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A new look at an old Australian raptor places "*Taphaetus*" *lacertosus* de Vis 1905 in the Old World vultures (Accipitridae: Aegypiinae)

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Abstract

The Australian Pleistocene fossil record of the Accipitridae (hawks, eagles and Old World vultures) is sparse and poorly known. Only two extinct confirmed accipitrid species have been described for this time period; both have received little investigation since their description. One is *"Taphaetus" lacertosus* de Vis, 1905, described from a distal humerus and a quadrate from north-eastern South Australia. While this species was verified as an accipitrid in subsequent studies, its more precise taxonomic affinities have remained conjectural. In this study, a new analysis incorporating newly referred material and phylogenetic analyses using a wide range of accipitriforms reveals that the lectotype humerus of *"T." lacertosus* is an Old World vulture in the subfamily Aegypiinae. The associated quadrate, one of two original syntypes from which de Vis named this species, is of an indeterminate species of ardeid. We erect the novel genus *Cryptogyps*, to accommodate the species '*lacertosus*', as it cannot be placed in *Taphaetus* de Vis, 1891, because the type species of this genus, *Uroaetus brachialis* de Vis, 1889, was transferred back to the genus *Uroaetus*, a synonym of *Aquila* Brisson, by de Vis in 1905. Further, *U. brachialis* is now considered a synonym of *Aquila audax* (Latham, 1801). Moreover, *Taphaetus* de Vis, 1891 is a senior homonym of *Taphaetus* de Vis, 1905, type species *Taphaetus lacertosus* de Vis, 1905, making the 1905 version of the genus unavailable. Newly referred fossils from Wellington Caves (NSW) and the Nullarbor Plains (WA) reveal this taxon had a wide geographical range across Pleistocene Australia. The referred tarsometatarsus lacks hyper-developed trochleae, indicating that *Cryptogyps lacertosus* (de Vis, 1905) comb. nov., was probably a scavenger like other aegypiines. Identification of *Cryptogyps lacertosus* as an aegypiine significantly expands the palaeogeographical range of the Old World vultures, hitherto unknown in Australia. The avian guild of large, obligate scavenging birds of prey, is currently absent in the modern Australian biota, but its former presence is not surprising given the megafauna-rich communities of the Pleistocene.

Key words: Pleistocene fossil birds, Accipitriformes, extinction, scavengers, biogeography, Australia

Introduction

Pleistocene Australian Accipitridae

Throughout most of Australia, the Pleistocene (2.56 Ma–11.7 Ka) epoch was marked by arid climatic conditions, with the environment dominated by grasslands, open woodland (Sniderman et al. 2007) and desert (Hesse et al. 2004), similar to the present day. The Australian megafauna, which included at least 20 genera of large mammals, four of large birds, and three of large reptiles (Wroe et al. 2013; Johnson et al. 2021), inhabited these environments until most of them went extinct between 50–40 Ka (Roberts et al. 2001; van der Kaars et al. 2017). The raptor guild of the Pleistocene can be assumed to have comprised most of the living Australian species, with fossil material of *Aquila audax* (Latham) (Wedge- tailed Eagle) at least 500–200 Ka old (Baird 1991; EKM, THW unpublished data). However, two extinct species that represent potential additional diversity have been described from this epoch; *Aquila brachialis* (de Vis, 1889) and *"Taphaetus" lacertosus* de Vis, 1905 (Gaff 2002 unpublished thesis; Boles 2006, 2017; Worthy & Nguyen 2020).

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The history of *"Taphaetus" lacertosus*

"Taphaetus" lacertosus de Vis, 1905 was described from a distal right humerus QM F5507, and a quadrate QM F5508, both collected from Kalamurina on the Warburton River in north-eastern South Australia (de Vis 1905). De Vis compared the fossil material with living Australian bird species of similar size and noted that the fossil humerus was not much larger than that of *Haliaeetus leucogaster* (J. F. Gmelin) (White-bellied Sea Eagle). However, it was also highly distinct from both those of that species and *Aquila audax*.

The generic assignment of *"T." lacertosus* is nomenclaturally problematic. The genus *Taphaetus* was first established by de Vis (1891) when he transferred *Uroaetus brachialis* de Vis, 1889, based on the holotype distal left humerus QM F1117, to the new combination *Taphaetus brachialis* (de Vis, 1889), thereby making it the type species for *Taphaetus* de Vis, 1891 by monotypy. The holotype of *Taphaetus brachialis* (de Vis, 1889) was reassigned back to *Uroaetus* by de Vis (1905). *Uroaetus* Kaup, 1844 is a junior synonym of *Aquila* Brisson, 1760, so *brachialis* is now listed in *Aquila* (see Worthy & Nguyen 2020) and is considered to be synonymous with *Aquila audax* (Latham, 1801) (see van Tets 1974; Condon 1975; Gaff 2002, unpublished thesis). In their review of the Australian fossil avifauna, Worthy & Nguyen (2020) noted that the reassignment of the type species of *Taphaetus* de Vis, 1891, i.e., *Uroaetus brachialis*, back to *Uroaetus*, meant that *Taphaetus* de Vis, 1891 then became a synonym of *Uroaetus* Kaup, 1844 and so is now a synonym of *Aquila* (see also van Tets 1974). However, de Vis (1905), after reverting *brachialis* back to *Uroaetus*, then (re)used the genus name *Taphaetus* for the description of *"Taphaetus" lacertosus* de Vis, 1905 based on another distal humerus, QM F5507, that was subsequently nominated as the lectotype by van Tets (1974), and a quadrate QM F5508, both from the Warburton River in Central Australia. As a result, *Taphaetus* de Vis, 1905, with the type species by monotypy *Taphaetus lacertosus* de Vis, 1905, is a junior homonym for *Taphaetus* de Vis, 1891, and so is unavailable as a genus name (ICZN 1999, Article 52.1).

De Vis (1889) also assigned a fossil left femur (minus the distal condyles; now QM F1118) from the Darling Downs, Queensland, to *Taphaetus brachialis* (de Vis, 1889). This femur was about the size of that of a female *Aquila audax* and was assessed by Gaff (2002) to have affinity with Old World vultures; at the time this included members of the present Aegypinae and Gypaetinae in one clade. This partial femur was unavailable to study, but as it has no nomenclatural significance, it is not considered further at this time. It will be assessed elsewhere, along with other similar-sized femora described by Mather (2021, unpublished thesis) that represent indeterminate large accipitrids.

The relationships of *"Taphaetus" lacertosus* were first discussed by van Tets (1974), when he designated the distal right humerus as the lectotype, and suggested it was a member of the living genus *Icthyophaga*, a genus of fish eagle now a synonym of *Haliaeetus*. Later, van Tets (1984) without rationale suggested it was related to the living accipitrid subfamily Gypaetinae, to which all accipitrid vultures were assigned at the time. In a review of avian taxa described by de Vis, van Tets and Rich (1990), described "*Taphaetus*" *lacertosus* as under study with unknown affinities within Accipitriformes. Priscilla Gaff, in her unpublished thesis (Gaff 2002), did not study the material (humerus, QM F5507 or quadrate QM F5508) on which *"Taphaetus" lacertosus* was based. Other works that also suggested the presence of Old World vultures in the Pleistocene Australian avifauna (Rich & van Tets 1982; Tedford & Wells 1990) were presumably alluding to this material, but the relationships of "*Taphaetus*" *lacertosus* remain unexamined.

Given that '*lacertosus*' is an available species name in nomenclatural terms, determining whether it is a species distinct from living and other fossil taxa, and thus its taxonomic (including generic) affinity, is a necessary precursor to investigating the diversity of Australian Pleistocene accipitrids and assignment of such fossils to taxa. Therefore, here we aim to redescribe the lectotype of '*lacertosus*', establish whether it is a distinct taxon, and if so, correct its nomenclature by assigning it to either an existing or a new genus as required. In doing so, other large accipitrid fossils from Pleistocene sites in Australia will be surveyed for possible assignment to the taxon and then the relationships reassessed for the taxon. The quadrate QM F5508 described by de Vis (1905) was unavailable for study due to closures of the collection at Queensland Museum between 2017–2021. Comparisons were instead made with extant specimens using the description and illustrations of the fossil in de Vis (1905).

Materials and methods

Abbreviations

Institution. Australian Museum, Sydney, NSW, Australia (AM); Australian National Wildlife Collection, Canberra, ACT, Australia (ANWC); University of Kansas Institute of Biodiversity, Lawrence, KS, USA (KU); Natural History Museum, London, UK (NHMUK); Museums Victoria, Melbourne, VIC, Australia (NMV); South Australia Museum, Adelaide, SA, Australia (SAMA); Queensland Museum, Brisbane, QLD, Australia (QM); Smithsonian Museum of Natural History, Washington DC, USA (USNM); Western Australian Museum, Perth, WA, Australia (WAM).

Nomenclature

The anatomical nomenclature advocated by Baumel & Witmer (1993) is followed for all bones. Accipitrid nomenclature follows Nagy & Tökölyi (2014) for subfamilial composition (excluding Milvinae), and Dickinson & Remsen (2013) for species, wherein the authors for living taxa can be found. Subfamily nomenclature differs from that in Mindell et al. (2018) by recognizing Haliaeetinae as distinct from Buteoninae, and Harpiinae from Aquilinae.

Comparative material

Specimens were obtained on loan from museums and other institutions from across Australia and overseas.

PHOENICOPTERIFORMES.

Phoenicopteridae. *Phoenicopterus ruber* Linnaeus SAMA B11552.

PELECANIFORMES.

Pelecanidae. *Pelecanus conspicillatus* Temminck SAMA B46635.

Ardeidae. *Ardea cinerea* Linnaeus SAMA B49222; *Egretta novaehollandiae* (Latham) SAMA B32854; *Botaurus poiciloptilus* (Wagler) SAMA B6971.

Threskiornithidae. *Threskiornis spinicollis* (Jameson) SAMA B48351.

CICONIIFORMES.

Ciconiidae. *Ciconia ciconia* (Linnaeus) SAMA B49223, SAMA B11601; *Ephippiorhynchus asiaticus* (Latham) SAMA B5098.

ACCIPITRIFORMES.

Cathartidae. *Coragyps atratus* (Bechstein) SAMA B36873.

Sagittariidae. *Sagittarius serpentarius* (J. F. Miller) USNM 223836.

Pandionidae. *Pandion haliaetus* (Linnaeus) SAMA B37096, NMV B30256.

Accipitridae specimens (in phylogenetic order):

Elaninae: *Elanus axillaris* (Latham) NMV B34037; *Elanus scriptus* Gould NMV B8617, NMV B30263, ANWC 22680. Perninae: *Elanoides forficatus* (Linnaeus) USNM 622340; *Chondrohierax uncinatus* (Temminck) USNM 289784; *Pernis apivorus* (Linnaeus) SAMA B59278; *Lophoictinia isura* (Gould) NMV B18533, ANWC 44373; *Hamirostra melanosternon* (Gould) ANWC (FALS-41), SAMA B36200. Gypaetinae: *Polyboroides typus* A. Smith USNM 430434; *Neophron percnopterus* (Linnaeus) SAMA B11449; *Gypohierax angolensis* (J. F. Gmelin) USNM 291316; *Gypaetus barbatus* (Linnaeus) NHMUK S.1972.1.59, NHMUK S.1896.2.16.120, NHMUK S.1952.3.61. Circaetinae: *Spilornis cheela* (Latham) USNM 562001; *Terathopius ecaudatus* (Daudin) NMV 18575; *Pithecophaga jefferyi* Ogilvie-Grant NHMUK S.1910.2.11.1a, NHMUK S.1961.23.1. Aegypiinae: *Necrosyrtes monachus* (Temminck) USNM 620646; *Gyps coprotheres* (J. R. Forster) ANWC 22724; *Gyps fulvus* (Hablizl) NMV 18574, NMV B30269; *Aegypius monachus* (Linnaeus) NMV R553; *Sarcogyps calvus* (Scopoli) NHMUK S.2013.22.1, NHMUK S.2007.30.1; *Trigonoceps occipitalis* (Burchell) NHMUK S.1954.30.54; *Torgos tracheliotos* (J. R. Forster) NHMUK S.1930.3.24.248, NHMUK S.1952.1.172. Aquilinae: *Aquila audax* (Latham) SAMA B46613, NMV B19228; *Aquila chrysaetos* (Linnaeus) NMV B32659, ANWC 22682 (FALS-123); *Aquila fasciata* (labelled as *Hieraaetus fasciatus*) Vieillot NMV B30575; *Hieraaetus morphnoides* (Gould) SAMA B47128, NMV B8643, NMV B20224; *Hieraaetus* (*=Harpagornis*) *moorei* (Haast) casts of original type material, NMV P33032 (tibiotarsus), NMV P33031 (pedal phalanx), NMV P33030 (tarsometatarsus), NMV P33029 (femur), NMV P33028 (humerus), NMV P33027 (femur), NMV P33026 (ulna); *Spizaetus tyrannus* (zu Wied-Neuwied) KU 35007; *Spizaetus ornatus* (Daudin) KU 72077. Harpiinae: *Morphnus guianensis* (Daudin) NHMUK 1851.12.2.10; *Harpia harpyja* (Linnaeus) NHMUK 1862.3.19.14, 1909.8.18.1. Haliaeetinae: *Haliaeetus leucogaster* (J. F. Gmelin) NMV B8847, SAMA B49459; *Haliaeetus leucocephalus* (Linnaeus) ANWC 22723 (16500), NMV B15601; *Haliaeetus albicilla* (Linnaeus) NMV B34417; *Haliastur indus* (Boddaert) ANWC 22719, NMV B13753; *Haliastur sphenurus* (Vieillot)

NMV B11661, SAMA B33998; *Milvus migrans* (Boddaert) SAMA B47130, NMV B20404. Accipitrinae: *Circus assimilis* Jardine & Selby SAMA B56454, ANWC 22727; *Circus cyaneus* (Linnaeus) ANWC 22735; *Circus aeruginosus* (Linnaeus) NMV B12891; *Accipiter fasciatus* (Vigors & Horsfield) NMV B13444, SAMA B36355; *Accipiter cooperii* (Bonaparte) ANWC 22764, ANWC 22765; *Accipiter striatus* Vieillot ANWC 22747, NMV B12666; *Accipiter novaehollandiae* (J. F. Gmelin) NMV B18401; *Accipiter cirrocephalus* (Vieillot) NMV B16071, NMV B10346; *Accipiter nisus* (Linnaeus) NMV B12413, ANWC 22742; *Accipiter gentilis* (Linnaeus) ANWC 22736, NMV B12927. Buteoninae: *Ictinia mississippiensis* (A. Wilson) ANWC 22681 (21655), NMV B13343; *Geranospiza caerulescens* (Vieillot) NHMUK S.1903.12.20.318; *Buteo buteo* (Linnaeus) SAMA B46558, NMV B24505; *Buteo lagopus* (Pontoppidan) NMV B24884, ANWC 22776 (21694); *Buteo nitidus* (Latham) NMV B13222; *Buteo rufofuscus* (J. R. Forster) NMV B24503.

Measurements

Bones were measured to an accuracy of 0.1 mm using digital callipers.

Photography and scanning

All photographs created at Flinders were taken using a focus stacking method using a Canon 5DS-r digital camera 50.0 MP and either a Canon EF 100 mm or 65 mm f2.8 IS USM professional macro lens. Multiple images were then compiled into a single photo using the program Zerene Stacker. The lectotype specimen for "*Taphaetus" lacertosus*, QM F5507, a distal left humerus, was photographed and surface scanned using an Einscan Pro+ handheld 3D scanner with an Industrial Pack tripod and turntable at the Queensland Museum by Isaac Kerr. The resulting point cloud scan files were then processed into triangle meshes in Einscan Software V3.0. This was then compiled into a 3D image accurate to roughly 200 microns, using the digital program Blender; this image was used to assess the morphological features of the fossil in a way that photography alone could not capture (see SI.4).

Phylogenetic methods

Morphological data

Three hundred morphological characters, from the cranium to the pedal digits, were coded for living species, and where applicable, in the fossil material. A total of 154 characters was derived from Migotto (2013, unpublished thesis), two from Elzanowski & Stidham (2010), two from Elzanowski & Zelenkov (2015), six from Gaff & Boles (2010), one from Worthy et al. (2016), and three each from Mayr (2014) and Mayr (2018). The remaining characters were novel traits derived from observations and comparisons between the living and fossil specimens (Mather et al. 2021).

Molecular data

Molecular data from Burleigh et al. (2015) were added to the morphological data to improve estimated relationships among living species (Lerner & Mindell 2005; Nagy & Tökölyi 2014; Burleigh et al. 2015). The following genes, well-sampled in accipitrids, were used: cytochrome b, cytochrome oxidase 1, NADH dehydrogenase 2, 12s RNA, RAG 1, and fibrinogen B beta introns 6 and 7 (Mather et al. 2021).

The following species were sampled for available genes from the above loci: *Ciconia ciconia*, *Coragyps atratus*, *Sagittarius serpentarius*, *Pandion haliaetus*, *Elanus caeruleus*, *Gampsonyx swainsonii*, *Elanoides forficatus*, *Chondrohierax uncinatus*, *Aviceda subcristata*, *Pernis apivorus*, *Lophoictinia isura*, *Hamirostra melanosternon*, *Polyboroides typus*, *Neophron percnopterus*, *Gypohierax angolensis*, *Gypaetus barbatus*, *Spilornis cheela*, *Terathopius ecaudatus*, *Pithecophaga jefferyi*, *Necrosyrtes monachus*, *Gyps fulvus*, *Gyps coprotheres*, *Aegypius monachus*, *Sarcogyps calvus*, *Trigonoceps occipitalis*, *Torgos tracheliotos*, *Harpia harpyja*, *Stephanoaetus coronatus*, *Aquila chrysaetos*, *Hieraaetus morphnoides*, *Aquila fasciata*, *Hieraaetus moorei*, *Spizaetus tyrannus*, *Spizaetus ornatus*, *Haliaeetus leucogaster*, *Haliaeetus leucocephalus*, *Haliaeetus albicilla*, *Milvus migrans*, *Melierax metabates*, *Kaupifalco monogrammicus*, *Circus aeruginosus*, *Circus cyaneus*, *Accipiter cooperii*, *Accipiter striatus*, *Accipiter novaehollandiae*, *Accipiter gentilis*, *Ictinia mississippiensis*, *Geranospiza caerulescens*, *Buteo buteo*, *Buteo lagopus*, *Buteo rufofuscus*, and *Platalea leucorodia*. To reduce missing data, genomic data from *Platalea leucorodia* was used instead of *Threskiornis spinicollis*, and *Elanus caeruleus* for *Elanus scriptus*, as these species pairs consist of closely related taxa (see Campbell & Lapointe 2009 regarding this method) (Mather et al. 2021).

Phylogenetic analysis

Forty-seven species of Accipitridae and one each from Pandionidae, Sagittariidae, Cathartidae, Threskiornithidae and Ciconiidae were sampled (Mather et al. 2021). The list of 300 morphological characters (67 ordered) is in SI.1, the data matrix is in SI.2, and the nexus input file is in SI.3. Phylogenetic relationships were assessed using the parsimony program PAUP 4.0a169, using a combined molecular-morphological dataset and heuristic searches. Each search comprised of 1000 random addition replicates, and enabled TBR branch swapping, with NCHUCK set to 1000 (Mather et al. 2021). Characters that were inapplicable to a specimen were coded using a '-', while missing data were coded as '?' for recording purposes, though PAUP treats these identically. The taxa *Threskiornis spinicollis*, *Ciconia ciconia*, *Coragyps atratus*, and *Sagittarius serpentarius* were set as outgroups to the Accipitridae plus Pandionidae. The support for clades on these trees was then assessed using bootstrapping via 1000 replicates, and the results were set to a conlevel of 50 (support shown on bootstrap consensus tree if >50%).

Fossil sites

Kalamurina, Warburton River

The Kalamurina locality is located near the Kalamurina Homestead, on the Warburton River approximately 55 km north-east of Lake Eyre in north-eastern South Australia. Fossils from this site were collected during an expedition in 1901–1902 led by J. W. Gregory, most likely from the riverbed beside fluvial deposits outcroppings on the riverbank just north of the homestead itself; these fossils constitute the Kalamurina Fauna (see Tedford et al. 1986; Tedford & Wells 1990). Tedford & Wells (1990) noted that the course of the Warburton River between Kalamurina and Toolapinna Waterhole cuts through the Katipiri Formation, from which the Kalamurina Fauna originates. The Katipiri Formation itself is now considered to be Middle to Late Pleistocene in age (Nanson et al. 2008; Megirian et al. 2010). The distal humerus QM F5507 and a quadrate QM F5508 are the only material that has been identified as accipitrid from the Warburton River sites (de Vis 1905).

Wellington Caves

The Wellington Caves are located in central-western New South Wales, seven kilometres south of the town of Wellington, and the fossiliferous deposits within are believed to have formed between the Pliocene and the late Pleistocene (Dawson et al. 1999; Megirian et al. 2010). The caves are formed in Devonian-age limestone at a boundary between facies of limestone-mudstone containing calcarenite (Frank 1971, 1975) and a thinly bedded limestone facies (Osborne 2007). Cathedral Cave, the largest of these caves, has yielded many fossils of great significance, most of them from the Cathedral Chamber and the Well Chamber (Dawson 1985; Dawson & Augee 1997; Prideaux et al. 2007a). An estimated 7–10 m of fossil-bearing sediment covers the floors of the Cathedral and Well Chambers (Osborne 1991). Fossils have also been found at other caves in this complex, most notably Bone Cave, Phosphate Mine and Mitchell's Cave (Osborne 1991, 1997). Mitchell Cave and Phosphate Mine are the source of huge collections of poorly provenanced Pleistocene material (Dawson 1985).

While numerous authors have attempted to date the stratigraphy of the Wellington Caves assemblages (see Dawson & Augee 1997), many of these dates are now regarded as problematic and are currently under revision (D. Fusco pers. comm.). The age of the fossils from the Wellington Caves deposits are therefore largely inferred based on biochronological comparisons with other sites (Megirian et al. 2010).

The accipitrid material from Wellington Caves has poor provenance data, with most fossils lacking both the identity of the source site and stratigraphic data. Three specimens from this site in the collections of the Australian Museum were identified as *"Taphaetus" lacertosus*; they include two distal humeri and a tarsometatarsus, which are part of the "Old Collection". The Old Collection refers to a large number of fossils that were excavated from the Wellington Caves throughout the mid-19th to early 20th centuries, most of which were not properly sorted or registered until 1926 (Dawson 1985). The accipitrid specimens reported herein were first transferred to the Australian Museum in 1976 and most likely were among the fossils acquired by the NSW Department of Mines between 1884 and 1917 (Dawson 1985). Due to their lack of precise collection data, their age can only be determined as Pleistocene.

Leaena’s Breath Cave

Leaena’s Breath Cave (alternate spelling; Leana’s Breath Cave) is a 73-m long limestone cave located in the Nullarbor Plains of Western Australia, located directly south of Old Homestead Cave, and is part of a collective of caves known as the Thylacoleo Caves. The cave itself has been dated as minimally four million years old using U-PB geochronology techniques on speleothems (Woodhead et al. 2006). Leaena’s Breath Cave was first discovered in 2002, and along with other caves in the Thylacoleo Caves complex, has yielded Pleistocene age fossils of remarkable quality, including complete skeletons (Prideaux et al. 2007b). The age of these fossils is thought to range between 400–200 Ka for specimens in the upper sediment of the excavation, based on optical dating, to as old as 780–400 Ka for those in the lower sediment, based on U-Th and palaeomagnetic dating (Prideaux et al. 2007b). Very little accipitrid material has been collected from Leaena’s Breath Cave, but that present has good provenance data. Only a proximal tarsometatarsus, identified as an indeterminate accipitrid by Shute (2018), is here attributed to *“Taphaetus”*.

Results

Systematic Palaeontology

Accipitriformes Vieillot, 1816

Accipitridae Vigors, 1824

The lectotype of *‘Taphaetus’ lacertosus* de Vis, 1905, a distal right humerus, QM F5507, is identified as an accipitrid based on the presence of the following characters: The distal margin of the fossa brachialis extends distal to the tuberculum supracondylare dorsale; a distinct sulcus scapulotricipitalis; the proximal margin of the condylus dorsalis is roughly level with the ventral tip of the epicondylus ventralis; a distinct circular dorsal insertion for the m. extensor metacarpi radialis on the dorsal projection of the tuberculum supracondylare dorsale; a distinct pit for the insertion of the m. pronator superficialis ventrally adjacent to and slightly proximal to the tuberculum supracondylare ventrale; and the epicondylus ventralis is markedly ventrally prominent.

This fossil is readily distinguished from the following similar-sized birds likely to be encountered in Pleistocene Australian fossil sites.

- From Ciconiidae (*Ephippiorhynchus asiaticus*) by the following characters (ciconiid state in brackets): The tuberculum supracondylare dorsale is strongly projecting (little to no projection); the dorsal sulcus of the m. humerotricipitalis is narrow, just under a third of the shaft width (broad, roughly half the shaft width); the ventral sulcus of the m. humerotricipitalis is broad, twice the width of the dorsal sulcus (narrow, half the width); the epicondylus ventralis and the tuberculum supracondylare ventrale are distinctly separated from each other (continuous/overlapping); the dorsal insertion of the m. extensor metacarpi radialis is oval restricted to the dorsal facies (circular with a ventrally projecting line leading onto the cranial facies).
- From Pelecanidae (*Pelecanus conspicillatus*) by the following characters (pelecanid state in brackets): The tuberculum supracondylare dorsale is strongly projecting (little to no projection); the origin of m. extensor digitorum communi is a small, circular pit on the dorsal facies between the tuberculum supracondylare dorsale and the epicondylus dorsalis (large, oval-shaped attachment scar); the tuberculum supracondylare ventrale is weakly projecting cranially (cranially flattened); there is no pneumatism of the distal end (pneumatic region present on cranial facies adjacent to tuberculum supracondylare ventrale); the epicondylus ventralis strongly projects ventrally (weak projection); the distal margin of the fossa brachialis is positioned distal to the tuberculum supracondylare dorsale (positioned proximal to the processus).
- From Phoenicopteriformes (*Phoenicopterus ruber)* by the following characters (phoenicopterid state in brackets): the epicondylus ventralis projects prominently ventrally (little to no projection), the dorsal sulcus for the m. humerotricipitalis is under a third of the shaft width (half of shaft width), the ventral sulcus for the m. humerotricipitalis is twice the width of the dorsal sulcus (half the width of the dorsal sulcus), the tuberculum supracondylare ventrale is weakly projecting cranially (cranially flattened), the condylus dorsalis and condylus ventralis are separated by a distinct, deep incisura (narrow, shallow incisura).

- From Ardeidae by the following characters (ardeid state in brackets): A deep fossa m. brachialis (shallow); a broad fossa m. brachialis, approximately two thirds of shaft width or more (narrow, one third of shaft width); a narrow sulcus for the dorsal belly of the m. humerotricipitalis (broad).

Several features of the bone, notably its large size, are only matched by *Aquila audax* and *Haliaeetus leucogaster* in the Australian fauna. However, the combination of a narrow dorsal part of sulcus humerotricipitalis, a markedly prominent epicondylus ventralis, the dorsally inflated facies between the tuberculum supracondylare dorsale and the epicondylus dorsalis, and a distally short processus flexorius, distinguish it from all other accipitrids. As this humerus is unambiguously identifiable as that of an accipitrid and is distinguished from all known genera and species, *'Taphaetus' lacertosus* is confirmed as a distinct taxon. However, it requires a new genus, as *Taphaetus* de Vis, 1905 is a junior homonym of *Taphaetus* de Vis, 1891, and the latter is a junior synonym of *Uroaetus* Kaup, 1844 and so of *Aquila* Brisson, 1760.

As the quadrate QM F5508 was inaccessible at the time of this study, we instead used the descriptions and illustrations in de Vis (1905) to assess if the original identification was valid. QM F5508 differs distinctly from quadrates of accipitrids, instead being similar to those of Ardeidae, particularly species in the genera *Ardea* and *Egretta*, by the following characters (accipitrid state in brackets): A large foramen pneumaticum caudomediale is positioned ventral to the capitulum oticum articular surface (no foramen pneumaticum, though a depressio caudomediale is present in some species); the capitulum oticum is positioned further dorsally relative to the capitulum squamosum (capitulum squamosum further dorsal); the width of the capitula and the width of the shaft are very similar, with little narrowing between the dorsal and ventral ends (shaft distinctly narrower than dorsal end); in caudal view, the condylus mandibularis medialis is positioned level with the condylus mandibularis lateralis, with both being equally visible (condylus mandibularis medialis set back rostrally, less visible than the condylus lateralis); the condylus mandibularis caudalis is prominently projecting caudally (projecting medially); the condylus mandibularis lateralis barely extends laterally from the shaft (extends prominently caudally); the condylus mandibularis medialis extends prominently medially from the shaft (little to no extension); a prominent secondary facet is present on the condylus mandibularis medialis (no secondary facet); in ventral view, the condyles project rostrally past the rostral margin of the articular surface (roughly in line with margin). The reported dorsal height of 22 mm is distinctly larger than that observed in the Australasian Bittern *Botaurus poiciloptilus* (~15–16 mm). While the morphology of QM F5508 is a better match for a heron, it is much larger than compared specimens of White-faced Heron *Egretta novaehollandiae* and Grey Heron *Ardea cinerea* but could potentially be a match in size to that of the Great-billed Heron (*Ardea sumatrana*). As QM F5508 is not of an accipitrid, it is not considered further here.

***Cryptogyps* Mather, Lee and Worthy 2022 gen. nov.**

http://zoobank.org/NomenclaturalActs/6CD1D60A-5B25-4431-8FB2-BD5EE5EAFE77

Type species: *'Taphaetus' lacertosus* de Vis, 1905: Annals of the Queensland Museum 6: 4, pl. 1, fig. 1.

Etymology: The name is derived from a combination of the Ancient Greek words '*kryptós*' (hidden) and '*gýps*' (vulture), in reference to the fact that this taxon was known for over 100 years but was generally believed to be an eagle. *Cryptogyps* also relates to the word 'crypt', a word used to describe an underground burial chamber, referencing the discovery of the new material in caves.

Revised diagnosis: A large accipitrid, similar in size to *Aquila audax*, with humeri differing from all other Accipitridae by the following combination of characters: **(1)** a prominent dorsal convexity of the facies between the tuberculum supracondylare dorsale and the epicondylus dorsalis; **(2)** a strongly dorsally projecting tuberculum supracondylare dorsale; **(3)** a distinct and deepened attachment for the origin of m. extensor digitorum communi; **(4)** a large, shallow, circular attachment scar for the origin of the proximal head of m. pronator superficialis (=pronator brevis); **(5) t**he epicondylus ventralis is strongly projected ventrally as a craniocaudally elongate peak; **(6) t**he processus flexorius is distally short, ending proximal to the distal margin of the condylus ventralis; **(7)** and it has a narrow sulcus/groove for the dorsal belly of the m. humerotricipitalis.

Cryptogyps lacertosus (de Vis, 1905) comb. nov.

Lectotype: QM F5507, distal R humerus (designated by van Tets, 1974, p. 58).

Type locality: Kalamurina, Warburton River, Kati Thanda–Lake Eyre Basin, SA. Collected by John W. Gregory in April 1902 (de Vis 1905).

Stratigraphy and Geological age: Katipiri Formation; mid- to late Pleistocene; the fossils are assumed to have derived from fluvial sediments that outcrop in the banks of the river at this point. The associated fauna comprises the Kalamurina Fauna and is typical of the late Pleistocene (Tedford & Wells 1990; Tedford et al. 1992).

Measurements (mm) of QM F.5507: preserved distal width 35.5, lateromedial width of the condylus dorsalis 9.1, depth of the condylus dorsalis 22.3, proximodistal length of the condylus dorsalis 12.3, width of the condylus ventralis 14.1.

Amended diagnosis: As for genus.

Description: In addition to the diagnostic characters described above, the following characters serve to distinguish the species: **(8)** the palmar attachment for the m. extensor metacarpi radialis (Figure 1A, C; PEMR) on the cranial facies immediately ventral of the tuberculum supracondylare dorsale (Figure 1A; TSD), is shallow, roughly oval-shaped, and orientated dorsoventrally; **(9)** the sulcus for the dorsal attachment of the m. extensor metacarpi radialis (Figure 1A, B; DEMR) is large and deep on the dorsal facies of the tuberculum supracondylare dorsale, and is directed dorsoproximally; **(10)** the epicondylus dorsalis is dorsally flat and does not project dorsally of the condylus dorsalis; **(11)** the fossa m. brachialis (Figure 1A; FB) is deep, with the distal margin positioned well proximal to the tuberculum supracondylare ventrale; **(12)** the dorsal margin of the fossa m. brachialis extends close to (~2 mm) the dorsal margin of the shaft; **(13)** the tuberculum supracondylare ventrale (Figure 1A; TSV) is not inflated ventrally and is moderately projected cranially; **(14)** the interior margin of the tuberculum supracondylare ventrale is aligned roughly parallel to the adjacent medial surface; **(15)** the attachment scars for the origin of the distal head of m. pronator superficialis and of m. pronator profundus are deep, with that for the former being deepest; **(16)** the incisura intercondylaris (Figure 1A; II) is relatively broad, roughly 3 mm in width, and distinctly separates the two condyles cranially; **(17)** the distal point of the condylus dorsalis (Figure 1A; CD) is set well proximal of the distalmost point of the condylus ventralis, with the distal margin forming a broad, shallow notch between the two condyles; **(18)** the distoventral margin of the condylus ventralis (Figure 1A; CV) is continuous with the entepicondyle; **(19)** and the sulcus scapulotricipitalis (Figure 1D; SST) is shallow and relatively broad.

Comparisons of the lectotype distal humerus QM F5507

Humerus. QM F5507, the lectotype of *Cryptogyps lacertosus* differs markedly from humeri of all species of accipitrid present in Australia. It is larger than all except those of *Aquila audax* and *H. leucogaster* and differs from these by the above diagnostic characters and especially **(1)** the convex projecting dorsal facies distal to the tuberculum supracondylare dorsale; **(12)** the more projecting epicondylus ventrale and **(7)**, the narrow groove for the dorsal belly of m. humerotricipitalis. The following comparisons, therefore, seek to establish to which subfamily it should be attributed. Referral of *Cryptogyps lacertosus* to the Elaninae, Perninae, Accipitrinae and Buteoninae can be excluded based on size, as all species in these subfamilies are significantly smaller than the fossil.

The Circaetinae, Aquilinae (e.g., *Aquila audax*), Harpiinae and Haliaeetinae (e.g., *Haliaeetus leucogaster*) can be excluded by the following differences exhibited by species in these groups: **(1)** the dorsal facies between the tuberculum supracondylare dorsale and epicondylus dorsalis has low dorsal convexity; **(2)** the tuberculum supracondylare dorsale is weakly to moderately projecting and flattened; **(4)** the attachment scar for the proximal head of pronator superficialis is small; **(5)** the epicondylus ventralis is weakly projecting ventrally; **(6)** the distal extent of the processus flexorius is equal to that of the condylus ventralis; **(7)** the dorsal sulcus of the m. humerotricipitalis is broad, occupying roughly half of the shaft width, while the ventral sulcus is quite narrow; **(13)** the tuberculum supracondylare ventrale is proximocranially prominent; and **(14)** the interior margin of the tuberculum supracondylare ventrale is aligned across the shaft at a low angle.

The humerus of *Cryptogyps lacertosus* most closely resembles those of species in the subfamilies Aegypiinae and Gypaetinae, with both subfamilies sharing similar states for the above diagnosis/description characters 6, 7, 9, 10, and 12; gypaetines in addition share states for characters 2, 11, and 18, and aegypiines share states for characters 1, 14, 16 and 19.

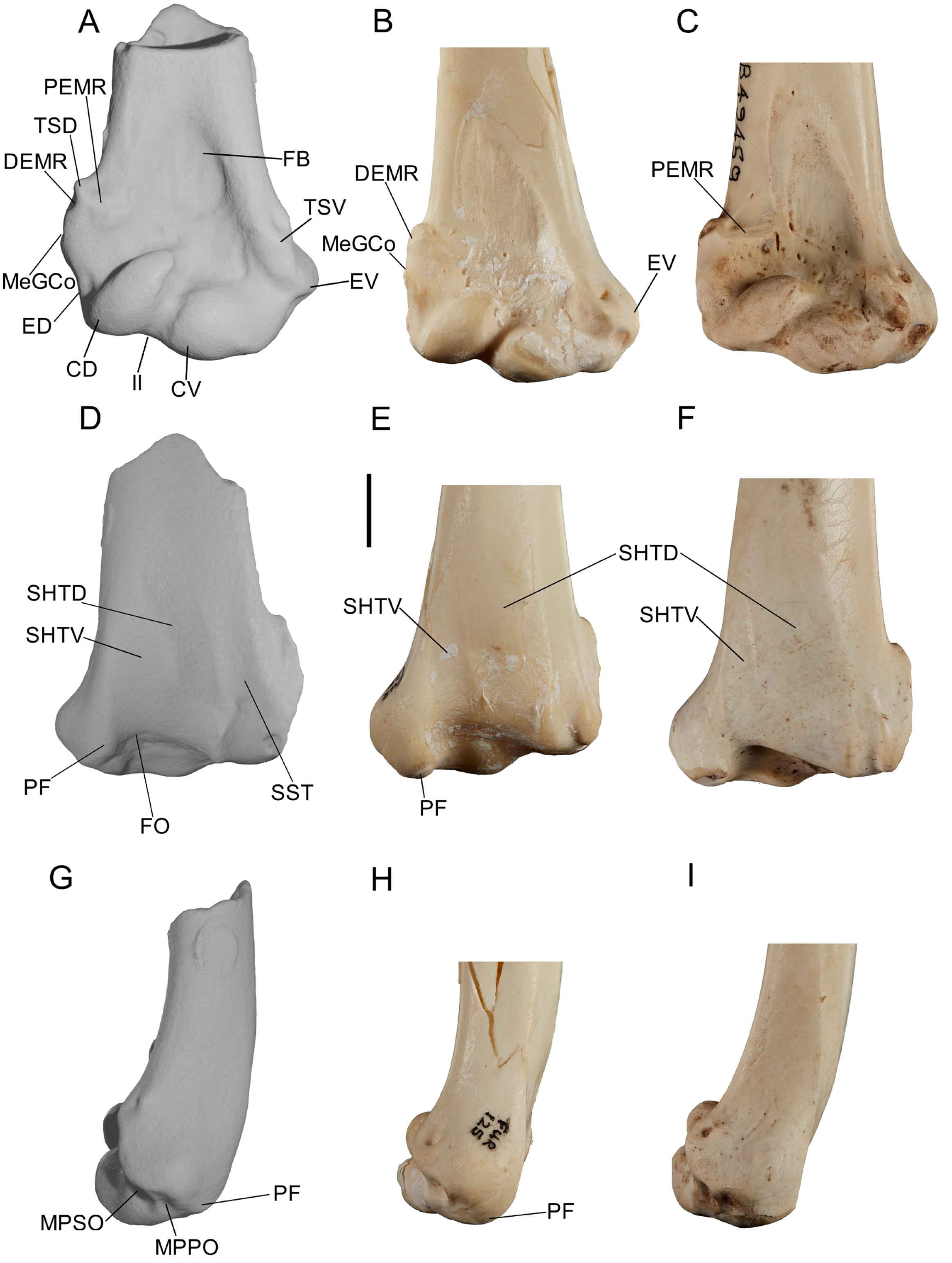

FIGURE 1. Comparisons of the distal humeri of *Cryptogyps lacertosus* QM F5507 (scanned, A, D, G), *Aquila audax* (B, E, H) and *Haliaeetus leucogaster* (C, F, I) in cranial (A, B, C), caudal (D, E, F) and ventral (G, H, I) view. Abbreviations: CD, condylus dorsalis; CV, condylus ventralis; DEMR, dorsal attachment m. extensor metacarpi radialis; ED, epicondylus dorsalis; EV, epicondylus ventralis; FB, fossa brachialis; FO, fossa olecrani; II, incisura intercondylaris; MeDCo, m. extensor digitorum communi origin; MPSO, origin of distal head of m. pronator superficialis; MPPO, m. pronator profundus origin; PF, processus flexorius; PEMR, palmar attachment m. extensor metacarpi radialis; SHTD, dorsal sulcus humerotricipitalis; SHTV, ventral sulcus humerotricipitalis; SST, sulcus scapulotricipitalis; TSD, tuberculum supracondylare dorsale; TSV, tuberculum supracondylare ventrale. Scale bar 10 mm.

The subfamilies differ from *Cryptogyps lacertosus* in the following characters:

Gypaetinae

(1) The dorsal facies between the tuberculum supracondylare dorsale and epicondylus dorsalis is less inflated as a convex surface compared to the fossil, barely projecting dorsal of these two points; **(3)** the insertion point for the m. extensor digitorum communi does not form a distinct pit; **(4)** the attachment scar for the proximal head of pronator superficialis is small and deep; **(5)** the epicondylus ventralis forms a moderate, rounded peak; **(8)** the palmar attachment scar of the m. extensor metacarpi radialis is small, circular and shallow in all species except *Polyboroides typus*, where it is circular, rather than broad, robust and elevated, as in the fossil; **(13)** the tuberculum supracondylare ventrale is more flattened, not elevated cranially; **(14)** the interior margin of the tuberculum supracondylare ventrale is oriented at a lower angle across the shaft; **(15)** the insertion scars of the distal m. pronator superficialis and profundus are roughly the same depth in *G. angolensis*, while that of m. pronator profundus is shallower in *P. typus* and *N. percnopterus*; **(16)** the incisura intercondylaris is broad in *N. percnopterus* (as in the fossil) and narrow in *P. typus*; **(17)** the distal margin forms a deep narrow notch between the condyles; **(19)** the two parts of the sulcus m. humerotricipitalis are shallow in all taxa, with the dorsal sulcus roughly one third of shaft width in *N. percnopterus* and half the width in *P. typus* and *G. angolensis*. The sulcus for the ventral belly is a third to a quarter of the shaft width in all species.

Aegypiinae

The Aegypiinae share states with the Gypaetinae for characters **(3)**, **(4)**, **(5)** and **(13).** The Aegypiinae differ in the following characters: **(2)** the tuberculum supracondylare dorsale does not project cranially in aegypiines; **(11)** the fossa m. brachialis is shallower than in *Cryptogyps lacertosus* in all species except those in *Gyps* and *Aegypius;* **(15)** only the origins for the distal m. pronator superficialis and profundus are distinct in *Necrosyrtes monachus*, while in all other taxa, the origin for the m. extensor metacarpi ulnaris is also distinct. The cranial-most attachment point is deeper than the caudal-most attachment, which latter is almost flat in *A. monachus*, *G. fulvus* and *G. coprotheres*, and the third insertion scar present in the aforementioned taxa is shallow; **(17)** the distal margin between the condyles forms a shallow, broad notch in the species of *Gyps* and *N. monachus* and is narrow and deep in *A. monachus*; **(18)** the distal margin of the condylus ventralis is not continuous with the entepicondyle in any species, except *N. monachus* (continuous).

Newly referred material

Localities and age: Leaena's Breath Cave, Nullarbor, WA, Australia, 31.4°S 128.1°E; excavation Pit B1, Unit 3, depth 115–120 cm; Pleistocene; collected by G. Prideaux et al. 2013, identified as an accipitrid by Shute (2018, Figure 4.44): WAM 15.9.73 proximal left tarsometatarsus.

'Old Collection', Wellington Caves, NSW, Australia, 32°31' S, 148°51' E; Pleistocene; likely acquired by NSW Mining Department 1884–1917: AM F.58093, left tarsometatarsus; AM F.58092, distal right and left humeri.

The new material has been assigned to *Cryptogyps lacertosus* for the following reasons: The two distal humeri fragments AM F.58092 are a similar size to (see Table 1) and have identical morphology to the lectotype QM F5507, and so are unambiguously referred to this same species. Specifically, these two fragments show the same unique sharp ventrally projecting entepicondyle and the same distally abbreviated processus flexorius (see Figure 2).

TABLE 1. Measurements (mm) of distal humeri of *Cryptogyps* (QM F. 5507, AM F. 58092) compared to *Aquila audax*. For *Aquila audax*, the data are the mean, number, range and standard deviation. *A. audax* specimen numbers: FUR 125, FUR 085, SAMA B46613, SAMA B49025, SAMA B47814, SAMA B39628, SAMA B46633, SAMA B55112, SAMA B31109, SAMA B46992. Abbreviations: CD, condylus dorsalis; CV, condylus ventralis.

Specimen	Distal width	CD width	CD length	CV width
QM F.5507	35.5	9.1	12.3	14.4
AM F.58092 R	31.8	9.2	13.3	13.7
AM F.58092 L	29.8	8.2	12.5	14.9
A. audax	30.3, (10), 28–32.3, 1.4	8.8, (10), 7.9–10.2, 0.8	10.7, (10), 10.2–11.7, 0.5	12.4, (10), 11.6–13.6, 0.7

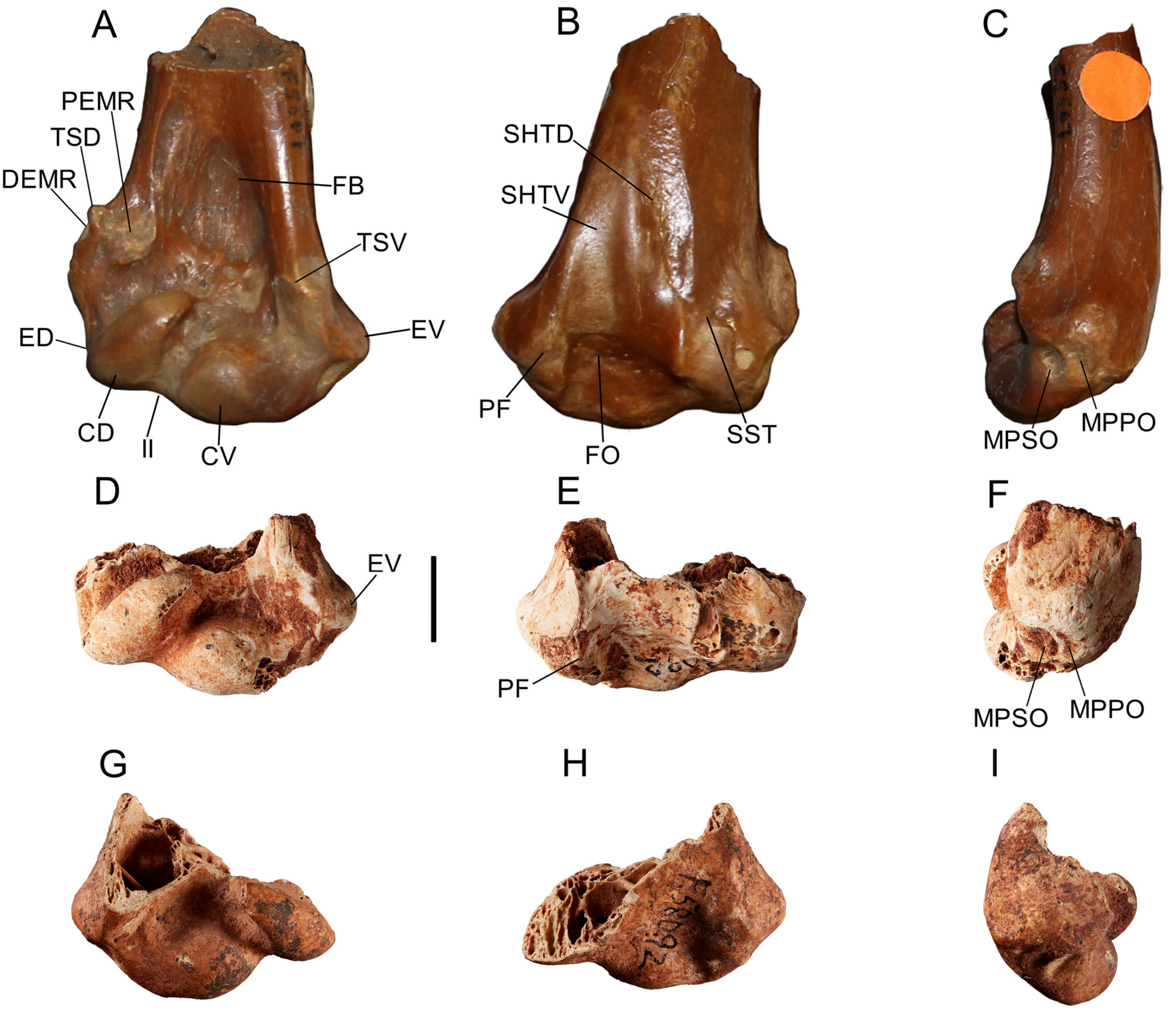

FIGURE 2. Photographs of *Cryptogyps lacertosus* lectotype QM F.5507 (A–C), right distal humerus AM F.58092 (D–F) and left distal AM F.58092 (G–I) in cranial (A, D, G), caudal (B, E, H) and ventral (C, F, I) views. Abbreviations: CD, condylus dorsalis; CV, condylus ventralis; DEMR, dorsal attachment m. extensor metacarpi radialis; ED, epicondylus dorsalis; EV, epicondylus ventralis; FB, fossa m. brachialis; FO, fossa olecrani; II, incisura intercondylaris; MPPO, origin of m. pronator profundus; MPSO, origin of distal head m. pronator superficialis; PF, processus flexorius; PEMR, palmar attachment m. extensor metacarpi radialis; SHTV, ventral belly of sulcus humerotricipitalis; SHTD, dorsal belly of sulcus humerotricipitalis; SST, sulcus scapulotricipitalis; TSD, tuberculum supracondylare dorsale; TSV, tuberculum supracondylare ventrale. Scale bar 10 mm.

The left tarsometatarsus AM F.58093 is associated with the distal humeri AM F.58092 in that it also derives from the 'Old Collections' from Wellington Caves. Its size (see Table 2, 3) is consistent with the size of the bird represented by the humeri, it differs markedly from all known taxa and has a morphology concordant with that of vultures, as does the humerus (see below). Moreover, it is from a distinctly smaller bird than another large accipitrid from Pleistocene deposits in Australia that will be described elsewhere. Therefore, it is considered more parsimonious to refer this tarsometatarsus to the same taxon as the humeri, rather than to erect a second similar-sized taxon. The proximal left tarsometatarsus WAM 15.9.73 from Leaena's Breath Cave has identical morphology to the Wellington Cave tarsometatarsus, and so is also referred to *Cryptogyps lacertosus*.

TABLE 2. Proximal and shaft measurements (mm) of tarsometatarsi of *Cryptogyps* (AM F.58093, WAM 15.9.73) compared to *Aquila audax*. For *Aquila audax*, the data are the mean, number, range and standard deviation. *A. audax* specimen numbers: FUR 125, FUR 085, SAMA B46613, SAMA B49025, SAMA B47814, SAMA B39628, SAMA B46633, SAMA B55112, SAMA B31109, SAMA B46992. Abbreviations: PW, proximal width; PD, proximal depth; CL, crista lateralis hypotarsi.

Specimen	Length	PW	PD (w/o hypotarsus)	PD (w hypotarsus)	CL length	Width (mid-shaft)
AM F.58093	91.4	22	11.9	15.5	10.4	12.8
WAM 15.9.73	NA	21.8	11.4	16.2 (preserved)	12.8 (preserved)	13.4 (preserved)
A. audax	104.1, (10), 101.5–108.2, 2.3	20.1, (10), 18.7–21.6, 1.1	8.6, (10), 7.7–9.1, 0.5	16.1, (10), 14.8–17.2, 0.9	6.4, (10), 5.1–7.5, 0.7	10.8, (10), 9.3–11.8, 1.0

TABLE 3 Distal measurements (mm) of tarsometatarsi specimens of *Cryptogyps* (AM F.58093) compared to *Aquila audax*. For *Aquila audax*, the data are the mean, number, range and standard deviation. *A. audax* specimen numbers: FUR 125, FUR 085, SAMA B46613, SAMA B49025, SAMA B47814, SAMA B39628, SAMA B46633, SAMA B55112, SAMA B31109, SAMA B46992. 'Flange' refers to the projection of bone out from the main trochlea. Abbreviations: DW, distal width; TII, trochlea metatarsi II; TIII, trochlea metatarsi III; TIV, trochlea metatarsi IV.

Specimen	DW (w/o flange)	DW (flange)	TII width (no flange)	TII width (flange)	TII height	TIII width	TIII height	TIV width	TIV height
AM F.58093	23	24.8	5.8	8.1	8.9	8.6	12.1	5.8	12.5
A. audax	20.2, (10), 18–22.1, 1.4	23.6, (10), 21.5–25.4, 1.5	5.5, (10), 4.7–6.3, 0.5	9.8, (10), 9.0–10.8, 0.6	8.1, (10), 7.5–8.8, 0.5	6.8, (10), 6.2–7.3, 0.4	10.1, (10), 9.3–10.9, 0.6	4.4, (10), 3.7–4.8, 0.4	12.5, (10), 11.2–13.3, 0.7

Tarsometatarsus (figures 3A, B, D, F, G, I).

The specimen AM F.58093 from Wellington Caves is near-perfectly preserved, missing only the crista medialis hypotarsi. The specimen from Leaena's Breath Cave WAM 15.9.73 preserves the proximal half of the tarsometatarsus except for the plantar parts of the hypotarsal crests.

These specimens reveal the following features: **(1)** the eminentia intercotylaris (Figure 3B; EI) projects proximally prominently; **(2)** the sulcus hypotarsi (Figure 3G; SH) is narrow in width; **(3)** the base of the sulcus hypotarsi (dorsal surface) is located plantar to the sulcus flexorius; **(4)** the fossa parahypotarsalis lateralis (Figure 3D; FPL) is shallow, about 5–6 mm wide between the crista plantaris lateralis and the base of the crista lateralis hypotarsi, extends about 25 mm distally to where the crista plantaris lateralis and the crista extending from the crista lateralis hypotarsi converge on the lateral margin; **(5)** the notch for the nervus peroneus (figures 3G, H; NP) in proximal aspect is shallow; **(6)** a sulcus for the musculus fibularis longus cannot be distinguished (in *Aquila audax* it is shallow and wholly on the lateral facies); **(7)** the cotylae are roughly level, not with the medial one relatively distally located; **(8)** the fossa infracotylaris dorsalis (Figure 3C; FI) is deepened proximally; **(9)** the impressio ligamentum collateralis lateralis (Figure 3A; IL) is laterally prominent (this margin is worn in AM F.58093); **(10)** the plantar facies of the crista lateralis hypotarsi is broadly ellipsoid (5.2 x 8.7 mm); **(11)** the distal end of the crista medialis hypotarsi is adjacent to the foramen vasculare proximale medialis; **(12)** the medial foramen vasculare is positioned medial to the crista medianoplantaris; **(13)** the medial shaft margin is relatively thick dorsal to the fossa parahypotarsalis medialis; **(14)** the proximal end of the fossa parahypotarsalis medialis (figures 3E, F; FPM) is deep and makes up over one third of shaft width; **(15)** the impressiones retinaculi extensorii (Figure 3C; IRE) are not discernible in either specimen; **(16)** the tuberositas m. tibialis cranialis (figures 3B, C; T) directly abuts the foramina vascularia proximalia in WAM 15.9.73, but in AM F.58093 the medial foramen is slightly separated proximally from the tuberositas (separated

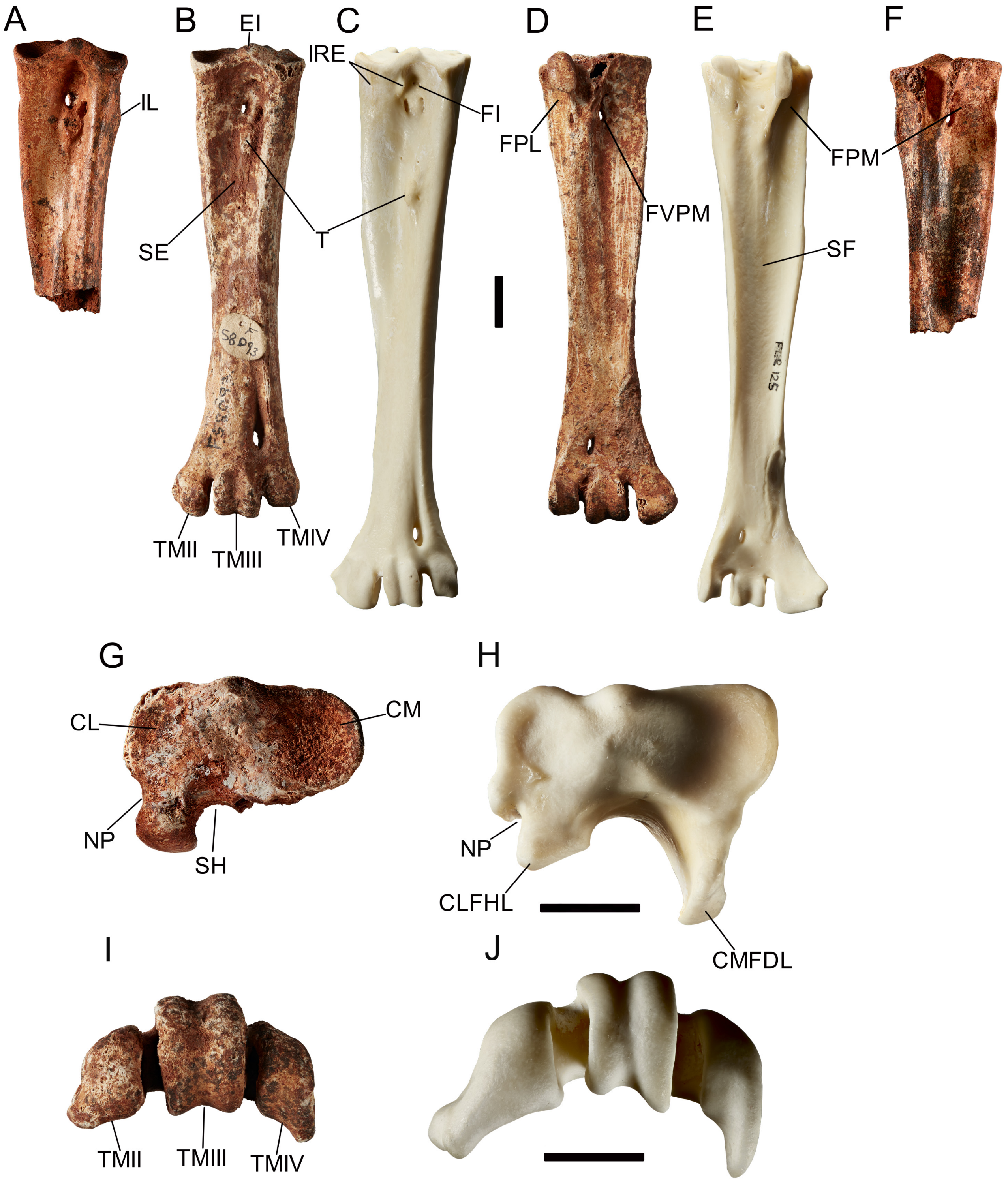

FIGURE 3. Tarsometatarsi of *Cryptogyps lacertosus* (A, B, D, F, G, I) compared to that of *Aquila audax* FUR 125 (C, E, H, J): left tarsometatarsus AM F.58093 (B, D, I); proximal tarsometatarsus WAM 15.9.73 (A, F, G); in dorsal (A–C), plantar (D–F), proximal (G, H) and distal (I, J) views. Abbreviations: Cl, cotyla lateralis; CLFHL, crista lateralis flexoris hallucis longus; CM, cotyla medialis; CMFDL, crista medialis flexoris digitorum longus; EI, eminentia intercotylaris; FI, fossa infracotylaris; FPL, fossa parahypotarsalis lateralis; FPM, fossa parahypotarsalis medialis; FVPM, foramen vascularia proximalia medialis; IL, impressio ligamentum collateralis lateralis; IRE, impressio retinaculi extensorii; NP, nervus peroneus notch; SE, sulcus extensorius; SF, sulcus flexorius; SH, sulcus hypotarsus; T, tuberositas m. tibialis cranialis; TMII, trochlea metatarsi II; TMIII, trochlea metatarsi III; TMIV, trochlea metatarsi IV. Scale bars 10 mm.

far from the foramina in *A. audax*); **(17)** the tuberositas is roughly ellipsoidal in shape; **(18)** the tuberositas is set roughly central in the shaft; **(19)** the sulcus extensorius (Figure 3B; SE) is moderately deepened and indistinct; **(20)** the sulcus flexorius (Figure 3E; SF) is slightly deepened and joins the medial facies by midlength; **(21)** the sulcus for the tendon of m. abductor digiti IV is broad and shallow, and opens laterally over a wide (10 mm) length of the shaft just proximal to TIV; **(22)** the trochlea metatarsi II (Figure 3I; TMII) is slightly longer than trochlea metatarsi III (Figure 3I; TMIII) by ~1 mm; **(23)** the relative distal extent of trochlea metatarsi II is slightly longer than trochlea metatarsi IV (Figure 3I; TMIV) by at least 2 mm; **(24)** the fovea lig. collateralium is shallow; **(25)** the plantar flange on trochlea metatarsi II is very short; **(26)** the plantar flange on trochlea metatarsi IV is short; **(27)** the trochlea metatarsi II is relatively narrow (compared with *A. audax*); **(28)** and the trochlea metatarsi IV is relatively broad (compared with *A. audax*).

The tarsometatarsi referred to *Cryptogyps lacertosus* can be excluded from any species in the Elaninae, Perninae, Accipitrinae and Buteoninae based on their much larger size, the lack of shaft width constriction immediately proximal to the fossa metatarsi I, and the positioning of fossa metatarsi I entirely on the plantar facies.

Species in the Circaetinae, Aquilinae, Harpiinae and Haliaeetinae are excluded as they do not have these characteristics of the fossil: **(2)** the narrow width of the sulcus hypotarsi; **(3)** the shallow depth of the sulcus hypotarsi; **(5)** the shallow notch for the nervus peroneus; **(15)** the absence of impressiones retinaculi extensorii; **(21)** the sulcus for the m. abductor digiti IV being broad; **(24)** the short plantar flange on trochlea metatarsi II; **(26)** the short plantar flange on trochlea metatarsi IV; **(21)** the relatively narrow width of the trochlea metatarsi II; **(28)** and the relatively broad width of the trochlea metatarsi IV.

The fossil shows the closest resemblance to species in the Gypaetinae and Aegypiinae, as compared below:

Gypaetinae.

The gypaetines share with the fossil the states of the following six tarsometatarsi characters: **(1)** the eminentia intercotylaris projects proximally as in the fossil in all species except *Polyboroides typus*, where it is hyper-protruding proximally; **(2)** a narrow sulcus hypotarsus; **(3)** the base of the sulcus hypotarsus is set plantar to the sulcus flexorius, though in *Gypohierax angolensis* it is to a lesser degree than in the fossil; **(8)** a deep fossa infracotylaris dorsalis; **(21)** the sulcus for the m. abductor digit IV being broad; **(22)** and the trochlea metatarsi II is slightly longer than trochlea metatarsi IV in *Gypohierax angolensis* and *P. typus* and is longer by at least half its length in *Neophron percnopterus* and *Gypaetus barbatus*.

Tarsometatarsi of gypaetines differ from the fossil as follows: **(5)** the notch for the nervus peroneus forms a shallow yet distinct notch in all species except *Gypaetus barbatus*, where it is deep;**(6)** the fossa parahypotarsalis lateralis spans a quarter of the shaft length or less in all species except *Neophron percnopterus*, where it spans a third of shaft length; **(9)** the impressio ligamentum collateralis lateralis is indistinct in all species except *P. typus*; **(10)** the plantar facies of the hypotarsus crista lateralis is wider than it is long in all species except *P. typus*, where it is longer than wide; **(13)** the medial shaft margin is thin dorsal to the fossa parahypotarsalis medialis in all species except *N. percnopterus*, where it is thick as in the fossil; **(14)** the proximal end of the fossa parahypotarsalis medialis takes up at least a third of the shaft width in all species, and is deep in all species except *G. barbatus*, in which it is shallow; **(15)** the impressiones retinaculi extensorii are present as small ridges in *P. typus* and *G. angolensis*, and practically absent in *G. barbatus* and *N. percnopterus*; **(16)** the tuberositas m. tibialis cranialis is separated distally from the proximal foramina by a distance equivalent to its length; **(17)** the tuberositas is oval in *G. barbatus* and *N. percnopterus*, and an elongate narrow ridge in *P. typus* and *G. angolensis*; **(20)** the sulcus flexorius is shallow in all species except *P. typus*, in which it is deep; **(22)** the trochlea metatarsi III has greater distal extent than trochlea metatarsi II in all species except *Gypohierax angolensis*, in which trochlea metatarsi II is longer; **(27)** the trochlea metatarsi II is relatively broad; **(28)** and the trochlea metatarsi IV is relatively narrow.

Aegypiinae.

The fossil is very similar to aegypiine species (see Figure 4), and consistent with them in the following 13 characters: **(2)** a narrow sulcus hypotarsus; **(3)** the sulcus hypotarsus is set plantar to the sulcus flexorius, though in species of *Gyps* and in *Aegypius monachus* to a lesser degree than in the fossil; **(5)** the notch for the nervus peroneus is very shallow in proximal view in all species, except those in *Gyps* and in *Sarcogyps calvus* (shallow but distinct notch); **(6)** the fossa parahypotarsalis lateralis extends over a third of the shaft length in all species except *Aegypius* *monachus*, in which it is barely present; **(8)** the fossa infracotylaris dorsalis is deepened proximally in all species except those in *Gyps* and *Necrosyrtes monachus*, in which it is shallow; **(13)** the medial shaft margin is thin dorsal to the fossa parahypotarsalis medialis; **(15)** the impressiones retinaculi extensorii are extremely flattened or absent; **(16)** the tuberositas m. tibialis cranialis directly abuts the foramina in all species except *Trigonoceps occipitalis* and *S. calvus* (separated by one tuberositas length); **(21)** the sulcus for m. abductor digit IV is broad; **(22)** the distal extent of trochlea metatarsi II is slightly longer than or roughly equal to that of trochlea metatarsi III in all species, except those in *Gyps*, *Aegypius monachus* and *Necrosyrtes monachus*, in which trochlea metatarsi III has slightly greater extent than trochlea metatarsi II; **(24)** the plantar flange of trochlea metatarsi II is short; **(25)** the plantar flange of trochlea metatarsi IV is short; **(27)** and trochlea metatarsi II is relatively narrow.

While, as shown, the lectotype and other fossils attributed to *Cryptogyps lacertosus* are broadly similar to those of aegypiines, they can be distinguished from those of all aegypiine genera as follows (aegypiine state in brackets).

The humerus has a more prominently projecting tuberculum supracondylare dorsale (tuberculum supracondylare dorsale non-projecting), moderate cranial projection of the tuberculum supracondylare ventrale (flattened or reduced cranial projection), a shallow, large attachment scar for the proximal head of pronator superficialis (small scar), and the epicondylus ventralis is highly distinct from the tuberculum supracondylaris ventralis. The tarsometatarsus has a prominent eminentia intercotylaris (flattened or barely projecting), medial and lateral cotylae of roughly equal depth (medial shallower), a deepened notch for the nervus peroneus (shallow or no notch), a broad and deep fossa parahypotarsalis lateralis (shallow), a deep sulcus extensorius (shallow), a deep sulcus flexorius (shallow), a shallow fovea lig. collateralis (deep in all species except *Gyps coprotheres*), and the length of trochlea metatarsi II being slightly greater relative to trochlea metatarsi IV (significantly longer than trochlea metatarsi IV). The fossil can further be distinguished from individual genera by the following characters:

From species of *Torgos*, *Trigonoceps*, *Sarcogyps*, and *Necrosyrtes* by a deeper fossa m. brachialis (shallow); from species of *Torgos*, *Sarcogyps*, *Aegypius* and *Gyps* by lacking a prominent, visible m. extensor metacarpi ulnaris origin (distinct); from *Torgos*, *Trigonoceps*, *Sarcogyps*, *Aegypius* and *Gyps* by the condylus ventralis being continuous with the entepicondyle (not continuous); from *Torgos*, *Trigonoceps*, *Sarcogyps*, *Aegypius* and *Necrosyrtes* by the trochlea metatarsi IV being relatively broad (narrow); from *Trigonoceps*, *Sarcogyps*, *Aegypius* and *Gyps* by the impressio ligamentum collateralis lateralis being prominent laterally (flattened); from *Torgos, Trigonoceps,* and *Sarcogyps* by the lateral crista hypotarsus being longer than wide (wider than long) and the tarsometatarsus being overall short and robust in length (comparatively long and elongate, narrows between proximal and distal ends); from *Necrosyrtes*, *Gyps* and *Aegypius* by a deep fossa infracotylaris (shallow fossa); from *Torgos* and *Necrosyrtes* by the convexity between the supracondylaris dorsalis and epicondylus dorsalis being relatively flattened (forms prominent peak); from *Torgos* and *Aegypius* by the flange of trochlea metatarsi II being extremely short (short but notably projecting medioplantarly from the trochlea); from *Torgos* and *Trigonoceps* by the crista medianoplantaris ending adjacent to the foramina vascularia proximalia (ending proximal to the foramina), and the foramen vasculare distale being set close to the incisura intertrochlearis lateralis (positioned well proximal to the incisura); from *Trigonoceps* and *Sarcogyps* by the position of the tuberositas m. tibialis cranialis being adjacent to the foramina proximalia (one tuberositas length distal) and the impressio ligamentum collateralis lateralis distinctly projecting dorsally (flat); from *Necrosyrtes* and *Gyps* by the length of trochlea metatarsi III being roughly equal with trochlea metatarsi II (trochlea metatarsi III longer than trochlea metatarsi II); from *Aegypius* by the broad and shallow notch distally between the condyles (deep and narrow).

Phylogenetic Analysis

The parsimony analysis of the combined molecular and morphological data resulted in three most parsimonious trees (MPTs), with a tree length of 1792, for which the strict consensus tree is shown in Figure 5.

The clade Accipitridae had very strong support (bootstrap 94%). Branching order for living forms is as for Mindell et al. (2018), as expected given the overlapping molecular data. Most subfamilies were well resolved with strong support greater than 60%, with the exception of Circaetinae (57%), Accipitrinae (57%), and Buteoninae (paraphyletic, *Ictinia mississippiensis* grouped closer to Haliaeetinae with 51% support).

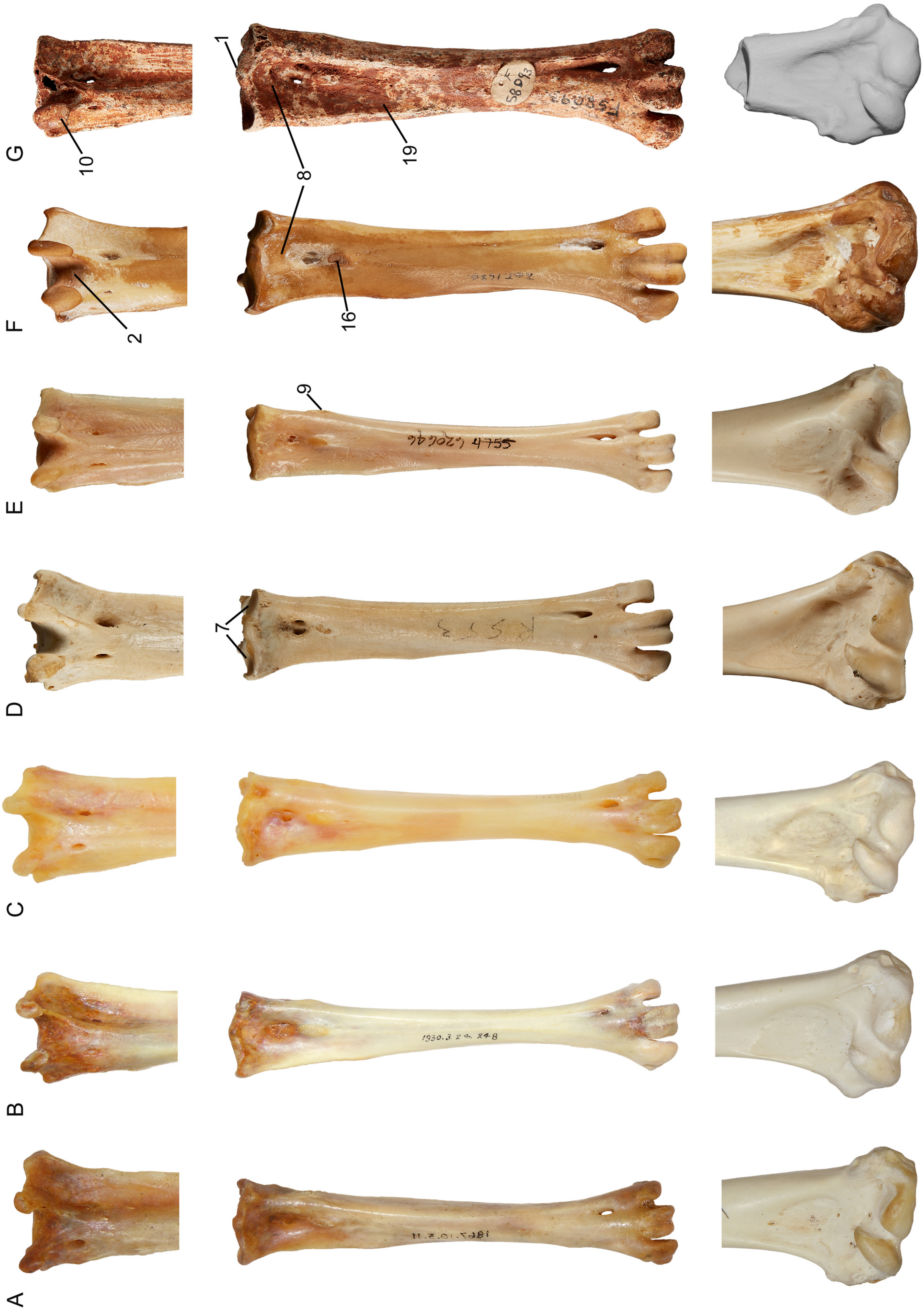

FIGURE 4. Comparisons of the elements of *Cryptogyps lacertosus* to those of six species of Aegypiinae, tarsometatarsus in plantar view to show structure of the hypotarsus (top), tarsometatarsus in dorsal view (middle) and distal humerus in cranial view (bottom): *Trigonoceps occipitalis* (A); *Torgos tracheliotos* (B); *Sarcogyps calvus* (C); *Aegypius monachus* (D); *Necrosyrtes monachus* (E); *Gyps coprotheres* (F); and *Cryptogyps lacertosus* (G). Numbers reflect the characters given in the tarsometatarsus description. Images are scaled to similar size.

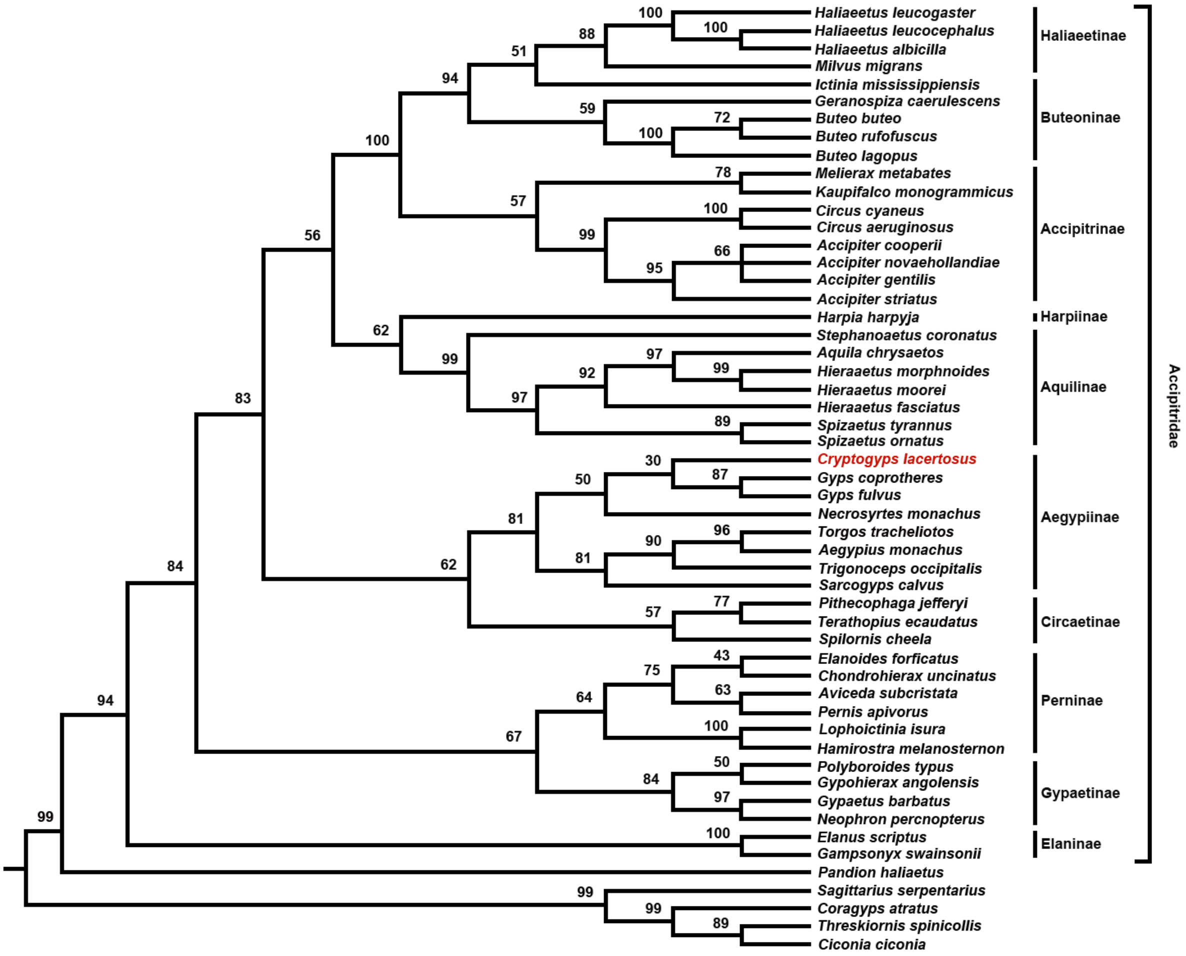

FIGURE 5. Parsimony analysis of morphological (ordered) data. Strict consensus of three most parsimonious trees. Tree length = 1792, MPT = 3, CI = 0.2176, HI = 0.7824, RI 0.5755. Bootstrap values are given at each node.

The fossil species *Cryptogyps lacertosus* was strongly supported as a member of the large accipitrid clade that includes Circaetinae and Aegypiinae (83%). Within this, it was moderately supported as a member of the aegypiine + circaetine clade (62%), strongly supported as an aegypiine (81%), and weakly supported as the sister group to the two sampled species of *Gyps* (30%).

Thirty-eight unambiguous (optimization-independent) morphological synapomorphies defined the Aegypiinae clade, but only eight were compelling (CI at least 0.5), and only the two for the tarsometatarsus were known for *Cryptogyps lacertosus* and appear to be the key drivers for the inclusion of this species in aegypiines: Character 37 state 1 (CI 0.5) (nares of rostrum partially covered by a caudal bone shield); 71 state 1 (CI 1.0) (sternum abutment of crista medialis to spina externa base); 101 state 1 (CI 0.5) (coracoid omal margin of processus procoracoideus oriented in distal slope relative to sternal margin); 102 state 0 (CI 1.0) (coracoid cotyla scapularis less than a quarter of the shaft width); 236 state 0 (CI 0.5) (tibiotarsus height to width ratio of medial condyle roughly equal); 237 state 0 (CI 0.5) (tibiotarsus height to width ratio of lateral condyle roughly equal); 261 state 0 (CI 0.5) (tarsometatarsus attachment ridges for impressiones retinaculi extensorii absent); and 274 state 1 (CI 0.5) (tarsometatarsus width of abductor muscle IV sulcus narrow).

Discussion

Implications for the ecology of *Cryptogyps lacertosus*

The morphology of both the humerus and the tarsometatarsus of *Cryptogyps lacertosus* are mostly consistent with that of aegypiine vultures. The reduced size of the flange on trochlea metatarsi II, the shallow fovea lig. collateralis, and the small, shallow sulcus hypotarsi show that the musculature on the limb was much weaker than in active hunters like *Aquila audax*. While the fossils of *Cryptogyps lacertosus* have comparatively deeper muscular sulci and fossae than most of its aegypiine relatives, it seems most likely that *Cryptogyps lacertosus* was still primarily a scavenger, and therefore probably flew great distances to locate dead or dying large vertebrates like most living vultures today.

Compared to most other aegypiines, *Cryptogyps lacertosus* was unusually small, despite being close in size to a Wedge-tailed Eagle. It was larger than the smallest aegypiine vulture, *Necrosyrtes monachus*, but smaller than species such as *Gyps fulvus* and *Aegypius monachus*. If it followed size-based dietary patterns observed among extant aegypiines, it can be predicted that *Cryptogyps lacertosus* might have had a 'gulper' or 'ripper' type diet (see Hertel 1994), feeding either on the soft viscera or the outer skin and flesh of carcasses.

Cryptogyps lacertosus, like many extant vultures, would have provided a valuable service to its native ecosystems through this scavenging by reducing the transmission of certain diseases (see Ogada et al. 2012) and facilitating energy flow through food webs (Wilson & Wolkovich 2011).

Cryptogyps lacertosus resolves phylogenetically as the sister group to the genus *Gyps*, though bootstrap support is low. It especially resembles *Gyps* in some features of the tarsometatarsus. Many species of *Gyps* are social, gathering in large numbers to feed at a single carcass, and are heavily reliant on the presence of conspecifics for successful foraging (Jackson et al. 2008; Dermody et al. 2011). There is no way to conclusively determine if *Cryptogyps lacertosus* behaved similarly, but such a strategy would no doubt have been quite useful in maintaining a competitive edge against other large raptors and mammalian scavengers.

The geographical range of *Cryptogyps lacertosus* has been expanded by the discovery of the new material. Previously known only from Kalamurina on the Warburton River in north-east South Australia (de Vis 1905), the newly referred material shows the species to have been present around the Wellington Caves in New South Wales and on the Nullarbor Plains of Western Australia. Both these sites are over a thousand kilometres from Kalamurina, though in terms of the flight range of a large accipitrid, this is not a great distance. There is no reason that *Cryptogyps lacertosus* could not have been widespread across Australia, foraging in grassland and open woodlands environments wherever they occurred, barring competitive exclusion via other species occupying the same niche.

Global Distribution of Scavenging Birds of Prey

The identity of *Cryptogyps lacertosus* as a member of Aegypiinae fills a prominent and puzzling ecological void in Pleistocene Australia. Living aegypiines are restricted to Africa, Europe and parts of Asia, but the fossil record reveals that their range once extended to the Americas (see Brodkorb 1964), leaving Antarctica and Australia as the only continents where they were apparently absent (Ferguson-Lees & Christie 2001; Bildstein 2017). While their absence from Antarctica is easily explicable based on environment, Pleistocene Australia had extensive areas of grasslands, open woodlands and desert, and a diverse assemblage of up to 27 genera of megafaunal mammals, birds and reptiles that would seem well suited to supporting vulture populations. Australia currently has only one large accipitrid living in inland terrestrial environments, the Wedge-tailed Eagle *Aquila audax*, which is both an active predator and a scavenger. The lack of other large, mainly scavenging birds filling the niche typically occupied by vultures in Australia makes this even stranger. Australia only has one documented species of stork (Ciconiidae), the Black-necked Stork *Ephippiorhynchus asiaticus*, which does not scavenge carcasses (unlike storks in the genus *Leptoptilus*). There is no evidence that any other lineages of large, volant scavenging birds, such as the Teratornithidae of the Americas, were ever present in Australia. The large, flightless Dromornithidae of Australia, despite some claims to the contrary, were herbivorous (Murray & Vickers-Rich 2004; Handley & Worthy 2021), unlike the flightless, predatory Phorusrhacidae from the Americas.

The Pleistocene avifauna of all continents outside of Antarctica and Australia has included multiple species of both vultures and large eagles. In Europe the vulture guild had at least one additional species, *Gyps melitensis* Lydekker, 1890, that presumably existed alongside the four species of vultures and ten eagles still present today (Dickinson & Remsen 2013). The African vulture guild similarly also had at least one additional species, *Aegypius varswaterensis* Manegold et al., 2014 alongside the 11 living vultures and 17 eagles (Dickinson & Remsen 2013). Mainland Asia had at least two extinct species of vultures, *Aegypius jinniushanensis* Zhang et al., 2012, and an unnamed species of *Torgos* (Zhang et al. 2012) alongside seven species of living vultures and 21 eagles (Dickinson & Remsen 2013), and throughout the south-east Asian islands, at least one fossil vulture, an unnamed species of

Trigonoceps (Meijer et al. 2013), existed along with 22 species of eagles (Dickinson & Remsen 2013). From North America, sites such as the Rancho La Brea tar pits demonstrate the existence of at least two species of accipitrid vultures, four cathartid vultures, two teratorns and six large eagles during the same time period (see Stock 1930; Howard 1930; Jefferson 1991). Compared to these diverse faunas (living and recently extinct species), the Australian accipitrid guild is extremely unusual, comprising only two large eagles, only one of which occurs inland, and until now, no vultures.

Cryptogyps lacertosus is the first recorded vulture species for the Australasian continental region (Australia and New Guinea, or Sahul), and its phylogenetic and morphological distinctiveness potentially indicates the existence of an endemic lineage of Australian or Australasian vultures. Most notably, it filled the ecological void of an obligate avian scavenger that is lacking in modern Australia. The extinction of *Cryptogyps lacertosus* was potentially related to the Australian megafaunal mass extinction ~50 Ka; the loss of up to 79 species of large-bodied mammals (Wroe et al. 2013) would have severely reduced the resources needed to support a scavenging species. Only five large-bodied species, all macropodids, survived, and these were not formerly found in the arid open lands that covered the vast majority of the continent, where one might expect vultures to mainly have lived. The surviving species of large kangaroos would eventually increase substantially in their range and numbers, but this might have happened too late to make a difference for *Cryptogyps lacertosus* and any other large raptors dependent on the megafauna for food.

The extinction of *Cryptogyps lacertosus* possibly resulted in the ecological release of now generalist accipitrid species like *Aquila audax*, allowing them to fulfil multiple roles as hunters and scavengers (Olsen 2005). *Aquila audax* is not unique in this regard; many species of *Aquila* and those in other genera of large eagles also scavenge frequently as part of their diet. In these species, scavenging is typically more frequent in winter seasons when live prey is scarce (Blázquez et al. 2009), or among younger individuals with lower hunting success than older adults (Margalida et al. 2017). In places such as Africa where large eagles and large vultures coexist, it has been noted that some vultures follow eagles to carcasses and then force them away (Kane et al. 2014). The relationship between *Cryptogyps lacertosus* and *Aquila audax* may have been similar in nature, with the extinction of the former possibly allowing the latter to use carcasses as extensively as it does in the present day.

Conclusion

"Taphaetus" lacertosus de Vis, 1905, is confirmed to be a valid species of extinct accipitrid, for which the new genus *Cryptogyps* is erected. *Cryptogyps lacertosus* (de Vis, 1905) is shown to be an aegypiine vulture that was widespread in southern Australia in the middle to late Pleistocene. The presence of Old World vultures (Aegypiinae) among Pleistocene Australian accipitrids indicates that their taxonomic and ecological diversity was significantly greater then than it is today; the extinction of *Cryptogyps lacertosus* likely had a distinct impact on those ancient ecosystems.

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Author contributions

EKM and THW designed the study. All authors contributed to the manuscript, with EKM writing the initial draft and THW and MSYL providing feedback, revisions and suggestions. EKM compared and described the fossil material, with THW providing corrections and feedback. MSYL suggested the inclusion of a phylogenetic analysis and collated the molecular data, while EKM collected the morphological data and performed the analyses, with MSYL and THW providing feedback.

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