

## A DOLICHOSAURID LIZARD FROM THE LATEST ALBIAN (MID-CRETACEOUS) WINTON FORMATION, QUEENSLAND, AUSTRALIA

JOHN D. SCANLON<sup>\*1,2</sup>, and SCOTT A. HOCKNULL<sup>3</sup>

<sup>1</sup>Riversleigh Fossil Centre, Outback at Isa, 19 Marian St, Mount Isa QLD 4825, Australia, \*Corresponding author riversleigh@outbackatisa.com.au; <sup>2</sup>School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney NSW 2052, Australia; <sup>3</sup>Geosciences, Queensland Museum, 122 Gerler Rd, Hendra QLD 4011, Australia, scott.hocknull@qm.qld.gov.au.

### INTRODUCTION

Most specimens of ‘dolichosaurs,’ Cretaceous aquatic platynotan lizards related to the much larger mosasaurs and also to snakes, come from shallow marine carbonate platforms of the western Tethys, but specimens have also been reported from the interior seaway of North America (e.g., Shimada and Ystesund, 2007) and from Japan (Evans et al., 2006). Here we report the first dolichosaur specimen (a single vertebra) from any non-marine Gondwanan deposits, from a fluvial deposit of the Winton Formation in central Queensland. It is also the oldest (or perhaps second-oldest) known Australian squamate: the only older confirmed lepidosaur record in Australia is Aptian, a poorly preserved but moderately large humerus ‘probably from a terrestrial lizard,’ from the Strzelecki Group in Victoria (Molnar, 1991, 2004). The Winton deposits are dated to latest Albian (ca. 100 Ma) on the basis of pollen zones, somewhat older than most other dolichosaurs (which are mainly Cenomanian–Santonian: for review, see Shimada et al., 2007) but younger than the Japanese fossil *Kaganaias* Evans, Manabe, Noro, Isaji and Yamaguchi, 2006 (Valanginian/Hauterivian: Evans et al., 2006). Another early record of a likely dolichosaur (Barremian of Spain) comes from a lacustrine deposit and was initially identified as a snake (Rage and Richter, 1994; Rage and Werner, 1999). Despite being the oldest known examples of the dolichosaur grade (basal Ophidiomorpha: sensu Palci and Caldwell, 2007), the occurrence of these three forms in freshwater continental deposits is likely to reflect independent incursions from marine habitats in a common ancestor because their localities were almost maximally separated by land routes.

### GEOLOGICAL SETTING

The specimen occurred in the lower part of the Winton Formation within the *Phimopollenites pannosus* Pollen Zone, and is considered to be latest Albian in age (Dettmann and Clifford, 2000; Clifford

and Dettmann, 2005). The fossil comes from a fossiliferous, silty claystone, which is part of a more extensive fluvial sequence containing several laterally discontinuous fossil-rich horizons. The specimen is associated with other fossil remains typically recovered from the Winton Formation. They include plants (McLoughlin et al. 1995), insects (Jell, 2004), molluscs (Hocknull, 1997, 2000; Cook, 2005), lungfish (Kemp, 1997), turtles (Molnar, 1991), crocodylians (Salisbury et al., 2006), ornithopods (Hocknull and Cook, 2008), titanosauriform sauropods (Coombs and Molnar, 1981), and some other archosaurs (e.g., pterosaurs, ankylosaurs, and theropods: Hocknull, unpublished data). The larger vertebrate fossils (e.g., sauropod bones) associated with the dolichosaur vertebra include reworked and transported elements, and as such indicate a mixture of burial ages. The vertebra was found during wet sieving of sediments associated with larger fossils. An ironstone encrustation forms around isolated bones in the deposit and such an encrustation is observed to fill the cotyle of the vertebra, making it highly unlikely that it was part of an articulated sequence when buried.

### SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811

PYTHONOMORPHA Cope, 1869

OPHIDIOMORPHA Palci and Caldwell, 2007

?DOLICHOSAURIDAE Gervais, 1852

cf. *CONIASAURUS* Owen, 1850

(Fig. 1)

**Material**—QMF52673, damaged posterior trunk vertebra, housed in the fossil collection of Queensland Museum, Brisbane, Australia.

**Occurrence**—Lower part of Winton Formation (latest Albian) at Belmont Station, central Queensland (22°5’S, 143°30’E: Queensland Museum Locality 1333).

**Description**—Procoelous vertebra missing left prezygapophysis and dorsal portion of synapophysis, distal portion of right prezygapophysis, right side of zygosphenon, right postzygapophysis and adjacent part of neural arch with zygantral facet, neural spine, condyle, and anteroventral margin including part of cotylar rim. Cotyle and anterior part of neural canal remain filled with matrix, and distal facets of synapophyses worn. Because of asymmetrical damage, only neural spine, anterolateral margin of zygosphenon, anteroventral margin of cotyle and synapophyses, and synapophyseal facets are unrepresented.

Vertebra of varanoid type, non-pachyostotic (sensu de Buffrénil and Rage, 1993), wider than high (excluding missing neural spine) and approximately 1.5 times as long as maximum width across (worn) synapophyses. Well-developed but shallow zygosphenon bearing ventrolateral facets separate from and approximately anti-parallel (i.e. facing, not divergent) to those of prezygapophysis. Zygosphenon wider than neural canal but slightly narrower than cotyle; part of anterior border preserved on left side indicating strong median notch. Neural canal arched at anterior and posterior ends, with acute ventrolateral angles bordering cotyle and condyle, respectively; canal oval at midlength, higher than wide. Prezygapophyseal and postzygapophyseal facets oval, with major axis approximately 30° from sagittal plane, and angled greater than 30° above horizontal in anterior and posterior views. Zygapophyseal facets define planes intersecting midline just below base of neural canal; zygosphenal facets define planes intersecting just below centre of canal. Interzygapophyseal ridge weakly developed (with no distinct epidiapophyseal ridge) and blunt, pierced by two relatively large lateral foramina on each side; several small foramina on each side also located in weakly defined depression between postzygapophysis and condylar neck, and several dorsolateral foramina near middle of broadly concave surface of neural arch on each side. Single pair of subcentral foramina in slight paramedian depressions on centrum; otherwise, smoothly rounded ventrally so that subcentral ridges and haemal keel are faintly defined. Numerous additional pits on ventral surface are asymmetrically distributed and probably resulted from abrasion of surface exposing underlying cancellous bone. Paracotylar, zygantral, and parazygantral foramina are absent, but pair of large parazygosphenal foramina is present at posteromedial margins of prezygapophyseal facets. Posterior part of neural arch upswep, suggesting presence of well-developed neural spine which has broken away for full length of neural arch, exposing cancellous bone within thick lamellar cortex. Regions of breakage

around left prezygapophysis and condyle show similar cancellous bone but cortex is thinner and not so obviously lamellar. Transverse processes are weakly developed and synapophyses do not appear to have projected laterally beyond prezygapophyses. Synapophyses are only partly preserved on each side, and rock matrix partially fills exposed cavities (unlike other areas of breakage which presumably occurred during sieving); they are higher than long, facing laterally and slightly ventrally, their centers located below posterior half of prezygapophyseal facets and extending ventrally as far as cotylar rim. There is little or no precondylar constriction; cotyle and broken base of condyle are wider than high, and cotyle is strongly oblique, facing more ventrally than anteriorly.

## DISCUSSION

Despite incomplete preservation of the single recovered vertebra, it exhibits a number of morphological features (including both apomorphic and plesiomorphic character states) indicative of its phylogenetic affinity. Rather than listing these exhaustively and conducting a phylogenetic analysis, we note that the vertebra is most similar in all respects to those of known ‘dolichosaurs’ (basal Ophidiomorpha) and further below, add remarks on features that may vary informatively among these taxa.

Some of these forms are represented by one or two isolated vertebrae like the present specimen, the others by articulated (partial to complete) skeletons preserved in a manner preventing complete examination of any single vertebra, and consequently none has yet been really adequately described. The taxa of interest for comparison include: *Adriosaurus* Seeley, 1881 (Lee and Caldwell, 2000; Palci and Caldwell, 2007), *Aphanizocnemus* Dal Sasso and Pinna, 1997 (Dal Sasso and Pinna, 1997), *Carentonasaurus* Rage and Néraudeau, 2004 (Rage and Néraudeau, 2004), *Coniasaurus* Owen, 1850 (Bell et al., 1982; Caldwell, 1999; Caldwell and Cooper, 1999; Liggett et al., 2005; Shimada and Bell, 2006; Shimada et al., 2006; Shimada and Ystesund, 2007), *Dolichosaurus* Owen, 1850 (Caldwell, 2000), *Kaganaias* (Evans et al., 2006), *Mesoleptos* Cornaglia and Chiozza, 1852 (Gorjanovic-Kramberger, 1892; Lee and Scanlon, 2002), and *Pontosaurus* Gorjanovic-Kramberger, 1892 (Kornhuber, 1873; Pierce and Caldwell, 2004; Caldwell, 2006) as well as unnamed forms discussed by Rage and Richter (1994), Albino (2000), and Averianov (2001).

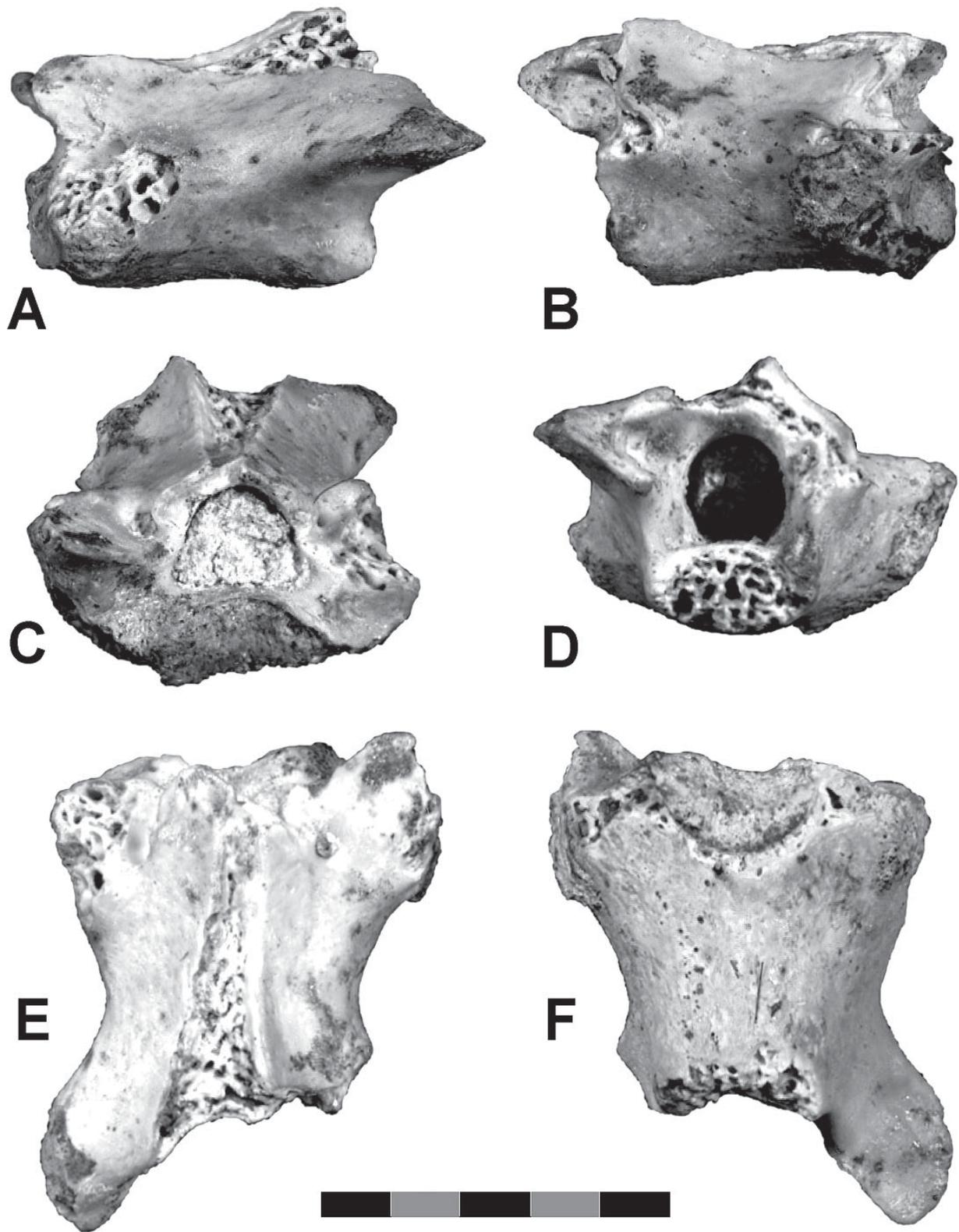


Figure 1. QMF52673, trunk vertebra of cf. *Coniasaurus* sp. from late Albian Winton Formation in western Queensland. A, left lateral view; B, right lateral view; C, anterior view; D, posterior view; E, dorsal view; F, ventral view. Scale equals 5 mm.

Most of these are from marine deposits, but contrary to Evans et al. (2006), a likely member of this assemblage was known from non-marine sedimentary rock prior to the discovery of *Kaganaias*. Rage and Werner (1999) note that “The hitherto earliest presumed snake (an unnamed form) was reported from the Early Cretaceous (Barremian) of Spain (Rage and Richter, 1994), but new data on mid-Cretaceous varanoid squamates cast doubt on the referral of this fossil to snakes.” The new data prompting this reassessment are not specified, but presumably the reference was to *Coniasaurus* vertebrae described around the same time (Caldwell and Cooper, 1999:444, make some comparisons, noting the notched zygosphenes of the Barremian specimens as a dolichosaur-like feature). The Uña coal deposit producing Rage and Richter’s (1994) specimens represents a lacustrine environment and the fauna includes both freshwater and terrestrial, but not marine elements.

Another possibly non-marine form described as a snake may also be a non-ophidian ophidiomorph. Albino (2000:250-251, fig. 3) reports an isolated vertebra from the Campanian-Maastrichtian La Colonia Formation in Patagonia and describes it as ‘*Serpentes incertae sedis*.’ However, it differs greatly from any known snake but rather resembles the specimen described here in almost all aspects. The only character in which the Patagonian specimen is more snake-like is the lack of a deep median anterior notch in the zygosphenes. If this specimen is regarded as a ‘dolichosaur’ rather than a snake, it represents the only post-Cenomanian record of this grade. The deposit was suggested to have formed in an estuary, tidal flat or coastal plain, and the fauna is predominantly terrestrial or fluvial, although at least some marine forms are present (Albino, 2000).

In the combination of relatively narrow and tapering centrum, only moderately prominent synapophyses, and (less certainly) the lack of pachyostosis, QMF52673 most closely resembles vertebrae assigned to *Coniasaurus* (figured by Caldwell, 1999; Caldwell and Cooper, 1999; Liggett et al., 2005; Shimada and Bell, 2006; Shimada et al., 2006; Shimada and Ystesund, 2007). Certain apomorphic conditions, such as lateral pockets as in *Kaganaias*, prominent epidiapophyseal ridges as in *Adriosaurus*, *Carentonosaurus* and some other dolichosaurs, and more snake-like zygosphenes as in the Patagonian form, are absent. Thus, there is no evidence for particular affinity with these derived taxa. Among similar known fossils, the most distinctive character is the presence of parazygosphenal foramina (also present in *Carentonosaurus* and a few snakes

including the early Cenomanian *Pouitella* Rage, 1988); however, the local polarity and informativeness of this feature are uncertain because, due to their state of preservation, such foramina could potentially have been overlooked in some other dolichosaurs.

The simplest model to explain the occurrence of dolichosaurs in widely distant freshwater deposits by the mid-Cretaceous is analogous to the process hypothesized for the Neogene genus *Crocodylus* (Brochu, 2003). Early pythonomorph diversity is highest in the western Tethys (southern Europe and the Levant) and this is the likely area of origin of ophidiomorphs, including dolichosaurs. Cosmopolitan invertebrate faunas from the mid-Cretaceous of Northern Australia and New Zealand share affinities to European faunas, suggesting an unrestricted oceanic circulation in the Tethys; these conditions were not available during the Aptian-Albian (Stilwell and Henderson, 2002). We suggest that marine *Coniasaurus*-like forms expanded their range and entered rivers and estuaries along the northern and southern coasts of Tethys, ultimately establishing multiple distinct populations in freshwater rivers and lakes as far apart as Japan and Australia.

The Australian dolichosaur represents the highest latitudinal occurrence for any platynotan squamate during the mid-Cretaceous (between 50°S and 60°S) (Jacobs et al., 2005). Cold sea-surface temperatures (SSTs) dominated the Aptian and early Albian of Australia; however, SSTs warmed toward the end of the Albian and reached optimum temperatures by the end of the Turonian (Clarke and Jenkyns, 1999). We suggest that the combination of warming SSTs and an unrestricted oceanic circulation provided optimal conditions for dolichosaur dispersal to Australia. Conversely, cold SSTs and insular oceanic conditions restricted dolichosaurs from entering into Australia during the Aptian-Albian.

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