

***Pygopus* (Squamata: Pygopodidae) from mid-Holocene cave deposits, Western and South Australia**

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Abstract – We report fossil remains of pygopodid lizards of known or probable Holocene deposits in Webbs Cave in Western Australia and Wombat Cave in South Australia. Knowledge of patterns of skeletal variation within and across pygopodid groups is insufficiently mature to permit species-level resolution. Confident identification of apomorphies to diagnose our specimens is limited by a general paucity of skeletal preparations of pygopodids. Preserved anatomical features on the fossils are interpreted in the context of published literature and putative apomorphies, and permit referral to the genus *Pygopus*. These specimens represent important additional records of *Pygopus*, and contribute to an improved understanding of the evolution of faunal communities in the Holocene of western and southern Australia.

INTRODUCTION

Several cave deposits in Western Australia were excavated since the 1950s for late Quaternary mammalian and archaeological remains, and produced a rich palaeontological record (Lundelius 1960; Dortch 1996, 2004). Marsupials and rodents were the focus of many of these studies, and extinctions and changes in their relative abundances through time are well documented. These changes serve as climatic proxies or to document zoogeographic range variations (Lundelius 1960, 1983; Balme *et al.* 1978; Baynes 1982). Squamate remains from these deposits also are abundant but have yet to be systematically studied in detail. Here we report the occurrence of pygopodid lizard remains recovered from cave deposits at Webbs and Wombat caves (Hampton Tableland).

Pygopods (flap-footed lizards) are a family of gekkonoid lizards endemic to Australia and New Guinea (Shea 1993). Over 38 species are currently recognized within the family, and are classified in seven genera (*Aprasia*, *Delma*, *Lialis*, *Ophidiocephalus*, *Paradelma*, *Pletholax*, and *Pygopus*; Jennings *et al.* 2003; Han *et al.* 2004; Maryan *et al.* 2007). Pygopods occur throughout most of Australia except for Tasmania, extreme southeastern Australia, and the rainforests of the

northeast (Shea 1993). Although today they are widespread throughout most of the continent, their fossil record is extremely sparse, with only one known fossil from the Miocene of Riversleigh, northwestern Queensland (Hutchinson 1997). Estimates of divergence times and mode of evolution and dispersal for the group are based mostly on inference from molecular data sets and tree topologies (e.g. Jennings *et al.* 2003).

Although superficially snake-like in appearance, pygopods retain a pectoral girdle with no external vestiges of front limbs and a pelvic girdle occasionally with hind limb remnants (Greer 1989; Shea 1993). Based on a sequence of molecular data (*12S rRNA* and *c-mos*) Donnellan *et al.* (1999) support the concept that Pygopodidae and Diplodactylidae are sister taxa. Similarly, the most recent taxonomic treatments recognize a monophyletic Pygopodidae as sister taxon to Diplodactylidae (Russell and Bauer 2002) or as sister to the padless Australian carphodactylines (Han *et al.* 2004). However, details of cranial osteology and myology are presently ambiguous in supporting a definitive sister-taxon relationship between pygopods and other groups of gekkonoids (e.g. Kluge 1987; Estes *et al.* 1988; Röhl and Henkel 2002). The historical uncertainty of higher-level

relationships of pygopods contributed to a variable taxonomy for the pygopods and diplodactyline geckos (see differing views in Kluge 1987; Bauer 1990; King and Mengden 1990; Hutchinson 1997).

CAVE DEPOSITS

Webbs Cave

Webbs Cave (6N 132; Western Australia; Figure 1) is situated on the Hampton Tableland south of the Nullarbor Plain at 31°46'S, 127°48'E, approximately 9.5 km north of Mundrabilla homestead. The entrance is an open, shallow sinkhole with abundant skeletal remains under overhangs. Passages go to small chambers with bones and speleothems; these chambers are ultimately terminated by roof collapse (Lundelius 1963; E. L. Lundelius field notes, May 1964; Vertebrate Paleontology Laboratory, Texas Natural Science Center, The University of Texas at Austin). Sixteen species of fossil mammals were recorded from the cave by Baynes (1987).

On top of a large collapse-boulder in the entrance sinkhole are many years of bone and sediment accumulation, and it is here that E. L. Lundelius recovered a *Sarcophilus* (Tasmanian devil) premolar in 1955 and conducted excavations in 1964. Bulk samples of bones and sediments were removed from five depth intervals. These were originally recorded in inches as 0–3, 3–6, 6–9, 9–12, and 12–15 inches below surface but are here treated as their metric equivalents of 0–7.5, 7.5–15.0, 15.0–23.0, 23.0–30.5, 30.5–38.0 cm, respectively. All sieved residue, charcoal, and bones are curated at the Texas Memorial Museum, Vertebrate Paleontology Laboratory, The University of Texas at Austin (TMM).

The principal agents of bone accumulation in the Nullarbor and Hampton Tableland caves were *Tyto alba*, *T. novaehollandiae* (masked owl) and *Falco cenchroides* (Australian kestrel; Baynes 1987). Lizard remains were common throughout the Webbs Cave sedimentary deposit. Two pygopod dentaries were recovered from the 15.0–23.0 cm and 30.5–38.0 cm intervals. Charcoal from the 15.0–23.0 cm interval produced an AMS radiocarbon intercept age of Cal BP 4,160 (Beta-214963), and represents a mid-Holocene record. With an assumption of a constant deposition rate, the skeletal remains in the undated 30.5–38.0 cm interval would be approximately 5,200 years old.

Wombat Cave

Wombat Cave (5N 264) is located approximately 42 km west of Koonalda on the Hampton Tableland in western-most South Australia (Figure 1). This small cavern has a low arched roof and three entrances, each with an associated debris cone. The

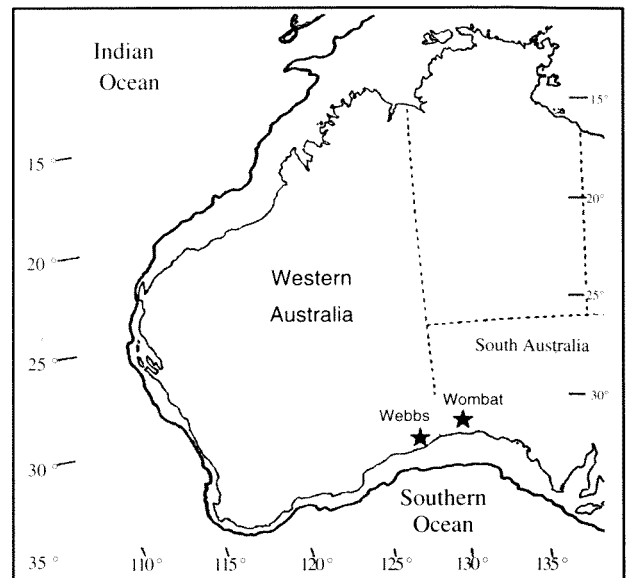


Figure 1 Map of Western Australia and adjacent regions showing the locations of Webbs and Wombat caves from which mid-Holocene *Pygopus* sp. lizard remains were collected. Heavy line represents the coastline position during the full glacial low-stand sea level (adapted from Dortch 1996).

basal edges of the debris cones are buried by reddish-brown silt of unknown age. The reddish-brown silt continues to a depth of about 92 cm (originally determined as 36 inches). *Lasiorhinus latifrons* (southern hairy-nosed wombat) dug extensively into this silt layer. Abruptly below the reddish-brown silt is a brighter red sand and clay unit (that shows no sign of wombat burrowing or bioturbation) containing limestone boulders and skeletal remains (E. L. Lundelius field notes, May 1964). Lizard remains, including one pygopod specimen, were recovered from 92–106 cm below surface, in the lower red sand and clay unit. The pygopod specimen from this lower unit is clearly not modern based on stratigraphic placement. The actual age is not known but is presumed to be from the Holocene, if not late Pleistocene. Clearly more work is needed in this cave. All fossils recovered by E. L. Lundelius in 1964 are curated in TMM.

Pygopod remains

Relatively few publications specifically address the osteology of pygopodid lizards. General aspects of skeletal morphology were discussed by Camp (1923; *Lialis*, *Pygopus*), Stokely (1947; *Aprasia*), Parker (1956; *Aprasia*), Underwood (1957; *Aprasia*, *Delma*, *Lialis*, *Pygopus*) and Moffat (1973; *Aprasia*, *Delma*, *Lialis*, *Pletholax*, *Pygopus*). Pectoral and pelvic girdle morphology were discussed by Fürbringer (1870; *Lialis*, *Pygopus*), Cope (1892; *Pygopus*) and Stephenson (1962; *Aprasia*, *Delma*, *Lialis*, *Pletholax*, *Pygopus*). General features of the

skull were noted by Kinghorn (1926) and Bellairs and Kamal (1981); more extensive coverage of particular taxa was provided by Jensen (1901; *Aprasia*), Kinghorn (1923; *Aprasia*), Broom (1935; *Pygopus*), McDowell and Bogert (1954; *Aprasia*, *Delma*, *Lialis*, *Pygopus*), Stephenson (1962; *Aprasia*, *Delma*, *Lialis*, *Pletholax*, *Pygopus*) and Rieppel (1984b; *Aprasia*, *Pletholax*, *Pygopus*). Detailed description of mandibular morphology was summarized by Hutchinson (1997). Additional published osteological data sets include vertebral morphology (Etheridge 1967; Hoffstetter and Gasc 1969), scleral ring formulae (Underwood 1970; *Aprasia*, *Delma*, *Lialis*, and *Pygopus*), and the detailed information on specific anatomical regions of the skeleton provided by Kluge (1976, 1987), Rieppel (1984a), and Lee (1998) as part of their phylogenetic studies of the group.

Our analysis of the pygopodid fossil remains is based primarily on published descriptions by Hutchinson (1997) and comparisons made with modern skeletal material. Identifications are based on morphological characters observed on modern specimens; an apomorphy-based approach was not possible because sufficiently detailed analyses of isolated skeletal elements of all pygopodids and their outgroups have yet to be conducted, and adequate skeletal collections of Australian gekkotans are lacking. Possible apomorphies are identified, and are combined with characters (the apomorphic status of which is not confirmed) that appear to exclude referral to one or other pygopod taxa. This approach permits referral to genus for all fossils considered here. We made no attempt to identify specimens to the species level.

Webbs Cave

One right dentary (TMM 41209-964; 15.0–23.0 cm interval) and one left dentary (TMM 41209-965; 30.5–38.0 cm interval) were recovered (Figure 2A, B). Both are complete and have the same osteological features. The groove for the Meckelian cartilage is completely enclosed by bone (a universal feature within gekkonoids, but also present in all dibamids and xantusiids, and variably present within gymnophthalmids, scincids, many non-acrodont iguanian groups and some amphisbaenians (Greer 1970; MacLean 1974; Gans 1978; Estes *et al.* 1988; Etheridge and de Queiroz 1988; Bell *et al.* 2003)). The angular process of each dentary is near-complete and positioned well posterior of the coronoid. The intramandibular septum is not extended posteriorly. The fossils do not belong to *Aprasia*, *Ophidiocephalus*, or *Pletholax* because the anterior contact for the splenial is ventral to the four posterior-most tooth positions. Loci for up to 15 teeth are present. The teeth are robust and each has an apical groove (see discussion in Sumida and Murphy 1987 and Hutchinson 1997). The posterior edge of the tooth row is raised dorsally to meet a high coronoid, a character found only in *Pygopus*. Teeth decrease in size and robustness from mesial to distal position. These features (possible apomorphies) on the two dentaries indicate that they belong to *Pygopus*.

Wombat Cave

A posterior fragment of a right dentary (TMM 41374-1 Figure 2C) was recovered from the red sand and clay unit at 92–106 cm below surface. The angular process of the dentary is near-complete and

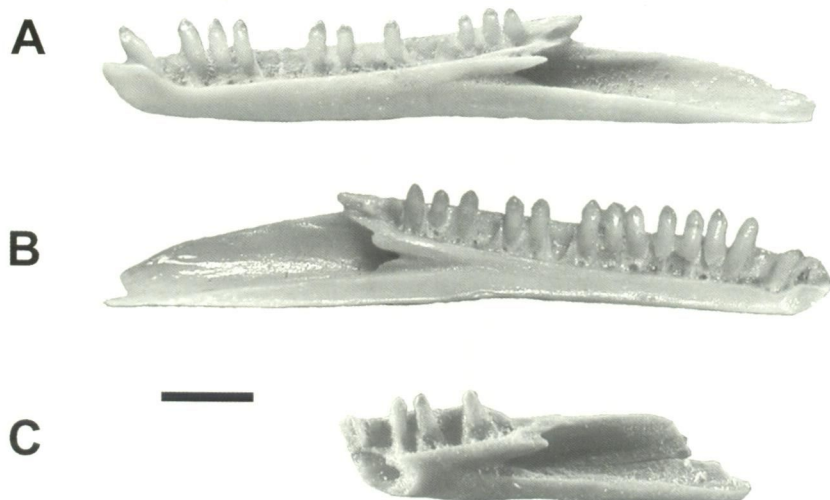


Figure 2 Pygopodid dentaries from mid-Holocene cave deposits. A, *Pygopus* sp., right dentary (TMM 41209-964) from the 15.0–23.0 cm level (Cal BP 4,120) and B, *Pygopus* sp., left dentary (TMM 41209-965) from the 30.5–38.0 cm level in Webbs Cave, WA. C, posterior fragment of a *Pygopus* sp. right dentary (TMM 41374-1) from the red sand and clay unit at 92–106 cm level in Wombat Cave, SA. Scale equals 1 mm.

extends well posterior to the coronoid. The intramandibular septum is not extended posteriorly. The fragment contains tooth loci for seven teeth (excluding referral to *Aprasia*). The splenial is not present but its articulation area is evident and shows that it probably separated the prearticular from the dentary (thus excluding referral to *Aprasia*, *Ophidiocephalus* or *Pletholax*); this feature is found in *Delma*, *Pygopus* and *Paradelma*. The anterior position of the splenial contact on the dentary is ventral to the four posterior-most tooth positions, and thus the specimen cannot represent *Aprasia*, *Ophidiocephalus*, or *Pletholax*, but is consistent with that condition found in *Delma*, *Pygopus* and *Lialis*. Although the posterodorsal area is somewhat damaged on TMM 41374-1, it shows the contact placements for both the labial and lingual projections of the coronoid to be at different elevations in the bone (versus the same elevation found on *Delma* and *Paradelma*). Tooth crowns are simple with blunt-pointed, slightly grooved apices, and are not recurved as found on *Lialis*. This combination of characters suggests that the specimen is a species of *Pygopus*.

DISCUSSION

The pygopods are a distinctive element of the modern lizard fauna in Australia. A phylogenetic analysis of pygopods based on mitochondrial DNA, nuclear DNA, and morphological data led Jennings *et al.* (2003) to support earlier studies that indicated that speciation of mesic-adapted biotas in the southeastern and southwestern corners of the continent occurred largely within those geographic regions between 23 and 12 million years ago as opposed to repeated dispersals between the regions. However, it is not clear whether or not dispersals occurred during cyclic changes from glacial to interglacial regimes of the latest Pliocene and throughout the Pleistocene. Cave sites along the greater Hampton Tableland (such as Webbs and Wombat caves; see others in Baynes 1987) and nearby Nullarbor Plain are positioned to record east-west dispersals (if they occurred) through these climatic cycles. The requirement of a detailed chronology for most of these sites has yet to be attained.

Pygopus was identified from Webbs and Wombat caves on the Hampton Tableland dating to Cal BP 4,160 (and possibly earlier at Wombat Cave). Species of pygopods living in the region today include *Aprasia inaurita*, *Lialis burtonis*, *Pygopus lepidopodus* (likely at the caves today) and *P. nigriceps* (Storr *et al.* 1990; Wilson and Swan 2003). Based on the known living fauna, and the mid-Holocene age of the remains, it is predictable that some species of *Pygopus* would be recovered from deposits within Webbs and Wombat caves.

The distance from the coast mostly determines the amount of rainfall on the Hampton Tableland and Nullarbor Plain, which in turn, controls the distribution of vegetation. The three vegetation zones recognized along the region are a mallee scrub zone located nearest to the coast, arid scrub, and a treeless plain found furthest from the coast (Martin 1973). During the mid-Holocene, vegetation patterns of the Nullarbor were broadly similar to those of today, suggesting that the climate of these times was not substantially different. Prior analysis of the recovered pollen from late Quaternary Madura Cave sediments (located 65 km south and west of Webbs Cave) provides a direct vegetation community reconstruction for the Nullarbor Plain (Martin 1973). We apply the results of that pollen analysis from Madura Cave to Webbs and Wombat caves because of their close proximity and roughly equal distance from the coastline.

Today Webbs and Wombat caves are about 35 km from the coastline. During glacial maximum, the coastline was approximately 160 km south of its present position along the Hampton Tableland and Nullarbor south of these caves. With the rise of sea level after the 18,000–15,000 yr B.P. low-stand, the coastline moved closer to the caves. The period between 9,000 and 4,000 yr B.P. was one of dramatic changes in the vegetation mainly in response to an increase in rainfall, and therefore, an increase in the mallee (eucalypt Myrtaceae) scrub community. After that time, the mallee scrub cover declined in abundance, followed by development of the arid scrub to treeless plain seen in the region today (Martin 1973).

Pygopus was differentiated and established in Australia by the Miocene (Hutchinson 1997); however, we do not know when *Pygopus* moved into the region around Webbs and Wombat caves. Our data document that they were present, if not established, by approximately 4,200 years ago. Both *P. lepidopodus* and *P. nigriceps* live today in the greater Nullarbor and nearby desert areas in mainly low shrubland with sandy soils (Storr *et al.* 1990; Wilson and Swan 2003).

CONCLUSIONS

It is interesting that only three dentaries of pygopods were identified from the thousands of bones recovered from both Webbs and Wombat caves. At the generic level, the mid-Holocene fossils are logical discoveries. The recovery of any pygopod remains is significant because all remains help reconstruct the timing for the development of the community mosaic that occurs today. Based on this scant and preliminary record, it appears that at least *Pygopus* inhabited the communities outside the caves, as they do today, by the middle to late Holocene.

It is apparent from our studies that a precise, isotopic-based chronology for each of the caves that contain fossil vertebrates is a prerequisite to truly understand the establishment of modern squamate community mosaics. Although this as yet has not been systematically implemented, it is beginning to be put into practice (see Prideaux *et al.* 2007a,b). Additional Pleistocene deposits with lizard remains are needed to assess the development of the current biotic communities and how the faunas responded to changing climate regimes and other influential factors. Not all paleontological deposits were screened through mesh sieves small enough (less than 500 μm) to recover isolated bones of small lizards. The use of micro-mesh screens is now a consistent practice at select excavations. The ability to reconstruct the development of the modern lizard communities and the community mosaic changes through time for Western and South Australia largely are dependant on the capability to identify accurately the recovered fossils. Ideally the identifications should be based on apomorphies, but that approach requires an extensive collecting and research program geared towards that goal. An important first step is an adequate comparative collection of articulated and disarticulated skeletons, and an appreciation of ontogenetic, sexual and individual variation within each species. Only with such a collection can palaeontologists begin to discover apomorphies in the anatomical systems (i.e. specific disarticulated skeletal elements) that we typically find preserved in the fossil record. Comprehensive skeletal comparative collections and descriptions now are beginning to be produced at the Western Australian Museum and exist at the South Australian Museum. Cranial osteology increasingly is being described for species of Australian lizards; and therefore, further discoveries are expected as the fossil specimens are compared with the known modern morphologies and described apomorphies.

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