibialis anticus* slightly closer to proximal foramen, shallower metatarsal facet.
King Island	FALS 269	Ulna, humerus, tibiotarsus	*Haliaeetus leucogaster*	**Humerus:** size, square pneumatic fossa, larger impression of brachialis anticus. **Ulna**: flat surface running along shaft. **Tibiotarsus:** tendinal groove proximal of bridge located to the internal side of the shaft.
Cemetry Bay, Norfolk Island (Midsands, Grab sample)		sternum, tibiotarsus	*Accipiter fasciatus*	
Norfolk Island	P164229, 163012, 162993	fragments of tarsometatarsus	*Accipiter fasciatus*	gracile, shallow metaarsal, shallow *fovea lig. collateralia* and tubercle for *tibialis anticus* closer to the proximal foramen

Table 9.2: Diagnosis of the elements of the Australian fossil material from extant accipitrids

Site	**Scientific no**	**Element**	**Species**	**Diagnosis**
Rocky Point, W. of Ceduna, a small cave.	P36735	two humeri	*Hieraaetus morphnoides (male)*	Deltoid crest not cut into (like Accipiter), similarly curved shaft, deep external tricipital groove, shallow brachial depression
Eucla Basin, WA.	68.3.105	skull	*Circus approximans*	size of naris, large vomer, wide posteriorly (from one postorbital process to the other), shape of palatine and size of premaxillary, lacking extended tympanic wing and temporal fossa
Eucla Basin, WA.	68.3.106	skull	*Circus cf. approximans*	vomer size, width across orbitals, connection between jugal and maxillary, lacking extended tympanic wing and temporal fossa

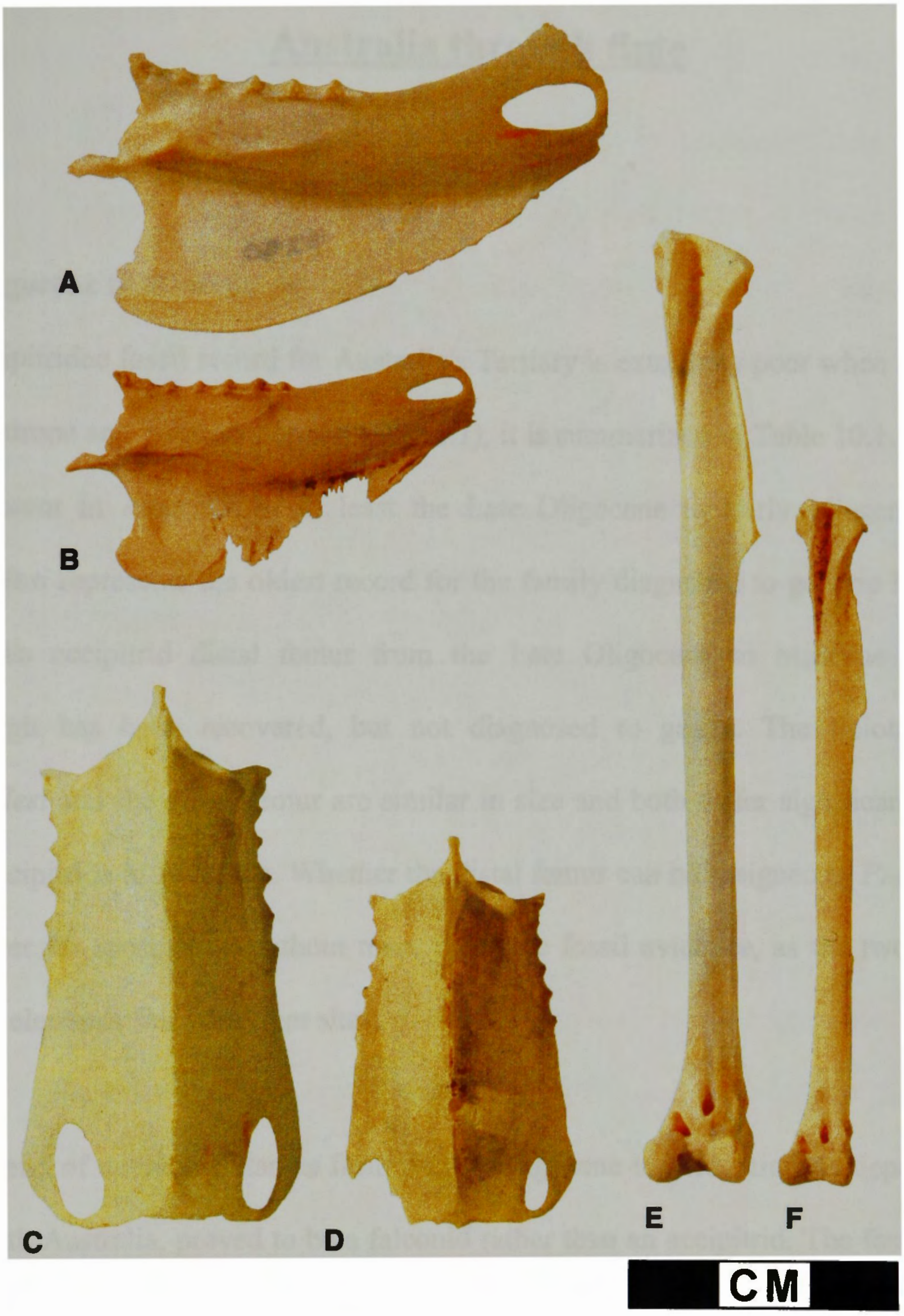


Plate 9.1: Subfossil material from Norfolk Island. Lateral view of the sternum A) *Accipiter fasciatus*, B) Subfossil; Anterior view of sternum C) *A. fasciatus*, D) subfossil; Tibiotarsus E) *A. fasciatus*, F) subfossil.

Chapter 10: Conclusions and discussion of the biogeographic and stratigraphic changes within the family Accipitridae in Australia through time

Late Oligocene to Miocene

The Accipitridae fossil record for Australia's Tertiary is extremely poor when compared to that of Europe and North America (Table 1.1), it is summarized in Table 10.1. Accipitrids were present in Australia by at least the Late Oligocene to Early Miocene. *Pengana robertbolesi* represents the oldest record for the family diagnosed to generic level (Boles, 1993). An accipitrid distal femur from the Late Oligocene to Miocene deposits of Riversleigh has been recovered, but not diagnosed to genus. The tibiotarsus of *P. robertbolesi* and the distal femur are similar in size and both differ significantly from all extant accipitrids in Australia. Whether the distal femur can be assigned to *P. robertbolesi* is a matter for speculation without more complete fossil evidence, as the two fossils are different elements from different sites.

A distal end of a tarsometatarsus from a Late Oligocene to Mid Miocene deposit, Steve's Site, South Australia, proved to be a falconid rather than an accipitrid. The fossil has been tentatively assigned to a new genus and species, *Palaeofalco richorum*, as it differs significantly from *Falco*, *Milvago* and *Polyborus*. However, future studies could include comparison of *P. richorum* to other members of the Falconidae to determine its taxonomic position within the Falconidae. *P. richorum* is the oldest record of the family Falconidae in

Australia, and it is amongst the oldest falconids in the world. Previously the only genus of falconid present in Australia was *Falco*.

Miocene

A distal humerus from Bullock Creek is the oldest evidence of large eagles in Australia, being mid-Miocene. The fossil shows most affinity with *Aquila*, and has tentatively been assigned to a new species, *Aquila bullockensis*. *A. bullockensis* was slightly smaller than the smallest members of *Aquila audax*. The genus *Aquila* had achieved a worldwide distribution by the Late Miocene, with *Aquila* fossils recovered from France (Gaillard, 1938), China (Li *et al.* 1985), and North America (Wetmore, 1923), as well as Australia. The Australian record appears to be the oldest; however, the fossil still needs to be compared to other members within the genus, so no conclusions can be made about the origin for this group of birds.

Claws from the Alcoota Local Fauna and Ringtail Site, Riversleigh, can be confidently assigned to the family Accipitridae. The size and degree of curvature of the claws, imply that these were large active predators. They differ enough from the extant Australian eagles, *Aquila audax* and *Haliaeetus leucogaster*, to be considered distinct taxa, but little can be said about their relationship within the Accipitridae, and diagnosis to the generic level is not possible.

Pliocene

A carpometacarpus from the Chinchilla Pliocene deposits shows most affinity to the monotypic genus, *Hamirostra*, but the fossil is considerably larger and differs enough morphologically from *Hamirostra melanosternon* to be considered a distinct species, and perhaps even a distinct genus. With such fragmentary remains, it is difficult to assess the most appropriate placement of this fossil.

Today Australia supports three endemic monotypic genera, *Hamirostra*, *Lophoictinia* and *Erythrotriorchis*, and four endemic species, *Aquila audax*, *Haliaeetus leucogaster*, *Elanus axillaris* and *Elanus scriptus*. With such a high level of endemic accipitrids in Australia today, a more diverse fossil record during the Late Tertiary would be expected particularly as the family Accipitridae had diversified and was widely distributed throughout the world (except Antarctica) by the Miocene Period (Table 1.1). The poor Tertiary fossil record for the accipitrids most likely reflects a scarcity of Tertiary sites producing fossil accipitrids rather than a poor diversity of accipitrids in Australia during this time. Moreover, predators are the top of the food pyramid and less abundant within populations, so are likely to be less plentiful in the fossil record.

Pleistocene

The Australian Pleistocene accipitrids were unique compared to those in the present day avifauna, although again, the Pleistocene fossil record is extremely poor and fragmentary relative to that of North America; and it is summarized in Table 10.1. Assigning the Pleistocene fossil material to distinct taxa has proven extremely difficult, as the only associated accipitrid material is the right and left ulnae, radi and carpometacarpi from Green Waterhole, South Australia. All other fossil material is represented by different elements from various localities; two distal tibiotarsi from Cooper Creek and Wellington Caves, one giant sternum from Mairs Cave, one femur from the Darling Downs, and one tarsometatarsus that may not even have come from Australia. This makes naming new species and designating paratypes extremely difficult and perhaps unwarranted.

The giant tibiotarsi from Cooper Creek and Wellington Cave (Chapter Five) remain unnamed. They are more closely related to the eagles rather than to the accipitrid vultures. The giant tibiotarsi are significantly larger than those of *Aquila audax,* to which they have been tentatively referred, but, based on the morphology and giant size, they could potentially be associated with the sternum from Mair's Cave, *Woltsha australensis*. To avoid splitting and naming too many species, the tibiotarsi have not been named as a new species at this stage. Further work and more fossil material are necessary to clarify the taxonomic relationships of these fossils within the Accipitridae.

The Green Waterhole material, named *Robustopternis marywaltersae*, was significantly smaller than the Mair's Cave sternum, *Woltsha australensis*, and the giant tibiotarsi (Chapter Five). All other taxa examined that possess a large sterna, for example *Gyps fulvus*, *Gypaetus barbatus* (Plate 6.1) and *Harpagornis moorei*, also possess proportionally large ulnae (Plate 7.3) and carpometacarpi (Plate 7.1). Based on the pattern of proportion observed in large accipitrids, *R. marywaltersae* is placed in a genus distinct from *W. australensis*.

Fossils of extant taxa, *Elanus scriptus*, and *Aquila audax*, were identified from Pleistocene deposits. The fossil of *Elanus scriptus* from Cooper Creek, South Australia, represents the oldest occurrence for the genus *Elanus* in the world. Today, *Elanus* contains four separate species, with Australia the only continent to support two species, *Elanus scriptus* and *Elanus axillaris,* both of which are endemic. This suggests a possible Gondwanan or even Australian origin for this group of kites. Alternatively, another possible explanation for two endemic species in Australia is a double invasion from the north.

Aviceda gracilis, described by de Vis (1905), was found to be an *Accipiter*, likely either *A. fasciatus* or *A. novaehollandiae*. The oldest records of *Accipiter* are from Pleistocene deposits (Table 1.1), by which time the genus was widely dispersed throughout Europe, Africa, North America and Australia, and had diversified into at least five different species. The genus today is cosmopolitan, and comprises at least 44 species. With such a wide distribution and high diversity during the Pleistocene and today, it is not possible to suggest a centre of origin without fossil material older than Pleistocene age.

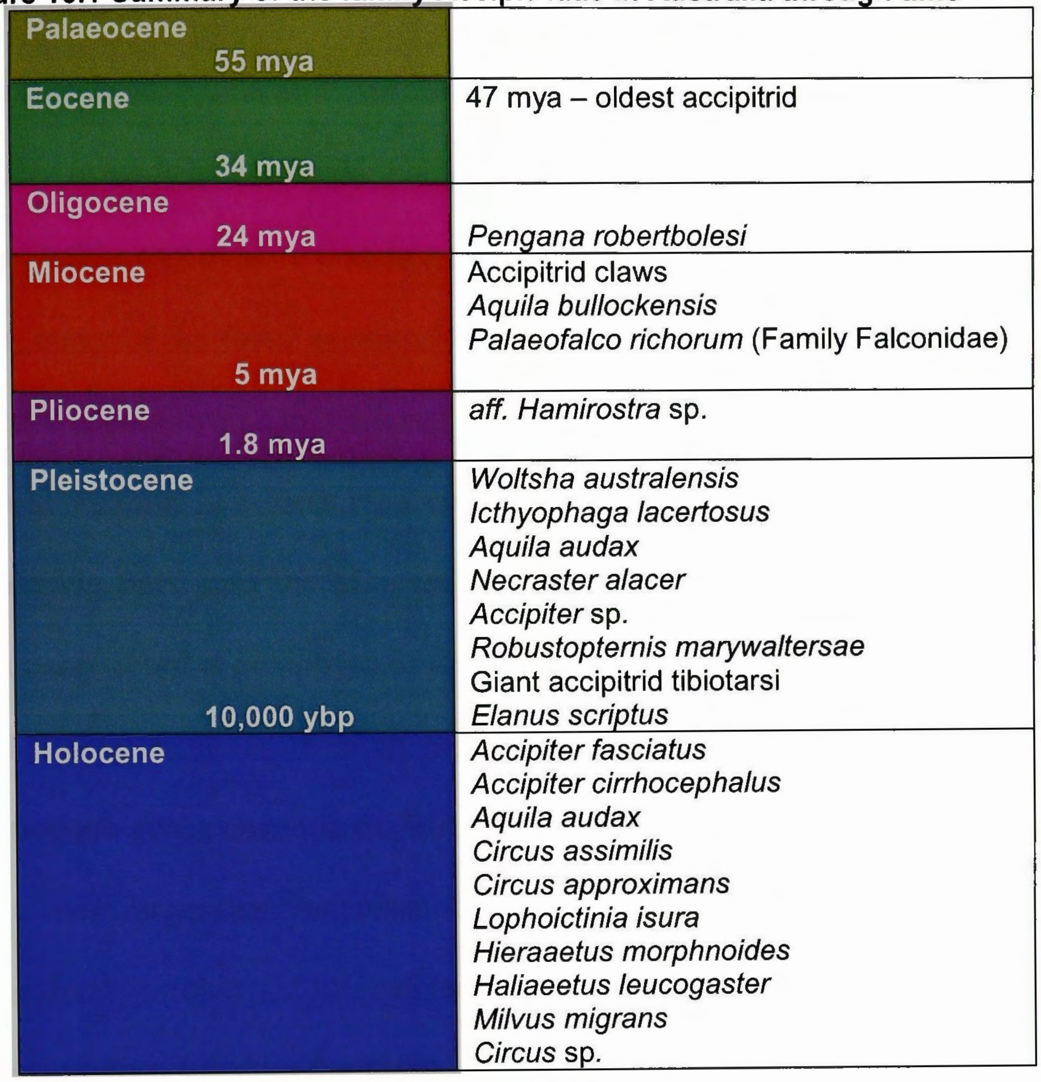
Necraster alacer (de Vis, 1892) was described on the basis of a proximal humerus. Unfortunately, the fossil material is not only fragmentary, but also not particularly diagnostic. Nevertheless, the material is considered different enough from extant Australian taxa to be considered a separate species. Recovery of better material would allow for a more accurate analysis of the taxonomic position of this species.

Taphaetus brachialis, described by de Vis (1891b), was nominally represented by two separate fossils, a humerus (QM F1117) and a femur (QM F1118). This humerus was reassigned by de Vis (1905) into *Uroaetus brachialis*. De Vis (1905) also placed the femur in a separate species, *Taphaetus lacertosus*, along with two other fossil specimens. Van Tets (1974) reassigned this species to *Icthyophaga*, becoming *Icthyophaga lacertosus*, and nominated a second fossilised humerus as the lectotype. This study showed that QM F1117 and QM F1118 are indeed from different taxa. The humerus (QM F1117) belongs to *Aquila audax*. Thus *Taphaetus brachialis* becomes a junior synonmy of *Aquila audax*. The femur (QM F1118) belongs to an accipitrid vulture, not an eagle as originally described by de Vis (1891b). The femur differs considerably from those of all accipitrid vultures to which it was compared, and a new name can be applied to this specimen. A tarsometatarsus (AM F58093) from an unknown locality may be allied with the femur, as the tarsometatarsus shows more affinity to the accipitrid vultures than to any other group within the Accipitridae. Unfortunately, the specimen was found in an 'old collection' in the Australian Museum and may not be from Australia. Again, as these two fossils are different elements, this makes the assignment of AM F58093 to the same taxon as QM F1118 debatable.

While there are no vultures in Australia today, there would have been several advantages for a vulture in the Pleistocene of Australia. The vulturine fossil material (QM F1118) suggests that this bird would have been similar in size to *Aquila audax*. The ancestors of this vulture may have specialized in feeding predominately on carrion, as there was an increased diversity of large-sized accipitrids during the Pleistocene (*Aquila audax*, *Woltsha australensis*, and *Robustopternis marywaltersae*) compared to today. One advantage a vulture would have over a mammalian scavenger is its method of locating prey. Via soaring thermals, expending minimal amounts of energy, vultures scan the ground to locate their prey. Therefore, a vulture could cover more area in search of food than a mammal, using less energy to do so. Such a large vulture would have been highly successful at locating megafauna carrion.

The presence of a vulture or a vulture-like bird during the Pleistocene in Australia contrasts dramatically with Australia's present day avifauna, which contains no Old World or New World vultures. QM F1118 could represent a product of convergent evolution, an eagle that has adapted to a niche of a vulture and in turn, the osteology of the bird has evolved along with the change in feeding style. Convergent evolution has been previously observed within the Order Falconidae. Feduccia and Voorhies (1989) described a Miocene hawk, *Apatosagittarius terrenus* (Family Accipitridae), which converged on the Secretarybird, *Sagittarius serpentarius*, (Family Sagittariidae). *A. terrenus* evolved and converged on the niche of a Secretarybird under selection pressure within a North American grassland community comparable to the habitat of the extant Secretarybird in Africa. QM F1118 could have evolved from vagrant accipitrid vultures from the North, as currently they inhabit South Thailand and Malaysia. Or perhaps, a vulture or vultures could have island-hopped or have been transported by a storm to Australia. Isolated from the Asian population, a distinct taxon of accipitrid vultures may have evolved. As QM F1118 shows more affinities to the accipitrid vultures than to the eagles, this suggestion is quite plausible. However, future discovers of fossil accipitrids are necessary to shed light on and determine more accurately the taxonomic position and evolutionary history of the unique palaeospecies of accipitrids from Australia.

Figure 10.1 Summary of the family Accipitridae in Australia through time



Palaeocene 55 mya	
Eocene 34 mya	47 mya – oldest accipitrid
Oligocene 24 mya	*Pengana robertbolesi*
Miocene 5 mya	Accipitrid claws *Aquila bullockensis* *Palaeofalco richorum* (Family Falconidae)
Pliocene 1.8 mya	*aff. Hamirostra* sp.
Pleistocene 10,000 ybp	*Woltsha australensis* *Icthyophaga lacertosus* *Aquila audax* *Necraster alacer* *Accipiter* sp. *Robustopternis marywaltersae* Giant accipitrid tibiotarsi *Elanus scriptus*
Holocene	*Accipiter fasciatus* *Accipiter cirrhocephalus* *Aquila audax* *Circus assimilis* *Circus approximans* *Lophoictinia isura* *Hieraaetus morphnoides* *Haliaeetus leucogaster* *Milvus migrans* *Circus* sp.

Conclusions

Accipitrids have inhabited Australia since at least the Late Oligocene, although their fossil history extends back into the Early Eocene in Europe. *Pengana robertbolesi*, an accipitrid quite unlike any modern taxa in Australia, is the oldest record of the family in Australia. In fact, many of the fossil accipitrids taxa are quite unlike any extant taxa in Australia. This 'theme' is comparable to the fossil record of the Accipitridae in North America, where Old World Vultures have been recovered from many sites, and have a long and diverse history extending back into the Miocene, despite their absence in North America today. The Miocene record is composed of three large claws, most likely from large active predators, and a large humerus from an eagle slightly smaller than *Aquila audax*. *Hamirostra*, a monotypic genus endemic to Australia, extends back into the Pliocene, but is represented by a taxon larger than the present day *Hamirostra melanosternon*. During the Pleistocene a considerably richer and more diverse record has been recovered compared with that of the Tertiary. Not only does the Pleistocene record differ from that of the Tertiary, but stands in stark contrast to the present assemblage of accipitrids in Australia. During the Pleistocene, a higher diversity of large to giant accipitrids survived in Australia. These species include a massive gliding accipitrid, *Woltsha australensis*, possibly with the potential to kill larger prey than could *Aquila audax* judging by the larger size of the claws (assuming the claws and sternum are associated). *Woltsha australensis* would have been similar in size to *Gyps fulvus* and possibly smaller members of *Harpagornis moorei*. A vulture similar in size to *Aquila audax*, represented by QM F1118, would have feed on the carrion of the megafauna and carcasses of smaller animals, perhaps competing for food with *Woltsha australensis*. Not all of the accipitrids would have fed predominantly on carrion. Active predators such as *Aquila audax* (Wedge-tailed Eagle), *Accipiter* sp. (Goshawk), *Elanus scriptus* (Letterwinged Kite), and *Necraster alacer* were present during the Pleistocene. *Robustopternis marywaltersae* was an unusual bird of prey, similar in size to the large eagles, such as *Aquila audax* and *Haliaeetus leucogaster*. *R. marywaltersae* could have been best suited to living in forest environments as opposed to open plains environments, as its rather short wing span differed in dimensions to the typical gliders, suggesting it was more likely to have used flapping flight. The end of the Pleistocene saw the end of the high diversity of large accipitrids in Australia, as was also so the case for North America. However, during the Holocene, Australia supported a higher diversity of smaller-sized diurnal birds of prey. *Accipiter fasciatus*, *A. cirrhocephalus*, *Circus assimilis*, and *C. approximans* were present in Australia, although they lack a fossil record older the Pleistocene. *Lophoictinia isura*, a monotypic genus endemic to Australia, has been recorded from Holocene deposits. *Milvus migrans*, reached Australia by the Holocene, possibly via a northern invasion, as *Milvus* extends back into the Early Miocene in Europe. *Hieraaetus morphnoides* and *Haliaeetus leucogaster* are both recorded from Holocene deposits, both are endemic to Australia, and both genera have a fossil record extending back into the Late Miocene in Europe. Members of each genus *Hieraaetus* and *Haliaeetus* could have a longer history in Australia as they have both changed significantly from those on other continents. Despite the fragmentary fossil record of the Accipitridae in Australia compared with that of North America, the Australian record provides evidence that this continent supported a diverse and unusual guild of diurnal birds of prey, some of which were quite unlike any other accipitrids in the world. Understanding their relationships within the Accipitridae proved to be extremely difficult with such little fossil material. However, there is hope that with future excavations of Tertiary and Pleistocene fossil sites, as was the case for Riversleigh sites, more accipitrid fossil material may be recovered, which will hopefully shed light on the understanding of these unique and unusual birds of prey.

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Appendix

Appendix 1. Comparison of the variation of the distal end of the tibiotarsus in some accipitrids

Species	number	number of ridges between the condyles, in the intercondylar fossa.	Location of the tendinal groove distal of the supratendinal bridge. **1**: mostly proximal of internal condyle. **2**: half over the intercondylar fossa and half over the internal condyle. **3**: mostly over the intercondylar fossa.	Supratendinal bridge location. **1**: similar to AM F 106562. **2**: P.25218	Projection of the supratenidinal bridge anteriorly of the shaft; **1**: similar to that of AM F 106562. **2**: similar to that of P25218	Rugose surface; 1:similar to AM F106562, 2:similar to P25218. Oval=o
Aquila audax	B19993	0	1	1	2	1 o
Aquila audax	B19993	0	1	1	2	1 o
Aquila audax	B8524	1	1 to 2	2	2	1 long o
Aquila audax	B8524	1	1	2	2	1 long o
Aquila audax	B13104	1	2	1 to 2	1	1 long o
Aquila audax	B13104	1	2	1	1	1 long o
Aquila audax	B708	0	2	2	2	2 narrow
Aquila audax	B708	0	2	2	2	2 narrow
Aquila audax	W4999	1	2	1 to 2	1	1 narrow
Aquila audax	W4999	1	2	2	1	1 narrow
Aquila audax	B4954	0	1	1		
Aquila audax	W3612	1	2	1	1	1 o
Aquila audax	W3612	1	2	1	1	1 o
Aquila audax	R10777	1	1	2	2	1 o
Aquila audax	R10777	1	2	2	2	1 o
Aquila audax	5403	1	3	1		
Aquila audax	5403	1	2	1		
Aquila audax	2354	1	2	2		
Aquila audax	2354	1	2	1		
Haliaetus leucogaster	B13631	0	2	1	2	large deep o
Haliaetus leucogaster	B13631	0	2	1	2	large deep o
Haliaetus leucogaster	B12814	0	2	1	2	2 faint
Haliaetus leucogaster	B12814	1	2	1	2	2 faint
Haliaetus leucogaster	B11537	1	2	1	2	2 faint
Haliaetus leucogaster	B11537	0	2	1	2	2 faint
Haliaetus leucogaster	B8847	0	2	1	2	1 o
Haliaetus leucogaster	B8847	0	2	1	2	1 o
Haliaetus leucogaster	B5	1	2	2		
Haliaetus leucogaster	B5	0	2	2		
Aquila chrysaetos	#1938	1	2 to 3	1		
Aquila chrysaetos	#1938	1	2 to 3	1		

Amendments

All changes regarding problems with nomenclature, with references, with presentation and specific problems suggested by Dr Walter Boles have been made in the body of the text where appropriate, and the thesis has been reprinted. However, not all of the suggested changes were made, and the reasons why are outlined below.

Problems with nomenclature

The changes to the problems with nomenclature as pointed out by Dr Walter Boles have been made in the text as prescribed. Dr Boles also stated the *Taphaetus brachialis* becomes the junior synonym of *Aquila audax*, and consequently the femur referred by de Vis to *Taphaetus brachialis*, which is distinct from *Aquila audax*, has no applicable generic or specific name. Subsequently, Dr Boles stated, "the author has complete freedom to create and apply novel names to this specimen". When publishing the work, I will name create and apply a new name to the specimen.

Additionally, Dr Boles states, "a further outcome is that the designation of the Cathedral Caves tibiotarsus as a paratype of *T. brachialis*, regardless of how that taxon is treated, has no validity". I think he is meaning to refer to the tarsometatarsus AM F58093 from an unknown locality, not the tibiotarsus. Dr Boles also points out "because the specimen was not part of the original description, at best it can be referred to this taxon. In either case, it has no nomenclatural status whatsoever". This specimen, AM F58093, where stated in the thesis as referred to *Taphaetus brachialis*, is not applicable and will in future be refer to the new species, with the type specimen the femur as originally described by de Vis.

As to the suggestion of changing the specific epithets *australensis* and *bullockensis*, while they are not particularly imaginative, I chose these names because they clearly allow the reader to gain information about the locality of the fossil.

Problems with presentation

With regards to the suggestion of the writing being tightened up and made more fluent, this suggestion is noted as valid and will be taken into consideration when publishing. The thesis has been edited many times by various palaeontologists, however, improvements have been made throughout the text.

The term significant was used in the thesis, where statistical tests were not used. Where this is the case the words "substantially" or "considerably" are interchangeable with the word significant in the thesis.

Specific Comments

1. On page 13, it states that there are 19 species of accipitrids in Australia. On page 15, it states that 20 of Australia's diurnal raptors, which refers to falcons and accipitrids, not exclusively accipitrids, furthermore it is a reference to the number of species Baker-Gabb (1984) used in his analysis, not the number present in Australia.