Re-discovery of the *Euparkeria* bonebed locality (Mid-Triassic) in Aliwal North, South Africa, with an update of the taphonomy and depositional environment

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Received 27 May 2022. Accepted 12 May 2023

Euparkeria capensis is an Early to Middle Triassic archosauriform reptile widely regarded as phylogenetically close to the base of the Archosauria. Fossils of this species are only known from a single locality in the townlands of Aliwal North, South Africa. The exact location was, until now, uncertain due to mis-reading of the field notes of the collector Mr Alfred 'Gogga' Brown and conflicting anecdotal information gleaned from local townsfolk. Careful transcription of the voluminous handwritten field notes, followed by archival research in the town museum, and ground-truthing of the targeted area, has led to the re-discovery of the *Euparkeria* type locality. Sedimentological facies analysis of the locality combined with taphonomic observations of the 38 fossil-bearing rock slabs collected by Brown, now housed in the Iziko South African Museum, reveal the following scenario for the origin of the *Euparkeria/Mesosuchus* bonebed: the bones are preserved within the base of two tabular massive sandstone beds in upper point-bar facies of a high sinuosity channel-fill. The stratigraphic position, sedimentology, and geometry of the sandstone beds with their interdigitation with overlying floodplain mudrocks is interpreted as part of an infilled chute-channel cutting across a point-bar of a meandering river. The taphonomic analysis of the main bonebed suggests that the initial concentration of tetrapod remains was controlled by a combination of a mass mortality event of a pack of *Euparkeria*, and a few *Mesosuchus* becoming overwhelmed by a flash flood, and the hydrodynamics of the small floating carcasses getting trapped within the confines of a downstream chute-channel. The re-discovered *Euparkeria* locality is stratigraphically positioned at the top of a locally significant sandstone marker bed informally named the Eldorado marker. This unit is generally accepted as the contact between the lower and middle Burgersdorp Fm. Biostratigraphically, the locality is positioned within the transition between the lower and middle subzones of the *Cynognathus* AZ, namely *Langbergia-Garjainia* below and *Trirachodon-Kannemeyeria* above. This is some 23 m lower in the stratigraphy than previously thought, and the possible association with *Langbergia*-type burrow casts leads us to tentatively place it within the lower subzone.

Keywords: archosauromorph, *Euparkeria /Mesosuchus*, type locality, bonebed, chute channel-fill, stratigraphy.

INTRODUCTION

The local postmaster and amateur natural historian Alfred 'Gogga' Brown first discovered fossils of the well-known and phylogenetically significant archosauriform *Euparkeria capensis* (Fig. 1) on 22 July 1907, within the townlands of Aliwal North in the Eastern Cape Province of South Africa (Fig. 2). The rocks that crop out in and around Aliwal North are predominantly mudrocks of the Early to Middle Triassic (Olenekian-Anisian) Burgersdorp Formation (Beaufort Group, Karoo Supergroup). According to the latest biostratigraphic scheme (Hancox *et al*. 2020) these exposures correlate with the upper *Langbergia-Garjainia* (*L-G*) and *Trirachodon-Kannemeyeria* (*T-K*) subzones of the *Cynognathus* Assemblage Zone (AZ). At the time of their first discovery, Brown was unaware of the taxonomic importance of the specimens and referred to them in his field notes as simply 'saurian' remains. He made additional finds in 1911 and 1912 at the same locality that were also recorded in his handwritten journals. In the following century of palaeontological fieldwork in the Karoo Basin, no more positively identified fossils of *Euparkeria* have been discovered. Furthermore, the exact location of the *Euparkeria* type locality within the commonage of Aliwal North has become obscured by the intervening years. Two factors are responsible for this confusion: increasing human occupation of the commonage, which has modified the topography and hidden the discovery site; and a succession of researchers making their own transcriptions of Brown's journals, leading them to propose two different sites that are at different stratigraphic levels (von Huene 1925; Ewer 1965).

One of the sandstone slabs collected in 1911, containing the intermingled skeletons of several individuals, was examined by D.M.S. Watson in 1911 (Watson 1912). At the time the specimens were largely unprepared, and Watson considered that all the individuals belonged to the same taxon, which he identified as *Mesosuchus browni*. When

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***Palaeontologia africana* 56: 118–132 — ISSN 2410-4418 [Palaeontol. afr.] Online only**
Permanently archived on the 21st of July 2023 at the University of the Witwatersrand, Johannesburg, South Africa
The article is permanently archived at: https://hdl.handle.net/10539/35707

Figure 1. **A**, *Euparkeria capensis* type specimen SAM-PK-5867 in dorsolateral view. **B**, *Euparkeria capensis* reconstruction in the African Dinosaur gallery of the Iziko South African Museum. Scale bar in A = 3 cm, in B = 10 cm.

Robert Broom visited Brown in Aliwal North in July 1913 he did more preparation on the slab and realized that it contained the remains of two different taxa. Subsequently, he described the second taxon as *Euparkeria capensis* (Broom, 1913). At the time, Broom recognized the phylogenetic importance of *Euparkeria* within the 'pseudosuchian' lineage and its significance regarding the origin of crocodilians and dinosaurs (including birds). Ewer (1965) performed the first full anatomical study of *Euparkeria capensis*. Today, ongoing studies of *Euparkeria capensis* are key in the understanding of the origin and evolution of the Archosauria (e.g. Nesbitt 2011; Ezcurra

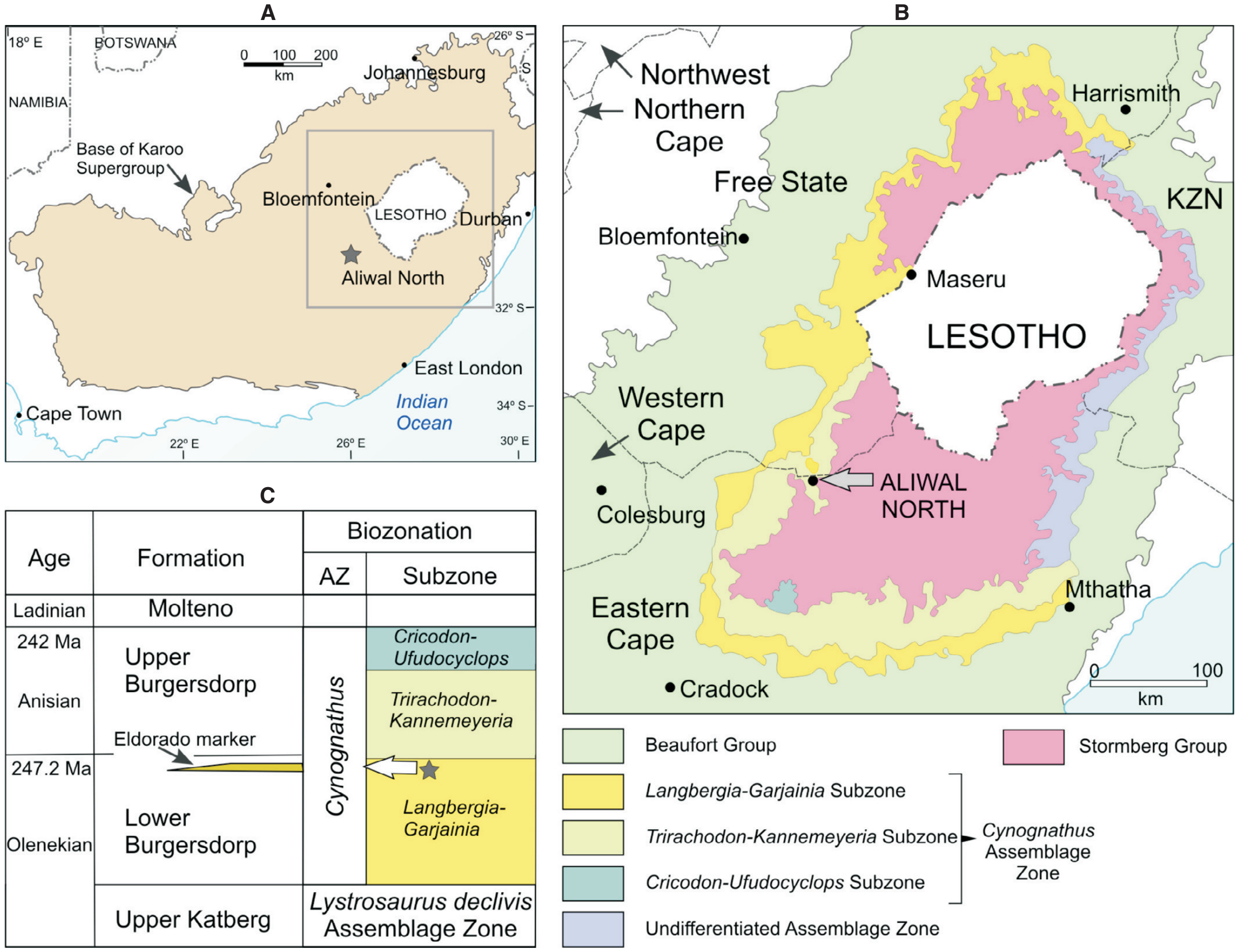

Figure 2. Geographic and stratigraphic position of *Euparkeria* type locality. **A**, Location of Aliwal North (star) within the outcrop area of the main Karoo Basin. **B**, Detail of square in (A) showing position of Aliwal North and the biostratigraphic subdivisions of the *Cynognathus* Assemblage Zone (after Hancox *et al* 2020). **C**, Stratigraphy of the Burgersdorp Formation in the study area with position of the re-discovered *Euparkeria* type locality (starred).

2016; Sobral *et al*. 2016; Sookias 2016; Demuth *et al*. 2020; Sookias *et al*. 2020; Spiekman *et al*. 2021). *Euparkeria* possesses several clear archosaur features (e.g. the presence of antorbital and mandibular fenestrae, serrated teeth), yet it phylogenetically predates the crocodile–bird split, and as such, represents a key taxon for understanding the origin of modern archosaurs.

The important events surrounding the discovery and identification of *Euparkeria* that led to the South African Museum acquiring Brown's fossil collection and his journals, are described in the Supplementary material: S1 — Historical note. The study of *Euparkeria* will be incomplete without a full understanding of the approximately 247-million-year-old taphonomic pathway that culminated in the preservation of multiple individuals in the sandstone slabs collected by Brown. To gain a full understanding of the origin of the *Euparkeria* bonebed, pinpointing the exact location of Brown's finds was considered paramount. Here, we summarize the controversies that surround the discoveries and present new evidence for the exact location of the *Euparkeria* and *Mesosuchus* type locality. This is followed-up by field investigations of the host strata and collection-based analysis of all the fossils that are used to reconstruct the depositional environment and taphonomic pathway leading to the preservation of the *Euparkeria* bonebed.

MATERIAL AND METHODS

Citing the handwritten journals of Alfred Brown, Haughton (1922) records the name for the *Euparkeria* locality as 'Krietfontein Spruit' within the Aliwal North commonage. A systematic manual search of Brown's original journals was performed to identify all mentions of *Euparkeria* or 'Saurian' and Krietfontein (or Krielfontein Spruit, as Brown did not consistently cross his longhand 't's'). The key paragraphs with these references were transcribed (see Fig. 3 and Supplementary material). The explicit locality information derived from this analysis was used to locate the potential site on historical aerial photographs (archived at the Aliwal North Municipal Museum), Google Earth Pro, and Google Maps. A field trip was undertaken in early December 2019 to visit the newly re-discovered locality. One of the Iziko specimens of a sandstone block containing a fragment of *Euparkeria* bone was taken to the field to find a matching sandstone bed with respect to colour and texture. When this was located, a cursory search yielded an *in situ* limb bone fragment that exactly matched that of the *Euparkeria*.

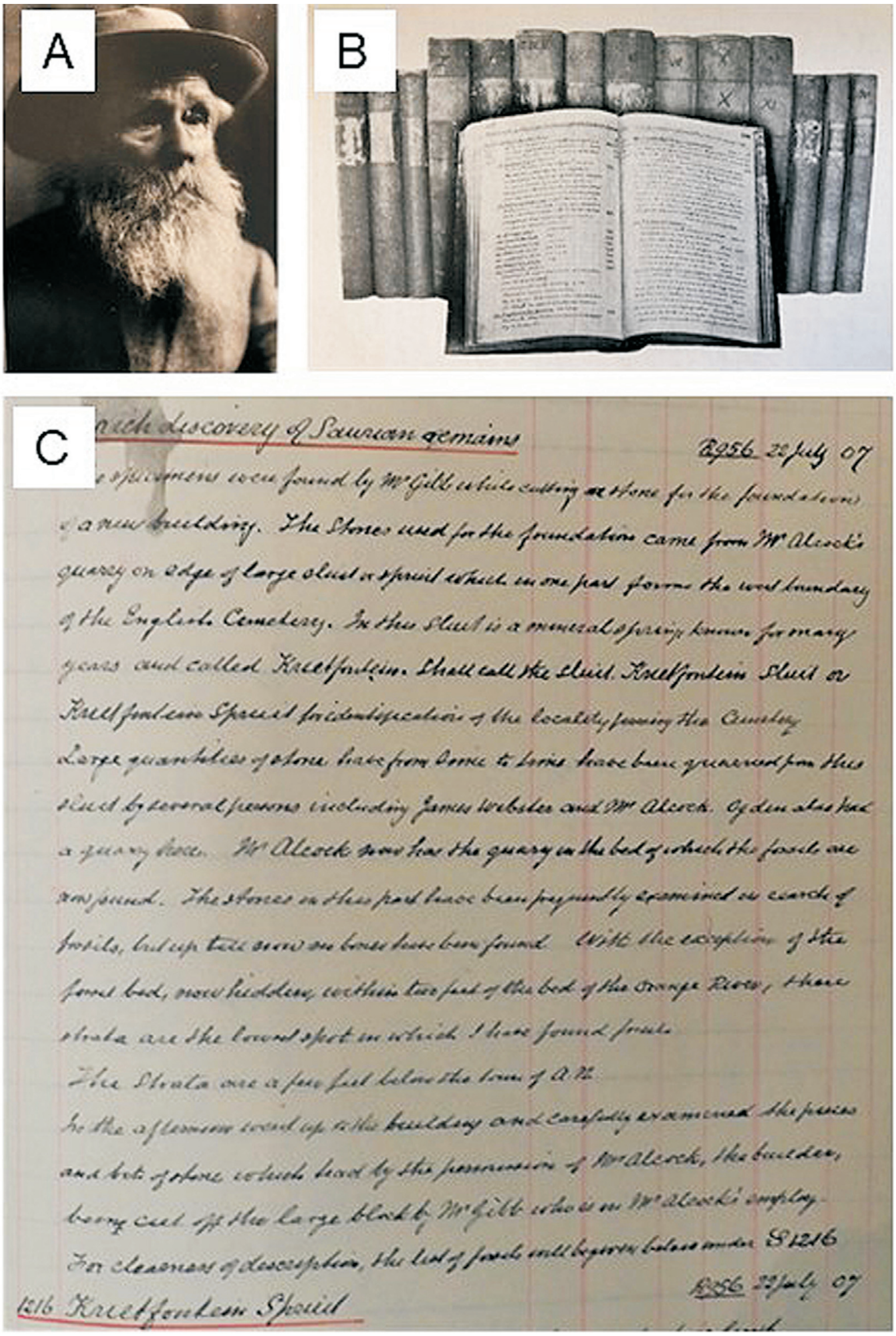

Figure 3. **A**, Alfred 'Gogga' Brown; **B**, his fifteen handwritten journals, and **C**, Brown's notes of 22 July 1907 recording the first discovery of *Euparkeria* (these notes appear twice in his journals, the second of which also contains a list of fossils). Our transcription is as follows:

1215 A rich discovery of Saurian remains *P956 22 July 07*

The specimens were found by Mr Gibb while cutting a stone for the foundation of a new building. The stones used for the foundations came from Mr Alcock's quarry on edge of large sluit or spruit which in one part forms the west boundary of the English Cemetery. In this sluit is a mineral spring known for many years and called Krietfontein. Shall call the sluit Krietfontein Sluit or Krietfontein Spruit for identification of the locality passing the Cemetery. Large quantities of stone have from time to time have [sic] *been quarried from this sluit by several persons including James Webster and Mr Alcock. Ogden also had a quarry here. Mr Alcock now has the quarry in the bed of which the fossils are now found. The stones on this part have been frequently examined in search of fossils, but up till now no bones have been found. With the exception of the fossil bed, now hidden, within two feet of the bed of the Orange River, these strata are the lowest spot in which I have found fossils.*

The strata are a few feet below the town of A. N.

In the afternoon went up to the building and carefully examined the pieces and bits of stone which had by the permissions of Mr Alcock, the builder, been cut off the large block by Mr Gibb who is in Mr Alcock's employ.

For clearness of description, the list of fossils will be given below under P1216

A sedimentological log of approximately 35 stratigraphic metres was measured along Krietfontein spruit from the water level of the Orange River up to a sandstone-capped hillock above the eye of the Krietfontein mineral spring. The log was recorded during drought with the Orange River water level near its minimum, which allowed access to the lowermost sandstone beds that are described in Brown's notes. Standard field methods, including Jacob's staff and Abney level, were used to record the sedimentary succession to an accuracy of 5 cm as well as a Munsell soil colour chart (2009 revision) to document the various rock colours. Bedding planes, rock textures, sedimentary structures and fossils were plotted onto the graphic log. A more detailed section was measured at the location of the sandstone bed containing the newly discovered archosaur limb bone fragment. This new fossil evidence combined with the archival research results we regard as confirmation that the *Euparkeria* type locality has been re-discovered. A second trip was undertaken in August 2021 to verify field observations made during the initial visit and to continue searching the local museum archives for independent information of when the quarries were active to cross-reference them with Brown's journals.

Taphonomic observations of the *Euparkeria* and *Mesosuchus* skeletons on the 38 sandstone slabs stored in the Iziko South African Museum's Karoo Palaeontology collection were made with a view to understanding their modes of death, disarticulation, and burial. This involved assessment of bone articulation (taphonomic class), skeletal element representation, spatial arrangement, bone breakage, and other bone surface modifications (e.g. invertebrate burrows, tooth marks etc.).

RESULTS

Re-discovery of *Euparkeria* type locality

Archival finds on Euparkeria *type locality*

Systematic review of the Alfred Brown Journals: It is generally accepted that all the positively identified *Euparkeria* and *Mesosuchus* specimens came from the same locality in Aliwal North (now the Walter Sisulu Municipality), Eastern Cape, South Africa, that was assigned to 'the *Cynognathus* zone of the Karroo System' by Watson (1912). However, our new transcriptions of various notes in the original handwritten journals of Alfred Brown indicate much more precisely where the *Euparkeria*-bearing sandstone slabs were collected. Brown's journals (and many of the fossils – see below) were taken into Iziko South African Museum's collections in 1921, a year after Brown's death, but have not been photocopied, digitized or fully-transcribed.

Brown's notes of 22, 23 and 26 July 1907 (Fig. 3) record that the first specimens of what was later named *Euparkeria* were discovered in Mr Alexander Alcock's stone quarry on the west bank of a 'sluit' (deep valley) along the western edge of the English Cemetery (see Figs 4 and 5). The source of the stream in this valley is a mineral spring that was known at the time as Krietfontein. Brown named the stream 'Krietfontein Spruit' in his written record of the locality at the time. The first specimens were found by one of the quarrymen, a Mr Gibb (no first name is known), on 22 July 1907, whilst he was excavating sandstone slabs for the foundations of a new building in the town of Aliwal North (near the Balmoral Hotel). Mr Alcock immediately informed Brown who was a well-known local natural historian. Further specimens were discovered in Alcock's quarry on 24 and 26 April 1911, this time in the stream bed several metres east of the quarry. The final discovery was made on 21 July 1912, this time in Webster's quarry which was excavated into the same sandstone beds on the eastern side of the valley directly opposite Alcock's quarry. Brown describes them as 'considerable fossil remains of a fine saurian', and working after-hours, a quarryman cut out the blocks for Brown.

Our re-examination and transcription of the journals confirms Haughton's (1922) name for the locality as 'Krietfontein Spruit' ('fontein' meaning 'water source' and 'spruit' meaning 'stream' in Afrikaans). As suggested by Ewer (1965), the transcription of the journals confirms that this is Brown's personal name for the stream running away from 'Krietfontein'. In notes that Brown entered in his journal on 6 and 20 December 1911, he identifies the exact location of the source of the spring as on the south side of the dolerite dyke that crosses the stream south of the quarries. He also states that 'The water smells strong like a rinsed-out gun barrel'. It is worth noting that the word for gunpowder in Dutch and Afrikaans is 'kruit', or 'buskruit'. The pronunciation of the words 'kruit' and 'kriet' by an English-speaking person would be similar. This may well be why the warm water emerging at this spring, one of many similar in the area that have a sulphurous odour, was known as 'Krietfontein'. The authors (R.M.H.S. & F.P.W.) have confirmed that this spring continues today to source the stream alongside which the *Euparkeria* quarry is located and is indeed sulphurous.

Up until Broom's third visit to Brown in July 1913, Brown referred to the specimens from Krietfontein as the 'Krietfontein saurians'. During this visit Broom inspected the specimens and shortly after that described and named the new taxon *Euparkeria capensis* (Broom, 1913). Brown revised his list of fossils in 1913, and it is here that he makes the important link between the 'Krietfontein saurians' and *Euparkeria*, *Browniella* and *Mesosuchus*. This journal entry also validates the exact location of the type locality of *Euparkeria* and *Mesosuchus*.

From this we surmise that the block containing *Euparkeria* SAM-PK-K8050 and *Mesosuchus browni* specimen SAM-PK-K8051 must have been part of the 1911 discovery (see Supplementary material: Transcript S13 of Brown's journal), as it was examined and noted by D.M.S. Watson in 1911 (Watson 1912); however, which other specimens were found in which year is still unknown pending further investigations of Brown's journals and correspondence.

The move of Brown's collection to the South African Museum: Alfred Brown died intestate in 1920 and his collections went to the highest bidder, the South African Museum

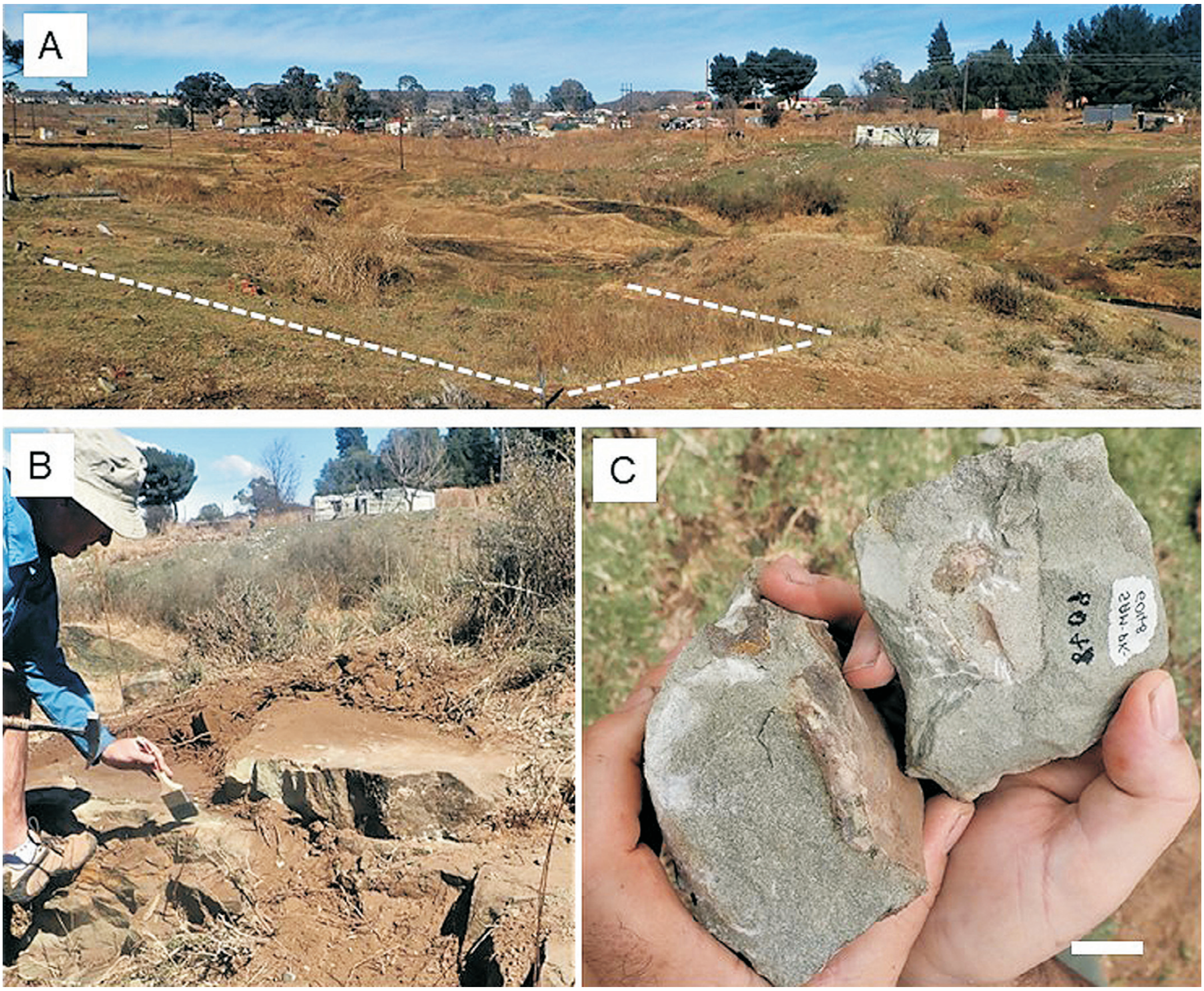

Figure 4. **A**, View south over Krietfontein spruit with remnants of Webster's quarry outlined in foreground. **B**, Cliff exposure of massive sandstone beds in Webster's quarry where new *Euparkeria* bone was found. **C**, *Euparkeria* hand specimen from Iziko collections (top right) and matching sandstone with similar limb bone fragment (lower left). Scale bar in C = 1.6 cm.

(SAM) in Cape Town in 1921 (see Supplementary Material: S1 — Historical note). Sidney Haughton immediately started work on the specimens and published his first results a year later (Haughton 1922). According to Ewer (1965), these specimens are labelled in the SAM catalogue as 'A. Brown collection, Krielfontein, Aliwal North'. In 1924 and 1925 more fossils were presented to the SAM by Mr Higgins, a lifelong friend of Brown (Ewer 1965). The 1924 consignment to the SAM is labelled 'Higgins collection, Krielfontein, Aliwal North' and that of 1925 labelled 'A. W. Higgins collection, Quarry, Commonage, Aliwal North' – indicating that both consignments were from the same locality as Brown had collected his specimens. It appears that in the transfer to the SAM 'Krietfontein' was misread as 'Krielfontein' likely because when writing with a dip-pen Brown commonly failed to cross his 't's'. Haughton (1922) correctly reported the locality as 'Krietfontein Spruit on the Aliwal North Commonage' and concluded that all *Euparkeria* specimens collected up until 1922 were from a single locality. Based on a communication from a certain Colonel de Wet, Ewer (1965) proposed that some, or even all, of the specimens labelled 'A. Brown collection' may have been actually collected by Higgins for Brown. This suggestion is not supported by Brown's notes; and given Higgins and Brown were friends, it seems unlikely he would have made such a mistake.

Tracking down additional specimens from the Euparkeria *type locality*: In 1911, Brown handed a specimen from the *Euparkeria* quarry to visiting scientist D.M.S. Watson who at the time was based at University College London. It was then transferred to the University Museum of Zoology in Cambridge (now UMZC T.692). Two specimens from Brown's collection (then SAM 7708 and 7698) were given by the SAM to the Institut für Geologie und Paläontologie at the University of Tübingen (renumbered GPIT/RE/12913 and GPIT/RE/15029). In 1913, four specimens from the quarry were received by the American Museum of Natural History (AMNH FARB 2238, 2239, 5548, and 19351); as part of a purchase of '200 South African fossils' from Robert Broom, who had visited Aliwal North in 1913 and

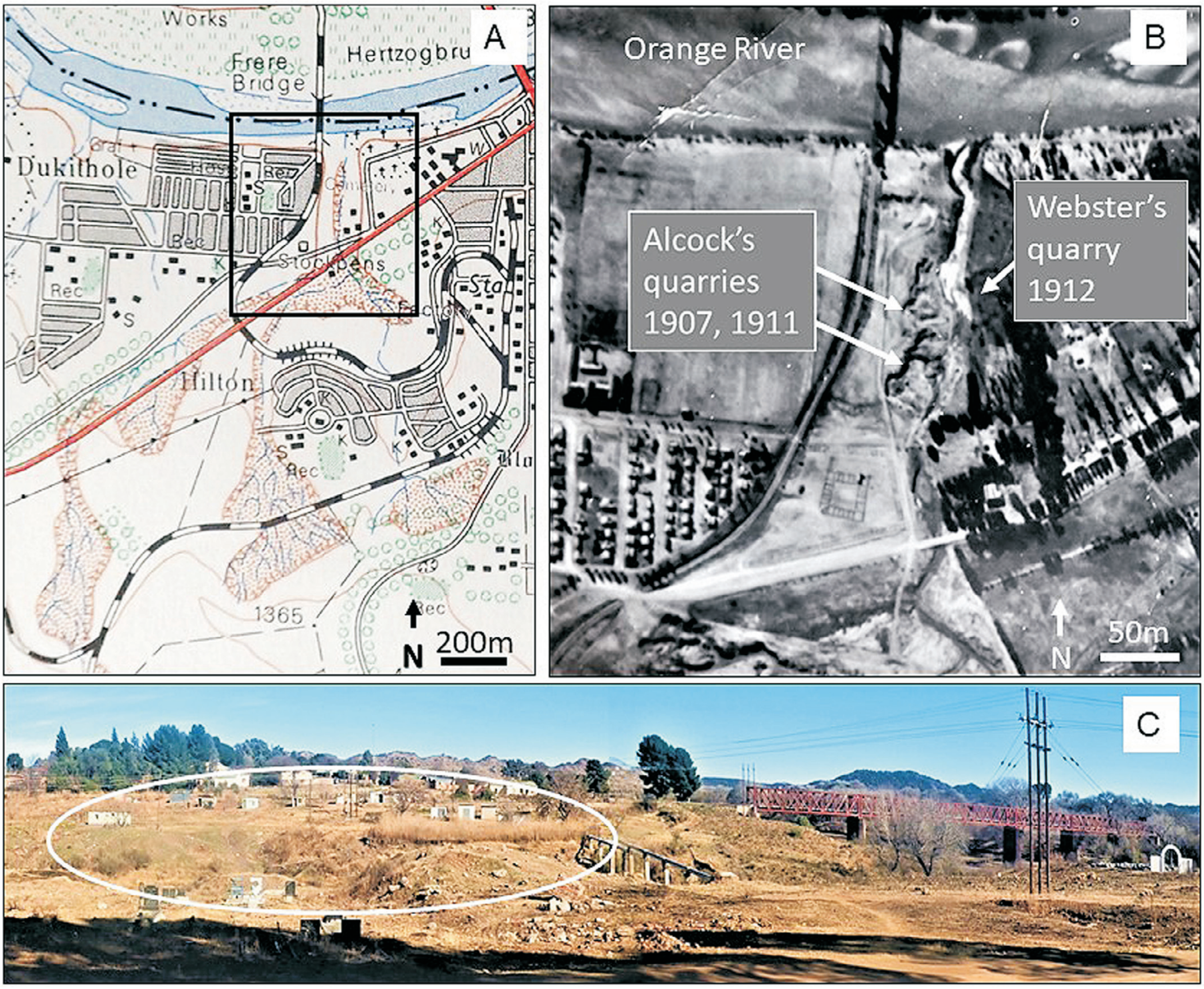

Figure 5. Re-discovered *Euparkeria* quarry: Archival research in Aliwal North Museum yielded (**A**) a detail of an old topocadastral map that delimits the Krietfontein spruit and its headwaters (shaded brown). Also, a detail from an aerial photograph archived at the Aliwal North Municipal Museum (**B**) taken before 1944 clearly shows the edges of Alcock's stone quarries on the western side of the stream identified in Brown's journals as the source of multiple *Euparkeria*/*Mesosuchus*-bearing sandstone blocks. Looking west from the English Cemetery today (**C**) Alcock's quarries have been substantially infilled (circled area in C) by a combination of natural soil erosion and human dumping activities. Abutments and piers of the Frere rail bridge across the Orange River, visible to the right, are built with sandstone blocks from these quarries.

presumably acquired the specimens directly from Mr Brown.

Field search for *Euparkeria* type locality

In 2019 the authors (R.M.H.S. & F.P.W.) followed the detailed directions from Brown's journal to an abandoned quarry site on the western bank of the stream running alongside of the English Graveyard in Aliwal North. Here, in what they identified as Webster's 1912 quarry, they came across a man-made cliff exposure of massive fine-grained sandstone identical in lithology, texture and colour to the matrix of the *Euparkeria* blocks in the Iziko South African Museum collections (see Fig. 4 and Fig. 1).

Closer inspection of the cliff face yielded an *in situ* limb bone that closely matched the morphology and preservation style of the *Euparkeria* specimens (see Fig. 4). Comparisons of the bone and matrix characteristics to those of the *Euparkeria* specimens in the Iziko Museum revealed a remarkably close correspondence, such that we can accept that this limb bone is from the same stratigraphic horizon as the *Euparkeria* bonebed. Side-by-side comparison of the new mid-shaft specimen with the right femur of the *Euparkeria* type specimen (see Supplementary material, Fig. S1) shows close similarity in length, width and curvature.

Following the 'ground truthing' of information gleaned from Brown's notes we conclude that the *Euparkeria*-bearing sandstone blocks in the collections of the Iziko South African Museum all came from Mr Alcock's, and later Mr Webster's, quarry. The precise location of the re-discovered quarry is corroborated by records kept in the Aliwal North Municipal Museum as well as Brown's journal, which state that the position of the quarry in Krietfontein Spruit is some 150 m upstream from the confluence with the Orange River, near the southern end of the old railway bridge (see Fig. 5). In the Aliwal North Municipal Museum an undated aerial photograph of the town taken after 1912 but before 1944 shows the outline of the abandoned quarry much more clearly than today (Fig. 5B). The conclusion regarding the date is based on the absence of the sewer aqueduct across Krietfontein Spruit (Fig. 5B) and its presence on photographs from 1944 onwards (e.g. Fig. 5C).

Stratigraphy of the *Euparkeria* type locality

The area that Ewer (1965), who was clearly unaware of the content of Brown's journals, proposed as the *Euparkeria* locality was based upon erroneous directions from a local resident. She reports the locality as 'on one of the commonages over the brow of a hill on the left of the road to Lady Grey just outside Aliwal North' (Ewer 1965, p. 381). This hill is 5 km away from the Krietfontein Spruit quarry, some 23 m higher in the succession. The exposed sandstone has no lithological similarity with the *Euparkeria* matrix, nor does it show signs of quarrying activity.

The quarry floor of the re-discovered *Euparkeria* type locality in Krietfontein Spruit is assigned to the upper *Langbergia*-*Garjainia* Subzone of the *Cynognathus* AZ (Hancox *et al*. 2020) close to, but still some 12 m below the transition with the overlying *Trirachodon-Kannemeyeria* Subzone. The bones are preserved in pale-olive fine-grained massive sandstone at the top of a laterally extensive >8 m-thick, multistoreyed channel sandstone body which we consider to be the lateral equivalent of an arenaceous unit of the mid Burgersdorp Formation informally referred to as the 'middle marker' (Hancox 1998) or 'Eldorado marker' (Neveling 2004; Fig. 6). The possible association of the stratigraphic equivalent of this marker with *Langbergia* type burrow casts on the Lemoenfontein farm supports our placing of the quarry floor within the lower subzone (Wolvaardt 2021; Wolvaardt *et al*. 2023). This marker sandstone corresponds to the last episode of Katberg-style deposition within the Tarkastad subgroup (Neveling 2004).

Our focussed transcription of Brown's journals also revealed the type localities of the therocephalian *Sesamodon* (now synonymized with *Microgomphodon*, Abdala *et al*. 2014), the brachyopid temnospondyl *Batrachosuchus* and the basal rhynchosaur *Howesia*. Brown used the names '*Sesamodon* Spot' or 'Theriodont Spot' for the *Sesamodon* locality. *Batrachosuchus* and *Howesia* are both from an exposure he named 'King's Grove' after a plantation of trees growing on the site. This discovery allowed the biostratigraphic positioning of these taxa relative to *Euparkeria* (see Fig. 6 and the Supplementary material). Brown described these localities as follows:

- The Theriodont (or *Sesamodon*) Spot is situated south of the De Wet homestead near the Aliwal North Hot Springs. It is bounded in the north by an east–west running dolerite dyke; in the south by a slow rise; in the east by a stone furrow next to the road connecting the Hot Springs to the town and a solitary flat-topped hill (now on the grounds of the hot springs resort); in the west by part of the sandstone ridge that forms the plateau at the top of the Aliwal North succession of beds.
- The King's Grove plantation extends southeast from the Aliwal North Railway Station and was established to arrest erosion on the south side of the railway line. These mudrock exposures are bounded in the south by the part of the sandstone ridge that forms the plateau at the top of the Aliwal North succession of beds; in the north by the railway line; and extends to just beyond the large railway culvert in the west.

The full transcription and GPS coordinates are provided in the Supplementary material (Transcript S12).

Sedimentology of the *Euparkeria* bonebed

Stonemasons Alcock and Webster were commissioned by the town council at various times to supply foundation stones and building blocks for municipal buildings and bridges in Aliwal North. For each new project the quarries in Krietfontein Spruit were re-opened and extended laterally along the outcrop of an approximately 2.5 m-thick interval of tabular massive and horizontally-laminated sandstone beds that had the optimal bed thickness, hardness and texture to be easily quarried, cut and dressed as dimension stone. Our field investigation of the abandoned Webster quarry yielded an *in situ* archosaur limb bone that not only matches the size and shape of *Euparkeria capensis*, but the colour and texture of the bone and the host matrix is indistinguishable from that of the *Euparkeria* specimens housed in the Iziko South African Museum (see Fig. 4 and Fig. S1).

The quarrymen exploited the uppermost levels of an at least 8 m-thick multistoreyed channel sandstone. An accurate thickness of the sandstone body at the study site is difficult to determine because the base is submerged beneath the Orange River. However, tracking the outcrop some 3.5 km northwestwards to a roadside outcrop on the farm Poortjie and on to correlate with the middle-marker (Hancox 1998) or Eldorado marker (Neveling 2004) on the farm Moerbeidal gives an estimated thickness of approximately 13 m.

The exposed upper part of the lower storey is dominated by vertically-stacked tabular beds of horizontally-laminated, medium-grained, pale-olive (5Y6/3) sandstone with abundant claystone pebbles and chips (Figs 7A, 8A, 8B). Lenses of intraformational conglomerate on the bedding planes are flanked by strongly N–S trending parting lineation. Manganese films blacken many of the weathered surfaces, becoming more pervasive on slickensided sub-vertical planes in a 30 cm thick dark reddish-brown (5YR 4/3) mudstone interbed (2.5 m on Fig. 7A). Above the mudrock interbed the sandstone becomes fine-grained, more olive-grey (5Y4/2) and structured with horizontal laminae with low angle intersections in places and no manganese dioxide staining. At 3.3 m an erosive disconformity is overlain by the upper storey that is dominated by sets of trough and planar cross-bedding with only minor horizontally laminated and massive sandstone towards the top. The vertically stacked trough cross-bedded, light olive-grey (5Y6/2), fine-grained sandstone units are approximately 50 cm thick with mudstone pebble conglomerate lining the scoured bases of each set. Towards the top of upper storey, the trough cross-bedded sets gradually become thinner and more tabular (see Fig. 8C) with the appearance of distinctive planar cross-bedding in places (see 6.75 m on Fig. 7A). The uppermost

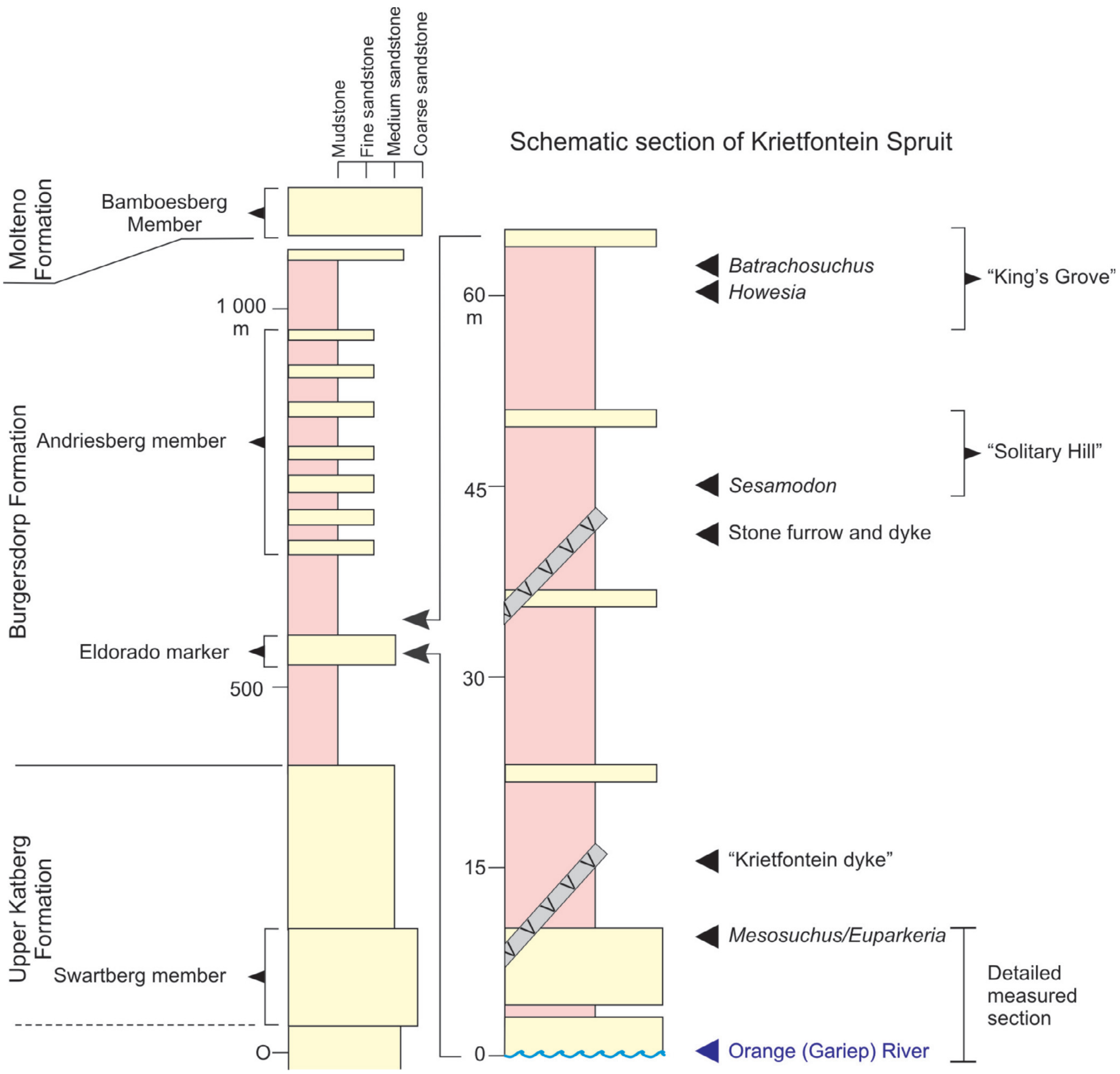

Figure 6. Stratigraphy of the *Euparkeria* type locality. Schematic lithostratigraphic section from Neveling (2004) (left) and a detailed schematic section of the outcrops on Aliwal North commonage (right) containing the topographic features used by Brown to describe the type localities of *Euparkeria*, *Mesosuchus*, *Sesamodon* (now synonymized with *Microgomphodon* (Abdala *et al*. 2014)), *Howesia* and *Batrachosuchus*.

2.5 m interval of sandstone immediately on top of a 0.5 m-thick planar cross-bedded, fine-grained, light olive-grey (5Y6/2) sandstone, comprises two massive sandstone sheets that proved not only to be the best dimension stone but also host for abundant *Euparkeria/Mesosuchus* bones (see detailed section of Fig. 7B). The bones occur at two levels in this interval, both associated with the bases of structureless very fine-grained sheet sandstones (see Fig. 8D). The lower level is, according to Brown's notes, where the true bone-on-bone bonebed accumulations were recovered whereas the upper level yielded mainly isolated bones such as the one found during our field investigation. Some wood impressions in a loose block in the abandoned quarry (Supplementary material, Figs S2 and S3) are likely what Brown records as tree stumps that were associated with the fossil bones.

DISCUSSION

Interpretation of *Euparkeria* bonebed palaeoenvironment

The *Euparkeria* bonebed occurs in the transition between lower and middle Burgersdorp strata which is interpreted as the switch from anastomosed and low sinuosity channels to more meandering river systems (Hancox 1998; Hancox *et al*. 2020; Neveling 2004). Our fieldwork confirms these findings and also suggests that the contact between lower and middle Burgersdorp systems is actually an erosive disconformity, and possibly also a temporal hiatus, within the Eldorado marker (3.3 m on Fig. 7A). The regional climate during accumulation of the lower Burgersdorp is considered to have been warm semi-arid with seasonal rainfall, becoming cooler and wetter during upper Burgersdorp-Molteno times (Retallack 2021; Wolvaardt 2021; Wolvaardt *et al*. 2023).

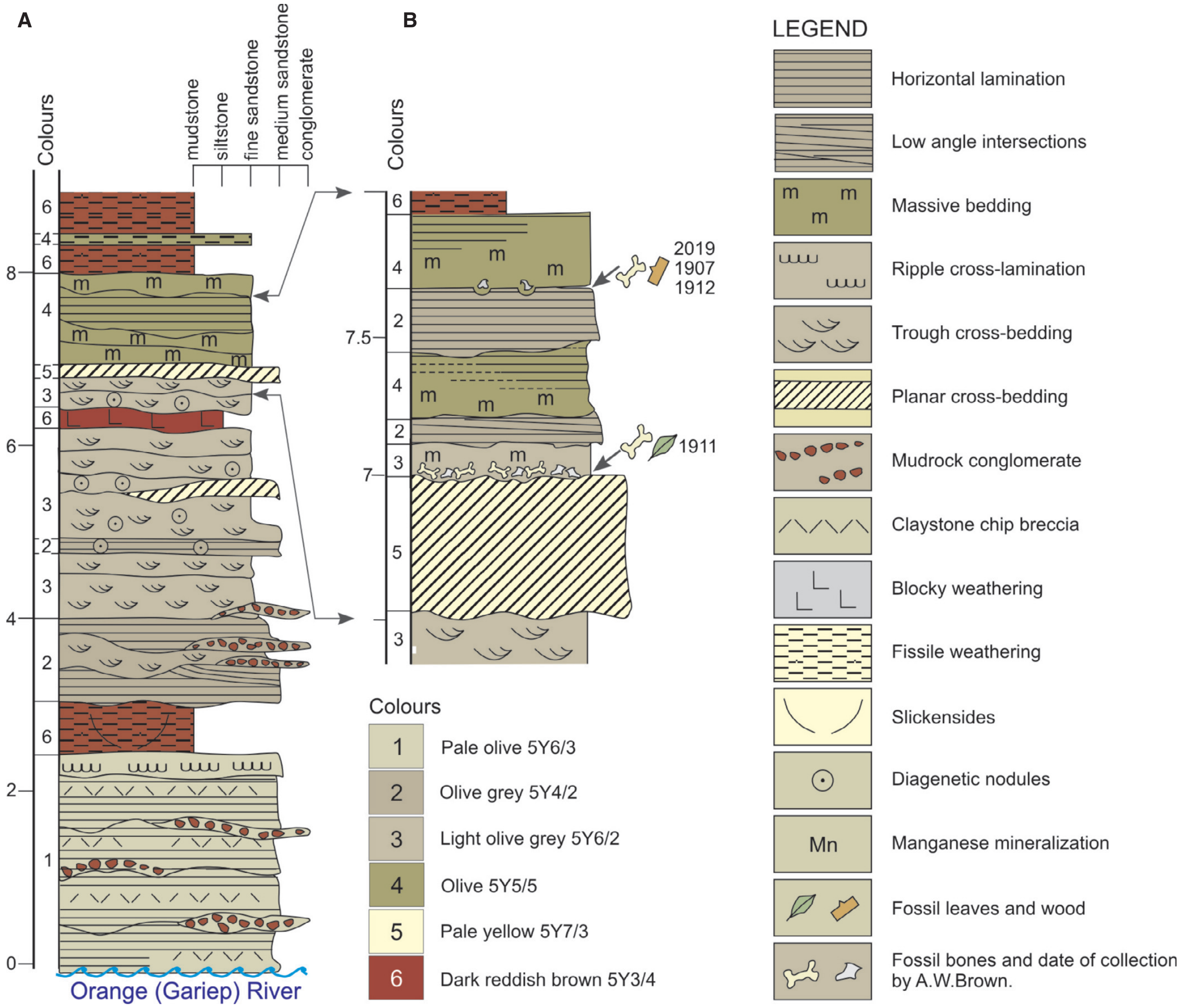

Figure 7. Sedimentology of the *Euparkeria* type locality. **A**, Sedimentological log of the uppermost 8 metres of a multistoreyed channel sandstone considered to be the lateral equivalent of the Eldorado marker of Neveling (2004). **B**, Detailed log of the wall of Webster's quarry indicating the position of the 2019 *in situ* archosaur bone, the corresponding positions of the 1907 and 1912 finds by Brown in the adjacent Alcock's quarry and position of the 1911 *Euparkeria/Mesosuchus* bonebed based on Brown's 1911 field notes.

The lower storey of the laterally extensive multistoreyed channel sandstone at the *Euparkeria* type locality is dominated by upper flow regime horizontal lamination with abundant mud chips and pebbles interpreted as in-channel deposits of a wide, shallow, low-sinuosity river system (Type 1 channel fill of Neveling 2004). However, the upper trough cross-bedded storey is of a different fluvial regime, interpreted as the in-channel deposits of a fluctuating, more turbulent flow in a sinuous meandering channel system. The tabular sandstone beds at the uppermost transition of the point-bar into the overlying floodplain deposits are an indication of gradual abandonment of the meander by chute or neck cut-off rather than a sudden avulsion (Fig. 9). In sand-bed river meanders undergoing chute cut-off it is notable that peak floods that flow into the chute channel rapidly lose competence and deposit their sandy bedload as structureless hyperconcentrated underflows (Schwendel *et al*. 2018). The stacked structureless tabular fine sandstone beds in the uppermost point-bar facies at the *Euparkeria* type locality host most of the tetrapod fossils. Here we interpret these beds as the basal units of a chute channel-fill that were deposited episodically by peak flood events during gradual abandonment of the river meander. It is notable that one of the prime controls of whether chute rather than neck cut-off takes place is the volume and intensity of high discharge events which are a characteristic of ephemeral rivers. Similar massive sandstone beds within Triassic fluvial channel fills in the Paraná Basin of Brazil have also been interpreted as a sedimentological indicator of an ephemeral flow regime (Horn *et al*. 2017).

We are confident the mid Triassic palaeoclimate in the adjoining Paraná basin of Brazil may be reasonably applied to the Burgersdorp Fm of the Karoo Basin as they were both in southwestern Gondwana lying between 34.6°S to 46.9°S paleolatitude (van Hinsbergen *et al*. 2015). Time equivalent strata to the upper Katberg-Burgersdorp formations in the Paraná basin comprise the middle-upper Santa Maria, Caturrita, and Mata formations. Through this sequence Holz & Scherer (2000) infer humid,

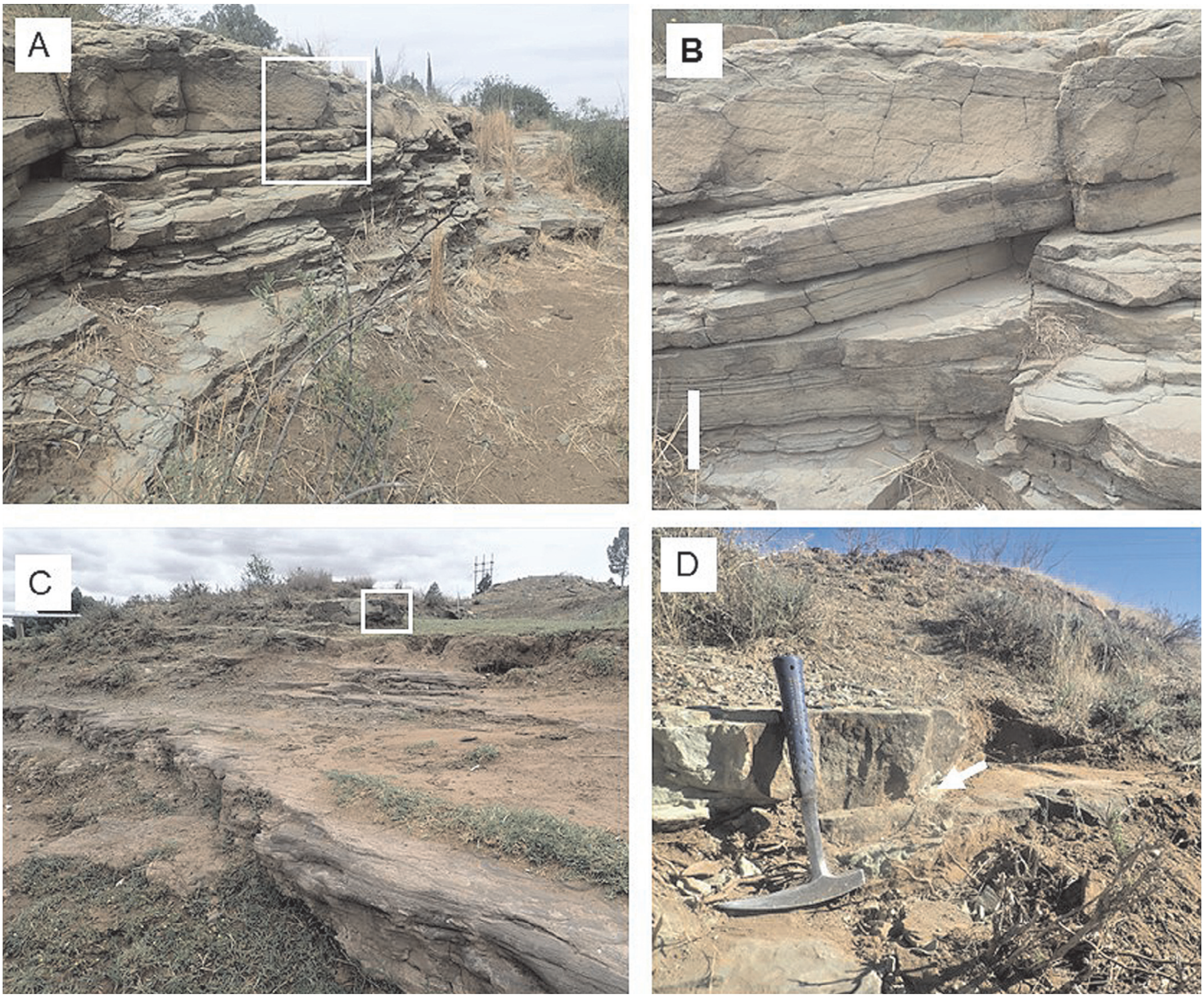

Figure 8. Sedimentology of the *Euparkeria* type locality. **A**, Lower part of the upper storey of the channel sandstone beneath the *Euparkeria*-bearing beds. **B**, Close-up of rectangle in A showing predominantly horizontally laminated medium-grained sandstone with low angle intersections. **C**, View of the top of the uppermost channel fill unit showing tabular planar and massively-bedded fine-grained sandstone beds. Rectangle indicates edge of Webster's quarry, **D**, Close-up of the structureless fine-grained sandstone beds that were preferentially quarried as dimension stone and host the *Euparkeria/Mesosuchus* bonebed. The newly discovered *in situ* archosaur bone is arrowed. Scale bar = 10cm, Geological pick = 33 cm long.

but still seasonal, conditions as fluvial architecture changed gradually from ephemeral braided to perennial braided, anastomosing, and finally meandering channels, with floral evidence of humidity. However, despite increasing rainfall, the floodplain water bodies appear to have remained seasonal for most of this succession. A similar conclusion was reached by Wolvaardt (2021) and Wolvaardt *et al*. (2023) through analysis of the taphonomy, palaeosols and palustrine carbonates at the Lemoenfontein procolophonid bonebed site in the lower middle Burgersdorp Fm, stratigraphically estimated to be about 10 m above the *Euparkeria* site based on the presence of the upper part of the Eldorado sandstone marker at both localities. Thus, our taphonomic analyses support Neveling (2004) in that the Katberg-Burgersdorp succession records a trend towards more humid floodplain environments yet still with strong seasonality.

Biostratigraphically there is a strong correlation of *Cynognathus* AZ taxa with the radiometrically dated Río Seco de la Quebrada Formation in Mendoza Province, Argentina where C*ynognathus* and *Diademodon* fossils have been found. They were considered early Anisian in age – earliest Middle Triassic, about 247 Ma (Martinelli *et al*. 2009). However, an ash bed below the Rio Seco de la Quebrada Formation was recently radiometrically dated as 235.8 Ma (early Carnian) some 10 Ma younger that had been generally accepted (Ottone *et al*. 2014). Should this new age in fact be corroborated by additional evidence, then the entire Burgersdorp succession could be a southwestern Gondwanan expression of the Pangea-wide mid–late Triassic pluvial conditions now widely accepted as the Carnian Humid Episode (e.g. Ruffell *et al*. 2016).

Taphonomy of the *Euparkeria/Mesosuchus* remains

The 38 fossil-bearing sandstone blocks from the *Euparkeria* quarry that are stored in the Iziko South African Museum display approximately 50 specimens of *Euparkeria* and *Mesosuchus* in different degrees of com-

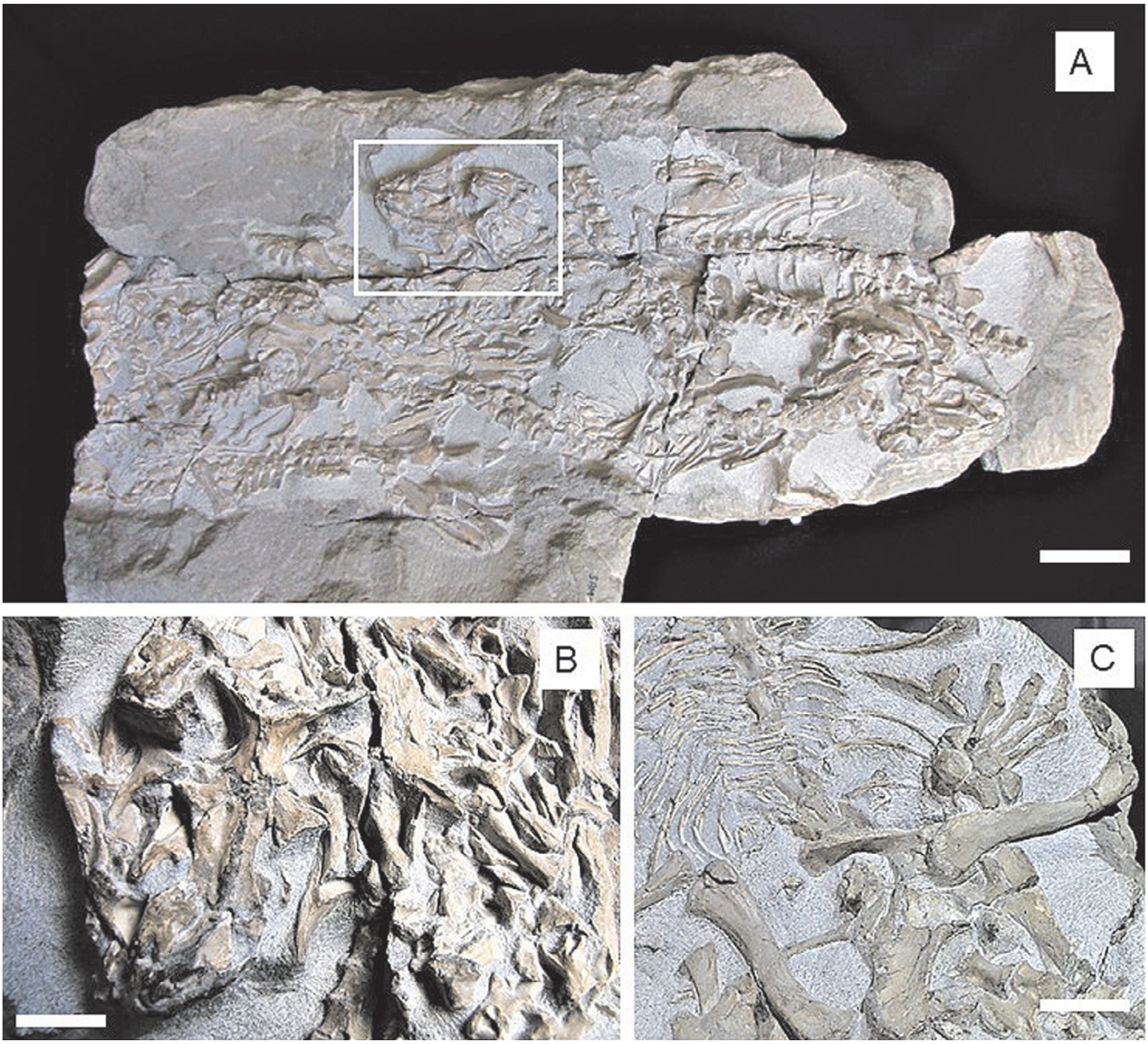

Figure 9. Taphonomy of the *Euparkeria/Mesosuchus* bonebed. **A**, The main *Euparkeria/Mesosuchus* bonebed block (SAM-PK-K8050 and 8051). Scale bar = 10 cm. **B**, Oblique view of dorsal up *Mesosuchus* skull (SAM-PK-K8051) outlined on the bonebed block in A. Scale bar = 2 cm. **C**, Detail of articulated gastralia and left pes of a ventral-up, partially articulated *Euparkeria* skeleton (SAM-PK-7696). Scale bar = 2 cm.

pleteness and articulation. Both taxa have approximately the same adult body size, but they have a different morphology in the skull and vertebral column. Each block was reviewed, photographed, the bone material described, and measured to determine the range of sizes of the specimens (Fig. 9A). Smith (1993) grouped repeated patterns of skeletal disarticulation of Karoo tetrapods into eight taphonomic classes, ranking from fully-articulated curled-up specimens (A), articulated skeletons with straight or reflexed spinal curvature (B), isolated skull with cervical vertebrae (C), with (D) or without (E) attached lower jaw, to isolated lower jaws (F), individual postcranial elements (G), and (more rarely) concentrations into bonebeds (H). All these classes are found within the available material from this site, presenting a wide diversity of taphonomic modes in one place. From the 12 skulls available, all of them have articulated lower jaws, four of them are crushed in the bonebed mode, but some of the specimens are perfectly preserved although laterally compressed, except for the most complete *Mesosuchus* skull (Fig. 9B). Gastralia are present, in marked contrast to similarly aged bonebeds elsewhere where they are rare. Significantly, two paired gastralia racks occur isolated but otherwise fully intact (Fig. 9C). This is a strong indication that the carcasses were desiccated before burial with strips of the skin having become separated. We interpret the presence of these articulated portions of skeletons as evidence of scavenging. Articular ends of the long bones are commonly fractured yet the delicate dorsal scutes are still articulated above the vertebrae of *Euparkeria* in their original position in most of the specimens. The former suggests a period of subaerial exposure in semi-arid climatic conditions whereas the latter suggests rapid burial possibly by trampling with minimum transportation of the carcasses.

The occurrence of bone accumulations in sand bed meandering river channels has been recorded in modern studies, in particular the Mara River of Tanzania (Dechant-Boaz 1982) where the primary agent of concentration is recurrent flood events with synchronous mass drowning of wildebeest. The carcass accumulation sites in this case are bank-attached rock outcrops and the inner bank bars of sharp bends downstream from the crossing points. It is interesting to note that as the carcasses disarticulate the bones become slightly dispersed, but most are incorporated as partially-articulated skeletons into the channel sediments at the site along with other flotsam such as tree trunks and plant debris. We report a similar association of numerous semi-articulated skeletons along with macro-plant debris at the *Euparkeria* locality such that we consider this corroborative evidence for mass-drowning events having been the main accumulating agency.

The common presence of halos of calcareous cement around bones (some with an outer fringe of tiny manganese dioxide dendrites) is indirect evidence for the presence of organic matter in and around the *Euparkeria* bones during and immediately after burial. These halos are interpreted as bacterially-induced local zones of reduction in the sediment surrounding the bone and decomposing tissue which caused the precipitation of calcium carbonate from the groundwater (Carpenter 2005; Daniel & Chin 2010; Smith 2000).

Figure 10 illustrates the interpreted depositional environment, and the following events summarize the reconstructed taphonomic pathway that led to the bone accumulation and final burial at the *Euparkeria* type locality.

1. A peak flood event temporarily inundated the entire point-bar which scoured out and widened the upstream side of a swale trough to form an incipient chute channel.
2. In the intervening low flow – and possibly no flow – stages the chute channel dried up, became vegetated and provided a local habitat for the indigenous tetrapods.
3. During a subsequent peak flood event some 50 *Euparkeria* and several *Mesosuchus* individuals drowned either during an attempted river crossing or they became trapped on a mid-channel island. Their floating carcasses, along with other flotsam such as plant debris and logs became trapped in a chute channel on top of a downstream point-bar.
4. Following the flood event, the chute channel retained a standing water body for some time before it dried up. Scavenging, desiccation and trampling of the carcasses resulted in a range of disarticulation stages in the surface bone scatter which at this bone accumulation site was dominated by remains of the medium-sized carnivore *Euparkeria* and the herbivorous (Ezcurra *et al*. 2016) *Mesosuchus*.
5. A subsequent sediment-laden flood event moved the smaller isolated bones into the axis of the chute, shifting the desiccated but still articulated full and partial carcasses into a current alignment before decelerating flow dumped a thick bed of fine sand over them. Importantly for fossilization there was minimal transportation with final burial all in the same flood episode.
6. Resident tetrapods re-occupied the chute channel after the flood subsided causing further disarticulation and crushing of the buried bones, mainly by trampling.
7. With increasing depth of burial beneath floodplain mudrock the lower bonebed horizon entered the water table where early diagenetic solution/precipitation processes led to the formation of incipient calcareous nodules around the bones especially those that still retained some organic matter.

The taphonomic analysis of the bonebed shows no evidence of reworking that would argue against the fact that *Mesosuchus* and *Euparkeria* were both part of the living tetrapod community on the Karoo floodplains during the late Olenekian. Their death accumulation on top of a large low-angled point-bar may indicate that their preferred habitats were the riparian forests that flanked the larger watercourses and vegetated stabilized sand bars within the channel itself. It is also quite feasible that packs of *Euparkeria* were the principal scavengers of the carcass accumulation causing the observed separation of articulated segments of skeletons and bone scatter.

SUMMARY AND CONCLUSIONS

The rediscovery of the exact locality where all the currently known specimens of the archosauromorphs *Euparkeria capensis* and *Mesosuchus browni* were collected has confirmed its stratigraphic position as at the transition between lower and middle Burgersdorp Formation at the top of a regionally extensive multistoreyed channel sandstone informally named the Eldorado marker (Hancox *et al*. 2020; Neveling 2004). This places the locality within the uppermost *Langbergia-Garjainia* Subzone of the *Cynognathus* AZ currently regarded as late Olenekian in age (Hancox *et al*. 2020).

The re-discovery also facilitated our investigation of the palaeoenvironment and taphonomic pathway that led to the *Euparkeria*-monodominant bonebed made up of numerous individuals of this iconic taxon. The analysis suggests that the initial concentration of tetrapod remains was controlled by a combination of a pack of *Euparkeria* getting drowned during peak flood discharge and the hydrodynamics of the small floating carcasses becoming trapped within the confines of a downstream chute-channel. Following the definitions in Rogers & Kidwell (2007), this type of bone accumulation mechanism can be categorized as intrinsic biogenic-behaviour as induced by environmental hazards.

Further concentration followed, after a period of scavenger-assisted disarticulation, when a subsequent hyperconcentrated sediment-laden flow rolled the isolated elements, and partially articulated desiccated skeletons, into the axis of the chute and buried them with structureless fine-grained sand.

Comparisons of the *Euparkeria* site with other Triassic bonebeds reveals a remarkable similarity in taphonomic mode to that of the Ghost Ranch *Coelophysis* bonebed in

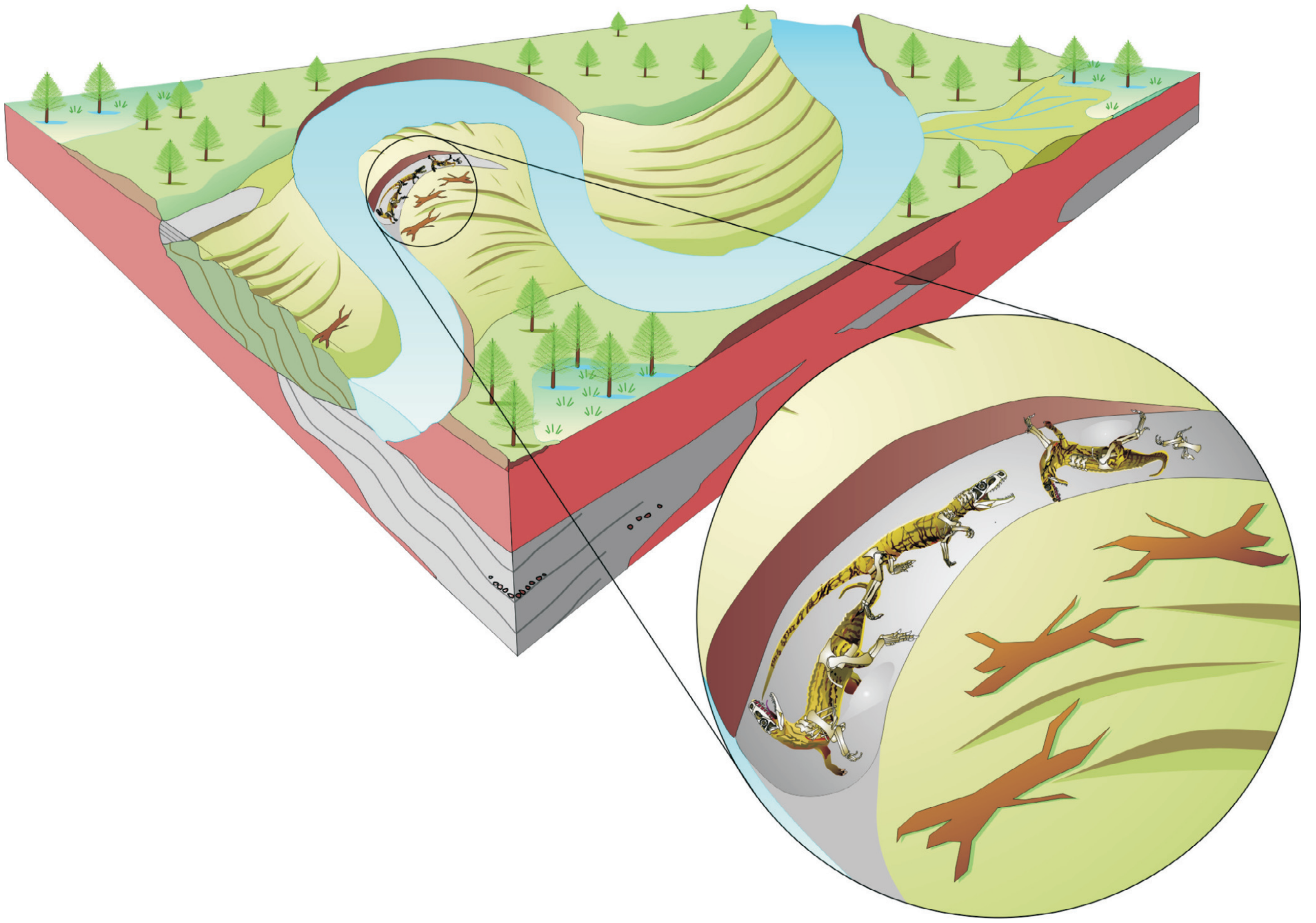

Figure 10. Palaeoenvironmental reconstruction of the *Euparkeria* type locality. The interpreted depositional setting for the *Euparkeria* bonebed within the upstream end of a chute channel eroded during extreme flood events into the surface of a low angle point-bar. Floating carcasses were concentrated by turbulent eddies in the chute channel during successive flood events then left stranded as floodwaters subsided. Each flood event rapidly deposited a layer of structureless fine sand. Flow is from left to right. In the vertical section the multistoreyed nature of the Eldorado sandstone is depicted as a change from low sinuosity vertically stacked medium-grained sand units to high-sinuosity laterally-accreted fine-grained units.

New Mexico not only in the dense, bone-on-bone packing of numerous skeletons, but their mode of occurrence is also interpreted as mass death and transportation during peak floods (Schwartz & Gillette 1994).

The observed worldwide increase in bonebed-type preservation of terrestrial tetrapods during the Triassic (Behrensmeyer 2007) may be a reflection of a significant change in rainfall seasonality and intensity linked to what has been dubbed the Triassic megamonsoon (Kutzbach & Gallimore 1989; Parrish 1993) causing increased surface run-off and the concentration of bones in depressions. Here we propose that the *Euparkeria*- and *Coelophysis*-dominated bonebeds may also exemplify the type of mass-drowning events that may have occurred with an increased frequency as a consequence of the monsoonal-type meteorological conditions that beset the inland areas of Pangea in the mid to late Triassic.

We thank Claire Browning of the Iziko South African Museum for access to the *Euparkeria* fossil collection and Alfred Brown's handwritten journals, especially Zaituna Skosan for managing to locate these journals during the museum renovations. Also, thanks to the volunteer staff of the Aliwal North municipal museum who provided access to written records about 'Gogga Brown' and to Léta and Jannie Joubert for hosting our field camps on their farm, Gladde Grond. F.P.W. extends his gratitude to Bruce Rubidge and Roger Smith for their years of encouragement and support through the process of developing an informal passion into a formally recognized qualification. He is particularly grateful to have been part of Prof. Smith's Karoo field team since 2003. R.M.H.S. would like to extend warmest appreciation for the many years of collegiate collaboration, fossil hunting and lasting friendship with Prof. Rubidge and thank him for his lifetime achievements that have significantly raised the profile of palaeontology, especially Karoo palaeontology, in South Africa and internationally. Funding was provided by the National Research Foundation of South Africa's African Origins Platform, grant UID117615 (RMHS).

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