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The biochronology and palaeobiogeography of *Baru* (Crocodilia: Mekosuchinae) based on new specimens from the Northern Territory and Queensland, Australia

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New records of the Oligo-Miocene mekosuchine crocodilian, *Baru*, from Queensland and the Northern Territory are described. *B. wickeni* and *B. darrowi* are accepted as valid species in the genus and their diagnoses are revised. Both species are present in Queensland and the Northern Territory but are restricted in time, with *B. wickeni* known from the late Oligocene and *B. darrowi* from the middle Miocene. The broad geographic distributions and restricted time spans of these species indicate that this genus is useful for biochronology. The record of *B. wickeni* from the Pwerte Marnte Marnte Local Fauna in the Northern Territory establishes that the species inhabited the northern margin of the Lake Eyre Basin drainage system. More southerly Oligo-Miocene sites in the Lake Eyre Basin contain only one crocodilian species, *Australosuchus clarkae*. The Pwerte Marnte Marnte occurrence of *B. wickeni* indicates that the separation of *Baru* and *Australosuchus* did not correspond with the boundaries of drainage basins and that palaeolatitude was a more likely segregating factor.

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Abstract

New records of the Oligo-Miocene mekosuchine crocodilian, *Baru*, from Queensland and the Northern Territory are described. *B. wickeni* and *B. darrowi* are accepted as valid species in the genus and their diagnoses are revised. Both species are present in Queensland and the Northern Territory but are restricted in time, with *B. wickeni* known from the late Oligocene and *B. darrowi* from the middle Miocene. The broad geographic distributions and restricted time spans of these species indicate that this genus is useful for biochronology. The record of *B. wickeni* from the Pwerte Marnte Marnte Local Fauna in the Northern Territory establishes that the species inhabited the northern margin of the Lake Eyre Basin drainage system. More southerly Oligo-Miocene sites in the Lake Eyre Basin contain only one crocodilian species, *Australosuchus clarkae*. The Pwerte Marnte Marnte occurrence of *B. wickeni* indicates that the separation of *Baru* and *Australosuchus* did not correspond with the boundaries of drainage basins and that palaeolatitude was a more likely segregating factor.

Introduction

Baru Willis, Murray and Megirian, 1990 is a distinctive deep-snouted mekosuchine crocodilian from the Oligocene and Miocene of northern and central Australia (Fig. 1a). The genus was first erected to encompass a single species, *B. darrowi* Willis, Murray and Megirian, 1990, which was recorded from terrestrial carbonate deposits in both the Northern Territory and Queensland (Willis, Murray and Megirian 1990). The holotype specimen is a large rostrum (Fig. 1b) from the Bullock Creek Local Fauna of the Northern Territory, while less complete specimens from Riversleigh Station (now Riversleigh World Heritage Area) of northwestern Queensland were designated as paratypes (Willis, Murray and Megirian 1990). The authors did note that there were proportional differences in the symphyseal region of the dentary and that the Bullock Creek specimens had minutely crenulated carinae on their teeth while those from Riversleigh were smooth. Nevertheless these differences were regarded as insufficient to establish separate taxa (Willis, Murray and Megirian 1990). At the time of description it was recognised that the Riversleigh *Baru*-bearing sites were older than the Bullock Creek Local Fauna, but the age difference was not considered remarkable for a crocodilian species (Willis, Murray and Megirian 1990).

Later in the same decade two additional species of *Baru* were described (Willis 1997a) on the basis of new material from Riversleigh and further study of the previous specimens. *B. wickeni* Willis, 1997a is a large species, similar in size to *B. darrowi*, which specifically includes the Riversleigh paratypes previously included in *B. darrowi* (Willis, 1997a). *B. huberi* Willis, 1997a is a much smaller form with a platyrostral snout that was found alongside *B. wickeni* (Willis 1997a). New evidence from a related species in the Bullock Creek Local Fauna indicates that *B. huberi* belongs to a distinct lineage more closely related to other mekosuchines than to *B. darrowi* (Yates and Lee, in prep.). Consequently *'B.' huberi* should be removed from the genus *Baru*. A revision of this species that will name a new genus and describe new species closely related it is in preparation and it will not be discussed any further here.

Our understanding of the stratigraphy and biochronology of the many vertebrate fossil sites in the Riversleigh WHA has greatly improved since *Baru* was first described. At the coarsest level the Oligo-Miocene sites can be divided into four faunal zones labelled A, B, C and D (Travouillon et al. 2006). We also recognise that these zones roughly correspond with the late Oligocene, early Miocene, middle Miocene and early late Miocene, respectively, based on biocorrelation with other mammal-bearing sites in Australian and direct radiometric dating of some Riversleigh sites (Travouillon et al. 2006; Woodhead et al., 2016). *B. wickeni* has only been identified in Faunal Zone A, mostly from Site D and White Hunter Site. Faunal Zone A includes of extensive fluviatile and lacustrine calcarenites and micrites with a notable aquatic component to the preserved faunas, such as large crocodilians, turtles and lungfish (Archer et al., 1989; Creaser 1997). Younger deposits consist mostly of laterally restricted pond and cave deposits that formed on a palaeokarst landscape (Archer et al. 1989; Creaser 1997; Arena et al. 2014). As a consequence crocodilians are less common and are of smaller size than those in Faunal Zone A deposits. Nevertheless a diverse fauna of small crocodilians has been recovered from the Faunal Zone C Ringtail Site (Willis 2001). This fauna includes a small maxilla and an even smaller dentary that Willis (2001) referred to *Baru* sp.. Willis (2001) declined to identify these specimens to species level because of their incompleteness. Specifically diagnostic *Baru* specimens from Riversleigh's Faunal Zone C would be highly desirable because the zone shares many mammal species with the middle Miocene Bullock Creek Local Fauna (Travouillon et al., 2006; Megirian et al. 2010) and it would be important to extend that correlation to crocodilians as well. The question of the specific identity of these specimens is revisited in this paper.

As records currently stand both *B. darrowi* and *B. wickeni* are known only from their respective type localities (or a cluster of geographically proximate and temporally equivalent sites in the case of *B. wickeni*). With only singular occurrences, little can be said about the geographic distribution or temporal range of these species. The difference in *Baru* species at the two localities may be due to the time difference between the two deposits (at least 10 million years) or the spatial separation (approximately 800 km) or a combination of both. Here I report on new occurrences of both species that strongly suggest that they had broad geographic distributions across the region but were confined to non-overlapping ranges of time.

Systematic Palaeontology

Crocodilia Gmelin, 1789

Mekosuchinae (Balouet and Buffetaut, 1987)

Baru Willis, Murray and Megirian, 1990

Baru wickeni Willis, 1997a

(Figs 2-6, 7c-e, 13)

Revised diagnosis. Distinguished from *B. darrowi* by: nasals extend to margin of external naris; strongly developed preorbital ridge on lacrimal, flanked by lateral depressions; deep ventrolateral ridge, forming pendent flange, extending from anterior end of jugal onto posterior end of maxilla; posterolateral squamosal boss absent; sixth, seventh and eighth maxillary teeth separated by gaps wider than length of preceding alveolus in adults; anterior process of palatines absent, palatine-maxilla suture linear; palatine-pterygoid suture level with posterior margin of suborbital fenestra; posterior pterygoid processes are elongate, finger-like projections in ventral view; dorsal posterior lobe of dentary symphyseal surface level with ventral lobe; splenial widely separated from symphyseal surface; all teeth with smooth carinae.

Type Locality. White Hunter Site, Riversleigh WHA, Queensland. Unnamed fluvio-lacustrine limestone, White Hunter Local Fauna, late Oligocene.

New material. NTM P2914-14, posterior end of left mandible. NTM P2914-16 and 17, fragments of left angular. NTM P2914-15, fragment of right jugal. NTM P6372, fragment of right squamosal from small juvenile. NTM P2815-18, isolated anterior tooth crown. NTM P2914-5, isolated anterior tooth crown.

NTM P6373, isolated posterior tooth crowns. Numerous other undiagnostic specimens from the site, including small shed teeth, incomplete vertebrae and osteoderms are not described here.

Locality and stratigraphic age of new material. Railside borrow pit on the new Ghan Railway line, approximately 40 km south of Alice Springs, Northern Territory. Unnamed fluvial deposit of calcite-cemented sandstones and conglomerates, Pwerte Marnte Marnte Local Fauna, late Oligocene (Murray and Megirian 2006).

Description of the Pwerte Marnte Marnte specimens. The jugal fragment comes from the anterior end of the right jugal, immediately anterior to the postorbital bar. The fragment is 67 mm deep dorsoventrally, suggesting a large, deep-snouted crocodilian. The medial side bears an enlarged medial jugal foramen, with a maximum internal diameter of 6.7 mm, nestled against the anterior side of the internal buttress for the postorbital bar. Laterally the external surface is ornamented with irregular pits and ridges. A broad shallow sulcus extends longitudinally under the orbital margin. This sulcus is separated from the ventral margin of the jugal by a well-developed longitudinal ridge. In more complete *Baru* specimens this ridge begins on the jugal at about the level of the postorbital bars and extends anteriorly onto the maxilla for a short distance. As in other *B. wickeni* specimens (NTM P8738-1, P8778-4; QM F16822), the peak of this ridge in NTM P2914-15 is directed ventrolaterally while its ventral surface is slightly excavated, giving the ridge the form of a pendent flange. The squamosal fragment bears large rounded pits on its dorsal surface and lacks differentiated marginal ornament. The dorsolateral margin is slightly raised above the dorsal surface but not to the degree that could be described as a squamosal horn. In dorsal view it does not bulge laterally as the posterior end of the dorsolateral margin does in *B. darrowi* (Fig. 7a-b) and an undescribed species of *Baru* from the late Miocene of Alcoota (NTM unregistered specimen).

The surangular of NTM P2914-14 is incomplete anteriorly and does not preserve any margins of the external mandibular fenestra. The anterior lateral surface is sculpted with elongate pits a ridges that become progressively deeper toward the level of the glenoid. Posterior to this level the lateral surface of the surangular is smooth and unornamented. The dorsal edge of the ornamented area is thickened and forms a low, laterally projecting ridge that begins at a point presumably level with the posterior margin of the external mandibular fenestra and extends posterior to the level of the glenoid. This ridge is not as sharply defined as in other *Baru* specimens but this difference is regarded as a relatively minor feature of individual variation. Unfortunately the dorsal part of the surangular adjacent to the glenoid is badly damaged so it is not possible to determine whether a dorsal pit was present as it is in other *Baru* or the height of the surangular extension up the posterior wall of the glenoid. Posterior to the glenoid the surangular tapers to form a thin splint that extends along the lateral surface of the retroarticular process, dorsal to the angular. The posterior end of the surangular is damaged and incomplete but facets on the angular and articular indicate that it would have extended close to the posterior end of the retroarticular process. Medially the surangular bears a large sutural scar where part of the anterior articular has broken away scar. This scar reveals that the articular had a semilunate lamina that projected anteriorly on the medial surface of the surangular, immediately below the dorsal margin (the 'crocodyline process' of Aoki, 1992). Imediately ventral to the scar is the surangular's half of the opening for the lingual articular foramen, indicating that in life this foramen opened on the articular-surangular suture. Anteriorly and ventral to the lingual foramen there is a small piece of the surangular that overlaps the medial surface of the angular indicating an oblique scarf joint was present between the two bones in this area. This fragment also indicates that the medial expression of the surangular-angular suture met the articular at its anterior tip. The posterior end of the angular is preserved on P2914-14. The lateral surface is flat and smooth from the glenoid region posteriorly to the end of the retroarticular process. Anterior of this level, ventral to the ornamented region of the surangular the surface becomes undulate and pierced by a couple of large neurovascular foramina. Medially there is a trough-like sulcus extending along the anterior part of the angular fragment, adjacent to the ventral margin, into which the anterior process of the articular sits. A separate fragment from a more anterior part of the angular (NTM P2914-16), which may well represent the same specimen as NTM P2914-14, shows that the lateral surface was ornamented with widely spaced deep pits. The ventral margin is broadly rounded. The articular is rather poorly preserved. It is crushed, broken and missing the medial edge of the retroarticular process, all of the glenoid and the anterior tip of the anterior process. The anterior process is more elongate than in extant *Crocodylus* and the sutural line with the medial side of the surangular descends less steeply ventrally from the dorsal margin of the jaw. The dorsomedial surface of the anterior process forms a simple slightly concave surface that lies against the medial surface of the surangular. There is no longitudinal sulcus adjacent to the articular-surangular suture as is present in some mekosuchines such as '*Baru' huberi* (QM F31072).

The isolated teeth from the site have elliptical cross sections with a labiolingual width that varies between 85 and 75 % of the antero-posterior length. The anterior and posterior edges bear a smooth carina. Posterior teeth have low rounded outline in lingual view while anterior teeth are tall and conical with a slightly lingually curved tip.

Remarks. The jugal fragment bears a flange-like pendent jugal-maxilla ridge which is an autapomorphic character of *Baru wickeni* that is present on all referred crania from Riversleigh that preserve a jugal (NTM P8738-1, P8778-4; QM F16822). The squamosal fragment lacks a laterally directed swelling on the posterolateral margin of the squamosal, which is a derived characteristic that is seen in *B. darrowi* and an unnamed *Baru* species from Alcoota but not *B. wickeni* (Fig. 7).

Similarly the known crocodilian teeth from the Pwerte Marnte Marnte local fauna have smooth carinae, a plesiomorphic characteristic of *B. wickeni*.

The lower jaw from Pwerte Marnte Marnte can be distinguished from all mekosuchine genera except *Baru* by the combination of its large size, lateral ridge along the dorsal margin of the ornamented area of the surangular, lack of a longitudinal sulcus on the articular adjacent to the surangular suture and location of the medial foramen for the articular artery and alveolar nerve on the surangular-articular suture. However there are no characteristics from this region of the jaw that would allow species identification.

Taken together, all of the known crocodylian remains from the Pwerte Marnte Local Fauna can be referred to *Baru*, or at least show anatomical characters consistent with it. Furthermore, all of the known elements are consistent with *B. wickeni* and one piece, the jugal, can be positively referred to this species on the basis of an autapomorphy. For these reasons the entire crocodilian sample from Pwerte Marnte Marnte is tentatively referred to *B. wickeni*.

Baru darrowi Willis, Murray and Megirian, 1990

(Figs 1a, 7a-b, 8-9)

Revised diagnosis. Distinguished from *B. wickeni* by: median sutural contact of premaxillae posterior to external naris; weakly developed preorbital ridge on lacrimal; low ridge extending from anterior end of jugal onto posterior end of maxilla; squamosal with laterally projecting, posterolateral boss; sixth, seventh and eighth maxillary teeth separated by gaps less than length of preceding alveolus in adults; acutely triangular anterior process of palatines; palatine-pterygoid suture anterior of posterior margin of suborbital fenestra; posterior pterygoid processes are low, blunt tubercles in ventral view; dorsal posterior lobe of dentary symphyseal surface overhangs ventral lobe; splenial closely approaching, or contacting symphyseal surface; larger teeth with minutely crenulated carinae.

Type Locality. Blast Site, Bullock Creek, Northern Territory. Camfield Beds, Bullock Creek Local Fauna, middle Miocene.

New material. QM F30319, a left premaxilla with an articulated fragment of the left nasal (Fig. 8). QM F 31013, a fragment of left maxilla. QM F31185, a complete left maxilla (Fig. 9).

Locality and stratigraphic age of the new material. Ringtail Site, Riversleigh WHA, Queensland. Unnamed calcareous pool deposit, Ringtail Local Fauna, Riversleigh Faunal Zone C, radiometrically dated to 13.56±0.67 ma, middle Miocene (Woodhead et al., 2016).

Description of the Ringtail Site specimens. The premaxilla (Fig. 8)is complete, save for the anteriormost surface and the second premaxillary tooth. Despite the missing surface it is apparent that, like other *Baru*, the anterior surface was both deep and close to vertical. The external naris faces dorsally and when complete would have been almost exactly as wide as it was long (determined by mirror imaging the complete left side of the opening) in the shape of a rounded trapezoid. The premaxillae completely surround the external naris and there is a short medial sutural surface behind the naris that where the opposite premaxilla would have contacted its partner. The premaxillary pair sent a short anterior spine from the posterior margin of external naris that protruded into the narial opening for a distance of 3.5 mm. On the ventral surface of this spur there is a sutural contact for the anterior tip of the nasal (which is itself missing due to breakage). This contact indicates that the nasals also reached the naris, albeit ventral to the superficial premaxillary cover and invisible in dorsal view. Ventrally the premaxilla bears four alveoli. There is a broad gap between the first and second alveolus indicating that, as in other crocodilians with four premaxillary teeth, it is the primitive second tooth that is missing. It is interesting to note that the loss of this tooth has to have occurred early in ontogeny because QM F30319 is a small juvenile. The horizontal premaxillary plate curves ventrally adjacent to the alveoli to form a lingual alveolar wall. The wall bulges lingually around the alveoli while narrow lingually facing depressions occur between alveoli two and three as well as three and four. A circular reception pit for the first dentary tooth occupies the space on the premaxillary palate between the first premaxillary alveolus anteriorly, the send premaxillary tooth laterally and the incisive foramen laterally. Unlike the old adult holotype of *B. darrowi* the floor of the pit is complete and separates it from the narial cavity, whereas it has merged with the incisive foramen in the holotype. Whether this difference is due to post-mortem damage to the holotype or absorbtion of bone during its life is not known. An irregularly spaced line of neurovascular foramina opens along the base of the alveolar wall. Mirror imaging indicates that the complete incisive foramen would have been broadly lanceolate with an elongated anterior point. The margins of the premaxillary symphysis anterior to the incisive foramen are not sharp so it is hard to judge exactly how far anteriorly the foramen extended but it is clear that the anterior end closely approached the lingual margins of the first premaxillary alveoli, if not actually abutting them. It is, however, clear that the incisive foramen did not intrude between this pair of alveoli. The posterior margin of the incisive foramen is level with the third, and penultimate, premaxillary alveolus. The anterior half of a ventrolaterally facing notch for receiving the fourth dentary tooth occurs between the fourth premaxillary alveolus and the maxillary suture. This notch is bounded dorsolaterally and ventromedially by thin, low, sharp ridges. The palatal premaxilla-maxilla suture is oriented medially in a roughly linear transverse line.

The maxilla (QM F31185, Fig. 9) has already been described by Willis (2001), so only a few salient points will be mentioned here. The number of maxillary alveoli cannot be observed directly because the region between the anterior and posterior festoons is crushed and the alveoli obscured. However the pattern of alveoli in this region is stable within *Baru* and the medial reception pits, which align with the gaps between alveoli, can also be observed. Thus it is clear that the crushed region is obscuring maxillary alveoli six and seven, while the first clear alveolus posterior to the crushed region is the eighth maxillary alveolus. As in other *Baru*, the eighth alveolus remains close to, but separated from, the closely spaced, enlarged alveoli of the posterior festoon (alveoli 9-11). Counting from alveolus eight it is clear that QM F31185 had 14 alveoli, which is one more than the old, adult holotype of *B. darrowi*. The loss of the posterior-most maxillary alveoli late in ontogeny occurs in extant crocodiles (pers. obs. of numerous *C. porosus* in NTM collections) and is not indicative of a taxonomic difference. The lateral wall of the narial canal, visible when the maxilla is viewed medially) is smooth and lacks any recesses. Also visible in medial view is the foramen for the n. alveolaris dorsalis caudalis. The opening occurs on the medial side of the dorsal lamina, above the alveoli and level with the anterior end of the ectopterygoid articulation. Unlike most other crocodilians, but like other *Baru*, the opening of this foramen faces dorsally and lies close to the dorsal edge of the maxilla. The sutural contact with the palatine is well preserved. It indicates that, like the holotype of *B. darrowi*, the anterior process of the palatine was a pointed, triangular process that extended anterior of the suborbital fenestra for the length of approximately one alveolus. Posteriorly the articular scar for the attachment of the ectopterygoid is well preserved. It indicates that the anterior tip of the ectopterygoid inserted into a notch in maxilla and was separated from the lateral margin of the suborbital fenestra by a short medial lamina of the maxilla. This is a derived condition seen in a number of mekosuchines including *B. wickeni* (number), *B. darrowi* (NTM P), '*B*.' *huberi* (QM F31063), *Mekosuchus sanderi* (QM F3118), *Pallimnarchus gracilis* (QM F1752) and *Kambara implexidens* (QM F29662).

Remarks. The deep, near vertical anterior profile of the premaxilla, the presence of just four premaxillary teeth at an early ontogenetic stage are derived characters that allow QM F30319 to be referred to *Baru*. The median premaxillary contact behind the external naris is an autapomorphic character that allows referral to *B. darrowi*.

Four other specimens from Ringtail Site were referred to *Baru* sp. by Willis (2001). Of these, two of the maxillae (QM F31013, F31185) can be referred to *Baru* on the basis of the combination of the following characters: rounded alveoli, well-developed festoons, anterior tip of the ectopterygoid inserting into the maxilla and separated from the lateral margin of the suborbital fenestra; medial foramen for the n. alveolaris dorsalis caudalis opens dorsally near the dorsal edge of the maxilla (Fig. 9b). The latter character has not been described before but is an apparent synapomorphy of *Baru* as it is present in the holotype of *B. darrowi* (NTM P8695-8) and an undescribed species from Alcoota (NTM P912) but not in other crocodilians including *Kambara implexidens* (QM F29662), *Quinkana meboldi* (QM F31056), *Mekosuchus inexpectatus* (= *kalpokasi*, Mead et al. 2002:fig. 3b), *Crocodylus novaeguineae* (QM J5332) and *Alligator mississippiensis* (NTM R36716). The maxillae can be specifically referred to *B. darrowi* on the basis of their short, but acutely triangular anterior palatine process that wedges between the maxillae (Fig. 9d). The process itself is not preserved in either specimen but its shape can be clearly deduced from the articular surfaces on the maxillae. In *B. wickeni*, and the undescribed *Baru* from Alcoota, the anterior end of the palatine pair is only gently convex or almost linear (e.g. QM F16822, NTM P5335).

The dentary (QM F31004; Fig. 10) that Willis (2001) referred to *Baru* presents a problem. Like *B. darrowi* it does possess an overhanging posterior dorsal lobe of the dentary symphyseal surface but unlike that species the anterior tip of the splenial is widely sepparated from the symphysis. The specimen also differs from all other *Baru* in being much smaller, and in having a highly dorso-ventrally compressed symphysial platform. Perhaps all of these discordant features are the result of an extremely early ontogenetic stage, though the anterior position of the splenial has not been documented to be an ontogenetically variable character in crocodilians. An alternative explanation is that the dentary actually belongs to *Trilophosuchus rackhami*, a very small mekosuchine that is also known from Ringtail Site (Willis, 1993). Not only is QM F31004 the right size to fit *T. rackhami*, the dorsoventrally compressed symphyseal platform matches the compressed platforms seen in the related dwarfed mekosuchine genus, *Mekosuchus*. Only further discoveries, either of *T. rackhami* with lower jaws or more complete, highly juvenile *Baru* can solve this question

Discussion

B. darrowi has been recorded from Riversleigh WHA before (Willis, Murray and Megirian 1990), but these specimens, which hail from Faunal Zone A, are now referred to *B. wickeni* (Willis 1997a). QM F30319 and F31185 from Ringtail Site indicate that *B. darrowi* was present in Faunal Zone C of the Riversleigh WHA. Fortunately Ringtail Site is one of the Riversleigh sites for which a radiometric date could be obtained (Woodhead et al., 2016). This date of 13.56 ± 0.67 ma, places the site about the boundary of the Langhian and Serravallian Stages in the middle Miocene (Woodhead et al., 2016). Bullock Creek, the type locality for *B. darrowi*, shares many mammal species with Faunal Zone C, particularly the younger interval zones within Zone C. Among the shared species are *Mutpuracinus archibaldi* Murray and Megirian, 2000, *Wakaleo vanderleuri* Clemens and Plane, 1974, and *Neohelos stirtoni* Murray et al., 2000. These marsupials are only known from younger Faunal Zone C deposits of the C2 and C3 intervals (Archer et al. 2006; Arena 2015). Although the mammalian fauna of Ringtail Site is insufficient to place it securely in an interval zone within Faunal Zone C (Arena, 2015) the radiometric date obtained from this site was one of the younger ones for Faunal Zone C, indicating that, like the Bullock Creek LF, this site probably correlates with the upper part of Faunal Zone C. Thus the occurrences of *B. darrowi* in the Northern Territory and Queensland are close to coeval. It is now apparent that *B. darrowi* was a widespread species in northern Australia around 13-14 ma (middle Miocene), stretching from at least Bullock Creek in the west to Riversleigh in the east, a distance of approximately 800 km (Fig. 11).

The presence of *B. wickeni* in the Pwerte Marnte Marnte LF is the first record for the species in the Northern Territory and indeed the first record outside of the Riversleigh WHA. The location of the Pwerte Marnte Marnte LF in central Australia not only represents a westward range extension but also a significant southerly extension, suggesting that its potential range may have encompassed the entire northern half of the continent. A significant detail of the Pwerte Marnte Marnte deposit is that it lies on the northern fringe of the Lake Eyre Basin (Fig. 12). Willis (1997b) noted that the well sampled Etadunna Formation in the Lake Eyre Basin of central South Australia contained abundant crocodilian remains attributable to the mekosuchine *Australosuchus clarkei* Willis and Molnar, 1991 but not a trace of any of *Baru*, or indeed any of the other the mekosuchines found at Riversleigh. Conversely, no trace of

Australosuchus has ever been recovered from the crocodilian-rich late Oligocene deposits of Riversleigh (Willis, 1997b). Time differences cannot explain this pattern because the upper part of the Etadunna sequence (Ngapakaldi and Ngama Local Faunas) correlates with Faunal Zone A of Riversleigh (Archer et al., 1989; Myers and Archer, 1997; Travouillon et al., 2006; Arena et al., 2015) and yet remain rich in *A. clarkae*. Willis (1997b) suggested that this distributional disparity was the result of aquatic taxa such as *Australosuchus* and *Baru* being restricted to separate and isolated drainage systems. The presence of *Baru wickeni* at the northern end of the Lake Eyre Basin falsifies this hypothesis. However *A. clarkae* and *B. wickeni* remain segregated by latitude, with the former not known north of 27° S and the latter not found south of 25° S. This suggests that it was palaeolatitude, and hence palaeoclimate, that separated these taxa, rather than access to drainage systems. Indeed the most southerly record for *A. clarkae*, Lake Pinpa, lies at 31° S and would have had a palaeolatitude between 45 and 50° S in the Oligocene (from McGowran et al. 2004, fig. 1). This exceeds the highest latitude obtained by a viable population of an extant crocodilian (36° N in *Alligator mississippiensis*, from distribution given in Neill 1971). Furthermore the Oligocene represents a cool period in the saw-tooth history of Australian palaeotemperatures (McGowran et al. 2004), indicating that *A. clarkae* may have been an unusually cold-tolerant crocodilian. This may explain the why *A. clarkae* is the sole crocodilian from the Etadunna Formation while adequately sampled crocodilian assemblages from the Oligo-Miocene of northern Australia usually contain multiple species.

The age of the Pwerte Marnte Marnte LF is a matter of some uncertainty. When the local fauna was first reported, Murray and Megirian (2006) determined that it was closest to, but nonetheless predated, the basal-most local faunas of the Etadunna and Namba Formations which date to the Late Oligocene (Woodburne et al. 1994). Murray and Megirian (2006) reached this conclusion based upon the apparent absence of any described species from other late Oligocene sites and the apparent plesiomorphic nature of the unnamed ilariid from the Pwerte Marnte Marnte LF. 'Stage-of-evolution' biochronology indicates that the age of the Pwerte Marnte Marnte LF is a greater than the oldest local fauna of the Namba Formation (Pinpa Local Fauna) which contains a more derived ilariid, *Ilaria ilumidens*. They also noted that the fauna must postdate the basal radiation of diprotodontan marsupials given the presence of diprotodontan subclades such as Ilariidae, Wynyardiidae, Diprotodontidae, Macropodoidea, Phalangeroidea and Petauroidea. Megirian et al. (2010) upheld Murray and Megirian's (2006) correlation when establishing a series of Australian Land Mammal Ages. The basal local faunas from the Etadunna and Namba Formations were placed in the Etadunnan Land Mammal Age while the Pwerte Marnte Marnte LF was regarded as pre-Etadunnan (Megirian et al. 2010).

On the other hand, Black et al. (2012) suggested that the Pwerte Marnte Marnte LF could be correlated with Riversleigh's Faunal Zone A, on the basis of the shared presence of the unusual marsupial *Marada arcanum*. As Riversleigh's faunal Zone A correlates with the Ngapakaldi and Ngama Local Faunas from higher in the Etadunna sequence (based on the shared presence of the marsupials *Ngapakaldia bonythoni* and *Kuterintja ngama*) this would place the Pwerte Marnte Marnte at a later time in the Oligocene, close to the Oligo-Miocene boundary (Woodburne et al. 1994). Regardless of how the Pwerte Marnte Marnte LF is correlated there is no disagreement that it is Oligocene, and probably late Oligocene in age. Thus, like the younger *B. darrowi*, *B. wickeni* appears to have been a geographically widespread species with known occurrences falling within a relatively narrow timespan, in this case the late Oligocene. One immediately usefull aspect of this biochronological information is the placement of 300BR, a Riversleigh site that could not be placed within the Riversleigh Faunal Zones due to a lack of informative mammal fossils (Travouillon et al. 2006). NTM P91171-1 is a magnificent, nearly complete, *Baru* skull collected by D. Megirian from 300BR (Fig. 13). The skull shows all the diagnostic features of *B. wickeni* including the autapomorphic ventrolateral flange at the anterior end of the jugal, indicating that 300BR belongs in Faunal Zone A.

Australia's record of Cenozoic terrestrial vertebrates consists largely of spatially and temporally isolated assemblages that present few opportunities for lithostratigraphic correlation using superposition (Megirian, 1994). Only a few sites have been dated absolutely with radiometric techniques (Black et al., 2012; Woodhead et al., 2016) leaving biochronological methods, particularly stage-of-evolution biochronology (Stirton, Woodburne and Plane, 1967; Megirian, 1994) or seriation based on taxon presence or absence (Travouillon et al., 2006; Megirian et al., 2010), as the main means placing these assemblages in a relative timescale. To date this work has been carried out exclusively with marsupial fossils but the observations presented here indicate that crocodilian lineages, such as the genus *Baru*, can also prove useful for this purpose.

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Figure 1

Baru Willis, Murray and Megirian, 2000 and its distribution.

A, Map of Australia showing Queensland and the Northern Territory and the sites where *Baru* has been found. Note that the occurrence at Alcoota represents a new species dating from the Late Miocene and is not discussed in this paper. **B**, Holotype rostrum of *B. darrowi* Willis, Murray and Megirian, 2000, the type species of the genus. Scale bar in B = 100mm.

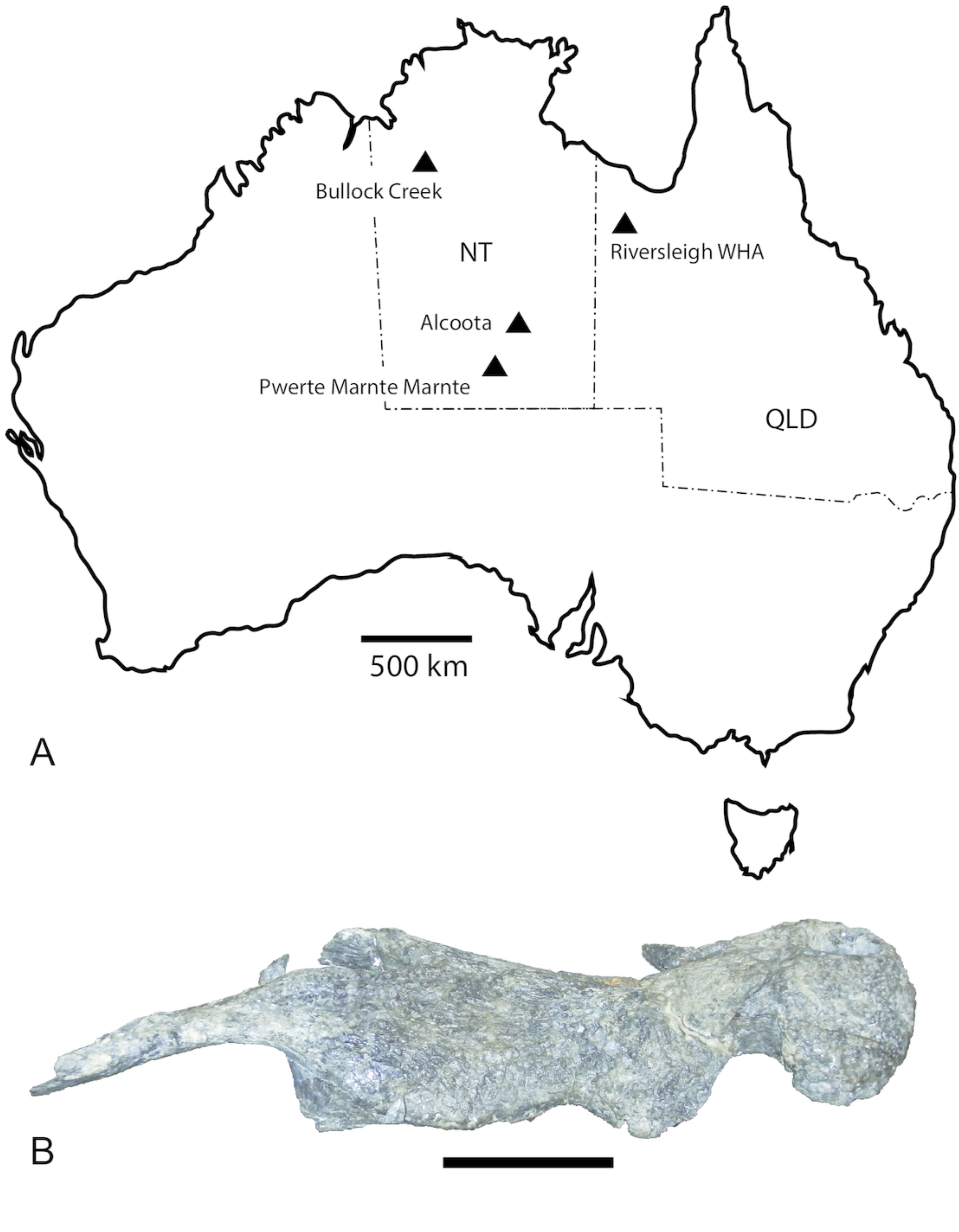
Bullock Creek
NT
Riversleigh WHA
Alcoota
Pwerte Marnte Marnte
QLD
500 km
A
B

Figure 2

Baru wickeni Willis, 1997a, NTM P2914-15, anterior fragment of the right jugal from Pwerte Marnte Marnte.

A, lateral view. **B**, medial view. **C**, anteromedial view. Abbreviations: eca, articular surface for the attachment of the ectopterygoid; lf, lateral fossa; mjf, medial jugal foramen; om, orbital margin; vlf, ventrolateral flange; vm, ventral margin. Scale bar = 50 mm.

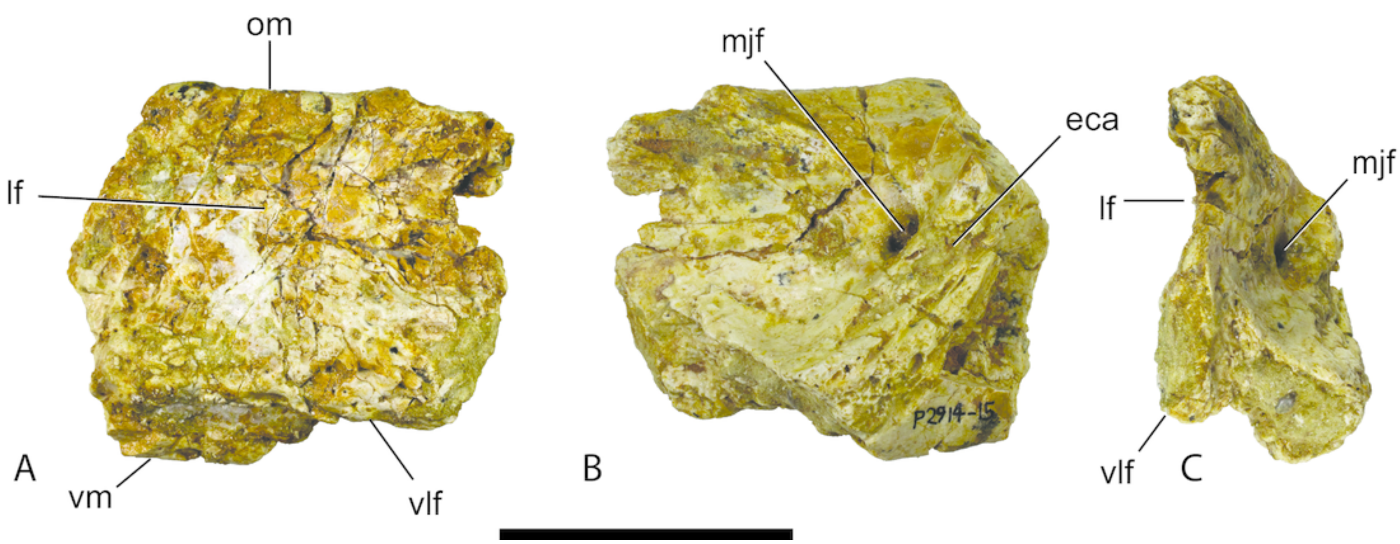

Figure 3

Baru wickeni Willis, 1997a, NTM P6372, posterior fragment of the right squamosal of a small juvenile from Pwerte Marnte Marnte.

A, dorsal view. **B**, posterior view. **C**, ventral view. Abbreviations: pa, articular surface for attachment of the parietal; plp, posterolateral process. Scale bar = 10 mm.

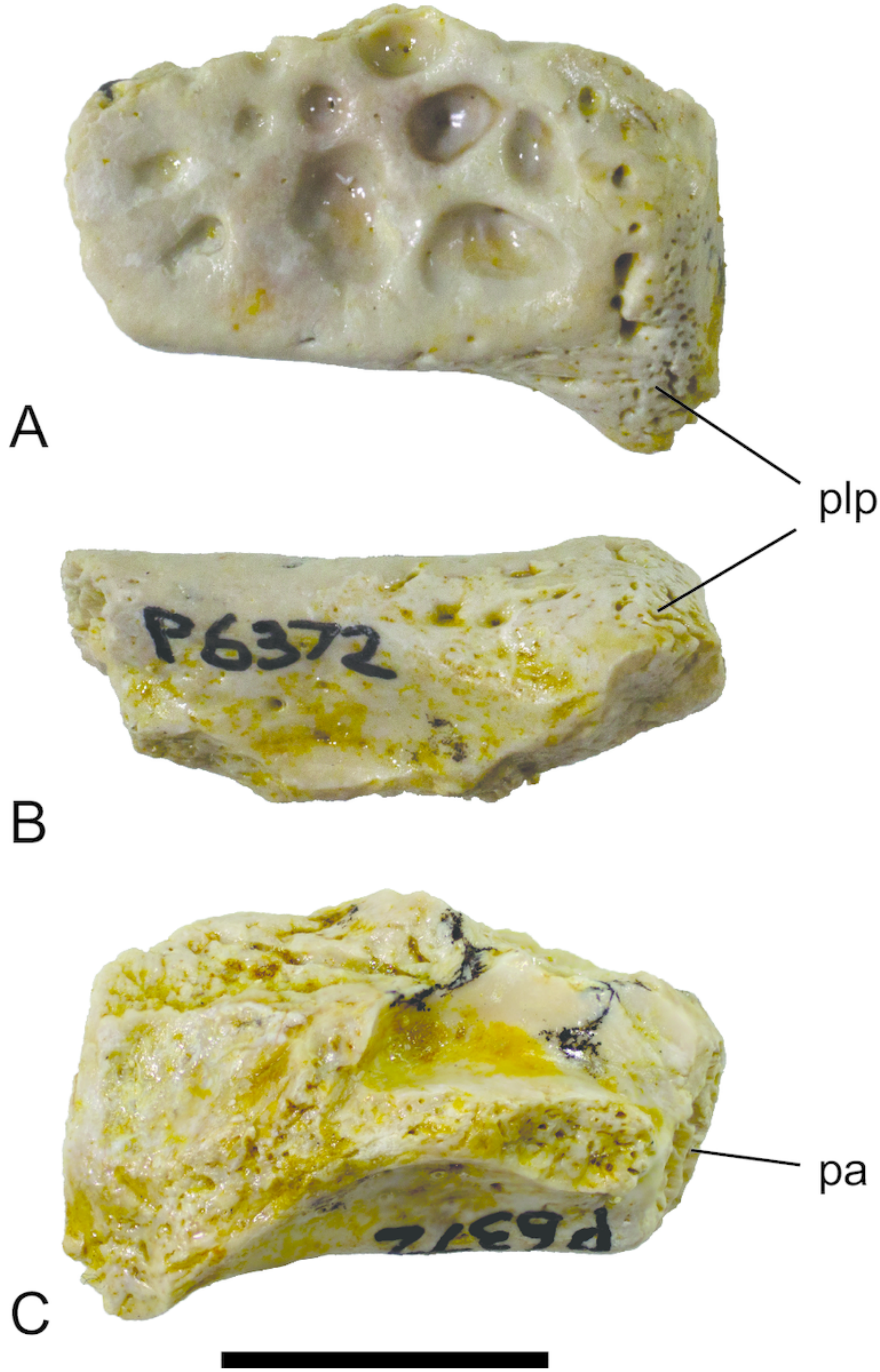
A
plp
P6372
B
C
P6372
pa

Figure 4

Baru wickeni Willis, 1997a, NTM P2914-14, posterior region of left mandible from Pwerte Marnte Marnte.

A, lateral view. **B**, medial view. **C**, dorsal view. Scale bar = 50 mm.

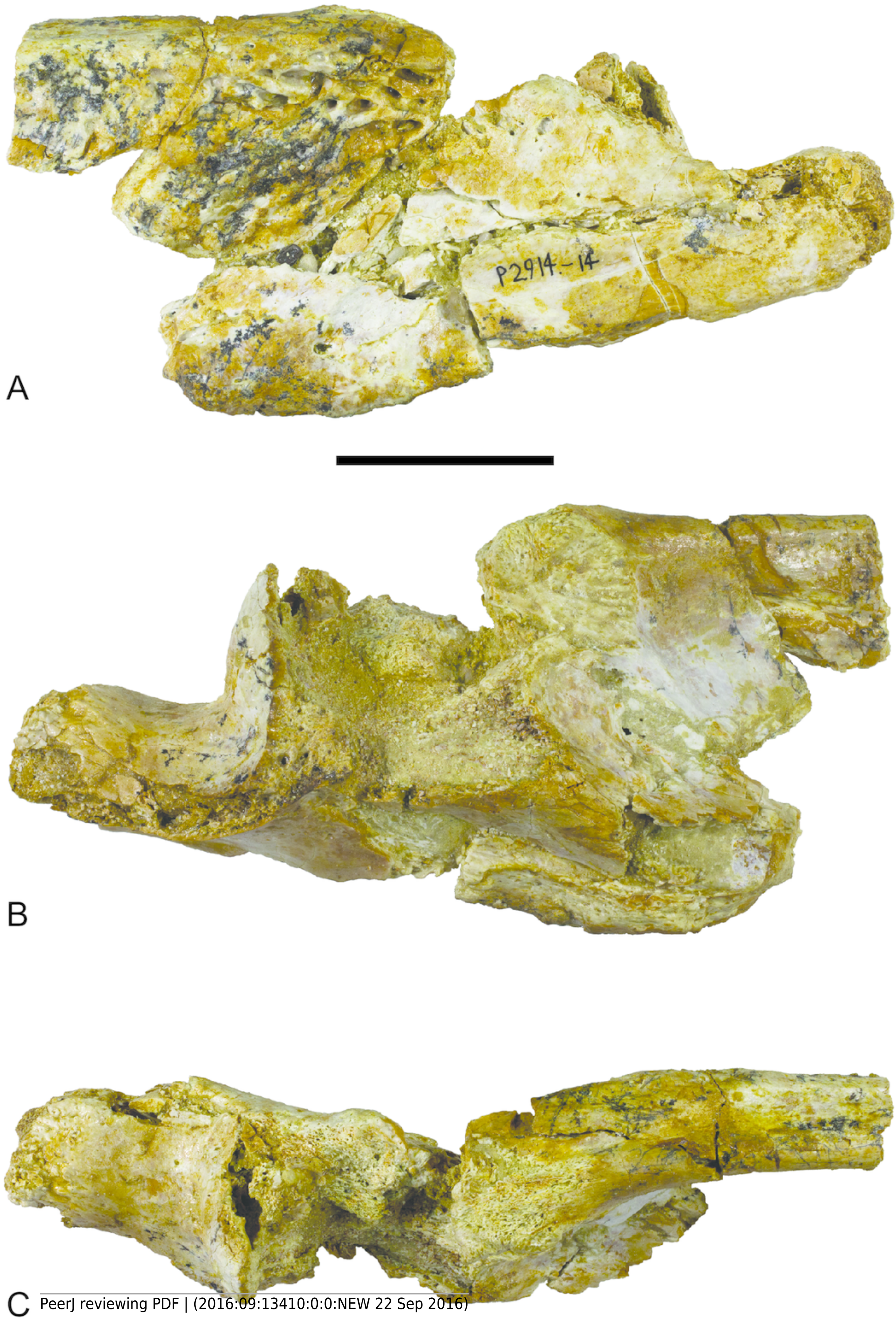
P2914-14
A
B
C

Figure 5

Baru wickeni Willis, 1997a, NTM P2914-14, interpretive drawings of posterior region of left mandible from Pwerte Marnte Marnte.

A, lateral view. **B**, medial view. **C**, dorsal view. Grey areas indicate patches of matrix and unassociated bone fragments. Hatched areas indicate broken bone surfaces. Abbreviations: an, angular; ana, articular surface for the attachment of the angular; ar, articular; ara, articular surface for the attachment of the articular; dla, articular surface for attachment of dorsal lamina of articular; dlr, dorsolateral ridge of the surangular; mf, medial foramen for articular artery and alveolar nerve; rap, retro-articular process; sa, surangular; saa, articular surface for the attachment of the surangular. Scale bar = 50 mm.

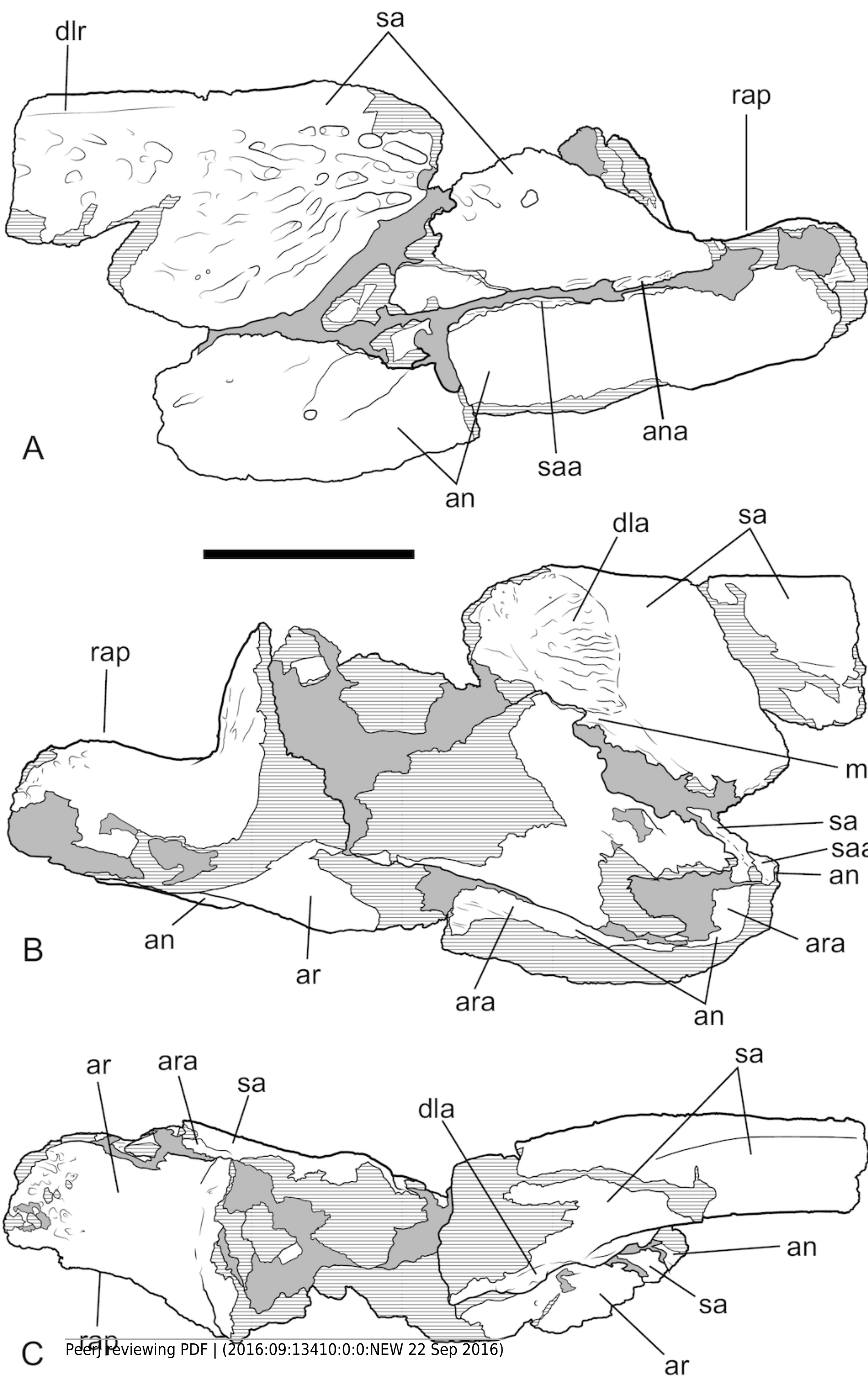
dlr
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Figure 6

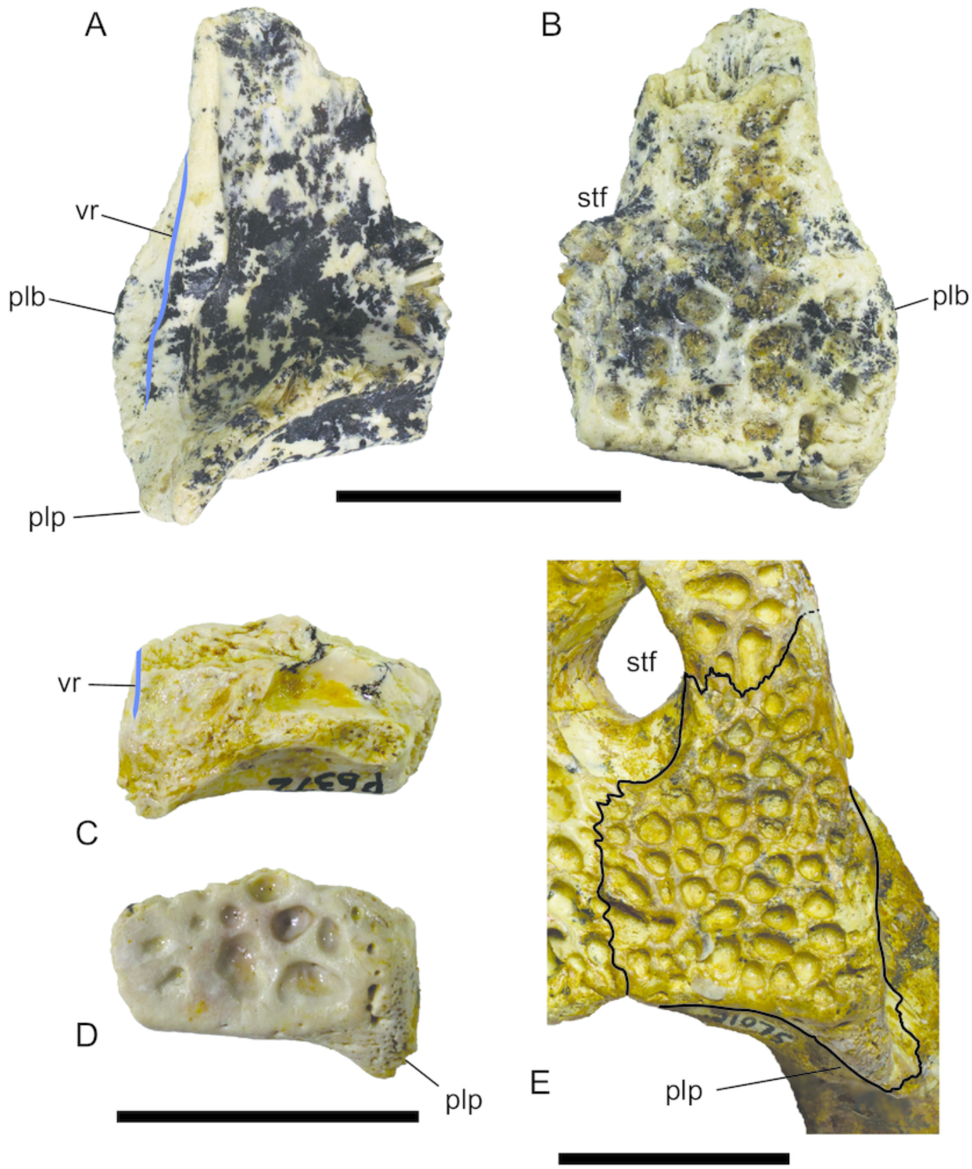
Baru wickeni Willis, 1997a, isolated teeth from Pwerte Marnte Marnte.

A-**B**, NTM P2914-5, anterior tooth in A, labial view and B, posterior view. **C**-**D**, NTM P6373, posterior tooth in C, occlusal and D, labial view. Scale bar = 10 mm.

Figure 7

Comparison of right squamosals of *Baru* Willis, Murray and Megirian, 1990.

A-**B**, *Baru darrowi* Willis, Murray and Megirian, 1990, NTM P2786-7, from Bullock Creek in A, ventral view and B, dorsal view. **C**-**D**, *Baru wickeni* Willis, 1997a, NTM P6372, fragment from Pwerte Marnte Marnte in C, ventral view and D, dorsal view. **E**, *Baru wickeni,* QM F31075, from White Hunter Site, Riversleigh World Heritage Area in dorsal view. Note the absence of a laterally protruding boss overhanging the lateral squamosal sulcus in the two *Baru wickeni* specimens. Abbreviations: plb, posterolateral boss of the squamosal; plp, posterolateral process of the squamosal; stf, supratemporal fossa; vr, ventral rim of the lateral squamosal sulcus. Scale bars = 20 mm.


A
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vr
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stf
E
plp

Figure 8

Baru darrowi Willis, Murray and Megirian, 1990, QM F30319, snout fragment of a juvenile including left premaxilla and nasal from Ringtail Site, Riversleigh World Heritage Area.

A, dorsal view. **B**, ventral view. **C**, lateral view. **D**, medial view. Abbreviations: 1-4, premaxillary alveoli; en, external naris; dps, dorsal premaxillary symphyseal surface; if, incisive foramen; ma, articular surface for attachment of the maxilla; n, nasal; na, articular surface for attachment of the nasal; nc, narial canal; pdp, posterior dorsal process of the premaxilla; pps, palatal premaxillary symphyseal surface; rn, reception notch for fourth dentary tooth; rp, reception pit for first dentary tooth. Scale bar = 20 mm.

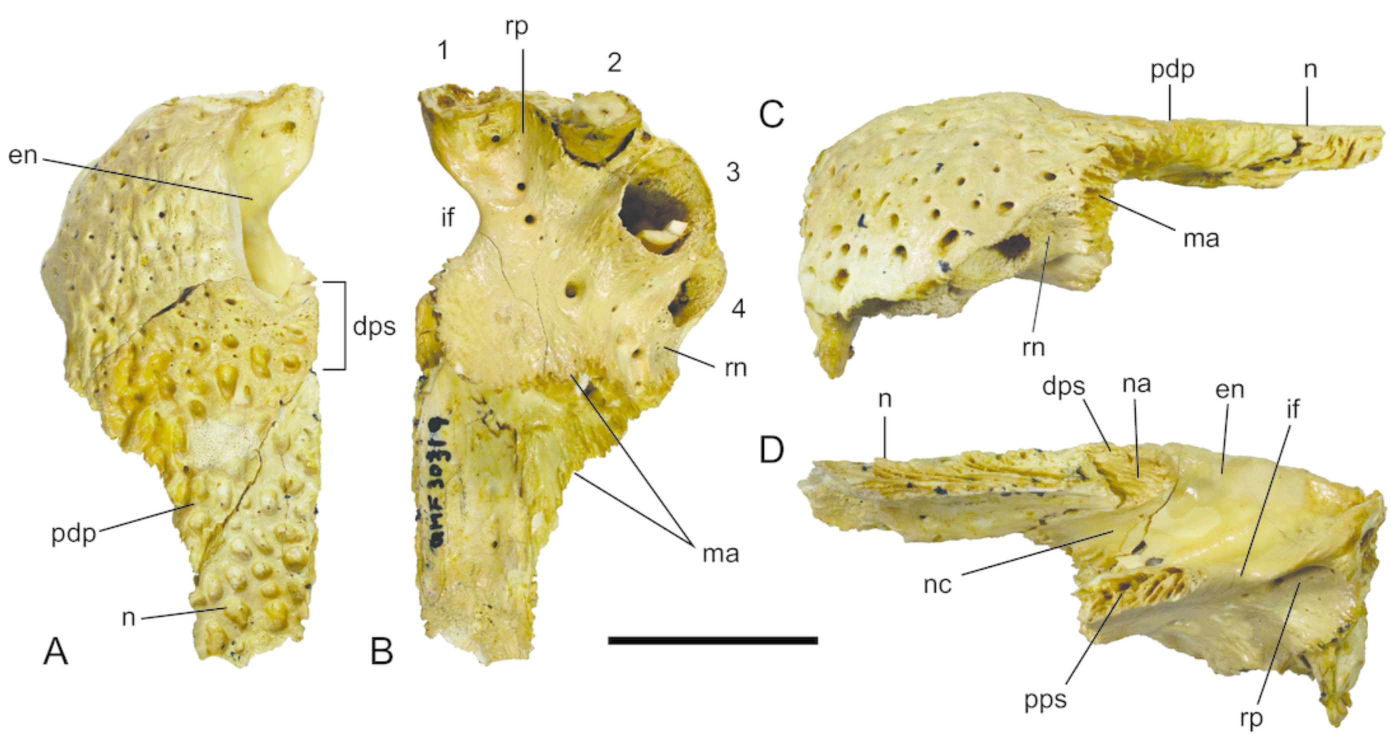
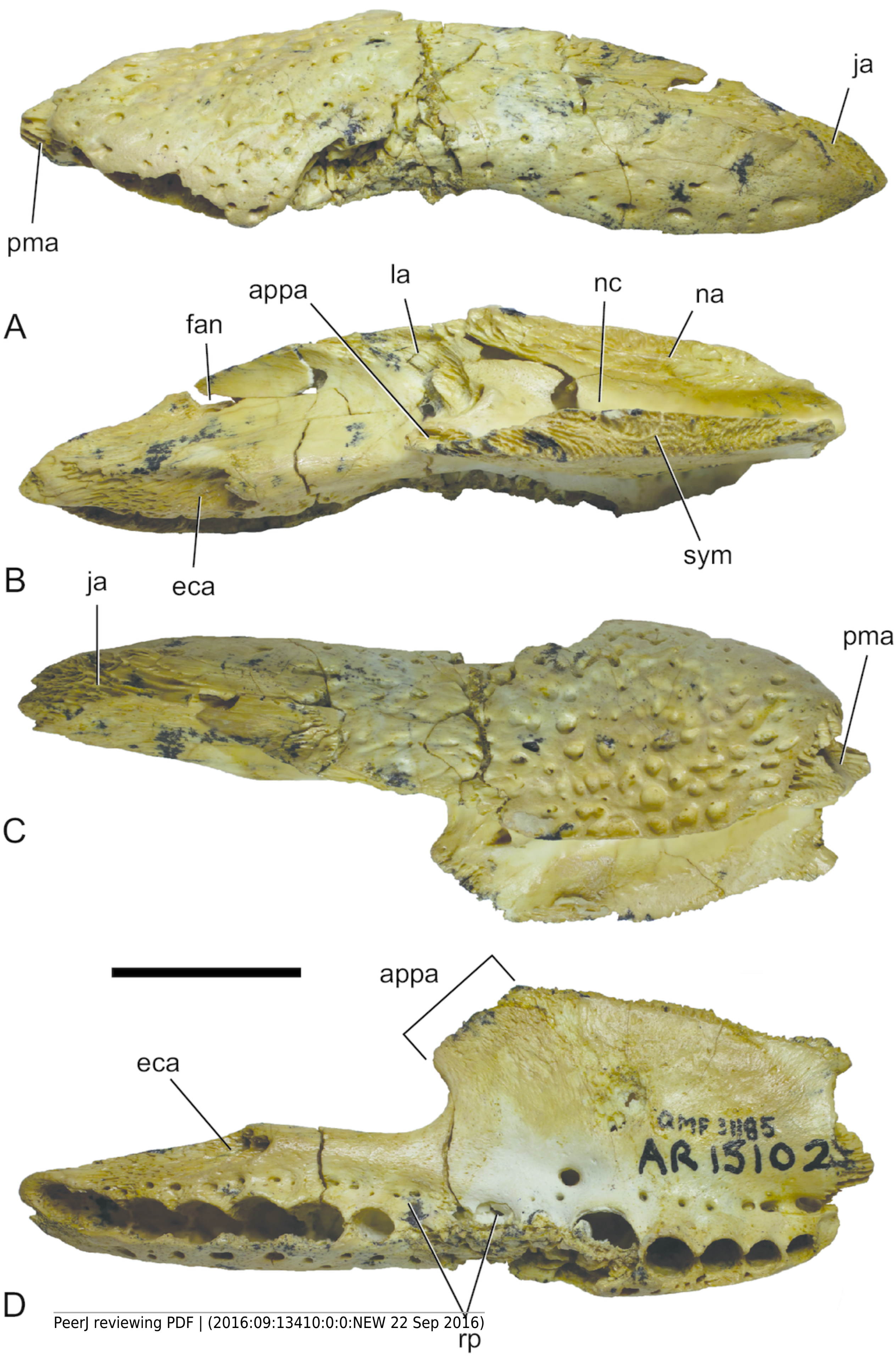


Figure 9

Baru darrowi Willis, Murray and Megirian, 1990, QM F31185, left maxilla of a juvenile from Ringtail Site, Riversleigh World Heritage Area.

A, lateral view. **B**, medial view. **C**, dorsal view. **D**, ventral view. Abbreviations: appa, articular surface for the attachment of the anterior process of the palatine; eca, articular surface for the attachment of the ectopterygoid; fan, foramen for n. alveolaris dorsalis caudalis; ja, articular surface for the attachment of the jugal; la, articular surface for the attachment of the lacrimal; na, articular surface for the attachment of the nasal; nc, narial canal; pma, articular surface for the attachment of the premaxilla; rp, reception pit for dentary teeth; sym, symphyseal surface. Scale bar = 20 mm.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AR 15102
rp
D

Figure 10

Mekosuchinae gen. et. sp. indet., QM F31004, right dentary from Ringtail Site, Riversleigh World Heritage Area.

A, lateral view. **B**, medial view. **C**, dorsal view. **D**, ventral view. Abbreviations: atsa, anterior tip of the articular surface for the splenial; emf, notch forming the anterior margin of the external mandibular fenestra; mc, meckelian canal; saa, articular surface for the surangular; sym, symphyseal surface of the dentary. Scale bar = 20 mm.

Figure 11

Geographic and stratigraphic distribution of *Baru darrowi* Willis, Murray and Megirian, 1990 and *B. wickeni* Willis, 1997a.

Map of Australia showing Queensland and the Northern Territory and the late Oligocene and middle Miocene sites that have produced these species.

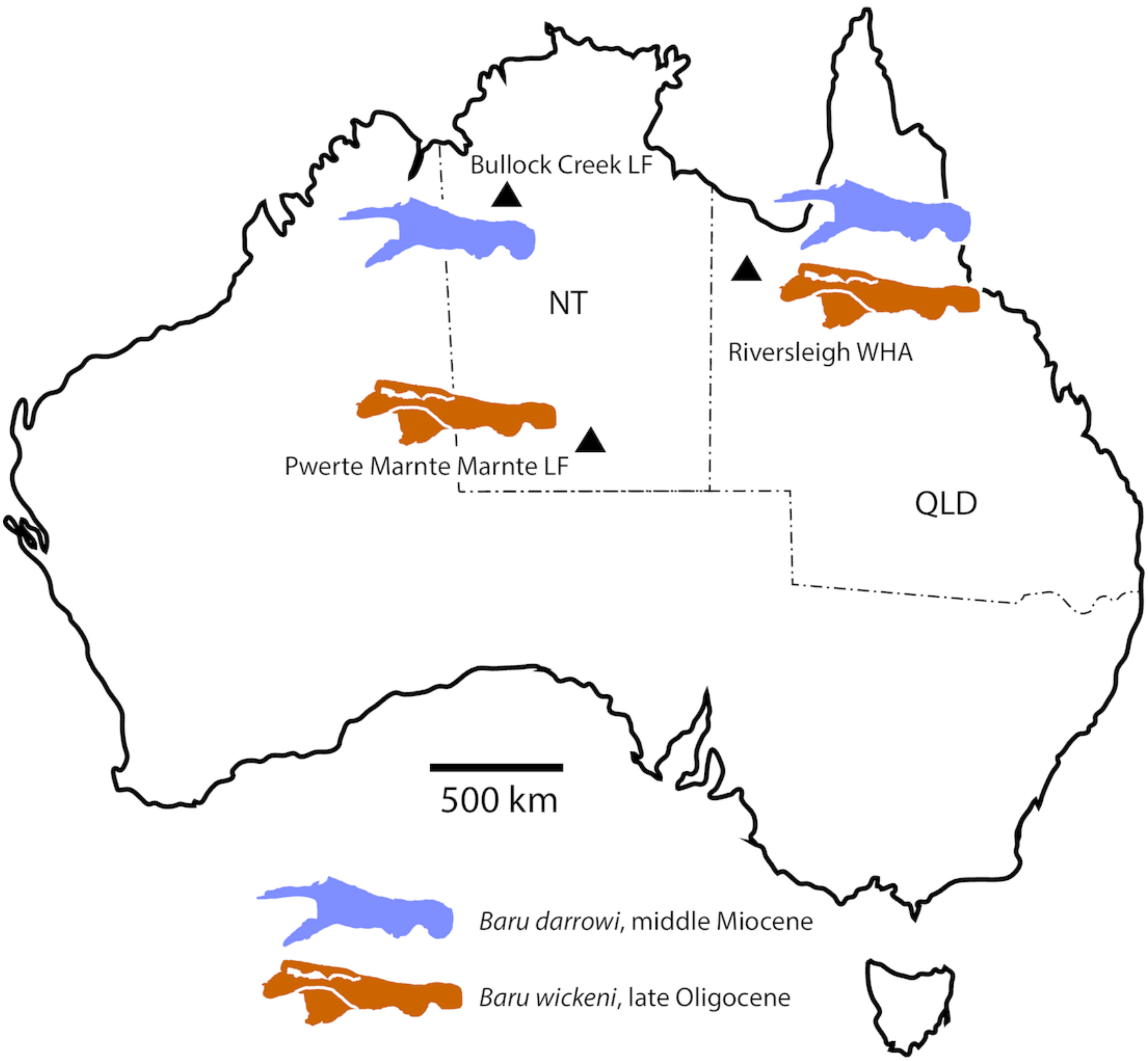

Figure 12

Geographic distribution of large mekosuchines in the late Oligocene of Australia.

Map of Australia showing position of the Lake Eyre Basin (pale brown) and the north/south division of *Baru wickeni* Willis, 1997a and *Australosuchus clarkae* Willis and Molnar, 1991 at about 26° S latitude (approximately 43° S palaeolatitude in the late Oligocene).

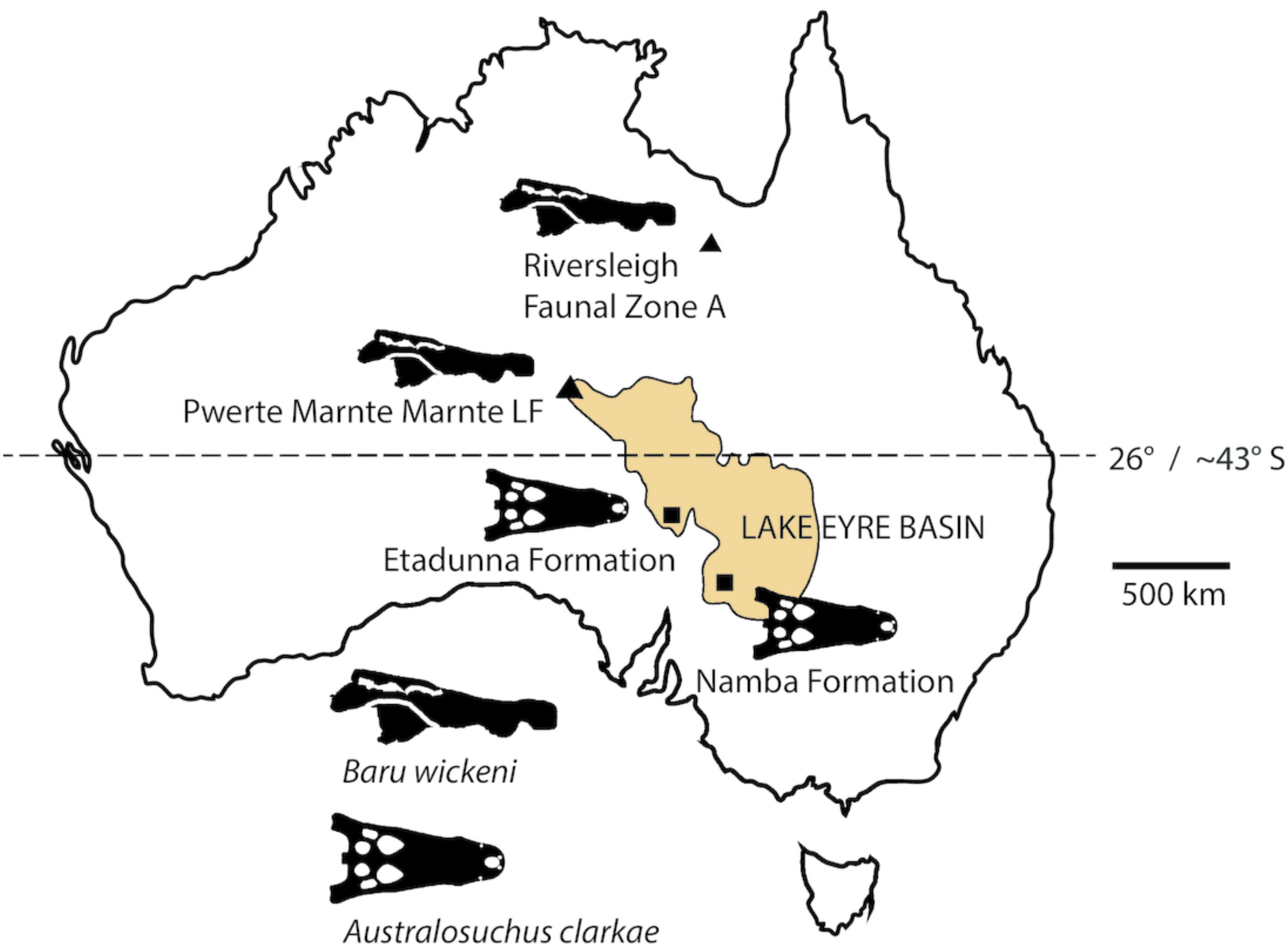

Figure 13

Baru wickeni Willis, 1997a, NTM P91171-1, near complete skull from 300BR Site, Riverseligh World Heritage Area.

A, dorsal view. **B**, right lateral view. **C**, ventral view. **D**, left lateral view. **E**, occipital view.

Abbreviation: vlf, ventrolateral flange. Scale bar = 200 mm.