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The first evidence of ankylosaurian thyreophorans from the Winton Formation (late Albian–Cenomanian) of central-western Queensland, Australia, reveals new information about the temporal and palaeobiogeographical range of these dinosaurs within Gondwana. The material, which comprises isolated teeth, is the youngest evidence of ankylosaurs in Australia. Although the Winton teeth exhibit a suite of pleisiomorphic characteristics that are also seen in other Australian and Gondwanan ankylosaur taxa, they are morphologically distinct and very likely represent a new taxon. Their discovery adds to the growing body of evidence indicating that thyreophorans, and in particular ankylosaurians, constitute a diverse and important component of Australia's mid-Cretaceous dinosaur fauna.

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WITH the exception of Africa, the remains of ankylosaurian dinosaurs are known from all the landmasses that were once part of Gondwana: South America (Coria 1994, Salgado & Coria 1996, Coria & Salgado 2001), Antarctica (Gasparini *et al*. 1996, Salgado & Gasparini 2006), India (Nath *et al*. 2002), New Zealand (Molnar & Wiffen 1994) and Australia (Molnar 1980, 1996, Dettmann *et al*. 1992, Barrett *et al*. 2010). Of these landmasses, Australia currently has the best preserved and most abundant material. *Minmi*, the only named Australian ankylosaur genus, is represented by seven specimens: QM F10329, *Minmi paravertebra* (an articulated series of thoracic vertebrae and associated dermal ossifications and a partial manus), QM F18101, *Minmi* sp. (a nearly complete articulated skeleton), QM F33286 (a partial thoracic region and articulated pelvis with associated dermal ossifications), AM F35259 (a partial series of ribs with ossicles), AM F119849 (assorted vertebrae, ribs and dermal ossifications), QM F33565 (a partial femur) and QM F33566 (a distal tibia). All these specimens come from the Early Cretaceous (Barremian–Albian; Gray *et al*. 2002) of Queensland (Fig. 1; Molnar 1980, 1996, Leahey *et al*. 2008, 2010). QM F18101, the skeleton referred to as *Minmi* sp., from the late Albian Allaru Mudstone of Marathon Station, near Richmond, central-western Queensland, currently represents the best-preserved Australian dinosaur, and is Gondwana's most complete ankylosaurian (Molnar 1980, 1996, Molnar & Clifford 2000, Leahey *et al*. 2008, 2010).

Dettmann *et al*. (1992), Weishampel *et al*. (2004) and more recently Barrett *et al*. (2010) have also reported the occurrence of indeterminate ankylosaurid material from the Early Cretaceous of southern Victoria, in the informally defined 'Wonthaggi formation' of the Strezlecki Group (Fig. 1; late Hauterivian–Albian: Wagstaff & McEwan Mason 1989, Tosolini *et al*. 1999) and the Eumeralla Formation of the Otway Group (Fig. 1; mid-late Aptian to early-middle Albian: Wagstaff & McEwan Mason 1989, Partridge 2006).

Here we provide a detailed account of isolated ankylosaurian teeth collected during screen-washing operations at the 'Elliot site', approximately 70 km northwest of Winton (Fig. 1). This material has been briefly mentioned (Salisbury 2006), but has never been described or discussed in any detail. This material represents the youngest occurrence of ankylosaurians in Australia, and indicates that the group persisted on the continent into at least the late Albian–Cenomanian.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, New York, USA; BYU, Earth Science Museum, Brigham Young University, Provo, Utah, USA; CEUM, College of Eastern Utah Prehistoric Museum, Price, Utah, USA; IMM, Inner Mongolian Museum, China; INBR, Victor Valley

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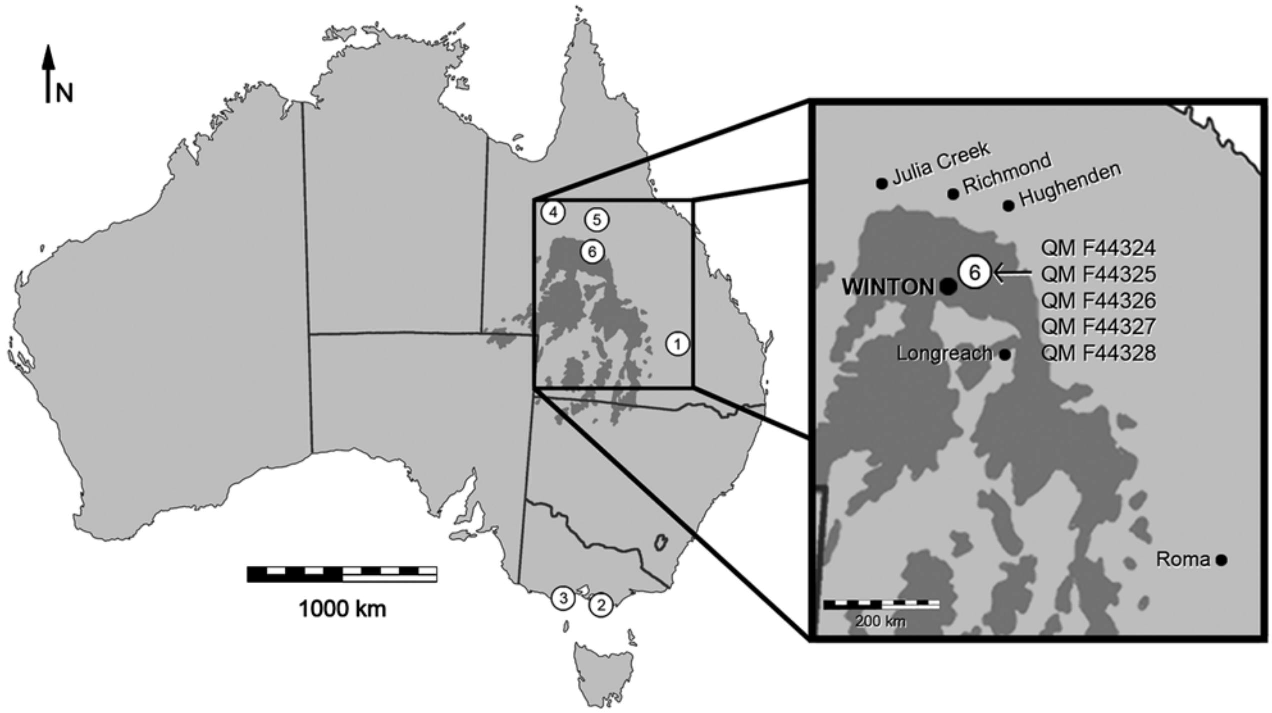

Fig 1. Map showing the geographic position of fossil localities in Australia that have produced material assignable to ankylosaurian dinosaurs. 1, Bungil Formation (Aptian), *Minmi paravertebra* (QM F10329); 2, 'Wonthaggi formation' (late Hauterivian–Albian), Ankylosauria indet. (for specimen numbers see Barrett *et al*. (2010); 3, Eumeralla Formation (mid-late Aptian to early-middle Albian), NMV P216739; 4, Toolebuc Formation (Albian), QM F33286; 5, Allaru Mudstone (late Albian), *Minmi* sp. (QM F18101), QM F33565, QM F33566, AM F35259 and AM F119849; 6, Winton Formation [latest Albian–Cenomanian] (dark grey), Ankylosauria indet. (QM F44324, QM F44325 and QM F44326). Shaded area represents exposures of the Winton Formation.

Museum, California, USA; KUVP, Museum of Natural History, University of Kansas, USA; NHMUK, Natural History Museum, London, UK (formerly BMNH, British Museum of Natural History); CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada (formerly the National Museum of Canada); PIN, Paleontological Institute, Moscow, Russia; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; OU, Ohio University, Colombus, Ohio, USA; QM, Queensland Museum, Brisbane, Australia (QM F, fossil; QM L, location); SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA.

Geological setting

The Winton Formation is the uppermost unit of the Manuka Subgroup within the Rolling Downs Group, and the youngest Cretaceous unit of the Eromanga Basin (Gray *et al*. 2002). Exposures extend over a vast geographic area, centred over western Queensland, but extending into the southeastern corner of the Northern Territory, the northeastern corner of South Australia and the northwestern corner of New South Wales (Fig. 1). The Winton Formation is currently regarded as being mid-Cretaceous (late Albian–Cenomanian) in age based on palynology, corresponding to the upper *Phimopollenites pannosus* and *Hoegisporis uniforma* (formerly the *Appendicisporites distocarinatus* Zone) spore-pollen zones (Helby *et al*. 1987, Dettmann *et al*. 1992, Partridge 2006), but McLoughlin *et al*. (2010) have noted that plant remains and palynological data have yet to obtain a definitive age determination of the upper part of the formation. The sediments comprising it include complex repetitive sequences of fine- to medium-grained feldspatholithic or lithofeldspathic arenite, siltstones, mudstones and claystones, with minor inclusions of thinly bedded mudclast conglomerates, and rare limestones, interpreted to have been deposited in alluvial to coastal plain deposits (Senior *et al*. 1978, Day *et al*. 1983, Dettmann *et al*. 1992, Gray *et al*. 2002, Romilio *et al*. 2013).

The Winton Formation is probably best known for the occurrence of dinosaur tracks at Lark Quarry Conservation Park, southwest of Winton (Thulborn & Wade 1984, Romilio & Salisbury 2011, Romilio *et al*. 2013). Prior to the start of the 21st century, the vertebrate body fossil record from the formation was limited to isolated remains of ceratodont lungfishes (Dettmann *et al*. 1992, Kemp 1997), a turtle (Molnar 1991), a possible neosuchian crocodyliform (Molnar & Willis 1996) and fragmentary sauropod material (Coombs & Molnar 1981, Molnar 2001, 2010, 2011, Molnar & Salisbury 2005). Recently, however, the Winton Formation has yielded a plethora of vertebrate fossils. New discoveries include, but are not limited to teleost fishes (Faggotter *et al*. 2007, Berrell *et al*. 2008), more complete sauropod remains (Salisbury *et al*. 2006b, Hocknull *et al*. 2009), a non-avian theropod dinosaur (Benson *et al*. 2009, Hocknull *et al*. 2009, Agnolin *et al*. 2010, White *et al*. 2012) and a basal eusuchian crocodyliform (Salisbury *et al*. 2006a). The Winton Formation has also yielded a wealth of plant macrofossils dominated by conifers and angiosperms, with rarer bennettitaleans, cycadophytes, ferns, ginkgoaleans and pentoxylaleans (Dettmann et al. 1992, 2009, McLoughlin et al. 1995, 2010, Pole 1998, 2000a, b, Pole & Douglas 1999, Dettmann & Clifford 2000, Clifford & Dettmann 2005). Non-marine invertebrates have also been described (Hocknull, 1997, 2000, Jell 2004, Cook 2005).

The ankylosaurian specimens described herein were collected during the 'Elliot Expeditions' between 2001 and 2004 as part of the 'Winton Dinosaur Project', and come from the 'Elliot/Mary sector' of the 'Elliot site' (QM L1333) on Belmont Station, approximately 70 km northeast of Winton, central western Queensland (Fig. 1). This locality has produced a wide range of vertebrate macro- and micro-fossils, including multiple partial skeletons of undescribed titanosauriform sauropods (Salisbury *et al*. 2006b), isolated teeth of non-avian theropod dinosaurs (Salisbury *et al*. 2011), an isolated vertebra of a dolicosaurid squamate (Scanlon & Hocknull 2008), teeth and postcranial remains of a likely non-mammalian cynodont (Musser *et al*. 2009), crocodilians, turtles, fishes and a possible plesiosaur (Salisbury 2006).

The fossils at QM L1333 derive from a thin, laterally continuous bed of fluvial siltstone, interpreted to be part of either a point bar deposit or an abandoned channel fill deposit associated with an ox-bow lake (Salisbury 2006). All were found within screen-washed sediments from the area immediately surrounding the bones of at least two titanosauriform sauropods (Molnar & Salisbury 2005, Salisbury 2006, Salisbury *et al*. 2006b). The degree of post-mortem wear displayed by many of the non-sauropod fossils (including the ankylosaurian teeth described here) suggests that they have been either reworked from older sediments or transported by flowing water to the site from upstream (Salisbury 2006, Scanlon & Hocknull 2008). QM L1333 is within 10 km of an exposed conformable contact with the underlying Mackunda Formation, a clastic sequence containing marine fossils, which acculumated in marine shelf and coastal environments (Senior *et al*. 1978). Clifford and Dettmann (2005) found that the subsurface sections of the Winton Formation at nearby localities were within the *Phimopollenites pannosus* spore-pollen zone, and on this basis proposed that the fossil-bearing sites in surface outcrops, such as QM L1333, were of a maximum latest Albian age (Helby *et al*. 1987, Burger 1990, 1993, Dettmann & Clifford 2000). Although it is conceivable that the vertebrate microfossils recovered from QM L1333 were reworked from older sediments in the Mackunda Formation, as yet there is no record of thyreophorans in this unit, and its shallow marine depositional origin makes the occurrence of these terrestrial dinosaurs within it unlikely (although we note that sauropod remains have been recovered from the Mackunda Formation; see Coombs & Molnar 1981, Molnar & Salisbury 2005). We, therefore, assume that the teeth described herein derive from the Winton Formation and that their age can be constrained to the late Albian–Cenomanian.

Material and methods

Material

Three isolated teeth: one from the left dentary (QM F44324), one from the right dentary (QM F44326) and one from the right maxilla (QM F44325). All specimens are accessioned to the Queensland Museum (QM), Brisbane Australia.

Methods

This study uses the standardized terminology of Smith & Dodson (2003) for anatomical and orientation descriptions of the fossilized teeth, together with standard terms used in the description of ankylosaurian teeth (Coombs 1990, Coombs & Maryańska 1990, Vickaryous *et al*. 2004).

This study involved the examination of thyreophoran teeth, particularly those from the continents that were once part of Gondwana. All comparisons were firsthand observations (see below), or where this was not possible, illustrations and descriptions provided in the literature. Due to the fragmentary and isolated nature of the Winton material, only the maximum mesiodistal length and labiolingual width of the teeth were measured.

Comparative material examined. Material examined firsthand included: *Ankylosaurus magniventris* (AMNH 5895); *Edmontonia rugosidens* (AMNH 5381; AMNH 5665); *Edmontonia longiceps* (AMNH 3076; CMN 8531, cast; viewed at NHMUK); *Gastonia burgei* (CEUM 1307 and BYU 14611, cast; viewed at OU); *Minmi* sp. (QM F18101); *Minotaurasaurus ramachandrami* (INBR 21004, cast; viewed at OU); *Pinacosaurus mephistocephalus* (IMM 96BM3/1, cast: viewed at OU); *Sauropelta edwardsi* (AMNH 3016); *Scelidosaurus harrisonii* (NHMUK R1111, viewed at NHMUK); *Silvisaurus condrayi* (KUVP 10296, cast; viewed at the NHMUK); *Tarchia gigantea* (PIN 3142/250, cast; viewed at OU).

Description

Preservation

The three teeth (QM F44324, QM F44325 and QM F44326; Fig. 2) are heavily abraded and generally very smooth. All of them have worn crown apices and lack the root apex. The enamel covers all the teeth symmetrically. All the teeth display wear facets (discussed below).

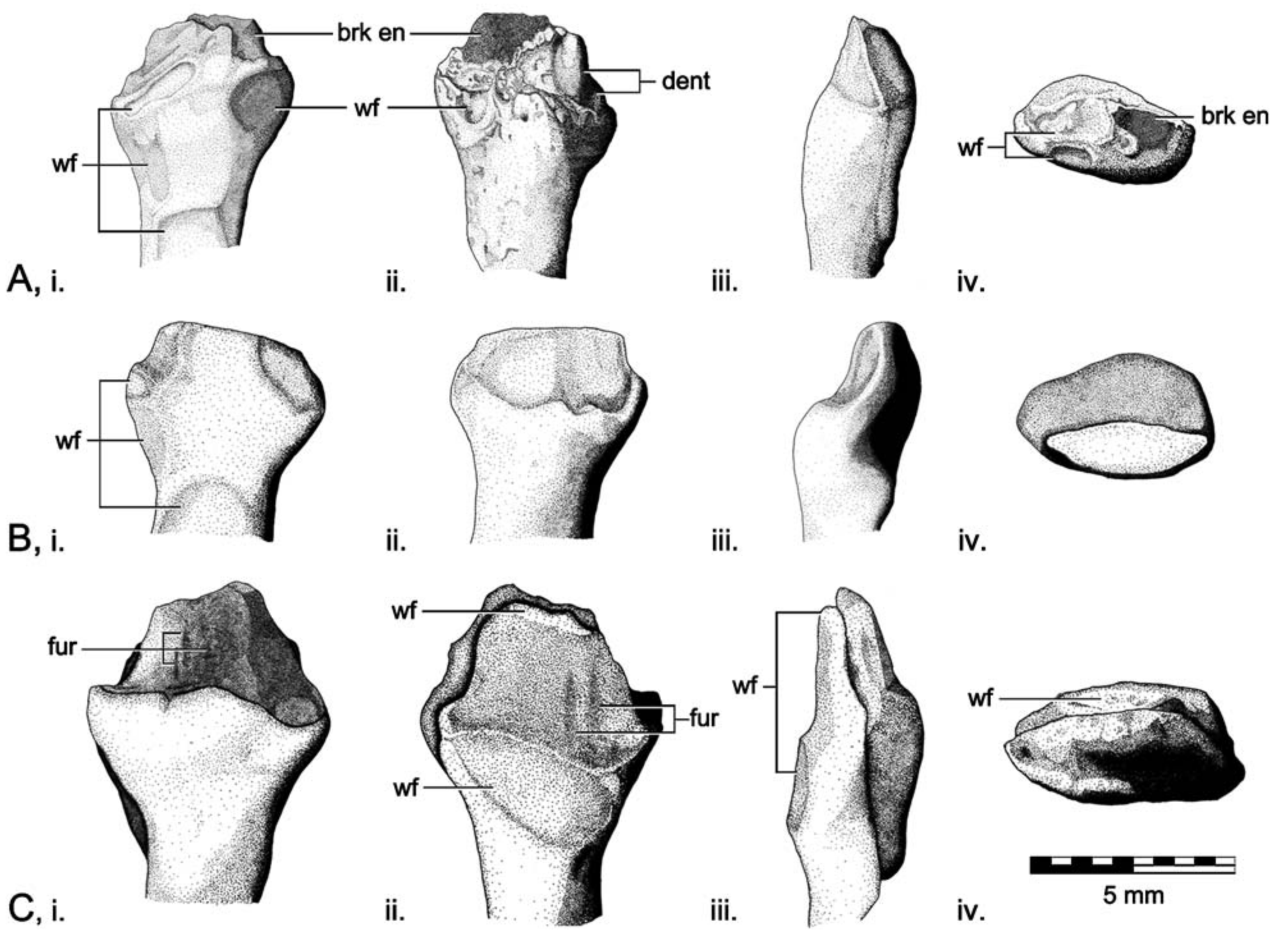

Fig 2. Ankylosauria indet. teeth from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Winton, central-western Queensland. **A**, QM F44324; **B**, QM F44326; **C**, QM F44325; i, labial aspect; ii, lingual aspect; iii, side aspect; iv, apical aspect. Abbreviations: brk en, broken enamel; dent, denticle; fur, furrow; wf, wear facet.

On the crown surface of QM F44324, a proportion of the enamel layer is missing. The right side of the crown on the labial surface is also missing approximately one-quarter of the enamel layer, whereas one-third is absent from the left side on the lingual surface. Two denticles are present on this tooth on the right side, visible in lingual aspect (Fig. 2A).

QM F44326 is the most worn of the three teeth (Fig. 2B). No denticles are preserved on either QM F44325 or QM F44326. However, there are shallow grooves on the crown surfaces of QM F44325. These are interpreted to be the worn remnants of the furrows associated with denticles. QM F44325 is broken along its mesiodistal plane. The crown has broken surfaces along the marginal side in both lingual and labial aspects (Fig. 2C).

Osteology

All the teeth have crowns that are asymmetrical, labiolingually compressed and phylliform. They also possess a distinct neck, which separates the crown from a cylindrical root. The cingulum is bulbous, forming a distinct shelf on the lingual surface, but less prominent and more apically situated on the labial surface.

QM F44324 (Fig. 2A) is the smallest of the Winton teeth, with a mesiodistal length of 4.58 mm and a labiolingual width of 2.73 mm. In mesial and distal aspect, the preserved portion of the crown is concave on the lingual surface, but convex on the labial surface. In lingual aspect, the crown is offset to the left, thereby indicating that the 'left' is the distal side of the tooth in lingual aspect (Coombs 1990). Two denticles are present on the mesial side of the crown in lingual aspect. The lingual cingulum is bulbous and twice as mesiodistally wide as it is labiolingually deep. In lingual aspect, the apical outline of the cingulum curves apically at the medial edges. The angle of this curve is greater on the distal side. In addition, shallow grooves occur at the centre of the cingulum. In labial aspect, the cingulum is angled apically on the distal side. The root of the tooth is sub-cylindrical in cross-section, except for the last 2 mm of the body on the labial surface, which forms a flat, quadrilateral-shaped area that is angled towards the core.

QM F44326 (Fig. 2B) is slightly larger than QM F44324 but smaller than QM F44325. The mesiodistal length is 4.92 mm and the labiolingual width is 2.79

mm. The crown is offset to the left in lingual aspect, indicating that the 'left' is the distal side of the tooth in lingual aspect (Coombs 1990). Its crown is concave on the lingual surface but convex on the labial surface. No denticles are preserved. The lingual cingulum is mesiodistally broad and bulbous, and protrudes prominently. The labial cingulum is considerably less pronounced, being only slightly raised from the surface of the tooth. The lingual cingulum arches apically at the mesial and distal margins of the tooth. It arches again at the central axis but is only one-third the height of the mesial and distal margins. The labial cingulum arches extensively towards the apex at the central axis to form a central eminence. The mesial side of the labial cingulum is more highly positioned than the distal side. Similar to QM F44324, the labial surface reflects inwards at the base of the root. Unlike QM F44324, however, the latter surface is oval-shaped.

QM F44325 (Fig. 2C) is the largest of the three teeth. The mesiodistal length is 6.06 mm and the labiolingual width is 3.10 mm. The preserved portion of the crown is as high as it is wide but only half as deep. The crown is offset to the left in lingual aspect; thus the left side of the tooth is the distal side in lingual aspect (Coombs 1990). The crown is slightly convex on the labial surface but relatively flat on the lingual surface. There are no denticles preserved, but shallow grooves are present on the crown on both the labial and lingual surfaces. These are interpreted as the worn remnants of the furrows associated with denticles. A large wear facet is present on its surface, so we are unsure of its original depth. The cingulum of the labial surface arches apically at the central axis of the tooth and at the most distal and mesial margins. However, the mesial arch is set more apically and is of a lesser angle than that of the distal side. The apical outline of the lingual cingulum plunges basally in the mesial two-thirds, with the lowest point at the mesial third of the cingulum's width.

Wear Faceting

All the teeth exhibit wear facets. On QM F44324, irregularly shaped wear facets are present on the apical surface of the crown (Fig. 2A, iv). An oval wear facet (0.95 × 0.9 mm) is present on the distal side of the labial cingulum, and two circular wear facets occur on the mesial side of the root in labial aspect. The flat, quadrilateral surface on the labial side at the base of the root may signify a wear facet (Fig. 2A, i). The lingual surface displays irregularly shaped wear facets on the distal side of the cingulum (Fig. 2A, ii).

QM F44326 has circular wear facets on the left side of the crown and the body, just basal to the crown, in labial aspect. The flat, oval surface on the labial side of the root is also interpreted as a wear facet (Fig. 2B, i).

QM F44325 has a wear facet on the apical surface of the crown that is at an oblique angle (Fig. 2C, iv). A large oblong wear facet is also present on the surface of the lingual cingulum (Fig. 2C, ii).

Comparisons

All three teeth possess a classically thyreophoran tooth form of a labiolingually compressed but mesiodistally expanded crown, a prominent cingulum and a peg-like root. Similarly shaped teeth are seen in basal thyreophorans such as *Scutellosaurus*, *Scelidosaurus* and *Emausaurus* (Barrett 2001, Norman *et al*. 2004). In these taxa, however, the labial surface has a triangular-shaped outline and the cingula are less prominent than on any of the Winton teeth (see Coombs *et al*. 1990, Barrett 2001, Norman *et al*. 2004). The Winton teeth do display similar wear faceting to *Scelidosaurus* (Barrett 2001).

Stegosaurian teeth differ from the Winton teeth, in that the former exhibit very little to no offset between the labial and lingual cingula (Gilmore 1914, Galton & Coombs 1981, Galton 1988). Similar to some stegosaurian teeth, however, the Winton teeth exhibit wear facets on the apex of the crown (Barrett 2001).

The Winton teeth compare most favourably to the teeth of ankylosaurians in their possession of an asymmetrical, phylliform, labiolingually compressed but mesiodistally expanded crown, a bulbous lingual cingulum, a cylindrical root and a well-developed neck that separates the root from the crown. Within Ankylosauria, ankylosaurids and nodosaurids each have characteristic tooth morphologies. QM F44325 and QM F44326 exhibit nodosaurid-like characteristics such as greater labiolingual compression and more prominent cingula. This contrasts with the less prominent cingula in QM F44324, which is more reminiscent of the condition in ankylosaurids (Coombs 1990, Coombs & Maryańska 1990, Baszio 1997, Vickaryous *et al*. 2004). Overall, the three new teeth from the Winton Formation share characteristics of both Ankylosauridae and Nodosauridae.

Comparisons with other Australian ankylosaurian teeth

There are two occurrences of ankylosaurian teeth in Australia: those preserved in the mouth of *Minmi* sp. (QM F18101; Molnar 1996) from Queensland and isolated teeth from the late Hauterivian–Albian (Wagstaff & McEwan Mason 1989, Tosolini *et al*. 1999) 'Wonthaggi formation' of the Strzelecki Group at Flat Rocks, southern Victoria, referred to Ankylosauria indet. (Dettmann *et al*. 1992, Barrett *et al*. 2010). The Winton teeth are much more worn than either those of *Minmi* or the Strzelecki specimens. Consequently, it is not possible to compare the usual finer characters of ankylosaurian teeth such as the shape of, or number of, denticles (Coombs & Maryańska 1990). The Winton teeth are approximately the same size as the other Australian material, mesiodistally within 1 mm of each other, yet they are proportionally more robust and the offset between the labial and lingual cingula is greater. They also display greater curvature along the apical outline of the cingula, particularly QM F44325. All three teeth also have a less constricted neck than both the teeth of *Minmi* and Ankylosauria indet. from the Strzelecki. Unlike the Winton teeth, the latter teeth exhibit denticulated cingula. It is unclear whether this absence of denticles on the cingula of the Winton teeth is an effect of post-mortem abrasion. Overall, the Winton teeth are unlike any ankylosaurian teeth found previously in Australia and are, therefore, likely to represent a new taxon.

Comparisons with ankylosaurian teeth from other parts of Gondwana

Ankylosaurian teeth are known from all Gondwanan continents except Africa and New Zealand (Dettmann *et al*. 1992, Gasparini *et al*. 1996, Molnar 1996, Coria & Salgado 2001, Nath *et al*. 2002, Salgado & Gasparini 2006, Barrett *et al*. 2010). India, Antarctica and South America have only one occurrence each in which teeth are preserved. The latter two have both been described as Nodosauridae indet. (Coria & Salgado 2001, Salgado & Gasparini 2006). The Indian material has yet to be fully described (Nath *et al*. 2002).

The Winton teeth differ from the described South American, Antarctic and the other known Australian teeth in that they have a less constricted neck. However, the teeth from South America and Antarctica are similar to those from Winton in being more robust and having more bulbous cingula compared with teeth from other Gondwanan ankylosaurian taxa. The Antarctic material is significantly larger than any of those from the other Gondwanan continents, including the Winton teeth (see Salgado & Gasparini 2006). The Winton teeth and the single South American tooth are similarly sized and both show extensive wear on their apical surfaces.

Overall, the Winton teeth share similarities with the other teeth found within Gondwana but are not an exact match for any of them.

Taxonomic conclusions

The Winton teeth possess characteristics of ankylosaurian dinosaurs: an asymmetrical, phylliform, labiolingually compressed but mesiodistally expanded crown; a bulbous lingual cingulum; a cylindrical root; and a well-developed neck that separates the root from the crown (Coombs 1978, 1990, Coombs & Maryańska 1990, Baszio 1997, Vickaryous *et al*. 2004). On this basis, we assign them to Ankylosauria (indet.). However, it must be noted that the Winton teeth are morphologically distinct from other Australian and Gondwanan specimens, and very likely represent a new taxon or taxa.

Discussion

The association of the teeth, to a single taxon, let alone the same animal can not be proven. Variation in the morphology and wear of ankylosaurian teeth within an individual animal is not uncommon (Coombs 1990, Coombs & Maryańska 1990, Barrett 2001). Despite the Winton teeth displaying slightly different morphologies to one another, they were nevertheless discovered close together (QM L1333), so their alliance can not be completely ruled out.

Wear facets

The Winton teeth have worn crown apices, discernible wear facets on the cingula and some evidence of wear facets on the root. Similar wear on the crown and cingula occurs in other ankylosaurians, stegosaurians and the basal thyreophoran *Scelidosaurus* (Barrett 2001).

In a study investigating the tooth wear and feeding mechanisms of *Scelidosaurus harrisonii* and other thyreophorans, Barrett (2001) found that in both *Scelidosaurus* and ankylosaurians the lingual surface of maxillary teeth occlude against the labial surface of the dentary teeth. These animals would thus have had a slight overbite. Consequently, maxillary teeth predominantly exhibit wear facets on the lingual, more prominent and basally positioned, cingulum, whereas the dentary teeth have worn labial cingula.

The wear facets on the crown apices, especially the bevelled apical surface of QM F44326, indicate the teeth underwent abrasional wear (tooth–food contact). The extraordinary worn surfaces of QM F44326, in comparison with the other Winton teeth, may indicate that the QM F44326 was a much older tooth within the jaw and thus subject to more wear. The sharp edges of the wear facets on the crown of QM F44324, and to some extent QM F44325, imply some attritional wear (tooth–tooth contact). Wear facets on the cingula of all the teeth suggest attritional wear. Furthermore, wear on both the labial and lingual surfaces suggest that the teeth would have met the corresponding teeth in the opposing jaw, as occurs in *Scelidosaurus*. Additionally, the high-angled planar wear facets on the crowns of QM F44324 and QM F44325 suggest they were once in a tooth row that exhibited precise and systematic occlusion. This combination of wear faceting also indicates a very efficient ‘puncture-crushing’ jaw movement, as is evident in *Scelidosaurus* and other ankylosaurians (Barrett 2001). Such effective mechanical processing of food is evident in *Minmi* (Molnar & Clifford 2000).

The wear facets on the sides of the tooth body of QM F44324 and QM F44326 also show signs of interdental pressure (see Thulborn 1974). The internally angled surfaces on the basal-most part of the preserved root of QM F44324 and QM F44326 may be explained as wear facets caused by newly erupting teeth. This feature, however, has yet to be described for any known thyreophoran teeth.

Tooth orientation

The original position of an isolated ankylosaurian tooth within a jaw can be inferred using a combination of characters: cingula, position of wear facets and a distally offset apex. First, the lingual cingulum of an ankylosaurian tooth is more prominent and is positioned basal to the labial cingulum (Coombs 1990, Barrett 2001). Thus, a tooth can be placed facing towards the cheek or tongue. Second, as discussed above, ankylosaurian maxillary and dentary teeth exhibit different wear faceting patterns. Maxillary teeth predominantly have wear facets on the lingual cingula, whereas dentary teeth have worn labial cingula (Barrett 2001). Consequently, a tooth may be placed in the corresponding jaw depending on wear facets. Third, ankylosaurian teeth generally have a distally offset apex (Coombs 1990). Subsequently, a tooth can be anatomically orientated. The combination of all three of these characters, therefore, can assign a tooth to a specific jaw. For example, a maxillary tooth (wear facets on the lingual cingulum) with an apex that is distally offset to the right in labial aspect, can be assigned to the right jaw, whereas a maxillary tooth with an apex that is distally offset to the left in labial aspect can be assigned to the left jaw. A dentary tooth (wear facets on the labial cingulum) with an apex that is distally offset to the right in labial aspect can be assigned to the left jaw, whereas a dentary tooth with an apex distally offset to the left in labial aspect can be assigned to the right jaw.

Winton teeth. Using the combination of characters discussed above, the isolated teeth from Winton can be interpreted as two dentary teeth and a maxillary tooth.

QM F44324 (Fig. 2A). In lingual aspect, the crown is offset to the left, thereby indicating that the 'left' is the distal side of the tooth in lingual aspect. The distally offset apical denticle, the position of the more prominent cingulum (lingual surface) and the distribution pattern of wear facets on the labial surface support the referral of this tooth to the left dentary.

QM F44326 (Fig. 2B). The crown is offset to the left in lingual aspect indicating, together with the more prominent lingual cingulum and the distribution of wear facets on the labial surface, that this tooth belonged to the right dentary.

QM F44325 (Fig. 2C). The crown is offset to the left in lingual aspect. This character, together with the position of the more prominent cingulum and the placement of wear facets on the lingual surface, indicates that this tooth belonged to the right maxilla.

Palaeobiogeographical implications

The teeth described here are the first evidence of ankylosaurian dinosaurs in the Winton Formation. They indicate that ankylosaurs persisted in Australia until at least the earliest Late Cretaceous (late Albian–Cenomanian; Gray *et al*. 2002), making them the youngest known evidence for the clade from the continent. The Winton Formation is the sixth formation within Australia to yield thyreophoran dinosaurs, the others being: (1) the Bungil Formation of Queensland (Valanginian–Aptian; Green *et al*. 1997), *Minmi paravertebra* (Molnar 1980); (2) the 'Wonthaggi formation' of Victoria (late Hauterivian–Albian; Wagstaff & McEwan Mason 1989, Tosolini *et al*. 1999), Ankylosauria indet. (Barrett *et al*. 2010); (3) the Eumeralla Formation of Victoria (mid-late Aptian to early-middle Albian; Wagstaff & McEwan Mason 1989, Partridge 2006), Genasauria indet. (formerly *Serendipacertops arthurclarki*; Agnolin *et al*. 2010) and Ankylosauria indet. (Barrett *et al*. 2010); (4) the Toolebuc Formation of Queensland (Albian; Gray *et al*. 2002), QM F33286 (Molnar 1996); and (5) the Allaru Mudstone of Queensland (late Albian), QM F18101, QM F33565, QM F33566, AM F35259 and AM F119849 (Molnar 1996). As the Winton ankylosaurian teeth are dissimilar to all other Gondwanan ankylosaurians, it is likely that they pertain to a new taxon or taxa, distinct from *Minmi* (Molnar 1980, 1996) and the indeterminate ankylosaurian material from the Strzelecki Group (Barrett *et al*. 2010). Thus, although the material is only fragmentary, it provides new information on the diversity and the geographic and temporal range of thyreophoran dinosaurs within Australia, and indicates that ankylosaurians constitute a diverse and important component of Australia's mid-Cretaceous dinosaur fauna.

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