

# Systematics of the fossil Australian giant megapodes *Progura* (Aves: Megapodiidae)

Walter E. Boles

Bird Section, Australian Museum, 6 College Street, Sydney, NSW 2010, Australia  
Walter.Boles@austmus.gov.au

**ABSTRACT** - Australia's largest megapode was *Progura gallinacea* De Vis, 1888, from Plio-Pleistocene deposits in south-eastern Queensland. A second species, *P. naracoortensis* van Tets, 1974, from southeastern South Australia, was initially distinguished by different leg proportions and size; it was later suggested that there might be only a single, sexually dimorphic species. An examination of extensive collections of unstudied material from the Naracoorte Caves indicates that there is only a single species, with size differences related to both moderate sexual dimorphism and individual variation. Comparisons of these specimens with the three living Australian megapode taxa show that the *Progura* is not separable from the modern genus *Leipoa*. The possibility that *Progura gallinacea* is the megafaunal representative of the living *Leipoa ocellata* Gould, 1838 (Malleefowl) is discussed.

**Key words** - megapode, *Progura*, *Leipoa ocellata*, megafauna, osteology

## Systematique des mégapodes fossiles géants d'Australie du genre *Progura* (Aves, Megapodiidae)

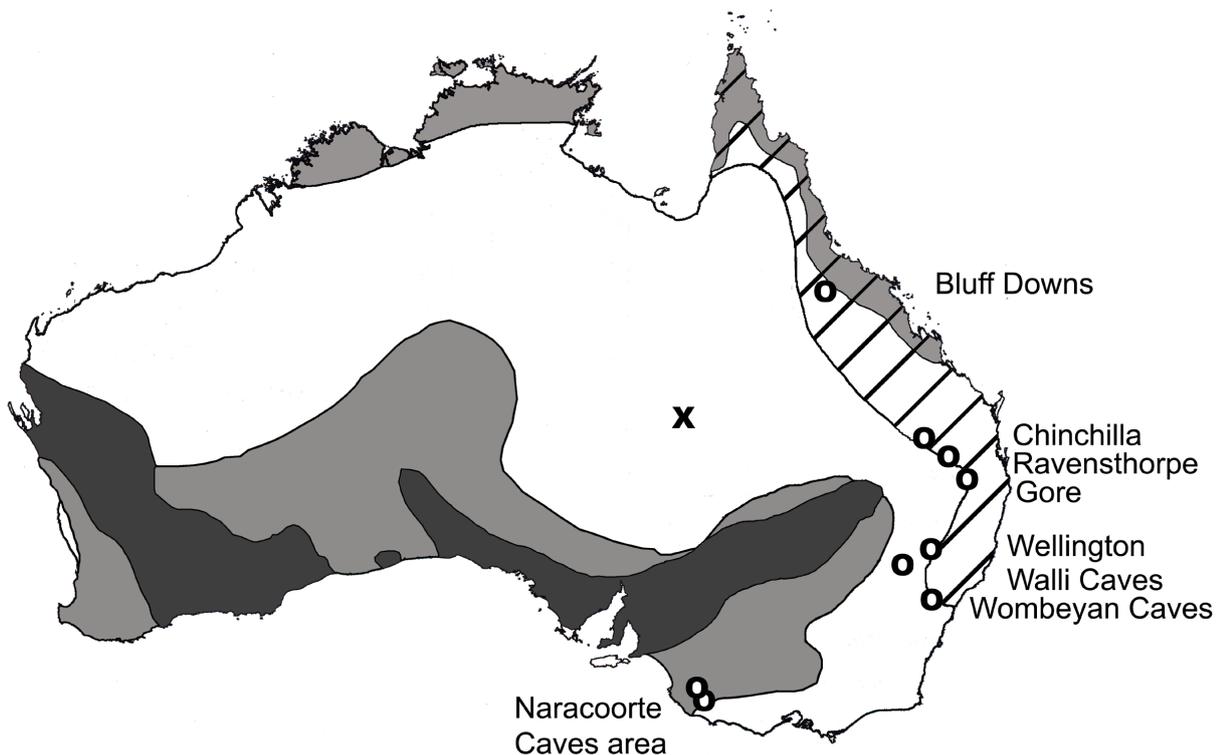
- *Progura gallinacea* De Vis, 1888, du Plio-Pléistocène du Sud-Est du Queensland, était la plus grande forme de mégapode d'Australie. Une deuxième espèce, *P. naracoortensis* van Tets, 1974, de la partie sud-est de l'Australie du Sud, a été décrite comme différente par sa taille plus faible et par les proportions de ses membres postérieurs. Mais il a été ensuite suggéré que ces deux formes pouvaient en réalité correspondre à une seule espèce présentant un dimorphisme sexuel. L'étude d'une grande quantité de matériel inédit provenant des grottes de Naracoorte, indique qu'il s'agit bien d'une seule espèce dont les différences de taille sont dues à la variation individuelle et à un dimorphisme sexuel modéré. La comparaison de ce matériel avec les trois genres de mégapodes actuels d'Australie montre que le genre *Progura* ne se distingue pas du genre actuel *Leipoa*. *Progura gallinacea* peut être considéré comme le représentant mégafaunique du *Leipoa ocellé* actuel (*Leipoa ocellata* Gould, 1838).

**Mots clés** - mégapode, *Progura*, *Leipoa ocellata*, mégafaune, ostéologie

## INTRODUCTION

The megapodes or mound-builders (Megapodiidae: Galliformes) are renowned for their use of external heat sources (rotting vegetation, sun, geothermal) for incubation, freeing the adults from any post-laying involvement with the eggs or chicks (Elliot 1994; Jones *et al.* 1995). There are 22 or so extant species classified in six or seven genera (Sibley & Monroe 1990; Elliot 1994; Jones *et al.* 1995). The centre of the family's taxonomic diversity is the Australo-Papuan region, with the distribution extending east to Tonga (with prehistorically extinct Holocene forms from as far as Samoa), north to the Philippine Islands and Palau and the Mariana Islands in Micronesia, and west through Sulawesi and Lombok, Indonesia, with isolated populations on the Nicobar Islands. Three living species occur in Australia: the Australian Brush-turkey *Alectura lathami*, the Malleefowl *Leipoa ocellata* and the Orange-footed Scrubfowl *Megapodius reinwardt* (Fig. 1).

Megapodes have an intriguing fossil record, including both living and extinct genera, most of which is confined to the Quaternary. This was recently reviewed by Steadman (1999), so is summarised only briefly below. Most fossil taxa are species of scrubfowl *Megapodius*, comprising mainly extinct forms. These are known from Oceania, from Palau and the Mariana and Caroline Islands in the northwest, southwards through the Bismarck Archipelago, Solomon Islands, Vanuatu and New Caledonia, and east through Fiji to Samoa and Niue (Balouet & Olson 1989; Worthy 2000; Steadman 1999 and references therein); most of these sites are of Holocene age. Aplin *et al.* (1999) aligned specimens from late Quaternary cave deposits in Irian Jaya, New Guinea, to the extant taxon *Aepyptodius arfakianus*. The other living taxon reported as a fossil is *Leipoa ocellata*, which was listed among late Pleistocene remains from the Victoria Fossil Cave, South Australia (van Tets 1974; van Tets &



**Figure 1** - Distribution of Australian fossil and living megapodes. Living megapodes (after Jones *et al.* 1995): *Alectura lathamii* – hatched; *Megapodius reinwardt* – pale grey; *Leipoa ocellata* – mid grey (former distribution), dark grey (current distribution). Localities from which *Progura* has been recovered (O). General locality of Darling Downs include area encompassing both Chinchilla and Ravensthorpe'. Naracoorte Caves World Heritage Area includes Henschke's Fossil Cave, Buckeridge Cave, Crawford's Cornucopia Cave, Victoria Fossil Cave and Big Bird Cave. Type locality of *Ngawupodius minya* (X), Etadunna Formation, Late Oligocene.

Smith 1974).

The earliest record of the family is *Ngawupodius minya*, recovered from the Late Oligocene Etadunna Formation of northeastern South Australia (Boles & Ivison 1999; Fig. 1); this form was notable for its diminutive size. The other extinct genera included the largest-bodied members of the family known. The large, unusual *Megavitiornis altirotis* comes from Late Pleistocene-Holocene deposits in Fiji (Worthy 2000). At one time considered to be a large, flightless megapode (Poplin & Mourer-Chauviré 1985), *Sylviornis neocaledoniae* of New Caledonia is best placed in its own galliform family (Balouet & Olson 1989; C. Mourer-Chauviré pers. comm.).

In Australia, the largest megapodes were in the genus *Progura* De Vis, for which two species have been named. *Progura gallinacea* was among the numerous taxa described by C.W. De Vis from Plio-Pleistocene deposits in the Darling Downs, Queensland (Figs. 1, 2). He assigned specimens of this species in four different groups of birds. (The problems with many of De Vis' identifications, and the modern equivalents, have been discussed by van Tets 1974 and van Tets & Rich 1990, among others.) *Progura gallinacea* was originally placed in the Columbidae (De Vis 1888a), where De

Vis considered it to be close to the crowned pigeons *Goura* of New Guinea, near the common ancestor of pigeons and poultry. He thought another bone represented an undetermined genus and species of bustard (De Vis 1888b). Subsequently he described other specimens as *Chosornis praeteritus*, a megapode, (De Vis 1889) and *Palaeopelargus nobilis*, a stork (De Vis 1891). Van Tets (1974) recognised that all of the specimens belonged to a single species of megapode, to which the senior synonym, *Progura gallinacea* De Vis 1888, applies. In his revision, he also assigned fossils from cave deposits in eastern New South Wales and southeastern South Australia to this species.

At the same time, van Tets (1974) named a second, smaller species of *Progura*, *P. naracoortensis*, based on material from cave deposits in the Naracoorte region of South Australia (Fig. 1). To this he referred fossils that previously had been attributed to the living *Alectura lathamii* (Lydekker 1891; Longman 1945). Van Tets (1974) distinguished the species on proportional differences in leg length, as well as size. Later, he (van Tets 1984) suggested that the two nominal species of *Progura* actually represented a single, sexually dimorphic species.

The only record of *Progura* from north of the Dar-

ling Downs comes from the Allingham Formation, north-eastern Queensland, the source of the Early Pliocene Bluff Downs Local Fauna (Fig. 1). Boles & Mackness (1994) assigned an incomplete carpometacarpus and proximal tarsometatarsus to *Progura* cf. *P. naracoortensis*, with the specific assignment being made on the basis of size, using the measurements given by van Tets (1974). Information on specimens of *P. gallinacea* and *P. naracoortensis* cited by van Tets (1974) and reported subsequently is given in Tables 1 and 2, respectively.

Since De Vis' original descriptions and van Tets' (1974) revision, little has been published on *Progura*, and its intergeneric relationships remain unstudied. Numerous unstudied specimens have been recovered from caves in the Naracoorte region of southeastern South Australia and greatly increase the skeletal elements that are now known, most of which are represented by larger sample sizes. It is the purpose of this study (a) to determine whether there are one or two species in this genus and (b) to examine its relationships to other Australian genera of megapodes.

## GEOLOGY AND GEOGRAPHICAL SETTING

Specimens of *Progura* have been found at several widely separated areas (Fig. 1), in two main types of deposits, fluvial sediments and cave accumulations.

*Qld: Darling Downs* De Vis described his original material of *Progura gallinacea*, *Chosornis praeteritus* and *Palaeopelargus nobilis* from several localities in the Darling Downs region of southeastern Queensland. The deposits bearing fossils are located in a rectangular band, about 200 km long and 80 km wide, and angled northwest-southeast, with the Condamine River running lengthwise, roughly parallel with the western boundary. The fossils are found in fluvial deposits comprising clays, sands and grits derived from Dividing Range, which borders the Darling Downs area to the northeast. The section west of the Condamine River, including Chinchilla, has Pliocene sediments yielding the Chinchilla Fauna, while the eastern section is of Pleistocene age and produces the Eastern Darling Downs Local Fauna. For more information on the geology and palaeontology of the Darling Downs, see Bartholomai (1976), Molnar & Kurz (1997) and Woods (1960), and references therein. *Progura* remains described by De Vis came from several sections of the Downs. The type locality of *Progura gallinacea* is at 'Ravensthorpe' (27°54'S, 152°10'E) near Pilton, in the southern section of the eastern Darling Downs. Chinchilla (26°45'S, 150°40'E), in the western Downs, is the type locality of *Chosornis praeteritus*. The type locality of *Palaeopelargus nobilis* was, like that of many De Vis taxa, given no more specifically than Darling Downs.

*Qld: Gore Limestone Quarries* Longman (1945) reported a single bird bone, referred to *Alectura lathami*, among vertebrate fossils at Cement Mills, Gore (28°18'S, 151°30'E), southeastern Queensland, near, but outside of, the southwestern corner of the fossil-producing area of the

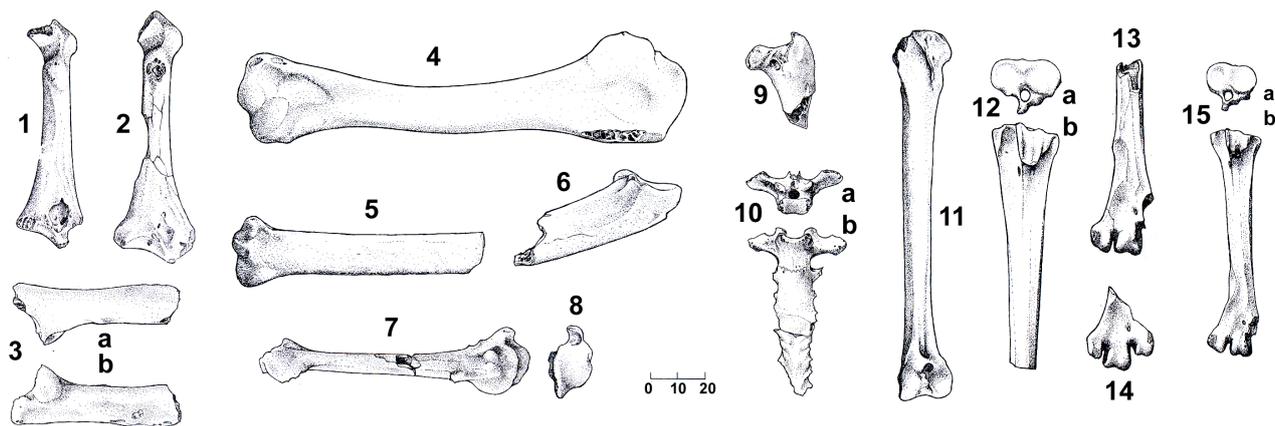
Darling Downs outlined above. These were encountered in restricted areas of limestone when quarrying activities intersected cave or fissure fills in the Palaeozoic rocks. Bartholomai (1977) interpreted the accumulation as a predator lair, with some in-washing. Compared with the Darling Downs, a relatively high proportion of taxa were recent species, or forms closely related to living ones, leading Bartholomai (1977) to consider the fossils to be Pleistocene, possibly very late and even extending into the Holocene.

*Qld: Bluff Downs* Boles & Mackness (1994) reported on the birds, including *Progura*, from Bluff Downs station, along the banks of the Allingham Creek, a tributary of the Burdekin River, northern Queensland (19°43'S, 145°36'E). The Allingham Formation is a lake and stream deposit, overlain by the Allensleigh 'flow' of the Nulla Basalt, radiometrically dated at 4.5–4 Myr. For a detailed discussion of the geology of this deposit, see Archer & Wade (1976), who first reported these fossils. The vertebrate component of this fossil assemblage, known as the Bluff Downs Local Fauna, consists (to date) of fish, turtles, crocodiles, several families of lizards and snakes, seven families in four orders of marsupials, one family of placental mammals, and birds. For a more detailed list of the fauna and relevant references, consult Boles & Mackness (1994) and Rich *et al.* (1991).

*NSW: Wellington Caves* The Wellington Caves are situated in a low, limestone outcrop 8 km south of Wellington, NSW (32°35'S, 148°51'E). They consist of at least five natural caves, from which vertebrate fossils have been collected since 1830. Phosphate mining operations in the early 1900s exposed additional sedimentary sequences, with material removed from the caves placed in spoil piles. The fossiliferous sediments formed during at least three episodes of deposition, ranging from the Pliocene to late Pleistocene. Unfortunately, the stratigraphic provenance of early collected fossils was not documented, nor from which cave they came or during which visit they were obtained; thus, the geological age of these specimens is not known. One *Progura* specimen was found among soil in the spoil piles. Another has its location listed as 'from a cave in Wellington Valley'. It is not possible to associate this within the stratigraphy of the region. See Osborne (1983, 1997) for references and current ideas on the Wellington Caves stratigraphy. The history of excavations and fossil discoveries and problems associated with the fossils were described by Dawson (1985).

*NSW: Walli Caves* Walli Caves (33°37'S, 148°51'E) are situated near the town of Walli, mid-western New South Wales. Over 40 cave entrances, potholes and dolines occur in approximately 1 km<sup>2</sup> of a limestone outcrop. The single specimen of *Progura* recorded from these caves has no more detailed provenance. The age is considered to be Pleistocene. Little work has been done on the vertebrate fossils from these deposits. The geology of the caves was described by Frank (1974).

*NSW: Wombeyan Quarry* Material comes from a marble quarry about 1.5 km west of the Wombeyan Caves Reserve (34°19'S, 149°56'E). During quarrying activities,



**Figure 2** - Selected specimens, including those of De Vis, incorporated by van Tets (1974) in his revision of *Progura*. Modified from van Tets (1974, figs. 2, 3 and 4). All are right elements except for 7 and 14, which have been reversed. For localities, see Tables 1 and 2. 1. coracoid, *P. naracoortensis* (SAM P16700), 2. coracoid, *P. gallinacea* (AM F54720), 3a,b. scapula, *P. gallinacea* (QM F5558), 4. humerus, *P. gallinacea* (SAM P71533), 5. ulna, *P. gallinacea* (AM F54721), 6. ulna, *P. gallinacea* (AM F54722), 7. carpometacarpus, *P. gallinacea* (QM F1132), 8. carpometacarpus, *P. gallinacea* (QM F1139), 9. femur, *P. naracoortensis* (SAM P17857), 10a,b. synsacrum, *P. naracoortensis* (SAM P18187), 11. tibiotarsus, *P. naracoortensis* (SAM P17152), 12a,b. tarsometatarsus, *P. gallinacea* (QM F1143), 13. tarsometatarsus, *P. gallinacea* (SAM P17856), 14. tarsometatarsus, *P. gallinacea* (QM F5557), 15a,b. tarsometatarsus, *P. naracoortensis* (SAM P17856).

a cave fill was uncovered, with the material removed and dumped near by. Several specimens were found among this discarded cave fill. Hope (1982) considered that this and other fossils were accumulated via pitfall into the cave. She interpreted the age of the deposit as Late Pleistocene. For information on the cave fill and other fossiliferous sediments at Wombeyan Cave, and the contained vertebrate fauna, see Hope (1982).

*SA: Naracoorte Caves* The most prolific source of *Progura* remains has been the caves of the Naracoorte region, southeastern South Australia. These were incised into the Miocene-aged Gambier Limestone during the Pliocene and Early Pleistocene. Some of the most productive and well studied caves form part of the Naracoorte Caves World Heritage Site (37°02'S, 140°47'E). Others occur on private property and are discovered accidentally. The main mode of fossil accumulation was by pitfall with some evidence of predator remains in particular caves. Dating has been carried out on fossil teeth and bones and associated speleothems using U/Th series and electron spin resonance. The only one yielding *Progura* that has been so dated is the Main Fossil Chamber of Victoria Fossil Cave, one of the richest deposits in the World Heritage Area. It has been dated at 280,000–500,000 years. Dates for neighbouring caves that have not produced megapodes are 125,000 years for Grant Hall, Victoria Fossil Cave, and 170,000–280,000 years for the Fossil Chamber, Cathedral Cave. Other caves in the World Heritage Area that have produced megapode remains are Fox Cave, Un-named Cave and Wombat Cave. Outside this Area, but still in the vicinity, are Buckeridge Cave, Big

Bird Cave and Crawford's Cornucopia Cave. Further information on the geology, dating and palaeontology of these caves is found in Ayliffe & Veeh (1988), Ayliffe *et al.* (1998), Grün *et al.* (2001), Moriarty *et al.* (2000), Reed & Bourne (2000) and Wells *et al.* (1984), and references therein.

Henschke's Fossil Cave (= Henschke's Fossil Quarry or Quarry Cave) (37°00'S, 140°45'E) was found in the outskirts of the town of Naracoorte, about 15 km west of the World Heritage Area. Fossils were found in a small cave uncovered during quarrying; the deposit no longer exists. Pledge (1990) and Barrie (1997) described the geology and fossil fauna of this site. Charcoal apparently associated with the fossils yielded a date of 32,000–40,000 years but there is uncertainty about these dates as they are at the limit of the carbon dating technique.

## METHODS

The type material of *P. gallinacea* is held in the Queensland Museum and that of *P. naracoortensis* in the South Australian Museum. All the specimens cited by van Tets (1974) in his revision were examined, with the exception of the coracoid mid shaft in the Natural History Museum (BMNH A3244), originally referred to *Alectura lathamii* by Lydekker (1891), a species not yet known from the fossil record (although there is no reason that it should not be represented). Additional specimens were examined in these institutions and in the Australian Museum and those currently held by E. Reed and S. Bourne. Comparative material of extant taxa was examined at or made available by the fol-

lowing institutions: Australian Museum, Sydney (AM); Australian National Wildlife Collection, Canberra (ANWC); American Museum of Natural History, New York (AMNH); Museum Victoria, Melbourne (MV); South Australian Museum, Adelaide (SAM). Measurements largely follow those illustrated by Steadman (1980) and were taken using digital calipers and rounded to the nearest 0.1 mm. Osteological nomenclature mostly follows Baumel & Witmer (1993), except that as terms of position and direction anterior is used rather than cranial and posterior rather than caudal. Adults among the fossil material examined and modern specimens used for comparisons were recognised on the basis of size and the absence of a pitted surface of the bone and incomplete ossification of the articular facets (Campbell 1979).

Ratio-diagrams of the log differences were constructed following the method of Simpson (1941). The selected measurements are converted to logarithms. One taxon is arbitrarily chosen as the standard, and the difference between its converted measurements and the corresponding ones for each taxon are calculated (the logarithms of the ratios). The standard taxon thus has all ratios of 0 (zero difference in logarithms), which when plotted along a vertical axis on arithmetic graph scale, form a straight line. The logarithmic ratios for each taxon are plotted horizontally such that the values of the same variable across the taxa line up vertically. Those values larger than the standard fall above the standard line, the smaller ones below it. The points of each taxon are connected with a line. Taxa with proportions identical to those of the standard taxon will have lines parallel to the standard's line. Variations from a parallel line are indicative of variations in the proportions from that of the standard taxon. Taxa with similar proportions will have approximately parallel plots, although these need not be straight. For the purposes of these comparisons, the values used were the means of the greatest lengths in Table 3 using all specimens.

Predicted body mass of *Progura gallinacea* was calculated using the method of Campbell & Marcus (1991) using the equation  $\log_{10}(\text{weight}) = a \cdot \log_{10}(\text{least circumference}) + b$ . Two sets of values determined by Campbell & Marcus (1991) were used, one for the composite of all birds (femur:  $a = 2.411$ ,  $b = -0.065$ ; tibiotarsus:  $a = 2.424$ ,  $b = 0.076$ ), the other for 'heavy-bodied terrestrial birds that are similar in morphology (short-legged and heavy-bodied)' (femur:  $a = 2.268$ ,  $b = 0.110$ ; tibiotarsus:  $a = 2.337$ ,  $b = 0.193$ ). The latter data set included a number of galliform groups, but not the Megapodiidae. String was wrapped around the bones at their least circumferences, marked at the point of overlap, straightened and measured with calipers. The resulting values were used in the equation to obtain the predicted body mass.

## DESIGNATION OF LECTOTYPE FOR *PROGURA GALLINACEA*

De Vis (1888b) described *Progura gallinacea* on the basis of two proximal fragments of left tarsometatarsi

(QM F1134 and F1143) and two distal parts of right tarsometatarsi (QM F5556 and F5557). He did not designate a holotype, thus these four specimens comprise the syntypes of the species. Because these syntypes are 'complementary fragments of the tarsometatarsus', van Tets (1974) chose not to select a lectotype. QM F1143 is the most complete syntype, preserving the proximal end and about 2/3 of the shaft, and exhibits characters sufficient to identify it as belonging to this taxon. It is selected as the lectotype of *Progura gallinacea* De Vis, 1888; the other three specimens become paralectotypes. The type locality – Ravensthorpe, Darling Downs – is unchanged.

## SYSTEMATIC PALAEOONTOLOGY

There are two major systematic questions regarding *Progura*. (1) How many species of *Progura* are there, i.e. is *Progura naracoortensis* a valid species? (2) What are the relationships of this genus to other taxa of the Megapodiidae?

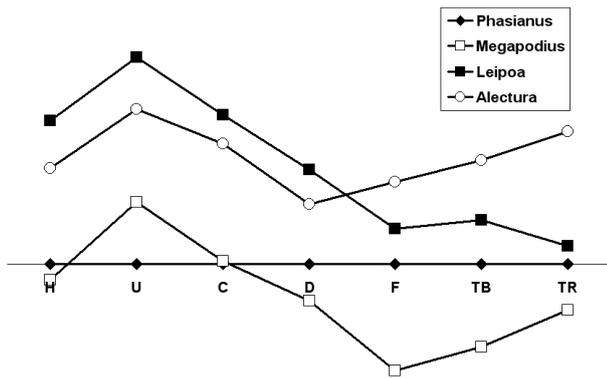
### Validity of *Progura naracoortensis*

Van Tets (1974) erected the *P. naracoortensis* on the basis of its supposed smaller size and relatively shorter tarsometatarsi compared to *P. gallinacea*. The latter was judged by comparing the length of the tarsometatarsus to that of the coracoid (*gallinacea* 1.6; *naracoortensis* 1.1). For each element length, van Tets only had available a single complete specimen (*gallinacea*: coracoid 94 mm, tarsometatarsus 148 mm; *naracoortensis*: coracoid 85 mm, tarsometatarsus 96 mm).

There are no associated specimens of coracoid and tarsometatarsus of *Progura*. Using the mean lengths of the coracoid (90.4 mm) and tarsometatarsus (96.7 mm) gives a ratio of 1.07. The respective ratios of the minimum and maximum lengths are comparable: 1.12 and 1.07. Comparing specimens of roughly equivalent sections of the size range produces broadly similar results. If, however, the maximum length of one element is compared with the minimum of the other, the range is much greater (0.88-1.37). Given the degree of individual variation exhibited, it would be possible to obtain a wide range of ratios of tarsometatarsus length to coracoid length if these skeletal elements were taken from different animals. It is not appropriate to use size ratios in this manner where they are based on bones not known to belong to the same individual.

Modern skeletons of *Alectura* and *Leipoa*, the bones of which are associated, give tarsometatarsus: coracoid ratios of 1.44-1.57 and 1.10-1.24, respectively. The coefficients of variation of the coracoids (3.9-4.6) and tarsometatarsi (5.0-5.6) of the living taxa are not dissimilar to those of the *Progura* specimens collectively (coracoid: 7.9; tarsometatarsus: 5.2). The degree of variation exhibited by *Progura* is comparable to that within single species of living megapodes. As there is no evidence that two species are represented, *P. naracoortensis* should be placed in the synonymy of *P. gallinacea*.

Van Tets (1984) subsequently raised the possibility



**Figure 3** - Simpson log-ratio diagram of *Megapodius reinwardt*, *Alectura lathamii* and *Leipoa ocellata* with *Phasianus colchicus* as standard. H, humerus; U, ulna; R, radius; C, carpometacarpus; D, phalanx I of the major digit; F, femur; TB, tibiotarsus; TM, tarsometatarsus. In this and the following figure, values above the standard line are larger than the standard, those below it are smaller.

that *P. gallinacea* and *P. naracoortensis* comprised a single, sexually dimorphic species because additional specimens demonstrated that both putative taxa were found together in most deposits and, furthermore, there were no characters, other than size, that consistently separated them.

Within modern megapodes, size variation is a mixture of varying degrees of sexual dimorphism, minor age-related differences and individual variation. In these species, sexual dimorphism is evident in element lengths – males averaging larger – but there is substantial overlap between the sexes and the differences are not significant. Dimorphism is more pronounced in *Alectura* than in *Leipoa*, and more obvious in the tarsometatarsus than in the humerus (Table 3). Where total length measurements can be taken, specimens of *Progura* exhibit a similar distribution to those of living megapodes, with comparable coefficients of variation. This suggests that this species also had moderate, but not significant, sexual size dimorphism.

Age-related size differences are minor once the bone is fully formed; however, one of the largest specimens of *Alectura* was a subadult bird still exhibiting some porosity of the bone surfaces. Whether there is a geographic component to the intraspecific differences is uncertain. Modern *Alectura lathamii* has two subspecies differing, in part, in size, whereas *Leipoa ocellata* shows no such variation. Another confounding aspect may be possible temporal variation, related to Late Pleistocene megafaunalisation and subsequent dwarfing (see below).

#### Generic relationships

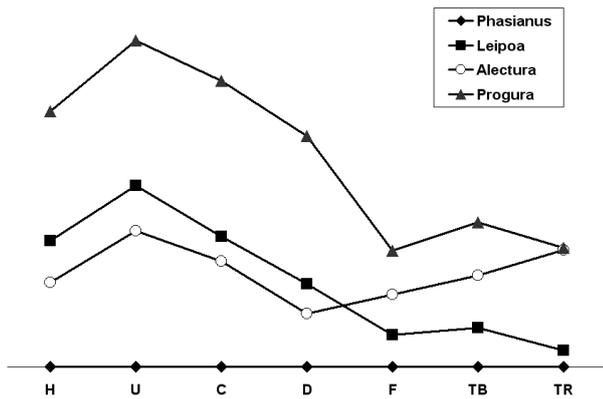
There have been several attempts at discerning the relationships between the genera of megapodes, although none of these has had an osteological component. Clark (1964a,b), using overall similarity of various morphological and proportional characters, discerned a division between the ‘scrubfowl’ (*Megapodius*, *Macrocephalon*) and the other taxa (*Alectura*, *Aepyodius*, *Talegalla*, *Leipoa*). This division was not confirmed by Brom & Dekker (1992), who based their study on many of the same characters but, unlike Clark, used outgroup comparisons in establishing their phylogeny. This phylogeny associated the two brush-turkeys (*Alectura*, *Aepyodius*), with *Talegalla* and *Leipoa* forming a trichotomy with

*Megapodius-Eulipoa-Macrocephalon*. Mey (1999) employed the taxonomy of megapode feather lice to assess that of their host taxa, concluding there was a split between *Megapodius-Eulipoa* and *Alectura-Aepyodius*. The positions of *Macrocephalon*, *Talegalla* and *Leipoa* were less certain but appeared aligned with the latter genera. In most recent study, Birks & Edwards (2002), using nuclear and mitochondrial DNA, confirmed a dichotomy between the scrubfowl and the other genera.

The relationships of *Progura* to living genera have not been examined previously. Van Tets (1974: 222) commented that ‘other than size there are no clear characters that separate *Progura* from the other genera of megapodes nor that indicate to which of these genera it is closest. Relative tarsometatarsal lengths do indicate similarities between *P. naracoortensis* and *Leipoa* and between *P. gallinacea* and the other two Australian megapode genera, *Alectura* and *Megapodius*. Until further fossil material becomes available for study and there is a modern revision of the mainly monotypic megapode genera, it is preferable to use the genus *Progura* for the two fossil megapod species, *gallinacea* and *naracoortensis*.’ Olson (1985), based on a cursory examination of specimens, commented on the possibility that two genera were involved with these species, although not indicating the basis for these remarks.

#### Osteological comparisons

Although cranial, sternal and pelvic fragments of *Progura* have been recovered, these are substantially damaged, limiting their value for assessing characters among taxa. Only bones of the fore- and hindlimbs and shoulder girdle are considered here. Comparisons of *Progura* specimens were made only with the three Australian species; however, these represent the major divisions within the family. Contrary to van Tets’ remark above, there are clear characters that separate members of these divisions. These, in turn, clearly align *Progura* with *Leipoa*. Other than size, no differences could be found between these two genera that could not be attributed to individual variation within and among the samples (Fig. 5). In contrast, the major skeletal elements of *Alectura* and *Megapodius* can be diagnosed from *Leipoa/Progura* and from each other by the suites of characters given below.



**Figure 4** - Simpson log-ratio diagram of *Progura gallinacea*, *Leipoa ocellata* and *Alectura lathamii* with *Phasianus colchicus* as standard. H, humerus; U, ulna; R, radius; C, carpometacarpus; D, phalanx I of the major digit; F, femur; TB, tibiotarsus; TM, tarsometatarsus.

Holman's (1964) study of galliform osteology included one specimen each of *Alectura lathamii*, *Leipoa ocellata* and *Megapodius freycinet*. Because his assessments of characters differentiating taxa were based on very limited sample sizes, they are potentially confounded by individual variation. In the following descriptions, disagreements with Holman arising from the more extensive material in this study are noted.

#### Coracoid

##### *Differences from Alectura*

The shoulder end is deeper from the edge of the facies articularis clavicularis across the processus acrocoracoideus, with a more pronounced triangular shape (shoulder view). The processus acrocoracoideus projects more anteromedially and is not as flattened. The impressio lig. acrocoracohumeralis is deeper. The area of the cotyla scapularis extends further from the shaft (dorsal view). The shaft is stouter and less attenuate towards the shoulder.

Holman listed as a difference the presence in *Leipoa* of a large pneumatic fossa on the distal dorsal face, which was absent in *Alectura*. This fossa occurs in some specimens of *Alectura*; in *Leipoa*, the degree of development is individually variable, in some cases being less extensive than in some specimens of *Alectura*. Another purported distinguishing character was a well developed terminal knob in *Alectura*, lacking in *Leipoa*. This feature also appears in some *Alectura*, although usually not as large.

##### *Differences from Megapodius*

The lateral border of the facies articularis humeralis is directed more ventrally (shoulder view) and is longer and blunter (ventral view). The shaft is proportionally wider throughout its length including the proximal end (ventral view). The facies articularis sternalis comprises a greater extent (2/3 vs 1/2) of the sternal border of the element. There is a pneumatic foramen of variable size in the distal dorsal face. The processus lateralis lacks a well developed terminal knob.

#### Scapula

##### *Differences from Alectura*

The acromion terminates in a narrower apex with

shorter, more rounded tip to the hook, and is directed more anteriorly. The blade is narrower and somewhat more attenuated towards the apex. Holman cited the blade of *Leipoa* as longer; with larger samples of these species, considerable overlap is evident (Table 3). There is a slight terminal expansion of the blade's apex as identified by Holman; however, this is minor and not obviously differing from the state in *Alectura*.

##### *Differences from Megapodius*

The acromion is directed more anteriorly, less ventrally. There is a pneumatic fossa in the ventral base of facies articularis humeralis. The area mediad to this facies lacks a slight depression (dorsal view). The blade is stouter, with the midsection more flattened and flared (dorsal view).

#### Humerus

##### *Differences from Alectura*

The caput humeri is more inflated, particularly anteriorly (proximal view). The crista bicipitalis does not project as far ventrally; it is less obviously demarcated from the caput humeri (the margin of the sulcus lig. transversus is weakly incised) and from the shaft. The crista deltopectoralis projects further. The scar for m. latissimus pars cranialis is broader and not as elongate. The condylus ventralis is more elongate, less globular (anterior view). The distal base of the condylus dorsalis is broader (distal view). The sulcus intercondylaris is narrower, less pronounced (distal view)

##### *Differences from Megapodius*

The caput humeri is more swollen, particularly on its posterior border (proximal view). The incisura capitis is deeper, extending further onto the ventral face. The crista bicipitalis starts more distally on the element; it is rounder in outline and projects further. The scar for m. brachialis is oriented more towards the midline of the shaft (less perpendicular to long axis). The distoventral corner (ventral to the condylus ventralis) is deeper, more produced dorsally and, particularly, ventrally. The condylus lateralis is deeper, projecting further dorsally.

#### Ulna

##### *Differences from Alectura*

The shaft is more bowed (posterior view). The dis-



**Figure 5** - Comparisons of skeletal elements of *Progura gallinacea* (Buckeridge Cave) and *Leipoa ocellata*: a. forelimb elements (humerus, ulna, carpometacarpus), b. hindlimb elements (femur, tibiotarsus, tarsometatarsus). In each, *Progura* is on the left, *Leipoa* on the right. Bar equals 10 mm.

tal end is shallower. The labrum condyli is flatter on the distoventral corner (posterior view).

*Differences from Megapodius*

The posterior margin of the olecranon and anterior margin of the shaft distal to the cotyla dorsalis are less curved. The cotyla dorsalis projects further dorsally. The condylus dorsalis ulnaris is rounder on its dorsal margin, joining the shaft more smoothly (dorsal view). The tuberculum dorsale is longer, extending further proximally along the shaft and merging more smoothly. The shaft is stouter.

Radius

*Differences from Alectura*

The distal end of the shaft is flatter, particularly the dorsal and ventral margins. The distal end is flatter, not curved on the distodorsal corner (posterior view).

*Differences from Megapodius*

The cotyla humeralis is rounder, less oval (proximal view). The shaft is thicker relative to the proximal end, and there is a less pronounced demarcation between them. The distal end is more produced dorsally.

Carpometacarpus

*Differences from Alectura*

The processus pisiformis is produced at the level of the ligamental attachment (anterior to the process in *Alectura*). The spatium intermetacarpale is narrower, not broadening as much across distal half and the os metacarpale minus is consequently less bowed. The synostosis metacarpalis distalis is proportionally longer. Holman stated that the processus intermetacarpalis is absent in *Leipoa* and represented as a minute point in *Alectura*; this feature is variable in both species and may be absent or minute in either.

*Differences from Megapodius*

The dorsal rim of the trochlea carpalis is more triangular, less rounded. The os metacarpale majus is stouter. The os metacarpale minus is more bowed on its distal half

and lacks a prominent bump at its proximal end.

Phalanx 1, major digit

*Differences from Alectura*

The broadest point of the blade is not situated as far distally, being located closer to the midline (dorsal view). The dorsal border of the facies articularis metacarpalis is slightly curved, not triangular (proximal view).

*Differences from Megapodius*

The deepest part of the blade is near the midpoint, rather than near the distal end; its dorsal surface (fossa dorsalis) is not as excavated, particularly at its distal end.

Femur

*Differences from Alectura*

The posteriolateral corner of the proximal end is more rounded (not flattened) (proximal view). The caput femoris is deeper (lateral view). The posterior edge of the facies antitrochanterica extends as a more or less straight ridge (more curved in *Alectura*), slanted downwards medially (posterior view) and extends closer to the caput femoris because the small sulcus between them is weakly expressed. The pneumatic foramen on the anterior face of the trochanter femoris is larger. The trochlea fibularis is more truncate posteriorly, not extending as far (lateral view).

*Differences from Megapodius*

The foramina below the crista trochanterica on the anterior face are more extensive distally and medially. The crista trochanterica is more extensive on its anteroproximal corner (medial view). The medial border of the facies articularis antitrochantericus is tilted more mediolaterally. The shaft is not as curved, the differences accentuated by the thicker portion at the proximal end distal to the caput femoris. The condylus medialis is broader on its anterior side (distal view), protruding much further posteriorly, with its posteromediodistal border flattened, rather than round; thus the condylus is more triangular distally and posteriorly,

not forming a rounded oval (medial view). The condylus lateralis is more truncate posteriorly (lateral view) and extends further distally relative to the condylus medialis. The trochlea fibularis does not extend as far posteriorly. The sulcus intercondylaris is broader. The fossa on the anterior face of the trochanter femoris can be pneumatic in *Leipoa* and *Megapodius*, contra Holman.

#### Tibiotarsus

##### *Differences from Alectura*

The crista cnemialis cranialis does not project as far anteriorly but extends further distally; the anterior border is straight (not triangular) (lateral view); it meets the proximal surface with a lateral extension along the edge. The crista cnemialis lateralis is thinner (proximal view) and the flattened tip is rectangular, rather than broadly circular (lateral view). The junction of the condylus medialis with the shaft is not as abrupt (medial view).

##### *Differences from Megapodius*

The anteromedial corner of the proximal end is more rounded (proximal view). The crista cnemialis cranialis projects further proximally and anteriorly but does not extend as far distally. The impressio lig. collateralis medialis is not as pronounced. The fossa flexoria is more excavated. The condylus medialis is proportionally broader. The distal end is squarer (width and depth subequal) rather than lateromedially elongate (distal view).

#### Tarsometatarsus

##### *Differences from Alectura*

The fossa parahypotarsalis medialis is not as excavated. The shaft is shorter and proportionally broader; its medial margin is more curved over most of its length (medial margin straighter in *Alectura* with curvature mostly restricted to proximal and distal ends). The trochlea metatarsi II extends further distally than trochlea metatarsi IV (subequal in *Alectura*) and flares medially to a greater degree.

Longman (1945) assigned a proximal tarsometatarsus (QM F2769) from the Gore Limestone Quarries, Queensland, to *Alectura lathamii*. Van Tets (1974) placed it with *Progura naracoortensis*; this was the only specimen he referred to this species that was not from South Australia. Re-examination confirmed the referral to *Progura*.

##### *Differences from Megapodius*

The hypotarsus is more expanded laterally but is shorter distally. The canales hypotarsi are proportionally larger. The shaft, particularly the proximal and distal thirds, are proportionally broader; the proximal half of its plantar surface is rounded. The trochlea metatarsi II is not as globular; it flares medially to a greater degree, causing the medial shaft margin to be more curved and less parallel with the lateral margin. The trochleae metatarsi II and IV are broader and the incisurae intertrochleares are thus narrower. The trochlea metatarsi III is longer. The trochlea metatarsi IV does not flare as much. Holman stated that trochlea metatarsi II is elevated above trochlea metatarsi IV in *Leipoa* (level in

*Megapodius*); both taxa agree in having trochlea metatarsi II extending further dorsally and distally than trochlea metatarsi IV.

#### Proportional comparisons

A Simpson log-ratio diagram was used to compare the relative proportions of the long bone lengths in the skeletons of the three living Australia megapodes, using the pheasant *Phasianus colchicus* as the standard (Fig. 3). This plot shows that the megapode species differ in the relative lengths of the fore- and hindlimbs. *Alectura lathamii* is a shorter winged, longer legged form. The plot for *Megapodius reinwardt* is roughly parallel with that of *Alectura* (although noting this bird's smaller size), indicating similar proportions of the wing and leg. In contrast, *Leipoa ocellata* has longer wings (both actually and proportionally than *Alectura*) but shorter legs. A second plot, omitting *Megapodius* but including *Progura* (and retaining *Phasianus* as the standard) demonstrates that *Progura* resembles *Leipoa* in the relative lengths of the long bones (Fig. 4). This is markedly different from the plot of *Alectura*.

The slight variations in the curves of *Progura* and *Leipoa*, particularly between the tibiotarsi, seem likely to be anomalies arising from different sample sizes. The value for the tarsometatarsus is based on 12 specimens, the tibiotarsus only three. Given the size variation within the population, a few individuals may comprise an unrepresentative sample. *Progura* is a notably larger bird than *Leipoa* but otherwise shows little difference in proportions.

#### *Relationships of Progura*

Based both on bone morphology and proportions, *Progura gallinacea* is closest to *Leipoa ocellata* among living Australian megapodes. Furthermore, the differences between these taxa do not justify recognition of two genera. Thus, *Progura* De Vis, 1888, is a synonym of *Leipoa* Gould, 1838, as are *Chosornis* De Vis, 1889 and *Palaeopelargus* De Vis, 1892.

#### SIZE OF PROGURA

*Progura* was easily the largest-bodied megapode in Australia and is only rivalled elsewhere by the Fiji *Megavitiornis*. Van Tets (1974) estimated the size of the two nominal species of *Progura* by assuming that the mass was proportional to the cube of the length of the coracoid. Using an average value for the modern *Leipoa ocellata* of 2 kg [1.5-2.5 kg (Marchant & Higgins 1993)] and of *Megapodius reinwardt* of 1 kg, he obtained figures of 5-7 kg for *gallinacea*, somewhat smaller than a Wild Turkey *Meleagris gallopavo*, and 4-5 kg for *naracoortensis*, based on coracoid lengths of 94 mm and 85 mm, respectively. The greater coracoid length measured in this study (c. 98.4 mm) would give an even larger bird using this method.

Predicted body masses of *Progura gallinacea* from the method of Campbell & Marcus (1991) were obtained



**Figure 6** - Left to right (not to scale), tarsometatarsi of *Ngawupodius minya*, *Leipoa gallinacea*, *Leipoa ocellata*, *Alectura lathami* and *Megapodius reinwardt*.

from specimens, a femur from Big Bird Cave (least circumference 46.6 mm) and tibiotarsus from Buckeridge Cave (41.7 mm). The resulting values from the femur were 7.8 and 9.1 kg from the composite bird equation and the heavy-bodied terrestrial bird equation, respectively. The tibiotarsus circumference gave 10.1 kg for each equation. The difference between the results from each element may be a result of the relative ages of the deposits (see below).

### MEGAFAUNA AND DWARFING

The similarities between *Leipoa ocellata* and *L. (Progura) gallinacea* in overall morphology and proportions are marked. In contrast, the differences are mainly quantitative (size), with qualitative differences being so small as to question whether these nominal taxa represent different stages on the same lineage undergoing megafaunalisation and subsequent dwarfing. (For convenience in the following discussion, *Progura* is used for the large, extinct form and *Leipoa* for the living form.) It has been well documented in Australia and elsewhere that Late Pleistocene members of many lineages (mainly mammalian) became significantly larger than their predecessors, a phenomenon known as megafaunalisation or gigantism; see Murray (1991) for a

review of Australian megafauna. Following the Late Pleistocene, these large forms met one of two fates. Many species became extinct. Some, however, underwent a reduction in body size, giving rise to smaller living forms, a process known as dwarfing. Marshall & Corruccini (1978) gave criteria for recognising dwarfing lineages: (1) other than size, the older forms and the smaller, surviving forms are virtually morphologically indistinguishable, and (2) modern forms do not occur together with the megafaunal form nor in deposits of comparable ages.

The extent of dwarfing between lineages varied considerably (e.g. Marshall & Corruccini 1978; Murray 1991). The Recent Eastern Quoll *Dasyurus maculatus* is only 5-6% smaller than its Late Pleistocene counterpart (Dawson 1982). This compares with markedly greater changes in the large macropine kangaroos: 29-30% in the Eastern Grey Kangaroo *Macropus titan/giganteus* and 30-35% in the Red Kangaroo *Macropus sp./rufa* (Marshall & Corruccini 1978; Horton 1984; Dawson & Flannery 1985).

The difference in size between *Progura* and *Leipoa* would indicate a striking degree of dwarfing: 30-40% based on the long bones. The largest Darling Downs specimen of *Progura* is about twice the size as living *Leipoa*, based on the proximal tarsometatarsal width (see below). Despite the

small samples, notable size differences can be detected between specimens from different sites (Table 3). In the Naracoorte area, Buckeridge Cave specimens average larger than those from Henschke's Fossil Cave. Unfortunately, only the caves from this region have produced fossils that are sufficiently intact to permit total length comparisons. The other sites, with the exception of the Darling Downs, do not allow comparisons because the material is scanty and there are few commonly represented skeletal elements. Even with the Darling Downs bones, the only measurement that can be used in comparison with Naracoorte specimens is the proximal width of the tarsometatarsus. The two values from Darling Downs bones are much larger than any from Naracoorte. These size variations between sites suggest that the deposits may be of different ages and thus at different stages along the gigantism-dwarfing path. Dating of these sites is too poorly known at present to permit any meaningful correlation between size and ages but this line of inquiry merits further examination.

The first criterion – that the larger and the dwarfed forms are virtually morphologically indistinguishable – has been met, as discussed above. The second could be compromised by the apparent co-occurrence of *Progura* and *Leipoa ocellata* from Victoria Fossil Cave. This record of *Leipoa*, identified by van Tets (1974) and van Tets & Smith (1974), consists of fragments of a juvenile skull; no reasons were given for this taxonomic allocation, although at the time of that study, skull material of *Progura* was not known. Also among the fossils recovered from this site were post-cranial elements of a very small juvenile megapode that could not be referred to any taxon within the family. Comparisons between skull material of subsequently acquired *Progura* from Henschke's Fossil Cave and modern *Leipoa* show that these cannot be separated other than by size. The putative fossil *Leipoa* material is sufficiently immature that it lacks any features that would distinguish these taxa. It is unlikely that skulls of these forms could be separated at this size, age and state of development. Consequently, *Leipoa ocellata* should be removed from the species list for Victoria Fossil Cave and, although it is very probably from *Progura*, the skull should be considered Megapodiidae indeterminate. On the basis of the material examined for this paper, there is no evidence of modern *Leipoa ocellata* occurring together with *Progura* nor from elsewhere in the Pleistocene or earlier; after this manuscript was initially submitted, T.H. Worthy (pers. comm.) has found additional specimens in the South Australian Museum, representing what he considers to be both *Progura* and *Leipoa* from the same sites. Thus, until further work can assess this putative co-occurrence, the second criterion for recognising *Progura gallinacea* as the megafaunal form of the *Leipoa ocellata* cannot be considered to be met.

Should *Progura* and *Leipoa* eventually be shown to represent different stages of the same lineage, there is the question of how this should be reflected taxonomically. Among Australian mammals, the relationship between megafaunal and younger dwarfed forms has been indicated

either by maintaining two species or by combining them specifically and recognising each as chronosubspecies. Criteria for treating the taxonomy of dwarfing lineages has been addressed by several authors (for example, see discussion in Marshall & Corruccini 1978). It has been proposed that a difference of 2.56 standard deviations be recognised at subspecific level and 4 standard deviations at specific level. Using this criterion, the relationship between the grey kangaroos, the Pleistocene *Macropus titan* and modern *M. giganteus*, would be maintained at subspecific level. Alternatively, other workers regard the absence of overlap in measurements as justification to retain separate species. The two grey kangaroos would be treated as specifically distinct by this principle. *Leipoa* and *Progura* resemble these in the magnitude of their differences.

## HABITAT

Van Tets (1974) suggested that, because *Progura gallinacea* had proportionally long legs like *Alectura* and *Megapodius*, like those taxa it was also a rainforest inhabitant. Conversely, the relatively shorter legs of *P. naracoortensis* were indicative of an open shrubland species. With the recognition that there is only a single, megafaunal representative of *Leipoa ocellata*, its possible palaeoecology can be re-examined in light of the current habitat preferences of this species. Despite its common name (Malleefowl), *L. ocellata* is not restricted to mallee, a scrubland of multi-stemmed *Eucalyptus* arising from underground rhizomes. Through much of its range in semi-arid zones of southern Australia, this species does occur in mallee-dominated environments, with good overhead cover, dense shrub understorey and open ground cover. In some areas, however, it is found in other types of dry non-mallee-form eucalypt woodland or occasionally, low woodland dominated by *Acacia* or other non-eucalypt species (Marchant & Higgins 1993).

The habitat in the Naracoorte region has been largely cleared for agriculture and viticulture. The remnant areas of native vegetation are more than half woodland, with the remainder comprising forest, grassland and swampland. At the time of European settlement, this region was dominated by open eucalypt forest/woodlands with intermittent tussock grasslands and sedgeland (Croft *et al.* 1990).

Reconstructions of the Middle to Late Pleistocene environment are based on the mammalian component of Victoria Fossil, Cathedral and Henschke's Fossil Caves. The large mammals were largely herbivores (macropodine and sthenurine kangaroos, diprotodontids), with grazing types predominating, but with some browsers also present, indicative of shrubs, trees and grasses. Small animal fauna and other minor components suggest that wetlands or swamps were also in the vicinity. The consensus palaeoenvironmental reconstruction is open forest and/or woodland, with grassy understorey and/or open areas, with some heath and wetlands/swamps (Wells *et al.* 1984, Pledge 1990, Barrie 1997, Brown & Wells 2000). The extant taxa in these de-

posits – including birds at Victoria Fossil Cave (van Tets & Smith 1974) – agree with this habitat interpretation. There is nothing in the reconstructed palaeohabitat of the Naracoorte region that is inconsistent with the occurrence of *Leipoa ocellata*.

The Bluff Downs records comprise the northernmost record of *Progura* by a considerable distance, there being a marked distributional gap from more southerly records. Based on the fossil bird community, the palaeoenvironment of Bluff Downs was interpreted by Boles & Mackness (1994) as a northern Australian, Kakadu-like wetland/floodplain. This is unlike that reconstructed for the habitat of *Progura* from southeastern Australia; however, almost all the avian taxa on which this interpretation was based were aquatic species. In contrast, the mammal fauna is representative of non-aquatic habitats and not dissimilar to the woodland that occurs in the area today (Rich *et al.* 1991).

The other localities producing *Progura* share with the Naracoorte deposits a number of the characteristic mammalian groups. Macropodine and sthenurine kangaroos and diprotodontids are indicative of similar palaeohabitats during at least part the accumulations. Evidence from several localities, including the Naracoorte region, implies that vertebrate remains were amassed over an extended period or across several episodes, encompassing fluctuations in climate and habitat; open woodland/forest suitable for *Progura* was present for prolonged durations, usually for the younger component of the accumulations.

## CONCLUSIONS

Most reported examples of megafauna in Australia are mammals. Among birds, the candidates as megafauna are few. Baird (1985) documented an average difference between Quaternary fossil and modern populations of the Long-billed Corella *Cacatua tenuirostris* of 4%, which he attributed to Late Pleistocene gigantism. The giant coucal *Centropus colossus* (Baird 1985) and large accipitrids (Gaff 2002) are among the few palaeospecies that may meet the criteria. It is uncertain, however, if the living coucal *C. phasianinus* is in the direct lineage of *C. colossus*. Likewise, the lineages to which the large raptors belonged are unknown. Boles (2005) speculated that *G. mortierii* may be the megafaunal member in the lineage of flightless gallinules starting with a smaller bird from the Oligo-Miocene. If the giant megapode *Progura gallinacea* were to be shown to the megafaunal representative of the living *Leipoa ocellata*, it would add another example to this list, one that is particularly notable for the extent of the post-Late Pleistocene dwarfing.

The diminutive fossil megapode, *Ngawupodius minya*, shares similarities with *Leipoa* and differs from *Megapodius*, *Alectura* and related brush-turkey taxa in the shape of the tarsometatarsus (Boles & Ivison 1999). Its broader, stouter shaft and medially flaring trochlea metatarsi II (Fig. 6) raise the possibility that this species was an earlier member of the *Progura-Leipoa* lineage. Miocene-aged

megapode fossils are needed to pursue this possibility.

Living taxa of Australian megapodes have not yet been reported from palaeontological sites, but there is no reason to doubt that these will be found with further work. Remains of megapodes are also recovered from archaeological sites, as are those of introduced, non-megapode galliforms. As an aid to separating these taxa, Appendices I and II present characters for distinguishing selected megapode elements from those of the pheasants (represented by Ring-necked *Phasianus colchicus*) and Wild Turkey (*Meleagris gallopavo*), respectively.

## ACKNOWLEDGEMENTS

I am very grateful to Liz Reed and Shane Bourne for starting me on this project by allowing me to study new specimens in their care and for discussion on the Naracoorte Caves and their contained vertebrate fossils. I thank B. McHenry and N. Pledge (SAM), J. Wilkinson and S. Hocknull (QM) and R. Jones (AM), for access to fossils of *Progura*; W. Longmore (MV), R. Palmer (ANWC), P. Horton (SAM), H. Janetzki (QM) and P. Sweet (AMNH) for access to comparative material; C. Mourer-Chauviré for her careful review of the manuscript; T. Worthy for information on additional SAM specimens; C. Bento and M. Allen for photography; and the Australian Museum for providing a venue in which to carry out this study.

## REFERENCES

- Aplin, K. P., Pasveer, J. M. & Boles, W. E. 1999. Quaternary vertebrates from the Bird's Head Peninsula, Irian Jaya, Indonesia, including descriptions of two previously unknown marsupial species. *In* Baynes, A. & Long, J. A. (eds). *Papers in Vertebrate Palaeontology. Records of the Western Australian Museum Supplement*, 57: 351-387.
- Archer, M. & Wade, M. 1976. Results of the Ray E. Lemley Expeditions, part I. The Allingham Formation and a new Pliocene vertebrate fauna from northern Queensland. *Memoirs of the Queensland Museum*, 17: 379-397.
- Ayliffe, L. K., Marianelli, P. C., Moriarty, K. C., Wells, R. T., McCulloch, M. T., Mortimer, G. E. & Hellstrom, J. C. 1998. 500 ka precipitation record from southeastern Australia: evidence for interglacial aridity. *Geology*, 26: 147-150.
- Ayliffe, L.K. & Veeh, H. H. 1988. Uranium-series-dating of speleothems and bones from Victoria Cave, Naracoorte, South Australia. *Chemical Geology (Isotope Geoscience Section)*, 72: 211-234.
- Baird, R. F. 1985. Avian fossils from Quaternary deposits in 'Green Waterhole Cave', south-eastern South Australia. *Records of the Australian Museum*, 37: 353-370.
- Balouet, J. C. & Olson, S. L. 1989. Fossil birds from Late Quaternary deposits in New Caledonia. *Smithsonian Contributions to Zoology*, 469: 1-38.

- Barrie, D. J. 1997. Climatic indicators within Henschke Fossil Cave system, Naracoorte, South Australia. *Quaternary Australasia*, 15: 45-57.
- Bartholomai, A. 1976. Notes on the fossiliferous Pleistocene fluviatile deposits of the eastern Darling Downs. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, 166: 153-154.
- Bartholomai, A. 1977. The fossil vertebrate fauna from Pleistocene deposits at Cement Mills, Gore, southeastern Queensland. *Memoirs of the Queensland Museum*, 18: 69-73.
- Baumel, J. J. & Witmer, L. M. 1993. Osteologia. In Baumel, J. J., King, A. S., Breazile, J. E., Evans, H. E. & Vandenberg, J. C. (eds). *Handbook of Avian Anatomy: Nomina Anatomica Avium. Publications of the Nuttall Ornithological Club*, 23: 45-132.
- Birks, S. M. & Edwards, S. V. 2002. A phylogeny of the megapodes (Aves: Megapodiidae) based on nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 23: 408-421.
- Boles, W. E. 2005. A new flightless gallinule (Rallidae: *Gallinula*) from the Oligo-Miocene of Riversleigh, northwestern Queensland, Australia. *Records of the Australian Museum*, 57: 179-190.
- Boles, W. E. & Ivison, T. J. 1999. A new genus of dwarf megapode (Galliformes: Megapodiidae) from the Late Oligocene of central Australia. *Smithsonian Contributions to Paleobiology*, 89: 199-206.
- Boles, W. E. & Mackness, B. 1994. Birds from the Bluff Downs Local Fauna, Allingham Formation, Queensland. *Records of the South Australian Museum*, 27: 139-149.
- Brom, T. G. & Dekker, R. W. R. J. 1992. Current studies on megapode phylogeny. In Dekker, R. W. R. J. & Jones, D. N. (eds). *Proceedings of the First International Megapode Symposium*, Christchurch, New Zealand, December 1990. *Zoologische Verhandelingen*, 278: 7-17.
- Brown, S. P. & Wells, R. T. 2000. A Middle Pleistocene vertebrate fossil assemblage from Cathedral Cave, Naracoorte, South Australia. *Transactions of the Royal Society of South Australia*, 124: 91-104.
- Campbell, K. E., Jr. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. *Royal Ontario Museum, Life Sciences Contribution*, 118: 1-203.
- Campbell, K. E., Jr. & Marcus, L. 1991. The relationship of hindlimb bone dimensions to body weight in birds. In Campbell, K. E., Jr. (ed.) *Papers in Avian Paleontology Honoring Pierce Brodkorb. Natural History Museum of Los Angeles County, Science Series*, 36: 395-412.
- Clark, G. A., Jr. 1964a. Ontogeny and evolution in the megapodes (Aves: Galliformes). *Postilla*, 78: 1-37.
- Clark, G. A., Jr. 1964b. Life histories and the evolution of megapodes. *The Living Bird*, 3: 149-167.
- Croft, T., Carruthers, S., Possingham, H. & Inns, B. 1999. *Biodiversity Plan for the South East of South Australia*. Department for Environment, Heritage and Aboriginal Affairs, Adelaide.
- Dawson, L. 1982. Taxonomic status of fossil devils (*Sarcophilus*, Dasyuridae, Marsupialia) from Late Quaternary Eastern Australian localities. pp. 517-525; In Archer, M. (ed.) *Carnivorous Marsupials*. Surrey Beatty & Sons Pty Ltd and Royal Zoological Society NSW, Sydney.
- Dawson, L. 1985. Marsupial fossils from Wellington Caves, New South Wales; the historic and scientific significance of the collections in the Australian Museum, Sydney. *Records of the Australian Museum*, 37: 55-69.
- Dawson, L. & Flannery, T. F. 1985. Taxonomic and phylogenetic status of living and fossil kangaroos and wallabies of the genus *Macropus* Shaw (Macropodidae: Marsupialia), with a new subgeneric name for the larger wallabies. *Australian Journal of Zoology*, 33: 473-498.
- De Vis, C. W. 1888a. Australian ancestry of the crowned pigeon of New Guinea. *Proceedings of the Royal Society of Queensland*, 5: 127-131.
- De Vis, C. W. 1888b. A glimpse of the post-Tertiary avifauna of Queensland. *Proceedings of the Linnean Society of New South Wales*, series 2, 3: 1277-1292.
- De Vis, C. W. 1889. Additions to the list of fossil birds. *Proceedings of the Royal Society of Queensland*, 6: 55-58.
- De Vis, C. W. 1891. Residue of the extinct birds of Queensland as yet detected. *Proceedings of the Linnean Society New South Wales*, series 2, 6: 437-456.
- Elliot, A. 1994. Family Megapodiidae (Megapodes); pp. 278-309. In Del Hoyo, J., Elliot, A. & Sargatal, J. (eds). *Handbook of the Birds of the World. Volume 2. New World Vultures to Guinea-fowl*. Lynx Edicions, Barcelona.
- Frank, R. 1974. Sedimentary development of the Walli Caves, New South Wales. *Helictite*, 12: 3-30.
- Gaff, P. 2002. *The Fossil History of the Family Accipitridae in Australia*. Unpublished MSc thesis, Monash University, Clayton.
- Grün, R., Moriarty, K. C. & Wells, R. T. 2001. Electron spin resonance dating of the fossil deposits in the Naracoorte Caves, South Australia. *Journal of Quaternary Science*, 16: 49-59.
- Holman, J. A. 1964. Osteology of gallinaceous birds. *Quarterly Journal of the Florida Academy of Sciences*, 27: 230-252.
- Hope, J. 1982. Fossil vertebrates from Wombeyan Caves; pp. 155-164. In Dyson, H. J., Ellis, R. & James, J. M. (eds). *Wombeyan Caves. Sydney Speleological Society Occasional Paper No. 8*. The Sydney Speleological Society, Sydney.
- Horton, D. R. 1984. Red kangaroos: last of the Australian megafauna; pp. 639-680. In Martin, P. S. & Klein, R. G. (eds). *Quaternary Extinctions*. University of Arizona Press, Tucson.

- Jones, D. N., Dekker, R. W. R. J. & Roselaar, C. S. 1995. *The Megapodes*. Oxford University Press, Oxford.
- Longman, H. A. 1945. Fossil vertebrates from Gore Quarries. *Memoirs of the Queensland Museum*, 12: 164.
- Lydekker, R. 1891. *Catalogue of the Fossil Birds in British Museum (Natural History)*. London: British Museum (Natural History).
- Marchant, S. & Higgins, P. J. (eds). 1993. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 2. Raptors to Lapwings*. Oxford University Press, Melbourne.
- Marshall, L. G. & Corruccini, R. S. 1978. Variability, evolutionary rates, and allometry in dwarfing lineages. *Palaeobiology*, 4: 101-119.
- Mey, E. 1999. Phylogenetic relationships of the Megapodiidae as indicated by their ischnoceran, in particular goniodid, chewing lice (Insecta: Phthiraptera). In Dekker, R.W.R.J., Jones, D.N. & Benshemesh, J. (eds). Proceedings of the Third International Megapode Symposium, Nhill, Australia, December 1997. *Zoologische Verhandelingen*, 327: 23-35.
- Molnar, R. E. & Kurz, C. 1997. The distribution of Pleistocene vertebrates on the eastern Darling Downs, based on the Queensland Museum collections. *Proceedings of the Linnean Society of New South Wales*, 117: 107-134.
- Moriarty, K. C., McCulloch, M. T., Wells, R. T. & McDowell, M. C. 2000. Mid-Pleistocene cave fills, megafaunal remains and climate at Naracoorte, South Australia: towards a predictive model using U-Th dating of speleothems. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 159: 113-143.
- Murray, P. 1991. The Pleistocene megafauna of Australia; pp. 1071-1164. In Vickers-Rich, P., Monaghan, J. M., Baird, R. F. & Rich, T. H. (eds). *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio, Melbourne.
- Olson, S. L. 1985. The fossil record of birds; pp. 79-238. In Farner, D. S., King, J. R. & Parkes, K. C. (eds). *Avian Biology*, vol. 8. Academic Press, New York.
- Osborne, R. A. L. 1983. Cainozoic stratigraphy at Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales*, 107: 131-147
- Osborne, R. A. L. 1997. Rehabilitation of the Wellington Caves Phosphate Mine: implications for Cainozoic stratigraphy. *Proceedings of the Linnean Society of New South Wales*, 117: 175-180.
- Pledge, N. S. 1990. The upper fossil fauna of the Henschke Fossil Cave, Naracoorte, South Australia. *Memoirs of the Queensland Museum*, 28: 247-262.
- Poplin, F. & Mourer-Chauviré, C. 1985. *Sylviornis neocaledoniae* (Aves, Galliformes, Megapodiidae), oiseau géant éteint de l'île de Pins (Nouvelle-Calédonie). *Geobios*, 18: 73-97.
- Reed, E. H. & Bourne, S. J. 2000. Pleistocene fossil vertebrate sites of the south east region of South Australia. *Transactions of the Royal Society of South Australia*, 124: 61-90.
- Rich, T. H., Archer, M., Hand, S. J., Godthelp, H., Muirhead, J., Pledge, N. S., Flannery, T. F., Woodburne, M. O., Case, J. A., Tedford, R. H., Turnbull, W. D., Lundelius, E. L. Jr., Rich, L. S. V., Whitelaw, M. J., Kemp, A. & Rich, P. V. 1991. Australian Mesozoic and Tertiary terrestrial mammal localities; pp. 1005-1070. In Vickers-Rich, P., Monaghan, J. M., Baird, R. F. & Rich, T. H. (eds). *Vertebrate Palaeontology of Australasia*. Thomas Nelson, Melbourne.
- Sibley, C. G. & Monroe, B. L. 1990. *Distribution and Taxonomy of the Birds of the World*. Yale University Press, New Haven.
- Simpson, G. G. 1941. Large Pleistocene felines of North America. *American Museum Novitates*, 1136: 1-27.
- Steadman, D. W. 1980. A review of the osteology and paleontology of turkeys (Aves: Meleagridinae). In Campbell, K. E. Jr. (ed.). Papers in Avian Paleontology Honoring Hildegard Howard. *Contributions in Science, Natural History Museum of Los Angeles County*, 330: 131-207.
- Steadman, D. W. 1999. The biogeography and extinction of megapodes in Oceania. In Dekker, R.W.R.J., Jones, D.N. & Benshemesh, J. (eds). Proceedings of the Third International Megapode Symposium, Nhill, Australia, December 1997. *Zoologische Verhandelingen*, 327: 7-21.
- Van Tets, G. F. 1974. A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura De Vis*. *Transactions of the Royal Society of South Australia*, 98: 213-224.
- Van Tets, G. F. 1984. A checklist of extinct fossil Australasian birds. pp. 469-475 In Archer, M. & Clayton, G. (eds). *Vertebrate Zoogeography and Evolution in Australasia*, ed. M. Archer & G. Clayton, pp. 469-475. Carlisle: Hesperian Press.
- Van Tets, G. F. & Rich, P. V. 1990. An evaluation of De Vis' fossil birds. *Memoirs of the Queensland Museum*, 28: 165-168.
- Van Tets, G. F. & Smith, M. J. 1974. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. III. Birds. *Transactions of the Royal Society of South Australia*, 98: 225-227.
- Wells, R. T., Moriarty, K. & Williams, D. L. G. 1984. The fossil vertebrate deposits of Victoria Fossil Cave. Naracoorte: an introduction to the geology and fauna. *Australian Zoologist*, 21: 305-333.
- Woods, J. T. 1960. Fossiliferous fluvial and cave deposits. In Hill, D. & Denmead, A. K. (eds). The Geology of Queensland. *Journal of the Geological Society of Australia*, 7: 393-403.
- Worthy, T. H. 2000. The fossil megapodes (Aves: Megapodiidae) of Fiji with descriptions of a new genus and two new species. *Journal of the Royal Society of New Zealand*, 30: 337-364.

## APPENDIX I -- SKELETAL DIFFERENCES BETWEEN THE MEGAPODIIDAE AND PHASIANIDAE.

Suites of characters by which the major elements of the Megapodiidae can be separated from those of similar-sized species of the Phasianidae (s.s.) (based on *Phasianus colchicus*).

**Sternum.** The entire element and the carina sterni are shorter. The spina interna is short and does not extend fin-like ventrally. The labra ventrales are broad, and extend dorsally, rather than anterodorsally. The sternal plate (corpus sterni) is entire for the anterior two-thirds of the carina sterni (about 10% in phasianids). The trabecula laterales are broader, particularly the anterior pair, and shorter, particularly the posterior pair; the pairs of trabeculae have separate origins on the sternal plate, that is, they are not joined at the base. The costal margin is longer, with more processus costales.

**Coracoid.** The processus lateralis is triangular, rather than hooked. The facies clavicularis is much broader. The impressio lig. acroracohumeralis does not occupy as much of the dorsal side of the shoulder extremity.

**Scapula.** The facies articularis humeralis is larger and rounder. The tuberculum coracoideum is larger and displaced somewhat towards the facies articularis humeralis. The acromion has the tip more extended as a flattened hook. The blade (corpus scapulae) is proportionally broader. The area on the posteromedial side of the facies articularis humeralis is strongly pneumatic.

**Humerus.** The caput humeri is inflated (proximal view). The tuberculum ventrale is not developed proximally (posterior view) because the caput humeri is extended dorsally, subsuming it. The crista deltopectoralis is longer (dorsal view) and extends further distally along the shaft; its profile is more rounded, less triangular, and the midpoint lacks a ventrally inflected section. The crista bicipitalis is rounder ventrally. The impressio coracobrachialis is flatter, less excavated and more level with the intumescencia. The posterior attachment of *m. latissimus dorsi* is slanted more posteriorly. The shaft is more curved (anterior view), particularly on the dorsal side. The processus flexoris is rounder, broader and less discrete from the condylus ventralis. The scars on the ventral face of distal end are located more towards the midline as opposed to the anterior border (ventral view). The scar for *m. brachialis* is longer and broader, extending to about the midline; in the phasianids, it is smaller and restricted to the ventral side, just in from ventral margin. The distal end is deflected anteriorly (ventral view) and does not project from the shaft as far ventrally.

**Ulna.** The impressio brachialis is more elongate, extending proportionally further distally. The anterior margin of the proximal cotylae is tilted distally. The apex of the olecranon is straighter (anterior view). The scar proximal to the impressio brachialis is triangular, rather than round. The labrum condyli dorsalis has rounder edges (distal view). The

impressio *m. scapulotricipitalis* is thin, straight and elongate proximodistally.

**Radius.** The proximal end is rounder, rather than oval (proximal view). The width of the shaft is more constant throughout its length, instead of tapering proximodistally. The tuberculum bicipitale is situated more dorsally. The rim surrounding the ventral edge of the cotyla humeralis is obsolete.

**Carpometacarpus.** A processus intermetacarpalis is absent. The os metacarpale minus is not as flattened nor as expanded dorsoventrally over its proximal half. The sulcus interosseus is deeper and more pronounced. The synostosis metacarpalis distalis is longer.

**Phalanx 1, major digit.** The dorsal side of the facies articularis metacarpalis is broader (proximal view) and extends further proximally (anterior view).

**Pelvis and synsacrum.** The posterior margin of the ala preacetabularis ilii (crista iliaca dorsalis) is curved concavely, not straight (anterior view). The alae ischii has straighter lateral and posterior borders (lateral view). A tuberculum preacetabulare is low and reduced, or absent. The foramen ilioischiatricum is much longer. The postacetabular portion is greater than 40% of the overall length. The ala postacetabularis ilii terminates posteriorly in a straight border oriented anterolaterally-posteromedially leading to a medially-directed point (posteriorly directed in phasianids). The borders of the synsacral vertebrae do not converge posteriorly, maintaining about the same distance apart through their lengths.

**Femur.** The proximal end is wider and deeper relative to the length of the element. The caput femoris is larger. The pneumatic foramen below the crista trochanteris on the anterior side is rounder (not oval nor proximodistally elongate). The impressio *m. iliotrochantericus caudalis* is more curved, rather than being proximodistally straight. The shaft is more robust (proportionally thicker) and straighter (both anterior and lateral views). The distal end is twisted laterally. The condylus lateralis projects further posteriorly. The distal margin of the condylus medialis is more angular and less round (anteriomedial view).

**Tibiotarsus.** The shaft and both ends are more robust. The proximal end is broader. In anterior view, the anterior margin of the crista cnemialis lateralis and the border of the articular surface medial to the crista cnemialis cranialis are roughly horizontal, forming a more or less straight line (not sloping distally on both sides, producing a rounded outline). The posterior margin or the proximal end extends further and is undercut by the fossa flexoria to a greater extent. The crista cnemialis cranialis is shorter and directed more proximolaterally, instead of projecting as far proximally. The border of the shaft is excavated between the rim of the facies articularis medialis and impressio lig. collateralis medialis (posterior view). The incisura tibialis is smoother from the articular surface to the side of the crista cnemialis lateralis because it is not interrupted by a pit and ridge (proximal view). The borders of the sulcus exten-

rius proximal to the pons supratendineus are low and merge smoothly into the sulcus (in phasianids, the medial border sharply demarcated ridge with scar at distal end). The pons supratendineus is narrower (not as long). The incisura intercondylaris and the sulcus extensorius are shallower. The posterior rims of the condyli are thicker lateromedially and do not extend as far. The posterior side of the distal end is flatter.

Tarsometatarsus. The hypotarsus does not extend as far distally, and the cristae hypotarsi do not run distally from its base. The canalis hypotarsi is larger, and is situated slightly lateral of the eminentia intercotylaris. There are three cristae hypotarsi; the medialmost is of moderate length, the other two are shorter; the middle crista is plantar to the midpoint of the canalis and the lateralmost roughly level with it (in phasianids, the lateral two cristae are more dorsally placed relative to the canalis and the middle crista is also situated more laterally).

The cotylae are not as deep, and thus less cup-shaped (dorsal view). The shaft is dorsoplantarly compressed. A spur is absent. The distal end is more splayed. The fossa metatarsi I is round, situated more proximally and laterally, at the proximal end of a large shallower scar; the medial border of the fossa is strongly developed, projecting beyond the border of the shaft (dorsal view). The foramen vasculare distale is round, not elongate proximodistally. The distal extent of the trochlea metatarsi II is subequal or greater than that of trochlea metatarsi IV (in phasianids, II is markedly shorter than IV).

## APPENDIX II -- SKELETAL DIFFERENCES BETWEEN MEGAPODIIDAE AND MELEAGRIDIDAE.

Suites of characters by which the major elements of the Megapodiidae can be separated from those of the Meleagrididae (based on *Meleagris gallopavo*).

Sternum. The entire element and the carina sterni are proportionally shorter. The spina interna is short and does not extend anteriorly. The processus cranio-lateralis is of moderate length and directed proximolaterally (substantially longer and more anteriorly directed in *Meleagris*). The apex carinae is about level with the spina interna (lateral view), rather than with a point between a 1/3 and 1/2 of the distance from the anterior end. The sternal plate (corpus sterni) is entire for the anterior 2/3 of the carina sterni (about 40% in meleagridids). The trabeculae laterales are broader, particularly the anterior pair, and shorter, particularly the posterior pair; the pairs of trabeculae have separate origins on the sternal plate, that is, they are not joined at the base. The posterior end is directed more or less posteriorly, not strongly curved dorsally.

Coracoid. The facies clavicularis is markedly thinner. The impressio lig. acrocoracohumeralis is smaller, occupying the central third of the medial side of the shoulder extremity instead of most of this surface. The linea muscularis is not as prominent (dorsal view). The facies articularis

sternalis extends further onto dorsal surface.

Scapula. The facies articularis humeralis is rounder. The acromion has the tip more extended and attenuated. There is no foramen on the proximal end of the dorsal surface medial to the facies articularis humeralis. The broadest section of the corpus scapulae is near the midpoint, not displaced 2/3 of the way towards the apex scapulae.

Humerus. The caput humeri is not as inflated (proximal view) and its distal projection is narrower and shorter, not extending to the distal border of the incisura bicipitalis (posterior view). The sulcus lig. transversus is deeper and more distinct from the caput humeri and intumescencia, with a more pronounced ridge separating it from the incisura bicipitalis. The posterior attachment of m. latissimus ventrale is on the dorsal side, rather than the ventral side, of the midline. The shaft is more curved (anterior view), particularly on the dorsal side. The processus flexoris is more rounded and does not project as far ventrally or distally. The scar for m. brachialis is narrower. The distal end is deflected anteriorly (ventral view) and does not project from the shaft as far ventrally. The condylus ventralis is more elliptical, elongate dorsoventrally.

Ulna. The apex of the olecranon is straighter (anterior view). The impressio m. scapulotricipitalis is thin, straight and elongate proximodistally (not circular). The sulcus intercondylaris is shallower. The condylus ventralis is low. The ventral half of the distal end (tuberculum carpale + condylus ventralis) is produced as a slender pyramid (heavy, blocky and subrectangular in meleagridids) (distal view).

Radius. The cotyla humeralis is circular, rather than oval (proximal view). The tuberculum bicipitale is less pronounced. The facies articularis ulnaris is much shallower. The ventral border of the distal end is straighter, not flaring outwards (posterior view).

Carpometacarpus. The distal rim of the trochlea carpalis is entire, not indented; the dorsal rim is more elliptical. There is no processus intermetacarpalis. The os metacarpale minus is not as flattened nor as expanded dorsoventrally over its proximal half. The sulcus interosseus is deeper and more pronounced. The synostosis metacarpalis distalis is longer. The facies articularis digitalis minor is proportionally shorter.

Phalanx 1, major digit. The dorsal border of the facies articularis metacarpalis projects further proximally (anterior view). The ventral border of the shaft distal to, and meeting, the rim of the facies articularis metacarpalis is more curved (anterior view).

Pelvis and synsacrum. The posterior margin of the ala preacetabularis ilii (crista iliaca dorsalis) is curved concavely, not straight (anterior view). The crista spinosa is discrete for most of its length, not fused with the cristae iliaca dorsalis. A tuberculum preacetabulare is low and undeveloped, or absent. The foramen acetabuli is proportionally smaller and located more ventrally relative to the foramen ilioischadicum. The cristae costalis of the lumbar and anteriormost sacral vertebrae are thinner (ventral view). The

alae ischii are positioned more medially relative to the cristae dorsolateralis ilii and form more pronounced angles at their juncture; the alae are more parallel, not bowing laterally (ventral view).

**Femur.** The proximal end, particularly the facies articularis antitrochanterica, is not as elongate lateromedially (proximal view). There is a pneumatic foramen below the crista trochanteris on the anterior side. The shaft is straighter in anterior view and more curved in lateral view. The linea intermuscularis cranialis is straighter and more parallel to the long axis of the shaft, rather than crossing the shaft proximolaterally-distomedially. The condylus lateralis projects further posteriorly. The condylus medialis is not as deep and is rounder on the posterior margin (medial view).

**Tibiotarsus.** The crista cnemialis cranialis is shorter and directed more proximolaterally, instead of projecting as far proximally (anterior view), and is less curved on its anterior border (medial view). The borders of the sulcus extensorius proximal to the pons supratendineus are rounded and merge smoothly into the sulcus (in meleagridids, the medial border is demarcated by a low ridge). The epicondylus medialis is situated further from the rim and more towards the

midpoint. The posterior rims of the condyli are thicker lateromedially and do not extend as far.

**Tarsometatarsus.** The hypotarsus does not extend as far distally, and no cristae hypotarsi run distally from its base. The sulcus hypotarsi is larger, and is situated slightly lateral of the eminentia intercotylaris. There are three cristae hypotarsi; the medialmost is of moderate length and level with the midpoint of the canalis (medial to midpoint in *Meleagris*); the other two are shorter and more dorsally placed relative to the canalis and the middle crista is also situated more laterally. The cotylae are not as deep, and thus less cup-shaped (dorsal view). The shaft is dorsoplantarly compressed, and its lateral margin is more curved (dorsal view). A spur is absent. The distal end is more splayed. The fossa metatarsi I is round, situated more proximally and laterally, at the proximal end of a large shallower scar; the medial border of the fossa is strongly developed, projecting beyond the border of the shaft (dorsal view). The foramen vasculare distale is round, not elongate proximodistally. The trochlea metatarsi IV projects distally about the same extent as the trochlea metatarsi II.

Element, Side, End	Reg. no.	Locality
Tarsometatarsus, P,L lectotype of <i>Progura gallinacea</i> (De Vis 1888a)	QM F1143	Qld: Ravensthorpe
Tarsometatarsus, P,L paralectotype of <i>Progura gallinacea</i> (De Vis 1888a)	QM F1134	Qld: Ravensthorpe
Tarsometatarsus, D,R paralectotype of <i>Progura gallinacea</i> (De Vis 1888a)	QM F5556	Qld: Ravensthorpe
Tarsometatarsus, D,R paralectotype of <i>Progura gallinacea</i> (De Vis 1888a)	QM F5557	Qld: Ravensthorpe
Carpometacarpus, P,R holotype of <i>Chosornis prateritus</i> (De Vis 1889); cited as 'left'; matching half of	QM F1132	Qld: Chinchilla
Carpometacarpus, P,R assigned to <i>Chosornis prateritus</i> (De Vis 1889)	QM F7005	Qld: Darling Downs unspecified
Carpometacarpus, D,R holotype of <i>Palaeopelargus nobilis</i> (De Vis 1891); matching half of F1132 (= Chinchilla)	QM F1139	Qld: Darling Downs unspecified
Ulna, D,R originally assigned to <i>Palaeopelargus nobilis</i> (De Vis 1891)	QM F5553	Qld: Darling Downs unspecified
Scapula, P,R originally assigned to Otididae undetermined genus and species (De Vis 1888b)	QM F5558	Qld: Chinchilla
Coracoid, C,L originally assigned to <i>Talegalla lathamii</i> (= <i>Alectura lathamii</i> ) 43879 (Lydekker 1891)	BMNH A3244	NSW: cave in Wellington Valley
Coracoid, C,R	AM F54720	NSW: Wombeyan Quarries
Ulna, P,R	AM F54721	NSW: Wombeyan Quarries
Ulna, D,R	AM F54722	NSW: Wombeyan Quarries
Ulna, D,R	AM F54723	NSW: Walli Caves
Tarsometatarsus, P,L	AM F54724	NSW: Wombeyan Quarries
Tarsometatarsus, D,L	AM F54725	NSW: Wombeyan Quarries
Tarsometatarsus, D,R	AM F54726	NSW: Wombeyan Quarries
Tarsometatarsus, D,R	AM F7033 (formerly QM F1134)	Qld: Ravensthorpe

**Table 1** - De Vis' specimens and other fossil material referred to *Progura gallinacea* by van Tets (1974). Institutional acronyms are AM (Australian Museum), BMNH (British Museum Natural History), QM (Queensland Museum) and SAM (South Australian Museum). Other abbreviations are P (proximal), D (distal), C (complete), L (left), R (right).

Element, End, Side	Reg. No.	Locality
Tarsometatarsus, C,R holotype of <i>Progura naracoortensis</i> (van Tets 1974)	SAM P17856	SA: Henschke's Fossil Cave
Tarsometatarsus, P,L originally referred to <i>Alectura lathami</i> (Longman 1945)	QM F2769	Qld: Gore Limestone Quarries
Coracoid, C,R	SAM P16700	SA: Victoria Cave
Humerus, C,L	SAM P17153	SA: Henschke's Fossil Cave
Humerus, D,L	SAM P17154	SA: Henschke's Fossil Cave
Humerus, D,L	SAM P17878	SA: Henschke's Fossil Cave
Humerus, D,R	SAM P18183	SA: Henschke's Fossil Cave
Ulna, C,R	SAM P17877	SA: Henschke's Fossil Cave
Ulna, D,L	SAM P17879	SA: Henschke's Fossil Cave
Ulna, D,L	SAM P18182	SA: Henschke's Fossil Cave
Radius, C,L	SAM P18184	SA: Henschke's Fossil Cave
Femur, P,R	SAM P17857	SA: Henschke's Fossil Cave
Femur, D,R	SAM P18186	SA: Henschke's Fossil Cave
Tibiotarsus, C,R	SAM P17152	SA: Henschke's Fossil Cave
Tibiotarsus, D,R,	SAM P17876	SA: Henschke's Fossil Cave
Tarsometatarsus, P,R	SAM P18185	SA: Henschke's Fossil Cave
Cervical vertebra	SAM P18181	SA: Henschke's Fossil Cave
Synsacrum, A	SAM P18187	SA: Henschke's Fossil Cave
Carpometacarpus, C	QM F23258	Qld: Bluff Downs (Boles & Mackness 1994)
Tarsometatarsus, P,L	QM F23259	Qld: Bluff Downs (Boles & Mackness 1994)

**Table 2** - Fossil material referred to *Progura naracoortensis*. Institutional acronyms are SAM (South Australian Museum) and QM (Queensland Museum). Other abbreviations are P (proximal), D (distal), C (complete), A (anterior), L (left), R (right). All references van Tets (1974) unless otherwise indicated.

**Table 3 (opposite)** - Measurements (mm) of *Progura gallinacea*, *Leipoa ocellata* and *Alectura lathami lathami*, giving mean, standard deviation, range and sample size. Method of each measurements taken is described in the text. Entries for *Progura* are all specimens combined and those from Henschke's Fossil Cave, Buckridge Cave and Darling Downs (where present). Abbreviations are cap. hum., caput humeri; cot. scap., cotyla scapularis; fac. art. hum., facies articularis humeralis; cond. dors., condylus dorsalis; troc. carp., trochlea carpalis; spat. inter., spatium intermetacarpale.

CORACOID	Greatest length	Cap. hum.–cot. scap.	Cap. hum.–f. art. hum.	Midshaft width	Sternal width
<i>Progura gallinacea</i>	90.4 ± 7.1	31.1 ± 1.8	22.3 ± 1.2	10.3 ± 0.7	28.8 ± 1.9
- Henschke's Fossil Cave	77.1-98.4; 10	27.6-34.2; 19	20.5-24.2; 12	8.8-11.6; 17	27.1-32.0; 5
- Buckeridge Cave	90.4 ± 7.1	31.1 ± 1.8	22.3 ± 1.3	10.3 ± 0.7	28.8 ± 1.9
	77.1-98.4; 10	27.6-34.2; 19	20.5-24.2; 10	8.8-11.6; 14	27.1-32.0; 5
	-	-	22.3 ± 1.6	10.4 ± 0.0	-
			21.2-23.4; 2	10.4; 2	
<i>Leipoa ocellata</i>	64.4 ± 2.2	19.3 ± 1.3	13.9 ± 0.5	6.5 ± 0.4	18.8 ± 0.8
<i>Alectura lathamii</i>	61.0-67.5; 9	16.9-20.9; 11	13.1-14.6; 10	5.7-6.8; 10	17.8-20.6; 11
	65.1 ± 3.2	17.7 ± 1.2	12.7 ± 0.6	6.1 ± 0.4	17.6 ± 1.3
	61.6-71.0; 12	16.4-20.2; 13	11.6-13.6; 12	5.4-7.0; 12	15.1-19.1; 13

SCAPULA	Greatest length	Acromion – fac. art. hum.	Width, fac. art. hum.	Depth, fac. art. hum.
<i>Progura gallinacea</i>	100.9	25.5 ± 1.6	12.3 ± 1.4	9.9 ± 1.2
	1	23.9-28.5; 7	11.2-15.2; 8	7.6-11.7; 9
- Henschke's Fossil Cave	100.9	25.2 ± 1.0	11.8 ± 0.7	9.5 ± 0.9
	1	24.0-26.1; 5	11.2-12.9; 7	7.6-10.3; 7
- Buckeridge Cave	-	28.5	-	11.5 ± 0.3
		1		11.3-11.7; 2
- Darling Downs (Chinchilla)			15.2	
			1	
<i>Leipoa ocellata</i>	82.2 ± 4.1	15.6 ± 1.1	7.7 ± 0.5	6.5 ± 0.5
<i>Alectura lathamii</i>	75.7-89.7; 10	13.5-16.6; 11	7.0-8.4; 10	5.4-7.0; 10
	82.8 ± 3.3	15.1 ± 0.8	8.1 ± 0.6	6.8 ± 0.5
	77.9-90.3; 13	13.9-16.4; 13	7.1-9.3; 13	6.1-7.5; 12

HUMERUS	Greatest length	Proximal width	Prox. depth (cap. hum.)	Midshaft width	Midshaft depth	Distal width	Distal depth (cond. dors.)
<i>Progura gallinacea</i>	143.9 ± 5.4	35.8 ± 1.5	16.7 ± 0.9	15.0 ± 0.7	11.4 ± 0.6	30.3 ± 1.2	16.6 ± 0.7
	137.8-150.6; 6	34.1-38.6; 13	15.3-18.9; 20	14.1-16.5; 12	10.5-12.6; 12	28.6-32.3; 22	15.1-17.7; 22
- Henschke's Fossil Cave	142.5 ± 5.8	35.1 ± 1.9	16.2 ± 1.3	15.0 ± 0.8	11.4 ± 0.5	30.0 ± 1.3	16.6 ± 0.7
	137.8-150.6; 4	31.3-38.6; 11	13.3-18.0; 18	14.1-16.5; 8	10.5-11.9; 8	27.6-32.3; 18	15.1-17.7; 17
- Buckeridge Cave	150.0	37.2 ± 1.7	18.1 ± 1.1	15.1 ± 0.6	11.8 ± 1.1	30.8 ± 0.5	16.9 ± 0.6
	1	36.0-38.4; 2	17.3-18.9; 2	14.6-15.5; 2	11.0-12.6; 2	30.4-31.1; 2	16.4-17.3; 2
<i>Leipoa ocellata</i>	103.1 ± 3.9	23.6 ± 0.9	10.9 ± 0.5	8.8 ± 0.7	7.6 ± 0.6	19.9 ± 0.6	11.0 ± 0.4
<i>Alectura lathamii</i>	96.6-107.9; 11	22.2-24.9; 11	9.9-11.6; 11	7.6-9.6; 11	6.4-8.3; 11	19.0-20.8; 10	10.5-11.7; 11
	92.6 ± 3.5	22.3 ± 1.0	9.4 ± 0.4	8.9 ± 0.5	6.8 ± 0.4	19.2 ± 0.8	10.3 ± 0.3
	88.5-99.0; 12	21.1-24.4; 12	8.4-10.0; 12	8.1-9.9; 12	6.4-7.5; 12	18.3-20.6; 12	9.7-10.8; 12

ULNA	Greatest length	Proximal depth	Proximal width	Midshaft width	Distal width	Distal depth
<i>Progura gallinacea</i>	155.5 ± 8.0	15.1 ± 0.9	23.9 ± 1.8	10.7 ± 0.8	19.5 ± 1.3	12.5 ± 0.8
	145.6-172.2; 9	13.2-16.3; 17	21.4-28.2; 16	9.3-12.6; 18	17.6-22.2; 22	11.3-14.0; 17
- Henschke's Fossil Cave	152.5 ± 5.2	14.8 ± 0.9	23.3 ± 1.4	10.4 ± 0.8	18.9 ± 1.0	12.2 ± 0.7
	145.6-160.2; 7	13.2-16.0; 13	21.4-25.3; 11	9.3-11.6; 11	17.6-21.3; 14	11.3-13.7; 13
- Buckeridge Cave	165.7 ± 9.2	16.0 ± 0.2	24.9 ± 2.2	11.3 ± 0.6	21.1 ± 1.0	13.6 ± 0.4
	159.2-172.2; 2	15.8-16.3; 4	23.5-28.2; 4	10.5-12.6; 7	20.2-22.2; 3	13.2-14.0; 3
- Darling Downs (unspecified)					20.0	15.2
					1	1
<i>Leipoa ocellata</i>	107.1 ± 4.1	16.8 ± 0.6	10.7 ± 0.3	7.1 ± 0.5	12.6 ± 0.3	8.8 ± 0.3
<i>Alectura lathamii</i>	100.5-113.1; 10	16.1-17.9; 11	10.4-11.4; 11	6.5-8.2; 10	12.0-13.1; 11	8.3-9.3; 11
	95.3 ± 3.5	14.4 ± 2.9	12.3 ± 3.1	7.0 ± 0.4	12.3 ± 0.5	8.3 ± 0.4
	89.5-102.1; 13	9.9-16.7; 13	9.7-17.5; 13	6.5-8.0; 13	11.7-13.5; 13	7.7-9.1; 13

RADIUS	Greatest length	Proximal width	Proximal depth	Distal width
<i>Progura gallinacea</i>	140.4 ± 4.6 135.4-144.5; 3	11.3 ± 0.5 10.4-11.7; 5	10.2 ± 0.7 9.3-11.1; 5	13.0 ± 0.8 12.1-14.2; 5
- Henschke's Fossil Cave	142.9 ± 2.3 141.3-144.5; 2	11.3 ± 0.6 10.4-11.7; 4	10.3 ± 0.8 9.3-11.1; 4	13.0 ± 0.9 12.1-14.2; 4
<i>Leipoa ocellata</i>	98.0 ± 4.0 91.4-103.7; 11	6.5 ± 0.3 6.1-7.0; 11	7.2 ± 0.4 6.1-7.6; 11	8.6 ± 0.3 7.9-8.9; 11
<i>Alectura lathami</i>	85.8 ± 3.5 81.0-92.2; 13	6.7 ± 0.3 6.3-7.3; 13	6.4 ± 0.4 5.6-7.0; 13	8.5 ± 0.5 7.8-9.3; 12

CARPOMETA-CARPUS	Greatest length	Proximal width	Prox. depth (troc. carp.)	Midshaft width	Max. width, spat. inter.	Distal width
<i>Progura gallinacea</i>	81.2 ± 4.8 75.0-91.4; 17	23.1 ± 1.9 20.5-26.5; 23	12.0 ± 0.9 10.8-14.4; 26	6.9 ± 1.0 5.8-10.6; 21	7.9 ± 1.2 6.8-9.2; 5	14.8 ± 1.3 12.7-17.9; 20
- Henschke's Fossil Cave	78.7 ± 2.9 75.0-83.9; 12	22.1 ± 1.1 20.5-24.4; 16	11.5 ± 0.5 10.8-12.8; 18	6.4 ± 0.3 5.8-6.8; 14	7.8 ± 1.1 6.9-9.0; 3	14.1 ± 0.7 12.7-15.1; 14
- Buckeridge Cave	87.7 ± 2.5 85.7-91.4; 4	25.9 ± 0.8 24.6-26.5; 5	13.2 ± 0.3 12.9-13.7; 4	7.2 ± 0.4 6.8-7.7; 5	9.2 1	16.4 ± 0.3 15.9-16.6; 4
- Darling Downs (Chinchilla)		26.0 1	14.4 1	10.6 1		17.5 1
<i>Leipoa ocellata</i>	54.5 ± 2.1 51.9-58.1; 10	15.0 ± 0.4 14.4-15.6; 10	7.9 ± 0.2 7.6-8.4; 10	4.4 ± 0.3 3.8-4.9; 10	4.7 ± 0.4 4.1-5.2; 10	9.3 ± 0.3 8.9-9.6; 10
<i>Alectura lathami</i>	51.1 ± 2.2 47.7-54.7; 13	13.9 ± 0.7 12.5-15.0; 13	7.3 ± 0.3 6.9-7.9; 13	4.0 ± 0.3 3.7-4.9; 13	5.1 ± 0.4 4.7-5.8; 13	8.2 ± 0.4 7.6-9.0; 13

PHALANX 1, DIGIT II	Greatest length	Width, blade	Proximal width	Proximal depth	Distal width
<i>Progura gallinacea</i>	27.5 ± 2.4 25.3-30.1; 4	11.7 ± 0.5 11.2-12.3; 4	8.7 ± 0.4 8.2-9.1; 4	8.3 ± 0.5 8.0-9.0; 4	9.1 ± 0.3 8.7-9.4; 4
- Henschke's Fossil Cave	27.5 ± 2.4 25.3-30.1; 4	11.7 ± 0.5 11.2-12.3; 4	8.7 ± 0.4 8.2-9.1; 4	8.3 ± 0.5 8.0-9.0; 4	9.1 ± 0.3 8.7-9.4; 4
<i>Leipoa ocellata</i>	18.8 ± 1.0 16.9-20.2; 10	8.9 ± 0.6 8.0-9.4; 10	6.2 ± 0.3 5.7-6.7; 10	6.2 ± 0.2 5.9-6.5; 10	4.3 ± 0.2 4.0-4.7; 10
<i>Alectura lathami</i>	17.4 ± 0.7 16.4-18.6; 13	8.4 ± 0.5 7.3-9.1; 13	5.9 ± 0.4 5.4-6.8; 13	5.9 ± 0.4 5.2-6.8; 13	3.5 ± 0.2 3.3-4.1; 13

FEMUR	Greatest length	Proximal width	Proximal depth	Midshaft width	Midshaft depth	Distal width	Dist. depth, lateral	Dist. depth, medial
<i>Progura gallinacea</i>	109.4 ± 6.0 100.5-113.7; 4	27.6 ± 2.7 23.3-30.7; 9	21.5 ± 2.7 18.4-25.5; 5	12.0 ± 0.9 10.6-13.3; 8	11.5 ± 0.8 10.6-13.0; 8	26.0 ± 1.5 24.5-29.6; 8	22.5 ± 1.8 20.2-25.5; 6	21.3 ± 2.1 19.1-24.8; 5
- Henschke's Fossil Cave	109.4 ± 6.0 100.5-113.7; 4	27.8 ± 2.6 23.3-30.7; 10	21.5 ± 2.7 18.4-25.5; 5	12.0 ± 0.9 10.6-13.3; 8	11.5 ± 0.8 10.6-13.0; 8	26.0 ± 1.5 24.5-29.6; 8	22.5 ± 1.8 20.2-25.5; 6	21.3 ± 2.1 19.1-24.8; 5
- Buckeridge Cave		31.6 1	18.9 1	13.9 ± 1.0 12.5-14.7; 4	13.2 ± 0.9 12.3-14.0; 4	26.9 1	21 - 1	
<i>Leipoa ocellata</i>	88.1 ± 3.9 81.6-95.5; 11	20.6 ± 0.7 19.3-21.6; 11	15.9 ± 1.3 14.1-18.3; 11	8.7 ± 0.6 7.9-9.5; 11	8.4 ± 0.8 7.2-9.6; 11	18.9 ± 0.6 18.0-19.9; 11	16.0 ± 0.8 15.1-18.0; 11	15.7 ± 0.7 14.5-16.8; 11
<i>Alectura lathami</i>	97.8 ± 4.8 89.8-107.6; 13	21.8 ± 1.1 19.4-23.2; 13	17.7 ± 1.4 14.4-19.2; 13	9.8 ± 0.5 8.8-10.7; 13	9.3 ± 0.5 8.6-10.7; 13	20.4 ± 0.9 18.8-21.6; 13	18.8 ± 0.8 17.7-20.2; 13	17.3 ± 0.8 15.7-18.4; 13

TIBIOTARSUS	Greatest length	Proximal width	Proximal depth	Midshaft width	Midshaft depth	Distal width	Distal depth, lateral	Distal depth, medial
<i>Progura gallinacea</i>	162.3 ± 6.7 158.0-170.1; 3	32.4 ± 2.5 29.7-36.3; 7	27.1 ± 3.0 21.8-30.2; 8	10.9 ± 0.8 9.7-12.2; 11	8.9 ± 0.6 8.0-9.6; 11	20.9 ± 1.3 18.9-22.8; 20	19.0 ± 1.2 17.4-21.2; 20	20.3 ± 1.1 18.4-22.3; 19
- Henschke's Fossil Cave	-	31.3 ± 1.7 29.7-34.0; 5	25.5 ± 2.6 21.8-28.4; 5	10.1 ± 0.5 9.7-10.8; 4	8.3 ± 0.3 8.0-8.7; 4	20.4 ± 1.0 18.9-22.4; 14	18.6 ± 1.0 17.4-21.2; 14	19.8 ± 0.8 18.4-21.3; 14
- Buckeridge Cave	164.1 ± 8.6 158.0-170.1; 2	35.3 ± 1.5 34.2-36.3; 2	29.8 ± 0.6 29.4-30.2; 2	11.5 ± 0.5 11.0-12.2; 5	9.3 ± 0.2 9.0-9.6; 5	22.5 ± 0.5 21.7-22.8; 4	20.4 ± 0.3 20.0-20.8; 4	21.5 ± 0.6 20.6-22.0; 4
<i>Leipoa ocellata</i>	123.6 ± 6.8 112.7-133.7; 11	22.0 ± 1.5 19.5-24.9; 10	23.0 ± 2.1 21.0-28.9; 11	7.5 ± 0.7 6.5-8.6; 11	6.1 ± 0.8 4.6-7.1; 11	13.8 ± 0.8 12.7-15.1; 11	12.9 ± 0.6 12.1-14.2; 11	14.1 ± 0.5 13.5-15.0; 11
<i>Alectura lathamii</i>	141.4 ± 7.6 130.6-156.3; 12	21.2 ± 2.3 19.1-26.5; 13	24.7 ± 1.2 22.8-26.5; 13	8.0 ± 0.7 6.6-9.3; 12	6.7 ± 0.7 6.1-8.6; 12	15.2 ± 0.7 13.9-16.1; 13	13.5 ± 0.9 11.8-14.9; 13	14.4 ± 0.7 13.3-15.6; 13
TARSOMETATA-TARSUS	Greatest length	Proximal width	Proximal depth	Midshaft width	Midshaft depth	Distal width	Distal depth	
<i>Progura gallinacea</i>	96.7 ± 5.0 86.2-105.7; 12	24.1 ± 2.2 21.8-29.6; 20	20.9 ± 1.5 19.0-23.8; 17	10.0 ± 1.0 8.9-12.6; 18	7.1 ± 1.0 6.1-9.3; 18	25.4 ± 1.8 23.4-29.3; 14	16.4 ± 1.5 15.0-21.6; 20	
- Henschke's Fossil Cave	94.6 ± 4.3 86.2-99.2; 7	23.0 ± 0.9 22.0-25.1; 12	20.3 ± 1.1 19.0-22.6; 11	9.4 ± 0.5 8.9-10.2; 10	6.8 ± 0.7 6.1-8.6; 10	24.5 ± 0.8 23.4-26.4; 10	15.8 ± 0.7 15.0-17.2; 15	
- Buckeridge Cave	100.5 ± 5.1 94.8-105.7; 4	24.9 ± 0.6 24.4-25.6; 3	22.5 ± 0.9 21.5-23.3; 3	10.4 ± 0.8 9.3-11.3; 5	6.9 ± 0.3 6.5-7.2; 5	25.8 ± 2.4 23.6-28.3; 3	18.0 ± 1.1 17.2-18.7; 2	
- Darling Downs (Ravensthorpe)		29.2 ± 0.6 28.7-29.6; 2	24.8 ± 0.9 24.1-25.4; 2	12.0 ± 0.9 11.3-12.6; 2	9.3 ± 0.1 9.2-9.3; 2	29.3 1	21.6 1	
<i>Leipoa ocellata</i>	74.3 ± 4.1 67.9-79.6; 11	15.6 ± 0.6 14.5-16.5; 11	14.5 ± 0.4 13.7-15.3; 11	6.9 ± 0.5 5.9-7.7; 11	4.3 ± 0.4 3.7-4.7; 11	17.3 ± 0.4 16.7-18.2; 11	11.8 ± 0.6 11.0-12.9; 11	
<i>Alectura lathamii</i>	96.1 ± 5.3 89.1-103.9; 12	16.9 ± 0.9 15.3-18.2; 13	14.8 ± 0.7 13.6-16.0; 13	7.2 ± 0.5 6.3-8.0; 13	4.6 ± 0.4 4.0-5.3; 13	17.4 ± 0.9 15.7-18.5; 13	13.6 ± 0.6 12.4-14.7; 13	