Reappraisal of *Austrosaurus mckillopi* Longman, 1933 from the Allaru Mudstone of Queensland, Australia's first named Cretaceous sauropod dinosaur

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Austrosaurus mckillopi Longman, 1933 was the first Cretaceous sauropod reported from Australia, and the first Cretaceous dinosaur reported from Queensland (northeast Australia). This sauropod taxon was established on the basis of several fragmentary presacral vertebrae (QM F2316) derived from the uppermost Lower Cretaceous (upper Albian) Allaru Mudstone, at a locality situated 77 km west-northwest of Richmond, Queensland. Prior to its rediscovery in 2014, the type site was considered lost after failed attempts to relocate it in the 1970s. Excavations at the site in 2014 and 2015 led to the recovery of several partial dorsal ribs and fragments of presacral vertebrae, all of which clearly pertained to a single sauropod dinosaur.

The discovery of new material of the type individual of *Austrosaurus mckillopi*, in tandem with a reassessment of the material collected in the 1930s, has facilitated the rearticulation of the specimen. The resultant vertebral series comprises six presacral vertebrae—the posteriormost cervical and five anteriormost dorsals—in association with five left dorsal ribs and one right one. The fragmentary nature of the type specimen has historically hindered assessments of the phylogenetic affinities of *Austrosaurus*, as has the fact that these evaluations were often based on a subset of the type material. The reappraisal of the type series of *Austrosaurus* presented herein, on the basis of both external morphology and internal morphology visualised through CT data, validates it as a diagnostic titanosauriform taxon, tentatively placed in Somphospondyli, and characterised by the possession of an accessory lateral pneumatic foramen on dorsal vertebra I (a feature which appears to be autapomorphic) and by the presence of a robust ventral midline ridge on the centra of dorsal vertebrae I and II. The interpretation of the anteriormost preserved vertebra in *Austrosaurus* as a posterior cervical has also prompted the re-evaluation of an isolated, partial, posterior cervical vertebra (QM F6142, the “Hughenden sauropod”) from the upper Albian Toolebuc Formation (which underlies the Allaru Mudstone). Although this vertebra preserves an apparent unique character of its own (a spinopostzygapophyseal lamina fossa), it is not able to be referred unequivocally to *Austrosaurus* and is retained as Titanosauriformes indet.

Austrosaurus mckillopi is one of the oldest known sauropods from the Australian Cretaceous based on skeletal remains, and potentially provides phylogenetic and/or palaeobiogeographic context for later taxa such as *Wintonotitan wattsi*, *Diamantinasaurus matildae* and *Savannasaurus elliottorum*.

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SAUROPOD dinosaur fossils were not reported from Australia until 1926, despite the fact that the first discovery of an Australian sauropod specimen was made in 1913. This incomplete humerus (QM F311)—found in Cretaceous strata near the town of Blackall in Queensland—was not determined to pertain to a dinosaur, let alone a sauropod, until 1980 (Molnar 2001b). The first Australian sauropod specimen that was recognised as such was discovered in 1924 near the town of Roma, Queensland. This partial skeleton (QM F1659) was designated the type of *Rhoetosaurus brownei* and remains one of only two Jurassic sauropod specimens known from Australia (Longman 1926, 1927a, b, 1929, Thulborn 1985, Rich & Vickers-Rich 2003, Nair & Salisbury 2012). The other, a distal caudal vertebra (UWA 82468), was found in the mid-1970s in Middle Jurassic rocks near Geraldton, Western Australia (Long 1992).

Cretaceous sauropod remains are only known from three Australian states. Footprints found in the Broome Sandstone (Valanginian–Barremian) of the Dampier Peninsula constitute the only evidence of Cretaceous sauropods in Western Australia (Thulborn *et al.* 1994, Thulborn 2012, Salisbury *et al.* 2017), whereas opalised sauropod teeth (AM F66769, AM F66770) from the Griman Creek Formation (middle Albian) of Lightning Ridge are all that has been reported from New South Wales (Molnar & Salisbury 2005, Molnar 2011b). In Queensland, the Griman Creek Formation has yielded two possible sauropod elements: a fragmentary right ischium (QM F54817) and a possible vertebral fragment (QM F11043; Molnar 2011b).

The Eromanga Basin in Queensland has produced the overwhelming majority of Australia’s sauropod skeletal remains. Rare specimens have been described from the Toolebuc Formation and the Allaru Mudstone, both of which constitute upper Albian marine deposits (Molnar & Salisbury 2005). However, the bulk of the known sauropod remains from the Eromanga Basin derive from the youngest Cretaceous unit preserved therein, the uppermost Albian–lower Turonian Winton Formation (Coombs & Molnar 1981, Molnar & Salisbury 2005, Greentree 2011, Bryan *et al.* 2012, Tucker *et al.* 2013, Tucker 2014), which evinces the existence of a vast floodplain. To date, three sauropod taxa have been reported from the Winton Formation: the non-titanosaurian somphospondylan *Wintonotitan wattsi* (Hocknull *et al.* 2009, Poropat *et al.* 2015a); and the titanosaurs *Diamantinasaurus matildae* (Hocknull *et al.* 2009, Poropat *et al.* 2015b, 2016) and *Savannasaurus elliottorum* (Poropat *et al.* 2016). However, the first Cretaceous sauropod, and indeed the first Cretaceous dinosaur, reported from Queensland was not from the Winton Formation: it was found in the Allaru Mudstone, and bears the name *Austrosaurus mckillopi* (Longman 1933).

===PLEASE INSERT FIGURE 1===

The type and only known specimen of *Austrosaurus mckillopi* was found in August 1932 on Clutha sheep station, 77 km west-northwest of Richmond, Queensland (Fig. 1). Clutha overseer Henry Burgoyne Wade (Fig. 2A) found fragments of fossilised bone near the southwest corner of Whitewood Paddock. He showed these to the station manager, Harley John McKillop (Fig. 2B), who contacted his brother, Dr Martin Joseph McKillop (Fig. 2C). Shortly afterwards, M. J. McKillop travelled from Brisbane to Clutha, helped H. B. Wade and H. J. McKillop to recover additional specimens, and sent a sketch of one to Heber Albert Longman (Fig. 2D), then director of the Queensland Museum. Longman requested that the specimens be sent to Brisbane, and they arrived in January 1933. By March 1933, Longman had correctly determined that the bones derived from a sauropod dinosaur and made them the type specimen of *Austrosaurus mckillopi*, honouring M. J. McKillop with the species epithet

(Longman 1933). A sign was erected by H. B. Wade and H. J. McKillop at the type site to demarcate its significance (Fig. 2E).

===PLEASE INSERT FIGURE 2===

In his original description of *Austrosaurus mckillopi*, Longman only mentioned three specimens (and figured two), all of which were presacral vertebrae (catalogued as QM F2316). It is probable that Longman received more than three specimens in the initial shipment from Clutha, given that contemporary newspaper articles stated that six vertebrae were preserved (Anonymous 1933b, a). However, only on the three specimens described by Longman is there evidence of “repeated soakings in shellac solution” (Longman 1933, p. 132). Correspondence between H. J. McKillop and Longman confirms that a second shipment of specimens was dispatched from Clutha to the Queensland Museum in June 1933. Molnar (2001b, p. 141, 2010, p. 423, 2011a, p. 332) and Molnar & Salisbury (2005, p. 456) suggested that this second shipment comprised five large and more than ten small pieces. However, in his letter to Longman on 23/05/1933, H. J. McKillop stated that the additional specimens were “smaller fossils from the same animal”, which suggests that all eight large portions of *Austrosaurus* vertebrae had been delivered to the Queensland Museum in the first shipment: furthermore, this implies that Longman did not describe all of the specimens at his disposal in March 1933. The total number of blocks presently catalogued under QM F2316 is 25: eight large, and 17 small (Appendix 1).

Longman never visited Clutha sheep station, possibly because H. B. Wade and H. J. McKillop left the property when it was sold in July 1933. Evidently, only two attempts were made by palaeontologists to revisit the *Austrosaurus* type locality prior to 2014. Tony Thulborn (then at The University of Queensland) and Mary Wade (then at the Queensland

Museum) attempted to relocate the site in 1976 (as alluded to by Molnar 1982b, p. 622, 2010, p. 423), immediately prior to their first excavation at the Lark Quarry Dinosaur Stampede (Thulborn & Wade 1979, 1984); however, they failed to find additional specimens (R. A. Thulborn, pers. comm. 2015). Ralph Molnar (then at the University of New South Wales), his wife Barbara, and Peter Bell (then a graduate student) visited Clutha in late June 1977, but they also failed to find any additional specimens (R. E. Molnar, pers. comm. 2016).

Perfunctory assessments of the vertebrae of *Austrosaurus* collected in the 1930s suggested that they represented part of an articulated series. This strongly implied that more of the same skeleton was preserved but remained unexcavated (as also suggested by Molnar 2010). Despite this, aside from a few brief considerations (Molnar 2001b, Molnar & Salisbury 2005, Molnar 2010, 2011a), the bulk of the *Austrosaurus* material has remained undescribed, and the specimen has never been rearticulated.

Longman (1933) published a map of Clutha Station (provided to him by H. J. McKillop) which included the paddock fence lines and an “X” marking the *Austrosaurus* site in the southwest corner of Whitewood Paddock (Fig. 3A). This map was overlaid onto Google Earth satellite images, which revealed that the fences on Clutha had not been moved since the 1930s. This implied that a search for the site could be constrained to a small section of one paddock. Clutha sheep station straddles two of the geological maps produced by the Bureau of Mineral Resources (Vine *et al.* 1963, 1970), both of which concur that the non-Quaternary sedimentary rocks exposed on the property, including the *Austrosaurus* type site, fall entirely within the bounds of the Allaru Mudstone (Fig. 3B).

===PLEASE INSERT FIGURE 3===

In December 1933, M. J. McKillop sent Longman a photograph of a sign, supported by two “gidgee” (*Acacia*) posts, which was erected by H. B. Wade and H. J. McKillop at the *Austrosaurus* site shortly after the taxon was described (Fig. 2E). No trace of the sign has been found; it is presumed to have disintegrated. However, the posts did not disintegrate, and they were known to John Wharton (mayor of Richmond Shire), who grew up on Clutha. Wharton and the last author (TH) attempted to relocate the site at ground level in early 2014. Although this proved futile, Wharton succeeded in finding the posts from the air with a helicopter. Nearby, he found fragments of mudstone which contained fossilised bone with camellate internal texture, showing nearly identical preservation to the type specimen of *Austrosaurus mckillopi*.

In July 2014, a team led by TH and SFP visited the presumed *Austrosaurus* site and recovered additional fragments of sauropod bone (rib and camellate internal vertebral fragments) from the topsoil. This was followed by a small-scale excavation in August 2014, wherein three fragmentary ribs were found next to each other. One rib portion was left *in situ* and covered with plaster in anticipation of a subsequent excavation. This transpired in July 2015, and the presence of six ribs was confirmed—three of these connected to rib portions excavated in 2014. All specimens were collected and donated to the Kronosaurus Korner Marine Fossil Museum (Richmond, Queensland), where they are presently on display.

The left ribs were preserved with their medial surfaces facing upwards and their tapered anterior margins directed to the northwest. A single right dorsal rib was found on top of the posteriormost left dorsal ribs preserved. The spacing between the left ribs was consistent with them having been derived from an articulated skeleton (as indicated by the vertebral centra originally described by Longman); however, no additional sauropod remains were found, despite extensive excavation around, and below the level of, the ribs. The immediate site is now considered to be exhausted of fossilised skeletal material, with the type of *Austrosaurus* having been augmented as much as possible. However, it is not infeasible that additional portions of the carcass might eventually be found further distant from the already excavated area. A comprehensive account of the discovery and rediscovery of the *Austrosaurus* site has been published elsewhere (Poropat 2016).

In this paper the augmented type specimen of *Austrosaurus mckillopi* is reappraised, and the first full description of this taxon is provided based on both external and internal characteristics (the latter having been visualised from CT data). The taphonomic processes which affected the *Austrosaurus* type specimen post mortem are considered and the implications of its preservation in a marine setting are explored. Comparisons of the type specimen of *Austrosaurus* with other sauropods from both Australia and elsewhere support the notion that it is a distinct, diagnostic taxon. This in turn has facilitated a reassessment of its phylogenetic placement, and has raised questions over its palaeobiogeographic and phylogenetic significance for other, geologically younger Australian sauropod taxa and for Early Cretaceous South American titanosauriforms. Finally, the possible referral to *Austrosaurus mckillopi* of the enigmatic “Hughenden sauropod”, represented by a single, incomplete, posterior cervical vertebra (QM F6142) from the Toolebuc Formation, is assessed.

Institutional abbreviations: AM, Australian Museum, Sydney, New South Wales, Australia; AOD, Australian Age of Dinosaurs Natural History Museum, Winton, Queensland, Australia; KK, Kronosaurus Korner Marine Fossil Museum, Richmond, Queensland, Australia;

MMCH, Museo Municipal 'Ernesto Bachman', Villa El Chocón, Neuquén, Argentina; MN, Museu Nacional, Rio de Janeiro, Brazil; MUCPv, Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina; QM, Queensland Museum, Brisbane, Queensland, Australia; UWA, University of Western Australia, Perth, Western Australia.

Geological and depositional setting and associated palaeofauna

QM F2316 was preserved in the Allaru Mudstone, the second youngest of the marine units preserved within the Eromanga Basin (Fig. 1). Much of the Allaru Mudstone was deposited below wave base in a low-energy marine setting, and comprises blue–grey mudstones and siltstones, some of which are calcareous (Exon & Senior 1976). However, its lowermost and uppermost sections are sporadically coarser-grained and contain sedimentary structures such as planar cross-bedding, hummocky cross-stratification and ripple cross-lamination, which suggests both initial and terminal shallowing during deposition. In the northern Eromanga Basin the Allaru Mudstone conformably overlies the Toolebuc Formation, whereas in the southern part of the basin (where the Toolebuc Formation is absent) it lies directly upon the upper Aptian–middle Albian Wallumbilla Formation (Gray *et al.* 2002). The Allaru Mudstone is conformably overlain by the marine Mackunda Formation, which is in turn overlain by the paralic–terrestrial Winton Formation.

Sauropod remains from the Allaru Mudstone are rare, with few specimens other than *Austrosaurus mckillopi* known (Poropat *et al.* 2014). The only other terrestrial tetrapod remains reported from the unit are: three ornithopod specimens (Molnar 1980, 1982b, 1984b, Lees 1986, Molnar 1996a, Agnolin *et al.* 2010), one of which has been designated *Muttaburrasaurus* sp. (Molnar 1996a); three ankylosaur specimens (Molnar 1984b, 1996b, Leahey & Salisbury 2013, Leahey *et al.* 2015), including the holotype specimen of *Kunbarrasaurus ieversi* [Leahey *et al.* 2015; formerly *Minmi* sp. (Molnar 1996b, Molnar & Clifford 2000, Molnar 2001a, Molnar & Clifford 2001)]; and fragmentary cranial elements which have been attributed to a late-surviving dicynodont (Longman 1916, Thulborn & Turner 2003) but also apparently compare favourably with baurusuchian crocodylomorphs (Agnolin *et al.* 2010, p. 293).

Unsurprisingly, remains of ancient marine vertebrates are far more common in the Allaru Mudstone than are those of terrestrial vertebrates. Polycotylid (Mobbs 1990, Hughes 2003), elasmosaurid (Persson 1960, Kear 2003, McHenry *et al.* 2005) and pliosaurid plesiosaurs (Holland 2015) are all represented, alongside ichthyosaurs (Longman 1943, Wade 1984, 1990, Zammit *et al.* 2010, Kear & Zammit 2014) and marine turtles (SFP and TH, pers. obs.). A variety of chondrichthyan and actinopterygian fishes has also been recovered from the Allaru Mudstone (Longman 1913, 1932, Bardack 1962, Bartholomai 1969, Lees & Bartholomai 1987, Kemp 1991, Bartholomai 2004, 2008, 2010b, 2012, Wretman & Kear 2014).

The Allaru Mudstone hosts a diverse fossil mollusc fauna, including squids (Wade 1993), ammonites (Day 1969, McNamara 1978, Henderson & Kennedy 2002, Henderson & McKenzie 2002), belemnites (Cook 2012), scaphopods (Stilwell 1999) and bivalves (Cook 2012). Non-molluscan invertebrates, such as crustaceans [brachyurans (Etheridge 1892, Woodward 1892, Etheridge 1917, Woods 1953, Glaessner 1980) and ostracods (Krömmelbein 1975)] and echinoderms (Cook 2008, 2012) are locally abundant, whereas corals are rare (Jell *et al.* 2011). Foraminifera from the Allaru Mudstone (Playford *et al.* 1975) indicate that the water temperature was cool, that the water salinity was lower than that of normal seawater, and that the seaway was shallow, probably less than 100 m deep (Haig 1979a, b). The abundance of planktonic organisms is also indicative of near-normal marine conditions (Exon & Senior 1976), whereas the abundance and diversity of benthic organisms (Haig 1980, 1982) appears to indicate well-oxygenated waters, at least during the early phases of deposition (Haig & Lynch 1993). Calcareous nannofossils suggest that the deposition of the lowermost Allaru Mudstone (at least) took place at a relatively high palaeolatitude (~55°; Seton *et al.* 2012) and/or in an environment characterised by cool near-surface water temperatures (Shafik 1985), an interpretation supported by analyses of isotope ratios in belemnite rostra (~19°C; Price *et al.* 2012).

Although terrestrial plant fossils are rare in the Allaru Mudstone [the cycadale *Nilssonia mucronatum* is one of the few described specimens (Rozefelds 1986)], studies of the palynomorphs have shown that this unit lies within the upper *Coptospora paradoxa* and *Phimopollenites pannosus* palynological zones (Burger 1986). The Allaru Mudstone is, consequently, ascribed a late Albian age, which is further reinforced by the presence of the ammonite *Goodhallites goodhallites* (Henderson & Kennedy 2002).

Systematic Palaeontology

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

SAUROPODOMORPHA von Huene, 1932

SAUROPODA Marsh, 1878

EUSAUROPODA Upchurch, 1995

NEOSAUROPODA Bonaparte, 1986

MACRONARIA Wilson and Sereno, 1998

TITANOSAURIFORMES Salgado *et al.*, 1997

?SOMPHOSPONDYLI Wilson and Sereno, 1998

Austrosaurus mckillopi Longman, 1933

Holotype. QM F2316: four partial, articulated presacral vertebrae, preserved within three blocks (Longman 1933: “specimens A–C”), comprising the posterior portion of the centrum of the posteriormost cervical vertebra, the centra and partial neural arches of dorsal vertebrae I and II, and a fragment of the centrum of dorsal vertebra III.

Hypodigm. QM F2316 and KK F1020, comprising the holotype and additional specimens referrable to the type individual: a series of articulated presacral vertebrae, comprising the posteriormost cervical vertebra and dorsal vertebrae I–V, associated with six dorsal ribs (left ribs I–V, right rib IV) and numerous additional fragments. QM F2316 comprises the six vertebrae and multiple associated fragments (including one small rib portion; Appendix 1), whereas KK F1020 comprises the six dorsal ribs, as well as additional rib and vertebra fragments.

Type locality. Southwest corner of Whitewood Paddock, Clutha Station (Fig. 3), ~55 km north-northwest of Maxwelton (~77 km west-northwest of Richmond), north-central Queensland, Australia (Fig. 1).

Type horizon. Allaru Mudstone (Lower Cretaceous; upper Albian).

Original diagnosis. "Dorsal vertebrae markedly opisthocoelous; centra with thin cortical walls, much enlarged at the enarthrodial articulations; intramural region a complex of small cavities; pleurocoeles[*sic*] prominent, with external and internal divisions. Neural arch with deep recess between the prezygapophyseal lamina and the infradiapophysial buttress" (Longman 1933, p. 132).

Comments on original diagnosis. Opisthocoelous anterior dorsal vertebrae are now recognised as being characteristic of most eusauropods (Wilson & Sereno 1998, Wilson 2002), whereas opisthocoelous middle–posterior dorsal vertebrae, although typical among macronarians (Wilson 2002), are also present in some non-neosauropod sauropods (Carballido *et al.* 2011b, p. 634). The combination of thin exterior walls, small internal cavities and prominent lateral pneumatic foramina (= pleurocoels) in the anterior dorsal vertebrae exemplifies the camellate internal texture now widely recognised in the presacral vertebrae of titanosauriform sauropods (Wedel 2003). Finally, several sauropod taxa are now known to possess a deep fossa [centrodiapophyseal fossa *sensu* Wilson *et al.* (2011b)] like that seen on Longman's "specimen A" between the "prezygapophyseal lamina" [= anterior centroparapophyseal lamina (ACPL)] and the "infradiapophysial buttress" [= posterior centrodiapophyseal lamina (PCDL)]. In sum, none of Longman's (1933) characters can be considered to be either autapomorphic or differentially diagnostic for *Austrosaurus* because all are more widely distributed within Sauropoda. However, these characters do suggest that *Austrosaurus* is a titanosauriform sauropod.

Revised diagnosis. A titanosauriform sauropod characterised as follows [potential autapomorphies are indicated with an asterisk (*)]: dorsal vertebrae I–II with ventral ridges flanked by shallow, circular fossae; dorsal vertebra I with accessory lateral pneumatic foramen situated anterodorsal to the parapophysis*; dorsal rib distal ends in cross-section ranging from plank-like (I–III) to semi-plank-like (IV) to subcircular (V).

Description

===PLEASE INSERT FIGURE 4===

Prior to our work on *Austrosaurus*, the number of vertebrae comprising the type series had never been established with certainty, nor had the vertebral column ever been successfully rearticulated. The type specimen of *Austrosaurus* was stated by Coombs & Molnar (1981, p. 358) to comprise “a series of six fragmentary dorsal vertebrae”, although further elaboration was not made. Molnar & Salisbury (2005, p. 456) and Molnar (2010, p. 423) claimed that at least eight vertebrae were present, although no evidence was presented to support this beyond the fact that there were eight large fragments containing portions of presacral vertebrae catalogued under QM F2316. Prior to the rearticulation of the specimen, all that could be stated with certainty was that five condyle-cotyle pairs were catalogued as part of the type series of *Austrosaurus*, indicating the presence of a minimum of six vertebrae.

The rearticulation of the vertebral column, successfully undertaken by SFP and JPN, revealed that the three specimens described by Longman (1933) were found to articulate with one another, with the undescribed condyle–cotyle pairs forming a sequence succeeding those three (Appendix 1). The preserved presacral series, as articulated, comprises the posteriormost cervical vertebra, and dorsal vertebrae I–V (Appendix 1; Fig. 4–8). On the left lateral side of the preserved vertebral column (Fig. 5), portions of two fragmentary ribs are preserved, not far removed from their *in vivo* positions. The recovery of several associated, effectively *in situ* left dorsal ribs from the *Austrosaurus* type site in 2014–2015 (Fig. 9) suggests that the carcass was buried with its left side lying on the seafloor (all of the left ribs were preserved with their medial surfaces up; Fig. 10). All but one of the right ribs are missing; it is likely that any others which were preserved were lost to erosion long before the specimen was discovered in 1932.

A fragmentary ammonite (registered as QM F2321) was found in association with *Austrosaurus*, whereas other mollusc specimens [*Inoceramus* (Bivalvia: Cryptodonta) and *Beudanticeras* (Cephalopoda: Ammonoidea)] remain embedded within matrix adhered to QM F2316 (Longman 1933, Molnar 2010). At least three additional ammonites, not visible on any exposed surface, have been identified through observation of the CT data. This associated invertebrate fauna clearly demonstrates that *Austrosaurus* was preserved in a marine setting.

Presacral vertebrae: general patterns. All preserved presacral vertebrae of *Austrosaurus mckillopi* are strongly opisthocoelous. The high degree of weathering to which the majority of the specimens has been subjected has exposed, and often accentuated, the camellate internal texture of the vertebrae. All of the vertebrae of *Austrosaurus* bear deeply-penetrating pneumatic foramina set within fossae (Fig. 5, 6). Few portions of the neural arches are preserved.

Several morphological changes are evident along the vertebral column. The first two dorsal vertebrae each possess a well-developed ventral median ridge, bounded on either side by circular depressions (Fig. 8); these ridges and depressions are absent in the succeeding dorsal vertebrae. The size of the vertebral condyle decreases in each successive vertebra in the preserved sequence (Fig. 7, 8), such that the anteriormost articulation (between the last cervical and the first dorsal vertebrae) is significantly broader transversely and taller dorsoventrally than the posteriormost (between dorsal vertebrae IV and V). The length of each centrum varies along the column, although the fragmented, yet articulated, nature of the series precludes accurate measurement in many cases (Fig. 4–8). Dorsal vertebra II appears to be shorter than either dorsal vertebra I or III (Table 1), and it is presumed that, when complete, the posteriormost cervical vertebra would have been anteroposteriorly longer than the first dorsal vertebra.

The parapophysis is located on the lateral surface of the centrum, anterior to the lateral pneumatic foramen, on dorsal vertebrae I and II; however, in dorsal vertebrae III–V, the parapophysis is situated entirely on the neural arch (Fig. 5, 6). This pattern of parapophyseal migration is consistent with the trend among transitional cervicodorsal vertebrae of sauropodomorphs in general (Upchurch *et al.* 2004). The shape and orientation of the pneumatic foramen varies with the position of the parapophysis: where the parapophysis is located on the centrum, the long axis of the pneumatic foramen is inclined anterodorsally–posteroventrally, whereas where the parapophysis is located entirely on the neural arch, the long axis of the pneumatic foramen is aligned anteroposteriorly (Fig. 5, 6).

Posteriormost cervical vertebra (“specimen c1”). The posterior cotyle of this cervical vertebra is preserved in articulation with the anterior condyle of dorsal vertebra I. The articulation is very slightly offset (Fig. 7, 8), as if the base of the neck of *Austrosaurus* was turned slightly to the left when the carcass was buried. The cotyle is wider transversely than it is tall dorsoventrally, as is often the case in sauropod posterior cervical vertebrae (Mannion *et al.* 2013). The preserved internal texture is camellate.

===PLEASE INSERT FIGURE 5===

Dorsal vertebra I (“specimens c2/b1 + b4”). Longman (1933, p. 136) incorrectly considered this vertebra and the preceding one to have been “from near the sacral region”, based on the fact that the centra are wider transversely than they are tall dorsoventrally. He also suggested that these vertebrae had been distorted dorsoventrally to such a degree that the matrix infilling the neural canal had been forced into the centrum; this is incorrect. The vertebra is largely undistorted—the neural canal was naturally set low in the centrum, such that the dorsal margins of the condyle and cotyle were shallowly concave (and therefore somewhat “heart-shaped” in anterior and posterior views) to accommodate the passage of the spinal cord.

The anterior portion of dorsal vertebra I is preserved in articulation with the preceding (cervical) vertebra, the cotyle of which obscures much of the succeeding anterior condyle. The centrum is opisthocoelous, and the anterior condyle is offset from the main body of the centrum by a pronounced rim around the lateral and ventral margins. This rim concomitantly forms the anterior margin of the ventral fossae (see below) and the anterior border of the lateral accessory foramina, close to where it presumably contacted (or even partially supported) the base of the parapophysis.

The anterior half of the ventral surface, posterior to the condylar rim, is occupied by a pair of fossae separated by a broad, anteroposteriorly-oriented ridge (Fig. 8). This ridge is truncated posteriorly by the breakage of the vertebra; nevertheless, both fossae are more or less completely preserved. The left fossa is deeper and larger than the right one. The anteroventral margin of the vertebra (i.e. the condyle) is expressed as a shelf that forms the anterior margins of the ventral fossae. Posterior to the fossae, the ventral surface of the centrum is transversely convex, as the aforementioned ridge expands transversely and flattens out, merging smoothly with the external surface of the posterior cotyle.

The majority of the external bone on the right lateral surface has been weathered away (Fig. 6), with the ventrolateral margin the only portion preserving the original external surface. Despite this, it is likely that only a thin veneer of superficial bone is missing given that the morphology of the preserved right lateral surface approximates that of a completely intact vertebral surface.

Two pneumatic features are present on the right lateral surface. The larger of the two is the elliptical lateral pneumatic foramen (90 mm × 40 mm), which is inclined anterodorsally–posteroventrally. The ventral surface of the lateral pneumatic foramen is bounded by a ridge (30 mm tall dorsoventrally). The second, smaller pneumatic feature is an accessory foramen (45 mm × 30 mm) that lies approximately 20 mm anterior to the lateral pneumatic foramen (Fig. 6). This structure is ovate, with its long axis aligned dorsoventrally, and bears surficial cortical bone around almost its entire circumference. Although it is not possible to quantify its total depth, it appears to have penetrated quite deeply posteromedially into the centrum.

The dorsal and posterior margins of the left lateral pneumatic foramen have been weathered away (Fig. 5). Consequently, the preserved margins can only be measured at a deeply inset level, such that the dimensions obtained (57 mm × 21 mm) understate its original size. The left lateral pneumatic foramen is not entirely visible in lateral view; it is best viewed in oblique posterior aspect without the posterior portion of the vertebra ("specimen b1") attached (Fig. 4 A2). This foramen is set within a fossa, and has an arc-like shape (with the concave margin of the arc facing posterodorsally). The anterodorsal margin of the pneumatic foramen, posteriorly adjacent to the parapophysis, penetrates most deeply. The left accessory foramen (which is visible in dorsal view; Fig. 7) is situated approximately 60 mm anterior to the lateral pneumatic foramen. It is ovate (45 mm dorsoventrally × 35 mm anteroposteriorly), with a well-defined posterior margin (preserved with external bone) and relatively indistinct anterior and dorsal margins.

The lateral accessory foramina preserved on both sides of this vertebra were not observed on any of the subsequent dorsal vertebrae. However, the possibility that lateral accessory foramina were present on the cervical vertebrae cannot be ruled out at present.

The bases of the parapophyses are incomplete, truncated by erosion (Fig. 5, 6). We infer that each occupied a position between the two lateral foramina present on each side of the centrum; it is possible that the division between the lateral pneumatic and accessory foramina formed a buttress extending from the body of the centrum to the parapophysis.

In dorsal view, very little exterior cortical bone is visible (Fig. 7). The neural arch has been almost altogether lost, fully revealing the hemispherical condyle–cotyle articulation between this and the preceding cervical vertebra, as well as the margins of the neural canal of this vertebra. The neural canal, represented by sedimentary matrix infill, is taller than wide.

Posteriorly, the preserved portion of the neural canal on “specimen c2” connects (imperfectly) to the portion of the first dorsal vertebra herein labelled “specimen b4” (Appendix 1), which represents the matrix between the first (“specimens c2/b1”) and second dorsal vertebrae (“specimens b2/a1”).

In posterior view, only camellate internal bone is visible on “specimen c2” (Figure 4 A2). The neural canal and the internal penetrations of the pneumatic foramina are the most prominent features. The posterior truncation of this portion of the vertebra highlights the asymmetry of the ventral fossae (since the ventral ridge is visible in cross-section) and of the placement of the neural canal opening.

Dorsal vertebra II (“specimen b2–4/a1”). The anterior portion of the second dorsal vertebra forms part of Longman’s (1933) “specimen B”, whereas the posterior portion forms part of his “specimen A”. Longman did not recognise the connection between these specimens, and in fact stated that they were not consecutive (Longman 1933, p. 136). The presence of a relatively ventrally positioned parapophysis on the centrum immediately anterior to the pneumatic foramen—but not at the anteroventral margin—is indicative of dorsal migration of the parapophysis relative to the preceding vertebra (Fig. 5, 6).

The anterior condyle is mostly obscured since it is articulated with the cotyle of the preceding vertebra. However, CT scans of this specimen demonstrate unequivocally that it is strongly opisthocoelous. The ventral surface of the centrum is transversely convex and anteroposteriorly concave, with a sagittal ridge (expressed more strongly anteriorly than posteriorly) as per the condition of the first dorsal vertebra (Fig. 8). The ventral fossae are extremely shallow, with each situated posterior to the annulus of the anterior condyle and lateral to the sagittal ridge. The right fossa is marginally deeper than the left, and is more clearly demarcated, as in dorsal vertebra I. However, the lateral margins of these fossae do not form strong ventrolateral ridges, distinguishing them from those present on the first dorsal vertebra.

In lateral view, the pneumatic foramen is situated at approximately the mid-length of the centrum (Fig. 5, 6). The surface of the centrum ventral to the pneumatic foramen is effectively flat and faces ventrolaterally. The lateral surface of the centrum is concave anteroposteriorly, as a consequence of the terminal flaring of the condyle and cotyle. The parapophysis is situated immediately posterior to the condylar annulus, and anterior to the pneumatic foramen. It is also broken at its base, revealing a camellate internal structure. At its truncated base, the parapophysis is relatively more elongated dorsoventrally than anteroposteriorly.

The lateral pneumatic foramen is semicircular in outline, with a slightly convex posterodorsal margin. Its long axis is oriented anterodorsally–posteroventrally (length: 65 mm), whereas its maximum dorsoventral height is 45 mm. The foramen is dorsoventrally deepest anteriorly and is posteriorly acuminate. Unlike the first dorsal, the posterior margin of the pneumatic foramen does not dissipate gradually; instead, it clearly terminates 80 mm anterior to the margin of the posterior cotyle.

“Specimen b3”, a fragment of matrix including a partial rib portion, keys into the left lateral pneumatic foramen of this vertebral centrum. The rib fragment houses a large (65 mm long) coel, infilled with calcite, which runs parallel to its long axis. A second smaller coel occurs slightly more distally. Another extraneous fragment occurs at the left dorsolateral margin of the cotyle. This fragment, which is approximately 95 mm wide, has a very compact and dense internal texture and might represent another rib portion.

The exposed neural arch, in anterior view (Fig. 4), presents the circumference of the neural canal, flanked by the pedicels. These presumably extended dorsally to form centroprezygapophyseal laminae (CPRLs); indeed, close to the medial edge of each pedicel, a slightly convex ridge is present which probably represents the CPRL base. The anterior neural canal opening is set within a broad, shallow fossa.

===PLEASE INSERT FIGURE 6===

Dorsal vertebra III (“specimens a2/h/e1”). The anterior portion of this vertebra, as well as the posterior portion of that preceding it, was described in detail by Longman (1933) as “specimen A”. Longman correctly recognised a portion of a rib preserved on the left side of the specimen, situated between the two vertebrae (Fig. 5).

Ventrally, the bony exterior of the condylar region has been damaged, revealing the pattern of the internal pneumatic coels (Fig. 8). The remaining preserved ventral surface is shallowly concave transversely and anteroposteriorly. Anteriorly, the internal coels are mediolaterally narrow and anteroposteriorly elongate, with the majority being approximately 4–10 mm wide and 15–25 mm long. Posteriorly, away from the anteriormost margin of the condyle, the coels seem to become anteroposteriorly shorter and more rounded in ventral profile. Further posteriorly still, the coels are not visible due to the presence of external bone. Ventrolateral ridges are only very weakly defined.

The left lateral surface (Fig. 5) is more intact than the right (Fig. 6), although it has been painted with consolidant (shellac), which has obscured some finer scale features. More of the condyle is exposed on the left side, including the full extent of the condylar rim, presumably due to the loss of part of the posterior cotyle of the preceding vertebra (Fig. 5). On both sides of the centrum, the lateral surface ventral to the pneumatic foramen (which extends for 80 mm dorsoventrally on the right side and 75 mm on the left side) is concave anteroposteriorly and very slightly convex dorsoventrally; on the left side, this convexity is asymmetrical, with its apex closer to the pneumatic foramen than the ventral margin.

The right lateral pneumatic foramen is anteroposteriorly elongate and posteriorly acuminate, with rounded anterior and dorsal margins and a straighter ventral margin (Fig. 6). The preserved internal dimensions are 55 mm × 37 mm, whereas the maximum external dimensions are estimated to be 80 mm × 80 mm. The anterior external margin of the right pneumatic foramen is situated 40 mm from the posterior margin of the cotyle of the preceding vertebra.

The left pneumatic foramen is both internally and externally defined, although the external definition is incomplete posteriorly, and the anterior margin merges imperceptibly with the annulus of the anterior condyle (Fig. 5). The maximum height of the left lateral fossa is 90 mm (measured externally, anterior to the mid-length), whereas the anteroposterior length can only be estimated at 110 mm. The left internal pneumatic foramen has an ovate outline (72 mm anteroposteriorly × 46 mm dorsoventrally), somewhat rounded anterodorsally and gently convex ventrally, and seems to have an acute—albeit not acuminate—posterior terminus. The total depth of the pneumatic foramen cannot be determined due to the presence of matrix; nevertheless a vertical partition can be observed within the foramen (at the mid-length), which has been slightly over-prepared and consequently damaged.

On the left lateral side, dorsal to the pneumatic foramen, the preserved neural arch has been painted over (Fig. 5). The left CPRL appears to become narrower towards the prezygapophysis; however, it is broken on its lateral surface, meaning that its true anteroposterior thickness cannot be ascertained. Posterior to the CPRL, the lateral surface of the neural arch is deeply embayed. This embayment is bounded posteriorly by a low ACDL. A third posteroventrally–anterodorsally oriented lamina, presumably the PCDL, arises approximately 120 mm posterior to the base of the CPRL. Although broken, the PCDL appears to intersect the ACDL, approximately 60 mm dorsal to the ventral margin of the embayment [positionally equivalent to a centrodiapophyseal fossa (CDF; Wilson *et al.* 2011b)], which is also the level from which both laminae originate. The diapophysis was presumably located dorsal to this intersection.

The external bone on the right half of the neural arch has been mostly lost (Fig. 6), with the exception of the anterior surface of the CPRL, which is smoothly mediolaterally convex lateral to the neural canal. The shallow CDF described for the left side (see above) appears to be replicated on the right side, although this can only be inferred on the basis of the morphology of the preserved sub-surficial bone.

Anteriorly, the bases of the CPRLs extend near-vertically at about 80° to the horizontal. The surface of the left CPRL base is flat, whereas the right is gently convex. The minimum mediolateral widths of the CPRLs are 70 mm (left) and 60 mm (right); these measurements were taken at a level that more or less coincides with the ventral surface of the neural canal (i.e. the likely position of the neurocentral juncture). Dorsal to this, the CPRLs expand mediolaterally; however, above the neural canal they are too incomplete to allow further observation. The outline of the anterior opening of the neural canal is circular (52 mm dorsoventrally × 50 mm transversely). A broad sulcus occupies the space on the neural arch dorsal to the neural canal and between the two CPRLs. The posterior neural canal opening is ovate (45 mm transversely × 33 mm dorsoventrally).

===PLEASE INSERT FIGURE 7===

Dorsal vertebra IV ("specimens e2/d/f1"). Dorsal vertebra IV is preserved in three pieces, although the majority of the specimen is confined to the anterior two portions. The condyle of this vertebra is mostly concealed by the cotyle of the preceding vertebra, although some of the condylar rim is visible, especially in ventral (Fig. 8) and right lateral views (Fig. 6).

The ventral surface is both transversely and anteroposteriorly shallowly concave between the condyle and cotyle (Fig. 8). The inflection point of the concavity is situated posterior to the mid-length. The concavity is approximately 150 mm long anteroposteriorly, whereas its minimum transverse width is 100 mm, measured at mid-centrum.

The left lateral surface of the centrum, ventral to the pneumatic foramen, is shallowly concave anteroposteriorly and flat dorsoventrally (Fig. 5). The minimum distance between the ventral margin of the centrum and the ventral margin of the pneumatic foramen is 60 mm internally and 65 mm externally. In left lateral view, much surficial bone remains intact, although matrix obscures the left lateral pneumatic foramen. The outermost surface of this fossa infill appears to preserve a sliver of surficial bone, presumably a shard of a rib shaft (distal to the rib head), which might have articulated in vivo with the succeeding vertebra (Fig. 5). Despite the persistence of matrix within the left pneumatic foramen, its form and depth can be gauged at the anterior break between "specimen e" and "specimen d" (i.e., more or less halfway through the vertebra; Fig. 4). The bilateral foramina almost meet internally and are separated only by a thin septum (20 mm wide). The left lateral pneumatic foramen projects 80 mm internally. In anterior cross-sectional view (Fig. 4), the foramen at depth has a horizontal ventral surface and a dorsally curved upper interior surface (similar in profile to that of the preceding dorsal—see Longman 1933, fig. 3). The external anteroposterior length of the left lateral pneumatic foramen was no more than 120 mm.

In right lateral view, the lateral surface ventral to the pneumatic foramen is dorsoventrally convex (~60 mm tall; Fig. 6). The right lateral pneumatic foramen is partially filled with matrix, mostly in its posterior half (the anterior half being shallowly exposed), although it was clearly elliptical with its long axis horizontal. The external margins of the pneumatic fossa (115 mm long anteroposteriorly) blend imperceptibly with the outer centrum wall and are poorly preserved anteriorly.

The neural arch preserves little surficial bone on all surfaces except for the ventral portion of the left lateral side (Fig. 5). Here, three buttress-like laminae originate approximately 150 mm dorsal to the ventral margin of the centrum. The anteriormost of these laminae, which is interpreted as a shared ACPL-PCPL base, is incompletely and poorly preserved but appears to be directed anterodorsally. The posterior margin of this shared ACPL-PCPL base is confluent with the base of the ACDL (which is directed posterodorsally), which in turn merges dorsally with the anterodorsally directed PCDL. The PCDL and ACDL define a shallow, dorsally tapering, triangular centrodiapophyseal fossa (CDF). Between the ACPL and ACDL, and anterior to the junction between the ACDL and PCDL, another anterodorsally–posteroventrally inclined lamina is present. This is interpreted as a second (stranded) PCPL, ventrally truncated by the ACDL. Between this PCPL and the conjoined ACPL-PCPL mentioned above, an anterodorsally–posteroventrally inclined, elongate posterior centroparapophyseal lamina fossa (PCPL-F) is present.

The posterior neural canal opening is sub-circular (47 mm dorsoventrally × 42 mm transversely). The surficial bone enveloping the bases of the centropostzygapophyseal laminae (CPOLs) is not preserved, although there are indications that the bases were approximately 55–60 mm wide mediolaterally. The medial margins of the CPOLs merge smoothly with the ventral margin of the posterior neural canal opening.

A large fragment of dorsal rib is preserved at the interface between dorsal vertebrae III and IV, with its long axis aligned dorsoventrally (Fig. 5). Despite its preserved position, the rib most probably relates to dorsal vertebra III. The preserved proximodistal length of the fragment is 175 mm and its internal structure is discernible, belying the presence of two large (30–40 mm long) coels, in addition to five smaller (<15 mm long) coels. Disregarding these coels, the internal structure of the rib is spongy towards the proximal end and much denser distally, such that it is almost solid.

===PLEASE INSERT FIGURE 8===

Dorsal vertebra V (“specimens f2 + k”). This vertebra comprises the anterior half to two-thirds of the centrum, in addition to an anteroposteriorly short section of the neural canal, preserved as a natural internal cast. The maximum preserved anteroposterior length of the specimen is 210 mm, whereas the maximum preserved transverse width of the anterior condyle is 240 mm. Surficial bone is only preserved on the condyle; the only other region of this vertebra preserving near-surficial bone is the left lateral surface, ventral to the left pneumatic foramen. The condyle is separated on the right side from the cotyle of dorsal vertebra IV by as little as 3 mm of matrix; ventrally, the intervening matrix is 8 mm thick.

The ventral surface of this vertebra is too poorly preserved to allow precise determination of its external morphology (Fig. 8). The exposed internal coels appear to be anteroposteriorly elongate, although their lengths cannot be determined accurately because of their poor marginal preservation and anastomosing nature. Generally, the mediolateral width of these coels is 10 mm.

The left lateral surface of the centrum is gently convex dorsoventrally, and is gently concave anteroposteriorly (Fig. 5). Matrix fills in and defines the shape of the left lateral pneumatic foramen, which presents a lenticular outline, oriented anterodorsally–posteroventrally (87 mm × 50 mm). On the right surface, no surficial bone is preserved (Fig. 6). However, the anteroventral half of the border of the external pneumatic foramen appears to be delineated, whereas the posterodorsal half is not.

The neural canal is represented by a short section of natural cast which is circular anteriorly (52 mm transversely × 50 mm dorsoventrally) and ovate posteriorly (46 mm transversely × ~40 mm dorsoventrally). The maximum length of the preserved natural neural canal cast is 75 mm.

Additional, positionally indeterminate vertebral specimens. A number of additional fragments smaller than the blocks comprising the main sequence of articulated vertebrae are present. Some of these might derive from dorsal vertebrae more posterior than dorsal vertebra V. Although only a few of these fragments are described below (others are too poorly preserved to be informative), a full listing is provided in the Appendix.

A fragment of dorsal vertebra (“specimen f”) preserves the right posteroventral portion of a centrum, including the posteroventral margin of the pneumatic foramen, the base of the posterior cotyle (which has mostly been lost to erosion), and matrix representing the position of the intervertebral disc. The internal camellate texture is clearly visible. The ventral surface was very shallowly concave anteroposteriorly and transversely, whereas the ventral portion of the lateral surface was dorsoventrally convex ventral to the pneumatic foramen; anteroposteriorly it was presumably flat. The long axes of the internal pneumatic coels run parallel to the cotylar margin, arranged in two concentric rings (ventrally) and four concentric rings (dorsally). Anterior to the cotylar margin, the coels become more elongate anteroposteriorly, more irregularly distributed, and less palisade-like in arrangement.

One narrow fragment comprises two thin slivers of possible vertebral centra with intervening sediment (“specimen q”). These vertebral portions could conceivably represent an articulation between two dorsal centra, implying that more than six vertebrae of *Austrosaurus* were originally preserved; this, however, is speculative. The concave element is extremely incompletely preserved, represented mostly by dense surface bone which forms a thin veneer; the convex element is more substantially represented. In cross-section, the surface is formed by a 3–5 mm thick section of dense bone, which is followed posteriorly by a palisade of internal coels. These coels are anteroposteriorly elongate (up to 37 mm anteroposteriorly × 16 mm mediolaterally; most are smaller), and are separated from their neighbours by 1–2 mm thin septa. The intervertebral matrix is between 10–20 mm thick and varies from one side of the specimen to the other.

A 120 mm deep fragment comprising the interface between two articular units and the intervening sediment (“specimen p”) seems to represent an articulated set of zygapophyses. The majority of the external surface has been lost; consequently, our interpretation is tentatively based on the morphology of the subsurface, which is presumed to replicate the original external morphology. The larger of the two preserved zygapophyses appears to represent a right postzygapophysis, embayed medially by an arc representing the right half of the spinopostzygapophyseal fossa (SPOF). This latter, medially facing surface retains a small section of external bone. Overall, the posterior/posterolateral surface of the postzygapophysis is convex, with the dorsal-most preserved portion being slightly more ridge-like. This morphology is consistent in general with sauropod postzygapophyses extending dorsally as narrowed spinopostzygapophyseal laminae. Thus, the more convex dorsal part of "specimen p" likely represents the base of that lamina. The counterpart right prezygapophysis is comparatively incomplete, but is separated from the postzygapophysis by a plane of sediment that is 10–20 mm thick, which likely conforms to an *in vivo* inter-articular gap. It appears that the internal coels of the postzygapophysis formed a palisade with their long axes perpendicular to the inter-zygapophyseal gap (the coels are about 20 mm dorsoventrally × 9 mm mediolaterally). Dorsal to the gap, the coels are larger in size (35 mm × 15 mm) and bear anteroposteriorly longer axes. The internal coel patterning is less well-defined for the prezygapophysis; there is a dense 5–10 mm thick layer of tissue at the prezygapophyseal articular facet, which thins medially.

===PLEASE INSERT FIGURE 9===

Dorsal ribs. A total of six dorsal ribs are preserved in the *Austrosaurus* hypodigm (Fig. 9). Five of these are from the left side, representing dorsal ribs I–V, whereas the other is interpreted to be right dorsal rib IV, based on the congruence between its morphology and that of left dorsal rib IV. The anterior four ribs are fairly consistent in their morphology. The proximal ends are thickened, subtriangular in cross-section, and each has a somewhat concave anteromedial margin near the point at which the capitulum and tuberculum would have met. In contrast, the distal ends (of dorsal ribs I–III, at least) are plank-like, being much longer anteroposteriorly than wide mediolaterally (anteroposterior:mediolateral ratio in dorsal rib I = 6.13; dorsal rib II = 4.87; and dorsal rib III = 3.14). The lateral surfaces of the ribs are flat, whereas the medial surfaces are convex. Distal to the rib head, each of the first four ribs bears a longitudinal groove on the posterior surface, which extends halfway down the shaft. In cross-section, each of the anterior four ribs is mediolaterally broadest in its posterior third, and the anterior margin of each is tapered. The portion of each rib bearing a posterior groove is arrowhead-shaped in cross-section, whereas distal to the groove the cross-section is "D"-shaped, with the lateral margin being straight. Dorsal rib V does not have a plank-like distal end, and also lacks the well-defined posterior groove present in dorsal ribs I–IV. At mid-length, the cross-section of this rib is almost circular. Distally, dorsal rib V is mediolaterally compressed but not particularly elongate anteroposteriorly.

The shafts of all six ribs are well preserved, whereas the proximal ends are not. The structure of the internal bone of several of the anterior dorsal ribs demonstrates that the proximal ends were pneumatised, a feature which can also be seen in some of the fragments collected in the 1930s. This pneumatisation presumably contributed to the poor preservation of the proximal ends.

Discussion

The taphonomy of the Austrosaurus mckillopi *type series*

===PLEASE INSERT FIGURE 10===

Generally, it is quite unusual to find sauropod skeletal remains in marine settings (Mannion & Upchurch 2010) because they were fully terrestrial animals. It is tempting to correlate the frequency of preservation of terrestrial vertebrate fossils in a marine setting with land area proximity. However, Buffetaut (1994) warned against drawing this conclusion too readily, noting that some workers had suggested that dinosaur carcasses could have been carried for hundreds or thousands of kilometres (Martill 1988).

Given that the type specimen of the terrestrial sauropod *Austrosaurus mckillopi* was found in the marine Allaru Mudstone, it is clearly allochthonous. As outlined above, QM F2316 constitutes an articulated sequence of vertebrae with ribs (KK F1020; Fig. 10); consequently, we were able to utilise the skeletal articulation and completeness metrics proposed by Beardmore *et al.* (2012) to elucidate its taphonomic history. Beardmore and colleagues' system separates the skeleton into nine skeletal units (head, neck, trunk, tail, ribs, left and right forelimbs + pectoral girdles, left and right hind limbs + pelvic girdles) and ranks articulation and completeness on a scale of 0–4, where 0 indicates low completeness and disarticulation, and 4 indicates high completeness and full articulation. We also adopted the classification system proposed by Syme & Salisbury (2014) to quantify the degree of articulation between skeletal units, where F denotes full articulation between adjacent units, P denotes partial articulation, and D denotes disarticulation.

The cervical and dorsal vertebrae have an articulation score of 4—fully articulated with no gaps or breaks—and the position of the ribs in the field suggests a similarly high articulation score. The neck and trunk skeletal units are fully articulated with one another (inter-unit articulation category F), and the rib and trunk skeletal units were either semi-articulated (inter-unit articulation category P) or fully articulated. Given that non-titanosaurian titanosauriforms had between 13 [*Giraffatitan* (Janensch 1950)] and 17 [*Euhelopus* (Wilson & Upchurch 2009)] cervical vertebrae, and that titanosaurs had between 14 [*Futalognkosaurus* (Calvo *et al.* 2007)] and 17 [*Rapetosaurus* (Curry Rogers 2009)] cervical vertebrae, we calculate that the completeness of the *Austrosaurus* neck is approximately 6–7%—a completeness score of 1. If the total number of dorsal vertebrae in *Austrosaurus* fell between the extremes known among titanosauriforms [10 dorsals in *Futalognkosaurus* (Calvo *et al.* 2007), *Overosaurus* (Coria *et al.* 2013) and *Trigonosaurus*

(Campos *et al.* 2005), and 13 in *Euhelopus* (Wilson & Upchurch 2009)], the completeness score would be between 38–50%—a completeness score of 2. Assuming that the number of dorsal ribs was precisely double the number of dorsal vertebrae, and given that six ribs were recovered, we calculate a percentage completeness ranging between 23–30% for the ribs—a completeness score of 1 or 2. Thus, QM F2316 displays relatively low completeness but relatively high articulation; this suggests that the carcass underwent a period of decay prior to burial in a low energy environment (Beardmore *et al.* 2012).

The body of *Austrosaurus* most likely drifted out to sea as a consequence of a process termed ‘bloat and float’ (Allison & Briggs 1991), wherein gas produced during endogenous decay built up in the body tissues and the digestive tract, which caused the body to swell and become positively buoyant in water (Schäfer 1972, Davis & Briggs 1998, Rogers & Kidwell 2007). The system of pneumatic diverticula present in sauropods (Wedel 2009), and the high level of postcranial pneumatisation developed in titanosauriforms (Wilson & Sereno 1998) and exemplified by titanosaurs (Cerda *et al.* 2012) would have affected the buoyancy of these dinosaurs (Henderson 2004a) and might have prolonged the duration of the flotation stage; however, the effect of this has not yet been quantified. As decay progressed and the integrity of the body tissues was compromised, gases would have escaped the carcass. This, along with continual saturation of body tissues, would have resulted in the carcass becoming negatively buoyant and caused it to sink (Fig. 11). For the last cervical vertebra, the first five dorsal vertebrae, and several ribs to have remained in articulation, some connective soft tissues must have been intact prior to the carcass settling on the sea floor (as suggested by Molnar 2010), left side down.

===PLEASE INSERT FIGURE 11===

It is possible that cranial and postcranial elements missing from the *Austrosaurus* site were detached by scavengers during the ‘bloat and float’ phase. In this scenario, the disruption of the integrity of the soft tissue by scavengers might have facilitated the separation and sinking of a portion of soft tissue containing presacral vertebrae and ribs; the remainder of the carcass would have been consumed and/or scattered. Another possibility is that the carcass progressed to the ‘advanced decay stage’, unaffected by scavenging, whereupon soft tissue decayed to such a degree that the carcass broke into discrete segments; the posteriormost ribs appear to have been ‘stacked’, so sufficient soft tissue must have decayed prior to burial to allow these elements to partially disarticulate. Given that the *Austrosaurus* site has been exhausted, and if we assume that the entire skeleton was buried and fossilised in life position laying on its left side, the missing elements must have eroded during post-diagenetic subaerial weathering. Although this might be true for elements positioned stratigraphically higher than the remainder of the recovered skeleton (such as the right ribs), for the rest of the skeleton we find this to be the least likely scenario because of our failure to discover additional skeletal material either vertically beneath, or laterally throughout, the soil profile at the site. It is important to note that the presence of a single right dorsal rib lying near to its in vivo position does not necessarily negate this interpretation, but rather suggests only enough soft tissue decay occurred to allow this single rib to disarticulate prior to burial. The lack of skeletal element transport after disarticulation also aligns with the interpretation of deposition below wave-base in a calm water environment.

===PLEASE INSERT FIGURE 12===

Given the presence of marine ‘reptile-fall’ type communities during the Mesozoic (Kaim *et al.* 2008, Wilson *et al.* 2011a, Danise & Higgs 2015), it is conceivable that any sauropod remains lying at the sediment-water interface would have been colonised by benthic communities, forming a ‘saurian deadfall’ [*sensu* Hogler (1994) and Reisdorf & Wuttke (2012)]. Colonisation might have taken place within weeks or months, resulting in bone surface modifications and bone erosion from chemical dissolution (Trueman & Martill 2002, Adams 2009, Anderson & Bell 2014). Although there is no evidence of encrusting biota or eroded bone on the *Austrosaurus* specimen, remains of the molluscs *Inoceramus* sp. and *Beudanticeras* sp. were recovered from the site and are preserved within matrix adhering to the vertebrae (Fig. 12). It is possible that the bacteriophage filter-feeding *Inoceramus* sp. [a mode of life proposed by Henderson (2004b)] were attracted to bacteria feeding on the decaying *Austrosaurus* remains. The apparent lack of other benthic scavengers, including crustaceans and teleost fish similar to those recovered from the underlying Toolebuc Formation (Wilson *et al.* 2011a, Smith & Holland 2016), could be a result of either true absence or preservation bias. There is also evidence of benthic feeding elasmosaurids and protostegid turtles occupying the Eromanga Sea at this time, with fossilised mollusc-rich gut contents and coprolites from both middle and upper Albian units including the Allaru Mudstone (McHenry *et al.* 2005, Kear 2006). If plesiosaurs [e.g. the pliosaur *Kronosaurus* (Longman 1924, 1930, White 1935, Romer & Lewis 1959, McHenry 2009, Holland 2015)] scavenged carcasses when they were available, and if the remains of *Austrosaurus* had a relatively long residence time at the sediment-water interface, they would most likely have been disarticulated and possibly destroyed before burial and fossilisation could occur. That the remains were preserved relatively intact suggests that this isolated portion of the *Austrosaurus* carcass was buried after only a short period of decay at the sediment–water interface during the ‘mobile scavenger stage’ or the beginning of the ‘enrichment opportunistic stage' (sensu Smith & Baco 2003, Kaim *et al.* 2008), before an abundant saurian deadfall community could form.

The phylogenetic position of Austrosaurus mckillopi

Previous opinions on the phylogenetic position of Austrosaurus mckillopi. When *Austrosaurus* was first described during the 1930s, sauropod inter-relationships in general were poorly understood. Longman (1933) considered *Austrosaurus* to be more specialised than *Rhoetosaurus brownei* (Longman 1926) on the basis of the more complex internal vertebral structure of the former, and specifically stated that the internal vertebral structure of *Diplodocus carnegii* (Hatcher 1901) was quite similar to that of *Austrosaurus*. Longman (1933) also suggested that *Austrosaurus* bore no close relationship to the Argentinean sauropods *Titanosaurus* (now *Neuquensaurus*), *Laplatasaurus* or *Antarctosaurus* (Huene 1929), and suggested that it was not a member of Titanosauridae. Instead, Longman (1933) tentatively suggested that *Austrosaurus* was an advanced member of the Cetiosauridae.

Coombs & Molnar (1981) were undecided on the phylogenetic placement of *Austrosaurus*, suggesting that classification as 'Sauropoda incertae sedis' was advisable if not satisfactory. In a non-technical summary of *Austrosaurus*, Thulborn (1987, pp. 44–46) provided a frank assessment of the then state-of-play of sauropod phylogenetics. His observations of the type specimen allowed him to state that *Austrosaurus* was not allied with diplodocids, camarasaurs or brachiosaurs, and that the classification of *Austrosaurus* as a cetiosaur was essentially meaningless, since at the time Cetiosauridae was "…really a waste-basket category for any generalised or primitive-looking sauropods that can't easily be classified elsewhere" (Thulborn 1987, p. 44).

Molnar (2001b, p. 141) suggested that *Austrosaurus* was a titanosaur, based on characters outlined by Salgado *et al.* (1997). Molnar (2001b, pp. 141, 143) regarded at least some of the preserved vertebrae as posterior dorsal vertebrae, and noted the presence of the following characters: centroparapophyseal laminae present; pneumatic foramina eye-shaped and deep; centra opisthocoelous; and “spongy” internal texture. Given that we now know that most of the preserved vertebrae of *Austrosaurus* are actually anterior dorsal vertebrae, the significance of many of these characters is greatly diminished.

The only phylogenetic analysis in which *Austrosaurus* has been included is that of Upchurch *et al.* (2004). On the basis of this analysis, *Austrosaurus* was recovered as a non-lithostrotian titanosaur (Upchurch *et al.* 2004, p. 310), an interpretation followed by Barrett & Upchurch (2005, p. 153). However, as has been mentioned elsewhere (Mannion *et al.* 2013, p. 154, Poropat *et al.* 2015a, pp. 92–93), the scores for this taxon relied heavily upon material referred to *Austrosaurus* sp. by Coombs & Molnar (1981), rather than the holotype. All specimens referred to *Austrosaurus* sp. by Coombs & Molnar (1981) were removed from *Austrosaurus* by Molnar (2001b); one of these (QM F7292) now constitutes the holotype of *Wintonotitan wattsi* (Hocknull *et al.* 2009, Poropat *et al.* 2015a).

Molnar & Salisbury (2005) discussed the phylogenetic placement of *Austrosaurus* in their revision of Australian Cretaceous sauropods. They noted the presence of three vertebral laminae on Longman’s (1933) Specimen A (here, dorsal vertebra III): the anterior centroparapophyseal lamina (ACPL), anterior centrodiapophyseal lamina (ACDL), and posterior centrodiapophyseal lamina (PCDL). More importantly, however, Molnar & Salisbury (2005) also incorporated some of the material not described by Longman (1933) in their assessment of *Austrosaurus*. Of especial note was their consideration of what has now been recognised as the middle section of dorsal vertebra IV ("specimen d"; see Appendix). In the text, Molnar & Salisbury (2005, pp. 456–457) state that "…it is unclear which end of the specimen is anterior", although they appear to contradict this statement by stating that "the right side is seen in Figure 20.1". However, if the laminae labels on their figure are taken at face value, then Molnar & Salisbury (2005) depicted the specimen in question in what can only be interpreted as left lateral view. On the basis of the identification of five laminae (ACDL, PCDL, prezygodiapophyseal lamina [PRDL], spinodiapophyseal lamina [SPDL], and postzygodiapophyseal lamina [PODL]), they suggested that *Austrosaurus* was a titanosaur; however, they did not specify which, if any, of these laminae lent support to this claim. Based on our observations, the majority of these laminae were either misidentified (PRDL, SPDL, PODL) and cannot be observed, or were incorrectly positioned (PCDL) by Molnar & Salisbury (2005).

Hocknull *et al.* (2009, p. 40) considered *Austrosaurus* as a nomen dubium because they regarded the holotype specimen as inadequate for diagnostic purposes; they also suggested that a neotype should be designated. In contrast, Agnolin *et al.* (2010, p. 262) regarded *Austrosaurus* as a valid taxon, assigning it to Titanosauriformes. Molnar (2011a), in another discussion of the holotype specimen of *Austrosaurus*, noted a personal communication from Zhao Xijin who "suggested that some of the vertebrae might be posterior cervicals" (Molnar 2011a, p. 322), a proposal with which we agree. Molnar stated that none of the preserved pieces of dorsal rib were pneumatised; this led him to suggest that *Austrosaurus* was a non-titanosauriform sauropod, since Wilson & Sereno (1998) and Wilson (2002) had earlier identified ribs with proximal pneumatic chambers as being synapomorphic of this clade. We disagree with the removal of *Austrosaurus* from Titanosauriformes on this basis: one specimen catalogued as part of the *Austrosaurus* type series appears to be close to the proximal end of a dorsal rib, and it is pneumatised, as are all of the rib proximal ends recovered in 2014–2015. One non-pneumatised rib portion is embedded in matrix in association with the articulated dorsal vertebrae of the type series; however, this rib segment represents a region somewhat distal to the proximal end, and would not have been expected to be pneumatised.

Mannion & Calvo (2011) tentatively agreed with the designation of *Austrosaurus* as a nomen dubium by Hocknull *et al.* (2009), but also assigned it with reservations to Titanosauria. In contrast, Mannion *et al.* (2013, p. 154) unequivocally regarded *Austrosaurus* as a nomen dubium, pending restudy, and considered it to be classifiable only as far as Titanosauriformes. Poropat *et al.* (2015a) also regarded *Austrosaurus* was a nomen dubium, pending reappraisal.

Phylogenetic distribution of key anatomical features. Some of the features observed in this study have potential significance for the phylogenetic position of *Austrosaurus mckillopi*. These include the ventral ridges on the anterior dorsal vertebrae, the internal pneumatic features of the vertebrae, and the morphology of the dorsal ribs.

(1) Ventral ridges on anterior dorsal vertebrae. The ventral surfaces of dorsal vertebrae I and II in *Austrosaurus* each bear prominent midline ridges, bounded on each side by a shallow fossa. None of the other dorsal vertebrae preserved appear to have had ventral ridges, although it is possible that ridges were present on vertebrae missing from the type series.

Although several titanosauriform taxa have ventral ridges in their middle–posterior dorsal vertebrae (e.g. the brachiosaurids *Brachiosaurus* and *Giraffatitan*; Upchurch 1998), far fewer possess these in their anterior dorsal vertebrae (Mannion *et al.* 2013, Poropat *et al.* 2016). In *Euhelopus*, a euhelopodid somphospondylan (D'Emic 2012), one of the vertebrae at the cervicodorsal transition (possibly the first dorsal, but probably the last cervical) bears a ventral median ridge set within a concavity (Wilson & Upchurch 2009, pp. 212, 219). This contrasts with the ventral ridges on the first two dorsals of *Austrosaurus*, which are not set within concavities.

Phuwiangosaurus is commonly resolved as a non-titanosaurian somphospondylan (Suteethorn *et al.* 2010, Carballido *et al.* 2011b, 2012b, D'Emic 2012, 2013, Mannion *et al.* 2013, Carballido & Sander 2014, Lacovara *et al.* 2014, Poropat *et al.* 2015b, Upchurch *et al.* 2015, Gorscak & O'Connor 2016, Poropat *et al.* 2016) or a basal titanosaur (Upchurch *et al.* 2004, Carballido *et al.* 2011a, 2015) in phylogenetic analyses. The description of a ventral ridge on an anterior dorsal vertebra (Martin *et al.* 1999, p. 47) in this taxon matches the morphology of the ventral ridges of *Austrosaurus*. In more posterior dorsal vertebrae, the ventral ridge was only faintly expressed (Martin *et al.* 1999, p. 49), whereas in a referred specimen of *Phuwiangosaurus*, it was determined that ridges were present on dorsal vertebrae III–VII (Suteethorn *et al.* 2009), demonstrating some intraspecific variation.

Relatively few titanosaurs are reported to have had ventral ridges on their anterior dorsal vertebrae. Exceptions include *Barrosasaurus* (Salgado & Coria 2009), *Overosaurus* (Coria *et al.* 2013) and *Lirainosaurus* (Díez Díaz *et al.* 2013), although perhaps most notable is *Opisthocoelicaudia* in which ventral ridges set within deep fossae are present on all dorsal vertebrae (Borsuk-Białynicka 1977). Among these titanosaurs, only the ventral ridges of *Lirainosaurus* approximate those of *Austrosaurus* in both morphology and distribution.

As the above summary suggests, the presence of a ventral ridge that is not set within a fossa in the anterior dorsal vertebrae of *Austrosaurus mckillopi* is unusual among Titanosauriformes, but not autapomorphic, given the presence of similar ventral ridges in the anterior dorsal vertebrae of *Phuwiangosaurus* and *Lirainosaurus*. Ventral ridges are not known in the anterior dorsal vertebrae of any other Australian sauropod, although this might simply be because no other Australian sauropod specimens described to date preserve dorsal vertebrae I or II. Additional specimens will be necessary to determine how widespread this feature was among Australian sauropods, if it was present in taxa other than *Austrosaurus* at all.

===PLEASE INSERT FIGURE 13===

(2) Internal texture of the vertebrae. The pneumatic nature of sauropod vertebrae, first observed by Seeley (1870), was also considered by Longman (1933) in his description of *Austrosaurus mckillopi*. However, Longman did not think that the internal cavities of the vertebrae connected with the pneumatic foramina: he instead tentatively supported Owen's (1876) suggestion that the internal spaces had been filled with "chondrine". The basis for this contention was that the chemical composition of the matrix within the coels was different from that surrounding the exterior of the specimen. Later, however, Longman changed his mind, possibly influenced by Janensch's (1947) work: in a 1949 newspaper article on *Austrosaurus*, he stated, "…the body of the vertebrae is composed of a multitude of small chambers, and it is also hollowed out on each side. Probably these chambers were filled with air in life." (Longman 1949, p. 2).

Wedel *et al.* (2000) determined that titanosauriforms show three types of internal texture in their presacral vertebrae: semicamellate, camellate, and somphospondylous. In the case of *Austrosaurus*, the preserved portions of the last cervical and first five dorsal vertebrae are camellate. Although it is probable that the presacral vertebrae of *Austrosaurus* were somphospondylous [following the criteria of Wedel *et al.* (2000) and Wedel (2003)], the incomplete preservation of the neural arches and the absence of neural spines prevent this from being demonstrated with certainty. Subsequently, Wedel (2003) highlighted the fact that the internal texture of the vertebrae of any given sauropod will show variation within the column, specifically stating that the internal texture of the posterior cervical vertebrae tended to be the most complex.

In order to further assess the internal texture of the *Austrosaurus mckillopi* type series, all specimens catalogued as QM F2316 were CT scanned at Greenslopes Private Hospital, Brisbane on a Siemens/Somatom Definition Flash CT scanner at 100 kV and 8 mAs, and 140 kV and 22 mAs, with a slice increment of 0.4 mm. Although the majority of the scans were affected by significant artifacts and failed to adequately resolve the internal structure of the specimens, some variation in the internal texture of each vertebra can still be seen (Fig. 13).

The laminae within the anterior condyles project posteromedially from the extremities towards the centre of the vertebra, forming an anastomosing network. The chambers between these partitions are dorsoventrally taller than they are long anteroposteriorly or (especially) wide mediolaterally. Particularly notable in axial section (Fig. 13A) is the fact that the camellae are most densely packed, into what appear to be three concentric layers, in the posterior cotyles. Similar observations to these were made by Molnar (2011a, pp. 332–333), based on inspection of the broken surfaces of the *Austrosaurus* type series. His recognition that a densely packed, concentric layer of camellae was also present in the posterior cotyle of a dorsal vertebra of *Saltasaurus loricatus* figured by Powell (1992, fig. 16d, 2003, pl. 30d) was particularly insightful. However, the CT scans have revealed that there were three concentric layers of camellae in the posterior cotyles of the dorsal vertebrae of *Austrosaurus*, whereas there is only one in those of *Saltasaurus*. It is probable that the reduced number of concentric layers of camellae in the posterior condyles of the dorsal vertebrae of *Saltasaurus* is a consequence of the significantly smaller size of this animal; taking this line of reasoning in the other direction, it would seem safe to presume that titanosauriforms larger than *Austrosaurus* would have had more strongly reinforced posterior cotyles, and that this strengthening might have been manifested as additional concentric layers of camellae. CT scans of the dorsal vertebrae of the Brazilian Cretaceous titanosaur *Austroposeidon magnificus* show concentric lamina rings that mirror the condyle/cotyle in shape (Bandeira *et al.* 2016), which would appear to support this hypothesis. However, Bandeira *et al.* (2016, p. 19) interpreted these laminae as “intercalated growth structures”. Studies on the internal structure of the presacral vertebrae of large titanosaurs [e.g. *Argentinosaurus* (Bonaparte & Coria 1993), *Puertasaurus* (Novas *et al.* 2005), *Futalognkosaurus* (Calvo *et al.* 2007), *Dreadnoughtus* (Lacovara *et al.* 2014), *Alamosaurus* (Fowler & Sullivan 2011, Tykoski & Fiorillo 2017)] and non-titanosaurian somphospondylans [e.g. *Daxiatitan* (You *et al.* 2008)] will be needed to test this hypothesis.

(3) Dorsal rib morphology. The dorsal ribs of very few titanosauriforms have been adequately described: normally, the presence of proximal pneumatisation, and a vague allusion to plank-like or non-plank-like distal rib ends, is all that is reported. Regarding one particular aspect of rib morphology in a broader taxonomic scope, few macronarian sauropods have had the cross-sectional shapes of their dorsal ribs documented in any detail. Exceptions include *Giraffatitan brancai* (Janensch 1950) and *Camarasaurus* sp. (Waskow & Sander 2014), for which multiple rib cross-sectional outlines have been illustrated, and

Opisthocoelicaudia skarzynskii (Borsuk-Białynicka 1977), for which the cross-sectional outline of each preserved dorsal rib was described.

As noted by Waskow & Sander (2014), each rib of *Camarasaurus* shows significant cross-sectional shape variation along its length, and the ribs show significant variability when considered collectively. Notably, the distal ends of the dorsal ribs of *Camarasaurus* appear to show the plank-like morphology generally considered to be a synapomorphy of Titanosauriformes (Wilson 2002). By contrast, the cross-sections depicted by Janensch (1950) of the anterior dorsal ribs of *Giraffatitan*—a titanosauriform by definition—do not conform to the criteria for being considered plank-like. *Opisthocoelicaudia*, however, possesses the distally plank-like anterior dorsal ribs typical of titanosauriforms: Borsuk-Białynicka (1977) observed that dorsal ribs III, IV and V had flattened distal ends; that rib VI was rounded along most of its length but flattened distally; and that ribs VII to IX were rounded in cross-section. The preserved ribs of *Austrosaurus* show a similar pattern to those of *Opisthocoelicaudia*, although the transition from plank-like to rounded was evidently completed by dorsal rib V.

===PLEASE INSERT FIGURE 14===

All of the dorsal ribs of the somphospondylan *Astrophocaudia* (D'Emic 2013), and all (except dorsal rib I) in the brachiosaurid *Cedarosaurus* (Tidwell *et al.* 1999), were described as not plank-like. Only the middle and posterior dorsal ribs of *Paludititan* were described as being plank-like—the anterior dorsal ribs were “…rounded oval in cross-section and not particularly flattened…” (Csiki *et al.* 2010, p. 304). All dorsal ribs of *Malawisaurus* (Gomani 2005) and *Rukwatitan* (Gorscak *et al.* 2014) were described as having flattened shafts irrespective of serial position. The dorsal ribs of *Epachthosaurus* appear to show some similarity to those of *Austrosaurus* inasmuch as the anteriormost elements were described as being distally plank-like, whereas the posteriormost were cylindrical in cross-section (Martínez *et al.* 2004). Dorsal ribs I and II of *Overosaurus* (Coria *et al.* 2013) are not plank-like at their distal ends, and both the anterior and posterior margins of dorsal ribs II and III in *Overosaurus* are expanded at the proximal end.

Among Australian sauropods, perfunctory comparisons can be made between those of *Austrosaurus mckillopi* and some of the preserved dorsal ribs of *Diamantinasaurus matildae* (Fig. 14; Hocknull *et al.* 2009, Poropat *et al.* 2015b). However, these are limited by the fact that the type specimen of *Diamantinasaurus* was not found articulated. As such, the eight *Diamantinasaurus* rib sections analysed herein were assigned a letter (from A–H) based on their presumed serial position (Fig. 14). Rib A appears to represent an anterior dorsal rib, possibly the anteriormost. The cross-section of this rib is crescentic—quite unlike any of those observed in *Austrosaurus*. It is possible that the corresponding section(s) of the anteriormost dorsal rib(s) of *Austrosaurus* were not preserved, hence the morphological incongruity. Rib B preserves a complete proximal end but is incomplete distally; that it appears to taper distally so rapidly might indicate that it was from the posterior half of the thorax. Rib C is morphologically congruent with dorsal rib III of *Austrosaurus* (Fig. 9). The ribs of *Diamantinasaurus* labelled D–F in Fig. 14 are presumably from the anterior half of the thorax, although their incomplete preservation makes it difficult to determine how close the portions were to the distal ends of their respective ribs. The ribs labelled G and H are interpreted to have been situated in the posterior half of the thorax based on their rounded cross-sections. Further work on the dorsal ribs of *Diamantinasaurus matildae* and *Savannasaurus elliottorum* (Poropat *et al.* 2016) will hopefully shed light on the variability within and between Australian Cretaceous sauropods.

Revised phylogenetic placement of Austrosaurus mckillopi. On the basis of the preserved remains, it can be demonstrated that *Austrosaurus mckillopi* is a titanosauriform sauropod. The pneumatisation of the proximal ends of the dorsal ribs (Wilson & Sereno 1998), along with the plank-like morphology of the distal ends of the anterior dorsal ribs (Wilson 2002), suggest titanosauriform affinities for *Austrosaurus*. The cervical and anterior dorsal vertebrae of *Galveosaurus herreroi*, a taxon resolved as the sister taxon to Titanosauriformes by Mannion *et al.* (2013), show camellate internal texture (Barco *et al.* 2006, Barco Rodriguez 2009); however, the dorsal ribs of *Galveosaurus* are not pneumatised. Therefore, the combination of features presented by *Austrosaurus* (i.e., presacral vertebrae with camellate internal texture + dorsal ribs with pneumatised proximal ends) allows it to be placed within Titanosauriformes.

Despite the augmentation of the *Austrosaurus mckillopi* type specimen, the remains of this sauropod are still frustratingly incomplete. Very few phylogenetic characters can be scored, and even fewer can be scored without reversion to estimation or approximation. Consequently, it is difficult to determine whether or not *Austrosaurus* is a titanosaur, let alone a somphospondylan. However, given that the presence of a ventral keel in anterior dorsal vertebrae is only known in somphospondylan titanosauriforms, we very tentatively suggest that *Austrosaurus* might be a member of Somphospondyli. Despite these difficulties, as elucidated above, the rearticulation of the specimen has facilitated the recognition of several features of *Austrosaurus mckillopi*, including one that appears to be autapomorphic (i.e., the accessory lateral pneumatic foramen on dorsal vertebra I).

Comparison of Austrosaurus mckillopi *with other Australian Cretaceous sauropods*

The fact that the type specimen of *Austrosaurus mckillopi* is limited to a posterior cervical vertebra, the first five dorsal vertebrae, the first five left dorsal ribs and right dorsal rib IV means that the scope for comparison with *Wintonotitan*, *Diamantinasaurus* and *Savannasaurus*—the only other named Australian Cretaceous sauropods to date—is limited. All three of these genera are derived from the Winton Formation, which is at least four million years younger than the Allaru Mudstone from which *Austrosaurus* was recovered. On the basis of this temporal separation alone, it might seem unlikely that *Austrosaurus* is congeneric with *Diamantinasaurus*, *Wintonotitan* or *Savannasaurus*; however, this cannot be ruled out a priori, especially given that several sauropod genera from the Upper Jurassic Morrison Formation of western North America have stratigraphic ranges that span five million years or more (Foster 2007).

The few recognisable portions of presacral vertebrae and ribs catalogued as part of the type specimen of *Wintonotitan wattsi* (QM F7292) are extremely fragmentary and poorly preserved, and the only additional specimen referred to *Wintonotitan* (QM F10916) comprises four caudal vertebrae (Hocknull *et al.* 2009, Poropat *et al.* 2015a). Consequently, substantive comparisons between *Wintonotitan* and *Austrosaurus* cannot be made at this time.

Of the two dorsal vertebrae from the type specimen of *Diamantinasaurus matildae* (AODF 603), one (dorsal vertebra B *sensu* Poropat *et al.* 2015b) is from the anterior half of the dorsal series (as interpreted by Poropat *et al.* 2016, p. 5) based on the position of the parapophysis (i.e., entirely on the neural arch). The few reasonably complete dorsal vertebrae preserved in a specimen referred to *Diamantinasaurus* (AODF 836) appear to have occupied positions posterior to dorsal vertebra IV (Poropat *et al.* 2016); thus, they cannot be substantively compared with *Austrosaurus*. The preserved dorsal vertebrae of *Savannasaurus elliottorum* have been interpreted as dorsals III–X (on the assumption that a total of ten dorsal vertebrae were present), meaning that the anterior three can be compared with *Austrosaurus* (Poropat *et al.* 2016), although the poor preservation in the latter of dorsal vertebra V precludes meaningful comparison.

As in *Austrosaurus*, the centra of dorsal vertebrae III and IV of *Savannasaurus*, and of III in *Diamantinasaurus*, lack ventral ridges (Poropat *et al.* 2015b, 2016). In the type specimen of *Diamantinasaurus*, the ventral surface is concave, both anteroposteriorly and transversely, and is bounded laterally by ridges (Poropat *et al.* 2015b); the same is true of dorsal vertebrae III and IV in *Austrosaurus*, whereas in *Savannasaurus* the ventral surfaces of the dorsal centra are transversely convex and anteroposteriorly concave (Poropat *et al.* 2016). In all three taxa, the centra of dorsal vertebrae III and IV are dorsoventrally compressed and strongly opisthocoelous, and the pneumatic foramina are set within fossae. Comparisons of the neural arches and laminae systems are limited because of the poor preservation of the *Austrosaurus* type series, although some observations can still be made.

The dorsal vertebral lamina systems of *Austrosaurus*, *Diamantinasaurus* and *Savannasaurus* show several similarities. In all three taxa, dorsal vertebra III appears to possess two PCPLs, one lower and one upper: the former runs effectively horizontally, dorsal to the pneumatic foramen, whereas the upper projects anterodorsally. Also projecting anterodorsally, albeit at a steeper angle than the upper PCPL, is the PCDL. The CDF, which is bounded by the upper PCPL and the PCDL, is very similar in morphology and position in both *Austrosaurus* and *Savannasaurus* but does not seem to be developed in *Diamantinasaurus*.

The congruence between the morphology of the dorsal vertebrae of *Austrosaurus*, *Diamantinasaurus* and *Savannasaurus* might be indicative of close phylogenetic proximity. However, it is also possible that these similarities are merely plesiomorphic characters, rather than shared derived features. None of the features that have been observed in the type series of *Austrosaurus* are autapomorphic for either *Savannasaurus* or *Diamantinasaurus*, and the possibility that any two or all three of these taxa are synonymous is remote in light of the morphological differences observed between *Diamantinasaurus* and *Savannasaurus* (Poropat *et al.* 2016) and the aforementioned stratigraphic and temporal separation of *Austrosaurus* (upper Albian, Allaru Mudstone) from *Diamantinasaurus* and *Savannasaurus* (Cenomanian–lowermost Turonian, Winton Formation). We regard *Austrosaurus* as a distinct, tentatively diagnostic taxon, clearly referable to Titanosauriformes. Given that Titanosauriformes by phylogenetic definition comprises the sister clades Brachiosauridae and Somphospondyli (Wilson & Sereno 1998), *Austrosaurus* by extension of this fact has its affinities within one of these two groups. The hypodigm of *Austrosaurus* does not present any unambiguous synapomorphies of the Brachiosauridae. However, absence of evidence alone is not sufficient grounds to conclusively exclude *Austrosaurus* from Brachiosauridae, especially given its incompleteness and the impossibility of verifying characters in materials that are not preserved. Nonetheless, several aspects of the morphologies we have discussed (i.e., ventral ridges, patterns of pneumaticity, and dorsal ribs profile) are more consistent with a patchy distribution among somphospondylan, rather than brachiosaurid, titanosauriform taxa. Thus, while acknowledging that these aspects of morphology do not represent unambiguous apomorphies of the clade, *Austrosaurus* is probably assignable to Somphospondyli (‘?Somphospondyli incertae sedis’). With future work on character distributions and discovery of new materials, *Austrosaurus* might in time even be shown to occupy a position within Titanosauria

Is the "Hughenden sauropod" cervical vertebra (QM F6142) referable to Austrosaurus*?*

===PLEASE INSERT FIGURE 15===

On the basis of our reassessment of the type specimen of *Austrosaurus mckillopi*, there is now arguably anatomical overlap between QM F2316, which includes the ultimate cervical vertebra, and the "Hughenden sauropod" (QM F6142) which solely comprises a posterior cervical vertebra, possibly the ultimate one. Their spatiotemporal proximity warrants an assessment of whether or not QM F6142 pertains to *Austrosaurus*, a suggestion tentatively made by Molnar (1982a, 1991).

The enigmatic "Hughenden sauropod" is represented only by a single, incomplete cervical vertebra (QM F6142; Fig. 15). This specimen was collected in 1955 by Jack Tunstall Woods [then Assistant Curator in Geology at Queensland Museum (Mather 1986)] near Pelican Bore on Stewart Creek, Dunraven Station, north of Hughenden, Queensland (as alluded to by Rich & Vickers-Rich 2003, p. 67, and Willis & Thomas 2005, p. 187). As far as we can ascertain, QM F6142 was first referred to in the literature by Molnar (1980, pp. 132, 136), who identified it as a sauropod from the Albian beds of Queensland and stated that it was distinct from the sauropods found near Winton. Bartholomai & Molnar (1981, p. 319) stated that QM F6142 derived from the Wilgunya Subgroup [which includes the Toolebuc Formation (Vine *et al.* 1967)], whereas Coombs & Molnar (1981, p. 351) simply noted that it was from the Lower Cretaceous.

Molnar (1982a, p. 201, 1991, p. 645) provided the first brief description of QM F6142, raising the possibility that it might represent an additional specimen of *Austrosaurus*, but also likening it to *Brachiosaurus brancai* [now *Giraffatitan* (Taylor 2009)]. Molnar (1982a, p. 198, 1991, p. 646) was also the first to illustrate QM F6142, and he reconstructed the vertebra as being extremely elongate.

Although QM F6142 was listed and briefly alluded to in several checklists of Australian fossil vertebrates (Molnar 1982b, 1984a, Lees 1986), and likened to brachiosaurids by Long (1998), it was not discussed by Molnar (2001b) in his otherwise comprehensive review of Cretaceous sauropod specimens from Queensland. Molnar & Salisbury (2005) provided a brief description of QM F6142, suggesting that it represented a brachiosaurid on the basis of several character states listed by Upchurch (1998), Wilson & Sereno (1998) and Wilson (2002). More recently, Mannion *et al.* (2013, p. 154) briefly reassessed QM F6142 and concluded that it was an indeterminate titanosauriform, noting that no brachiosaurid synapomorphies were observable.

TITANOSAURIFORMES Salgado et al., 1997

Titanosauriformes indet.

Material: QM F6142 (“Hughenden sauropod”), posterior portion of a posterior cervical vertebra.

Locality: Pelican Bore, Stewart Creek, Dunraven Station, Hughenden, Queensland, Australia. Collected by Jack Tunstall Woods in 1955.

Horizon: Toolebuc Formation, upper Lower Cretaceous (upper Albian).

Associated vertebrate fauna: Fossil vertebrates recorded from the Toolebuc Formation on Dunraven Station (as mapped by Vine *et al.* 1970) include: at least six genera of fish (Lees & Bartholomai 1987, Bartholomai 2004, 2010a, b, 2012, 2013); turtles (Gaffney 1981), including *Bouliachelys suteri* (Kear & Lee 2006); the ichthyosaur *Platypterygius australis* (Kear 2001a, 2005, Zammit *et al.* 2010, Kear & Zammit 2014); an indeterminate elasmosaurid (Kear 2001b, 2003, Zammit *et al.* 2008); the pliosaur *Kronosaurus queenslandicus* (McHenry 2009); and an ankylosaur [represented by at least two specimens (AM F35259, AM F119849)] previously assigned to *Minmi* sp. (Molnar 1996b, Leahey & Salisbury 2013, Leahey *et al.* 2015). The only other sauropod specimen known from the Toolebuc Formation on Dunraven Station is an isolated, amphicoelous caudal centrum (QM F13712; Molnar & Salisbury 2005).

Description: QM F6142 preserves the posterior cotyle, both postzygapophyses, the partial neural spine, and portions of several laminae. The posterior cotyle is dorsoventrally compressed and strongly concave; this latter observation suggests that the centrum was opisthocoelous, as are all sauropod post-axial cervical vertebrae (McIntosh 1990, Upchurch *et al.* 2004). Small sections of the dorsal margin of the cotyle have been broken, revealing large (35–45 mm long), triangular internal pneumatic coels. The ventral surface of the centrum is transversely and anteroposteriorly concave, and the preserved portion lacks a ventral midline ridge. On the ventrolateral surface of the centrum, a horizontal posterior centroparapophyseal lamina (PCPL) can be observed, strongly suggesting that the parapophyses were located at the anteroventral corners of the centrum, as in all sauropod cervical vertebrae. The lateral faces of the centrum are otherwise dominated by posteriorly acuminate pneumatic fossae; the anterior extent of the pneumatic foramen within each fossa is obscured on both sides by matrix. On the left side of the vertebra, an accessory fossa (40 mm long) is present near the anteroventral margin of the pneumatic foramen, set within the pneumatic fossa; this fossa is evidently quite shallow and might simply have been cut off from the main fossa by an oblique lamina. The posterior centrodiapophyseal laminae (PCDLs) are well-developed and oriented anterodorsally–posteroventrally. An essentially vertical anterior centrodiapophyseal lamina (ACDL) can also be observed; the triangular area ventral to the intersection of these laminae at the diapophysis is filled with matrix but was evidently a deep centrodiapophyseal fossa (CDF), ventrally bounded by a thin ridge which separates the CDF from the lateral pneumatic fossa of the centrum. The CDF is best observed on the left side of the vertebra.

The neural canal is oval in posterior aspect (slightly broader transversely than tall dorsoventrally), being bounded laterally by the centropostzygapophyseal laminae (CPOLs). The dorsal margin of the neural canal is obscured by matrix, as are the seemingly shallow postzygapophyseal centrodiapophyseal fossae (POCDFs). The CPOLs are oriented vertically, and each CPOL is broad ventrally and narrows dorsally; both are broken at their narrowest points. The CPOLs deflect slightly laterally at their apices to contact the medial margins of the postzygapophyses.

The large, flat articular facets of the postzygapophyses face ventrally and somewhat laterally. The postzygapophyseal facets are ovate, with the lateral margin of each being more rounded than the medial one. Each postzygapophysis is significantly wider mediolaterally

(164 mm) than long anteroposteriorly (82 mm). The postzygapophyses are attached to the neural spine via spinopostzygapophyseal laminae (SPOLs). The SPOLs are as broad ventrally as their respective postzygapophyseal facets and narrow only slightly as they approach the summit of the neural spine, each being broader than the neural canal where they converge with the neural spine; consequently, the SPOLs in QM F6142 would be better referred to as buttresses rather than laminae. Epipophyses are not present on the postzygapophyses or on the SPOLs. Towards the summit of the neural spine, both SPOLs split into two branches, defining spinopostzygapophyseal lamina fossae (SPOL-Fs), which are filled with matrix; the depth of these cannot be ascertained. The SPOLs and the dorsal margin of the neural canal define the boundaries of the spinopostzygapophyseal fossa (SPOF), which is not deeply invaginated on the posterior surface of the neural spine. No trace of a postspinal lamina (POSL) is preserved within the SPOF. At the anterior margin of the right postzygapophysis, a posterodorsally–anteroventrally extending postzygodiapophyseal lamina (PODL) is preserved. On its anterolateral surface, the right SPOL defines a narrow ridge that represents the posterior margin of an apparently short, rounded spinodiapophyseal fossa (SDF), which was bounded ventrally by the PODL. The anterior extent of this SDF is unknown because of the incompleteness of the specimen. As far as we can determine, the neural spine of QM F6142 was not bifid. If it were, the notch would have been small and restricted to the summit of the spine.

Most of the anterior portion of QM F6142 is missing, and this surface has also only been incompletely prepared; nevertheless, some observations can be made. The junction of the truncated PCPLs and the truncated combined base of the ACDLs and centroprezygapophyseal laminae (CPRLs) defines an X-shape in anterior view. As far as they are preserved, the bases of the CPRLs are broad mediolaterally. On the lateral surface, shallow triangular fossae appear to be defined on both sides by the ACDLs (posteroventrally) and CPRLs (anteroventrally); prezygodiapophyseal laminae (PRDLs) are presumed to have been present and would have formed the dorsal margins of these fossae (the base of the right PRDL has been tentatively identified). Consequently, we interpret these fossae as prezygapophyseal centrodiapophyseal fossae (PRCDFs), assuming no additional laminae were present that would warrant alternative identifications (as per Wilson et al. 2011b). On the right side, the CDF and PRCDF are similar in size. The exposed neural canal opening is oval (being wider transversely than tall dorsoventrally).

Comparisons: The SPOL-Fs of QM F6142 appear to be autapomorphic. Although SPOL-Fs have been reported in other sauropods (Wilson *et al.* 2011b, Ibiricu *et al.* 2013, Mannion & Barrett 2013), these are morphologically divergent from those of QM F6142 and are present only in the posterior dorsal vertebrae.

The widely-spaced, ventrally-facing postzygapophyses indicate that QM F6142 is a posterior cervical vertebra—potentially the posteriormost. Consequently, it is possible that QM F6142 overlaps anatomically with the anteriormost vertebra preserved in the *Austrosaurus mckillopi* type specimen. The accessory fossa within the lateral pneumatic fossa observed on the left side of QM F6142 does not seem to be homologous with the accessory foramen identified in dorsal vertebra I of *Austrosaurus*—that in QM F6142 was situated posterior to the parapophysis, not anterior to it as in *Austrosaurus*. The posterior cotyles of both QM F2316 and QM F6142 are dorsoventrally compressed, and the internal texture of both specimens is camellate; these observations are, however, not sufficient to unequivocally refer QM F6142 to *Austrosaurus*. Future discoveries in the Toolebuc Formation and the Allaru Mudstone might shed further light on the diversity of sauropods in the latest Early

Cretaceous of northeast Australia, and on whether or not QM F6142 is referable to *Austrosaurus*. If a series of presacral vertebrae were discovered, wherein SPOL-Fs were present in the posterior cervicals and accessory lateral pneumatic foramina were found anterior to the parapophyses in dorsal vertebra I, then referral of QM F6142 to *Austrosaurus mckillopi* could be confirmed.

The pneumatic fossae on both sides of QM F6142 appear to be almost completely preserved. This, coupled with the observation of the posteriormost section of the PCPL on the left lateral surface, suggests that QM F6142 was not as elongate as restored by Molnar (1982a, 1991). Furthermore, the posterior cotyle of the “Hughenden sauropod” (Table 3) is actually smaller than the posterior cotyle of the posterior cervical of *Austrosaurus mckillopi* (Table 1). Size estimates of the sauropod from which QM F6142 derived [20 m according to Molnar (1982a, 1991)] are, therefore, probably excessive.

Possible biogeographic links between Austrosaurus mckillopi *and South American Early and earliest Late Cretaceous titanosauriforms*

Poropat *et al.* (2016) suggested that some sauropod clades, specifically titanosauriforms, might have taken advantage of late Albian–Turonian warming to migrate between South America and Australia via Antarctica, with *Austrosaurus* possibly representing one such migrant. Testing this hypothesis is, however, difficult because of the relative dearth of Early Cretaceous titanosauriform body fossils from South America, and the complete lack of such fossils from Lower Cretaceous Antarctic and pre-Albian Australian strata. The oldest known titanosauriform specimens from South America are of Hauterivian–Barremian age, and only seven pre-Cenomanian deposits have yielded titanosauriforms to date (de Jesus Faria *et al.* 2015). The specimens from these units, along with those from the lower Cenomanian Candeleros Formation (Rio Limay Subgroup, Neuquén Group), are briefly discussed here to provide somewhat limited phylogenetic and biogeographic context for *Austrosaurus* and other mid-Cretaceous sauropods from Australia.

Two presacral vertebral centra, a tibia and an indeterminate limb bone from the Hauterivian–Barremian Puesto La Paloma Member of the Cerro Barcino Formation of Chubut (Rauhut *et al.* 2003) constitute the oldest reported body fossils of titanosauriforms from Argentina. Although these specimens were originally described as pertaining to titanosaurs, the justification for this referral is weak. The morphology of the lateral pneumatic foramen of the centrum (elongate and eye-shaped) was the only character used to support titanosaur affinities for the vertebrae (following Salgado *et al.* 1997); however, the actual shape of the foramina in these vertebrae was not observed—it was inferred on the basis of their length (Rauhut *et al.* 2003). Furthermore, some non-titanosaurian titanosauriforms also possess this feature [e.g. *Chubutisaurus* (Carballido *et al.* 2011a), *Europasaurus* (Carballido & Sander 2014), *Sauroposeidon* (D'Emic & Foreman 2012)], so it is more appropriate to consider these Argentinean specimens as indeterminate titanosauriforms.

A right fibula and a partial skeleton from the Rio Piranhas Formation (Hauterivian–Barremian) of Paraíba constitute the oldest reported titanosauriform body fossils from Brazil (Ghilardi *et al.* 2016). The isolated fibula was described as a titanosaur; however, the evidence for this is weak. Ghilardi *et al.* (2016) suggested that the distal end being triangular, and the overall shape of the fibula being sigmoidal, were sufficient grounds for referral of this element to Titanosauria. However, sigmoidal fibulae were found to be synapomorphic for Somphospondyli/Titanosauria by Mannion *et al.* (2013) in their LCDM analysis [wherein

Somphospondyli and Titanosauria were interchangeable because *Andesaurus delgadoi* (the most basal titanosaur by definition) clustered with a group of sauropods otherwise commonly resolved as non-titanosaurian somphospondylans], whereas D'Emic (2012) identified sigmoidal fibulae as synapomorphic for an unnamed clade comprising *Tastavinsaurus*, Euhelopodidae, *Chubutisaurus* and Titanosauria, thereby encompassing most of Somphospondyli. It is unlikely that the fibula described by Ghilardi *et al.* (2016) will ever be referred unequivocally to Titanosauria; it is, however, possible to tentatively refer it to Somphospondyli.

Also from the Rio Piranhas Formation is the type specimen of *Triunfosaurus leonardii*, which comprises a right ischium, three caudal vertebrae, three chevrons and three isolated neural spines (Carvalho *et al.* 2017). *Triunfosaurus* was interpreted as a titanosaur on morphological grounds, and was resolved as such in a phylogenetic analysis [based on the data matrix of Carballido & Sander (2014)] by Carvalho *et al.* (2017). However, the case for *Triunfosaurus* as a titanosaur is weak. The pubic articulation of the right ischium is longer than the anteroposterior length of the iliac peduncle, a feature used by Carvalho *et al.* (2017) to justify referral to Camarasauromorpha [following Salgado *et al.* (1997)]. The neural arches of the caudal vertebrae are situated upon the anterior halves of the centra, a feature used by Carvalho *et al.* (2017) to refer *Triunfosaurus* to a clade comprising *Europasaurus holgeri* and all more derived camarasauromorphs [following Carballido & Sander (2014)]. The proximal articular surfaces of at least one of the chevrons were each divided into two discrete surfaces by a furrow, and Carvalho *et al.* (2017) used this to support the notion that *Triunfosaurus* was a titanosaur, citing Mannion & Calvo (2011) to support this. However, the feature Mannion & Calvo (2011) described as being present in *Andesaurus* was a strong convexity dividing the two surfaces, as also observed in *Tastavinsaurus* (Canudo *et al.* 2008) and the non-neosauropod *Cetiosaurus* (Upchurch & Martin 2002). The furrow morphology is present in some titanosaurs [e.g. *Aeolosaurus* (Powell 2003, Santucci & Arruda-Campos 2011) and *Epachthosaurus* (Poropat *et al.* 2016)]; however, it has also been identified in the non-titanosaurian somphospondylans *Phuwiangosaurus* and *Tangvayosaurus* (D'Emic 2012). Consequently, this feature supports the inclusion of *Triunfosaurus* within Somphospondyli but does not allow unequivocal referral to Titanosauria. Carvalho *et al.* (2017) also suggested that the caudal prezygapophyses, which project anteriorly, are reminiscent of Aeolosaurini. The caudal centra were interpreted as opisthoplatyan [the anterior articular surfaces could not be observed, according to Carvalho *et al.* (2017)], separating *Triunfosaurus* from the majority of titanosaurs (Upchurch *et al.* 2004), and the dorsoventral height of the haemal canal was found to be less than 50% the overall length of the chevron, in contrast to Titanosauria as characterised by Wilson (2002); however, the latter feature has been shown to much more variable (Mannion *et al.* 2013). There are a number of features of these caudal vertebrae which were not mentioned by Carvalho *et al.* (2017), which are quite notable: 1) the caudal vertebrae have prominent transverse processes, connected to the prezygapophyses by pronounced PRDLs, which terminate in deep diapophyses (for middle caudal vertebrae); 2) the prezygapophyses are connected to the neural spine by well-developed SPRLs [which are omitted from the schematic provided by Carvalho *et al.* (2017, fig. 4)]; 3) the ventrolateral surface of the centrum appears to be deeply excavated (Carvalho *et al.* 2017, fig. 4); and 4) the anterior margin of the postzygapophyseal facet is situated in line with the midlength of the centrum. All of these features are unusual in middle caudal vertebrae of sauropods generally. Furthermore, the presence of such a prominent transverse process implies that these vertebrae were situated more anteriorly within the tail than postulated by Carvalho *et al.* (2017, fig. 7). If we presume that this was so, then these caudal vertebrae are perhaps too small to be associated with the ischium. In sum, *Triunfosaurus* is a problematic taxon, albeit one which appears to be referable to Somphospondyli.

Several teeth from the Barremian–lower Aptian La Amarga Formation of Neuquén, Argentina have been assigned to Titanosauria (Apesteguía 2007). However, this interpretation has been questioned (Zaher *et al.* 2011), with some workers explicitly removing them from Titanosauria (D'Emic 2012) and others hesitating to classify them beyond Titanosauriformes (Gallina 2016). *Amargatitanis macni*, a sauropod also derived from the La Amarga Formation, was originally described as a titanosaur (Apesteguía 2007); however, a full reappraisal of the type specimen has revealed it to be a chimaera, as suggested by D'Emic (2012), with the majority of the remains actually pertaining to a dicraeosaurid diplodocoid (Gallina 2016).

The titanosauriform *Padillasaurus leivaensis* was erected on the basis of fourteen vertebrae (two dorsals, four sacrals and eight caudals) from the Barremian–Aptian Paja Formation of Colombia, and referred to Brachiosauridae (Carballido *et al.* 2015). The internal morphology of the vertebrae, which have coels both large (camerae) and small (camellae) and are therefore semicamellate, lends support to this interpretation. However, another feature utilised by these authors to support its referral to Brachiosauridae, i.e. the blind lateral fossa in the caudal centra, is also present in the titanosaur *Savannasaurus* (Poropat *et al.* 2016), and a recent analysis has recovered *Padillasaurus* as a non-titanosaurian somphospondylan (Mannion *et al.* 2017).

Tapuiasaurus macedoi is represented by a complete skull and partial skeleton from the Aptian Quiricó Formation of Minas Gerais, Brazil (Zaher *et al.* 2011, Wilson *et al.* 2016). Although the postcranial skeleton of this taxon has only been perfunctorily described to date, it has been made clear that the presacral vertebrae have camellate internal texture, the proximal ends of the dorsal ribs are pneumatised, and the distal ends of the anterior dorsal ribs are plank-like in cross-section (Zaher *et al.* 2011, Wilson *et al.* 2016). *Tapuiasaurus* has consistently been recovered within Titanosauria in phylogenetic analyses. However, although virtually every phylogenetic analysis in which it has been included has resolved it within Lithostrotia (Zaher *et al.* 2011, Carballido & Sander 2014, Gorscak *et al.* 2014, Lacovara *et al.* 2014, Carballido *et al.* 2015, Poropat *et al.* 2015b, Díez Díaz *et al.* 2016, González Riga *et al.* 2016, Gorscak & O'Connor 2016, Martínez *et al.* 2016, Poropat *et al.* 2016, Filippini *et al.* 2017, Tykoski & Fiorillo 2017), more recent research on the cranial remains suggests that *Tapuiasaurus* might occupy a basal position within Titanosauria (Wilson *et al.* 2016), outside Lithostrotia [or within Somphospondyli but just outside Titanosauria—the omission of *Andesaurus* from the phylogenetic analyses of Wilson *et al.* (2016) means that the placement of the node Titanosauria is subjective].

The upper Aptian–lower Albian Lohan Cura Formation of Neuquén, Argentina, has produced abundant sauropod remains, including *Agustinia ligabuei* (Bonaparte 1999, Salgado & Coria 2005, Salgado & Bonaparte 2007) and *Ligabuesaurus leanzai* (Bonaparte *et al.* 2006, Martinelli *et al.* 2007). The type specimen of *Agustinia* is incomplete, poorly preserved and difficult to interpret; consequently, it has variously been regarded as an indeterminate neosauropod (D'Emic *et al.* 2009), a nomen dubium (D'Emic 2012), and an indeterminate somphospondylan (Mannion *et al.* 2013). D'Emic *et al.* (2009) questioned the interpretation of the osteoderms, suggesting that they might perhaps be hypertrophied ossifications, whereas Mannion *et al.* (2013) suggested that the elements represented dorsal ribs and pelvic girdle elements. A recent histological study of the type specimen (Bellardini & Cerda 2017) has concluded that Mannion *et al.* (2013) were correct: the supposed armour of *Agustinia* comprises misinterpreted ribs and pelvic girdle elements, thereby undermining the evidence for its inclusion in Lithostrotia.

Ligabuesaurus is known from more complete and better preserved material than *Agustinia* and has generally been resolved as a basal somphospondylan (Bonaparte *et al.* 2006, D'Emic 2012 and references therein, Mannion *et al.* 2013, Carballido & Sander 2014, Poropat *et al.* 2015b, Díez Díaz *et al.* 2016, González Riga *et al.* 2016, Poropat *et al.* 2016), although a small number of analyses have placed it within Titanosauria (Carballido *et al.* 2015, Gorscak & O'Connor 2016). The type specimen of *Ligabuesaurus* includes an anterior dorsal vertebra; unfortunately, the ventral surface of the centrum was not described by Bonaparte *et al.* (2006), and the presence or absence of a ventral ridge could not be determined even through firsthand personal observation of the specimen (by PDM).

The lower/middle Albian Itapecuru Group of Maranhão, Brazil has produced very fragmentary sauropod remains that have been assigned to Titanosauria (Castro *et al.* 2007). The dorsal vertebrae were classified as such on the basis of their internal texture, which is semicamellate, whereas the amphicoelous caudal centrum was assigned to Titanosauria because the neural arch is situated anteriorly. Both of these features are now known to occur more widely in Titanosauriformes, suggesting that these specimens cannot be referred unequivocally to Titanosauria.

The lower Cenomanian Candeleros Formation of Neuquén, Argentina has produced *Andesaurus delgadoi* (Calvo & Bonaparte 1991, Mannion & Calvo 2011), the most basal titanosaur by definition (Wilson & Upchurch 2003). *Epachthosaurus sciuttoi*, a titanosaur best known from the Lower Member of the Bajo Barreal Formation (Cenomanian–Turonian) of Chubut, Argentina (Powell 1990, 2003, Martínez *et al.* 2004), has also been reported from this unit (Salgado & Coria 2005, Salgado & Bonaparte 2007); however, the specimens that might indicate its presence in the Candeleros Formation have never been described. An indeterminate titanosaur (MUCPv 271; now stored at MMCH), initially reported by Calvo (1999) as an additional specimen of *Andesaurus*, is represented by a partial pelvis and several caudal vertebrae. On the basis of the morphology of the pubis, Mannion & Calvo (2011) assigned MUCPv 271 to 'Titanosauriformes indet.'—the caudal vertebrae previously reported could not be located. Another specimen once referred to *Andesaurus*, comprising a series of caudal vertebrae and associated chevrons (MMCH-Pv 47), was regarded as an indeterminate titanosaur by Otero *et al.* (2011).

At this stage, meaningful comparison between *Austrosaurus* and the majority of the known South American Early Cretaceous titanosauriform specimens is not possible because few of the specimens overlap anatomically. Despite this, our brief summary of the Early Cretaceous South American titanosauriform body fossil record demonstrates that multiple titanosauriform taxa existed in South America prior to the end of the Albian. Any or all of the clades to which these taxa pertain might have been able to take advantage of high latitude dispersal routes to Australia via Antarctica when conditions were favourable. However, because the precise position of *Austrosaurus* within Titanosauriformes is unknown, and is difficult to resolve on the basis of the type material alone, we will be forced to rely upon future discoveries to precisely determine the palaeobiogeographic significance of *Austrosaurus*.

Conclusion

The sauropod taxon *Austrosaurus mckillopi* is of historical significance to Australian palaeontology as the first Cretaceous dinosaur recognised in Queensland, and the first Cretaceous sauropod ever reported from the entire continent. The augmentation, articulation and description of the type material have helped to shed light on the phylogenetic position of *Austrosaurus*, unequivocally placing it within Titanosauriformes, and probably as a member of Somphospondyli. The identification of an autapomorphic auxiliary pneumatic foramen in dorsal vertebra I means that the referral of other sauropod specimens to *Austrosaurus* should be possible in the future, although this feature is not presently observable in any other Australian sauropod specimen. The morphological congruence of the posteriormost cervical vertebra of *Austrosaurus* with QM F6142 (the "Hughenden sauropod") might represent grounds for the referral of the latter to the former, although this cannot be demonstrated unequivocally. Lastly, despite its fragmentary nature, *Austrosaurus* appears to share several features with the type specimens of both *Diamantinasaurus* and *Savannasaurus*, possibly indicating a close phylogenetic relationship.

The fragmentary nature of the type series of *Austrosaurus* has impeded, and will continue to restrict, efforts to precisely resolve its phylogenetic position within Titanosauriformes. Consequently, the palaeobiogeographic significance of *Austrosaurus* is poorly understood, a situation worsened by the relative rarity of Early Cretaceous titanosauriforms in South America and the lack of such in Antarctica. Nevertheless, the presence of numerous titanosauriform lineages in the Early Cretaceous of South America provides some context for Australian Early Cretaceous titanosauriforms like *Austrosaurus*, and also for the mid-Cretaceous Winton Formation fauna, which appears to have been dominated by titanosaurs with amphicoelous (rather than procoelous) caudal vertebrae.

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Figure captions

Figure 1: Geological map of the Julia Creek–Richmond region of North West Queensland, showing the position of Clutha Station (geological outcrop data from Vine *et al.* 1963, 1970). Scale bar = 10 km. <FULL PAGE WIDTH>

Figure 2: *Austrosaurus mckillopi*, historical overview. A) Henry Burgoyne Wade (1902–1970; courtesy Peter Wade), B) Harley John McKillop (1888–1967; courtesy Elizabeth Cleary [née McKillop]), and C) Dr Martin Joseph McKillop (1893–1980; courtesy Elizabeth Cleary [née McKillop] and Kathryn Evans [née McKillop]) discovered and excavated the *Austrosaurus mckillopi* type specimen in the early 1930s. D) Heber Albert Longman (1880–1954) named *Austrosaurus mckillopi* on March 14th, 1933 (courtesy Queensland Museum). E) The gidgee (*Acacia*) post-supported sign at the *Austrosaurus* type site in 1933 (courtesy Peter Wade). <FULL PAGE WIDTH>**Figure 3:** A) Map of Clutha Station showing the *Austrosaurus mckillopi* type site (marked with an ***X***), supplied by H. J. McKillop to H. A.

Longman, who published it in the original description of *Austrosaurus* (Longman 1933). B) Geological map of Clutha Station showing the lithology (Kla = Allaru Mudstone), paddock fence lines, creeks, and location of the homestead (image compiled from Vine *et al.* 1963, 1970). <SINGLE COLUMN WIDTH>

Figure 4: Rearticulated vertebral column of the *Austrosaurus mckillopi* type specimen (QM F2316) in left lateral view, with anterior and posterior views of each block. A1) anterior view of cross-section through the posteriormost cervical vertebra; A2) posterior view of cross-section through dorsal vertebra I; B1) anterior view of cross-section through dorsal vertebra I; B2) posterior view of cross-section through dorsal vertebra II; C1) anterior view of cross-section through dorsal vertebra II; C2) posterior view of cross-section through dorsal vertebra III; D1) anterior view of cross-section through dorsal vertebra III; D2) posterior view of cross-section through dorsal vertebra IV; E1) anterior view of cross-section through dorsal vertebra IV; E2) posterior view of cross-section through dorsal vertebra IV; F1) anterior view of cross-section through dorsal vertebra V; F2) posterior view of cross-section through dorsal vertebra V. UCV = ultimate cervical vertebra; DV # = dorsal vertebra #. Scale bar = 200 mm. <FULL PAGE WIDTH>

Figure 5: Rearticulated vertebral column of the *Austrosaurus mckillopi* type specimen (QM F2316) in left lateral view: A) photograph; B) schematic. UCV = ultimate cervical vertebra; DV # = dorsal vertebra #. Hatched sections on schematic indicate matrix. Scale bar = 100 mm. <FULL PAGE WIDTH>

Figure 6: Rearticulated vertebral column of the *Austrosaurus mckillopi* type specimen (QM F2316) in right lateral view: A) photograph; B) schematic. C) Posterior portion of ultimate cervical vertebra and anterior portion of dorsal vertebra I showing the autapomorphic lateral

accessory foramen anterior to the lateral pneumatic foramen. UCV = ultimate cervical vertebra; DV # = dorsal vertebra #. Hatched sections on schematic indicate matrix. Scale bar = 100 mm. <FULL PAGE WIDTH>

Figure 7: Rearticulated vertebral column of the *Austrosaurus mckillopi* type specimen (QM F2316) in dorsal view: A) photograph with blocks of neural arches in place; B) photograph with blocks of neural arches removed; C) schematic. UCV = ultimate cervical vertebra; DV # = dorsal vertebra #. Hatched sections on schematic indicate matrix. Scale bar = 100 mm. <FULL PAGE WIDTH>

Figure 8: Rearticulated vertebral column of the *Austrosaurus mckillopi* type specimen (QM F2316) in ventral view: A) photograph; B) schematic. UCV = ultimate cervical vertebra; DV # = dorsal vertebra #. Hatched sections on schematic indicate matrix. Scale bar = 100 mm. <FULL PAGE WIDTH>

Figure 9: Dorsal ribs of the *Austrosaurus mckillopi* type specimen (KK F1020) in lateral view, each of which includes several cross-sections. The medial surface of each cross-section is directed towards the top of the page. DR # = dorsal rib #. Scale bar = 200 mm. <SINGLE COLUMN WIDTH>

Figure 10: Retrospective map of the *Austrosaurus mckillopi* type site. The positions of the ribs (KK F1020) were plotted using hand-drawn site maps and photographs from the 2014 and 2015 excavations, whereas the rearticulated presacral vertebrae (QM F2316) were emplaced on the basis of their interpreted serial position and information derived from the rib fragments embedded in matrix adhered to the vertebrae. Scale bar = 200 mm. <FULL PAGE WIDTH>

Figure 11: Reconstruction of the possible sequence of events that led to the preservation of the carcass of the sauropod *Austrosaurus mckillopi* in the Eromanga Sea. A) *Austrosaurus* as a living animal on land; B) freshly deceased *Austrosaurus* prior to bloating; C) bloated *Austrosaurus* carcass washed out to sea, where it was possibly scavenged by marine reptiles like *Kronosaurus*; D) the partially defleshed but still effectively intact thoracic portion of the *Austrosaurus* carcass is picked at by sharks as it sinks to the seafloor; E) the thoracic portion of the *Austrosaurus* carcass is buried along with several ammonites (*Beudanticeras*) and bivalves (*Inoceramus*) which were possibly drawn to the carcass as it decayed. Reconstruction by Travis R. Tischler. <FULL PAGE WIDTH>

Figure 12: A, B) Two views of an ammonite (*Beudanticeras* sp.) preserved within the matrix adhering to “specimen g”; and C) inoceramid bivalve (*Inoceramus* sp.) shells in cross-section, preserved within the matrix adhering to “specimen a” (i.e. between dorsal vertebrae I and II). Scale bar = 10 mm. <SINGLE COLUMN WIDTH>

Figure 13: CT rendering of the rearticulated vertebral column of the *Austrosaurus mckillopi* type specimen (QM F2316) in A) axial (viewed dorsally) and B) sagittal (viewed left laterally) mid-line sections. Both the axial and sagittal vertebral series were assembled from individual CT scan images of each bone (taken through the pneumatic foramina in the case of the axial section, and through the neural canal in the case of the sagittal section), hence the imperfect articulation. Scale bar = 100 mm. <FULL PAGE WIDTH>

Figure 14: Eight of the dorsal ribs from the type specimen (AODF 603) of *Diamantinasaurus matildae*. Ribs A, D–F and H are portrayed in lateral view (with the medial surfaces of the cross-sections directed towards the top of the page); Ribs B and G are portrayed in medial view (with the medial surfaces of the cross-sections directed towards the

bottom of the page); and Rib C is portrayed in posterior view (with the medial surface of the cross-sections directed towards the left of the page). Scale bar = 200 mm. <FULL PAGE WIDTH>

Figure 15: Cervical vertebra of the “Hughenden sauropod” (QM F6142) in A) dorsal; B) anterior; C) anteroventral; D) left lateral (with schematic below); E) posterior (with schematic below); F) right lateral (with schematic below); and G) ventral views. H) close-up of the neural spine in posterior view showing SPOL-Fs. Scale bar at bottom left for A–G = 100 mm; scale bar at top right for H = 50 mm. <FULL PAGE WIDTH>

Tables

Measurements (mm) *Incomplete measurement.			Cervical vertebra	Dorsal vertebrae				
			Ultimate	I	II	III	IV	V
Centrum	Length (including condyle; ventral midline)		100*	320	260*	280	210*	210*
	Length (including condyle; left lateral)		-	-	-	265	-	-
	Length (excluding condyle; ventral midline)		-	250	230*	217	-	-
	Length (excluding condyle; left lateral)		-	-	185	220	-	-
	Anterior (condyle)	Maximum width	-	-	-	-	-	240
	Posterior (cotyle)	Maximum dorsoventral height (left lateral)	235	211	-	-	F: 250	-
		Maximum transverse width (ventral)	322	301	-	-	-	-
		Ratio H:W	0.73	0.7	-	-	-	-
Neural canal (anterior)	Maximum transverse breadth		-	-	67	52	-	52
	Maximum height of neural canal		-	-	50	50	-	50
Neural canal (posterior)	Maximum transverse breadth		-	54	41	45	42	46
	Maximum height of neural canal		-	43	54	33	47	40
Pneumatic foramen (left lateral)	Maximum anteroposterior length		-	57	65	110	120	70
	Maximum dorsoventral height		-	21	45	90	65	70
Pneumatic foramen (right lateral)	Maximum anteroposterior length		-	90	86	80	115	-
	Maximum dorsoventral height		-	40	53	55	77	-

Table 1. Measurements of the vertebrae of *Austrosaurus mckillopi* (QM F2316, holotype) in millimetres.

Measurements	Left dorsal ribs				
	I	II	III	IV	V
Preserved proximodistal length	781	1347	1379	1484	1702

Table 2. Measurements of the dorsal ribs of *Austrosaurus mckillopi* (QM F2316, holotype) in millimetres.

Measurement			QM F6142
Centrum	Preserved anteroposterior length		279
	Posterior (cotyle)	Maximum height	199
		Maximum width	275
Pneumatic fossa	Maximum length		195
	Maximum height		74
Postzygapophyses	Combined transverse width		383

Table 3. Measurements of the cervical vertebra of the “Hughenden sauropod” (QM F6142) in millimetres.

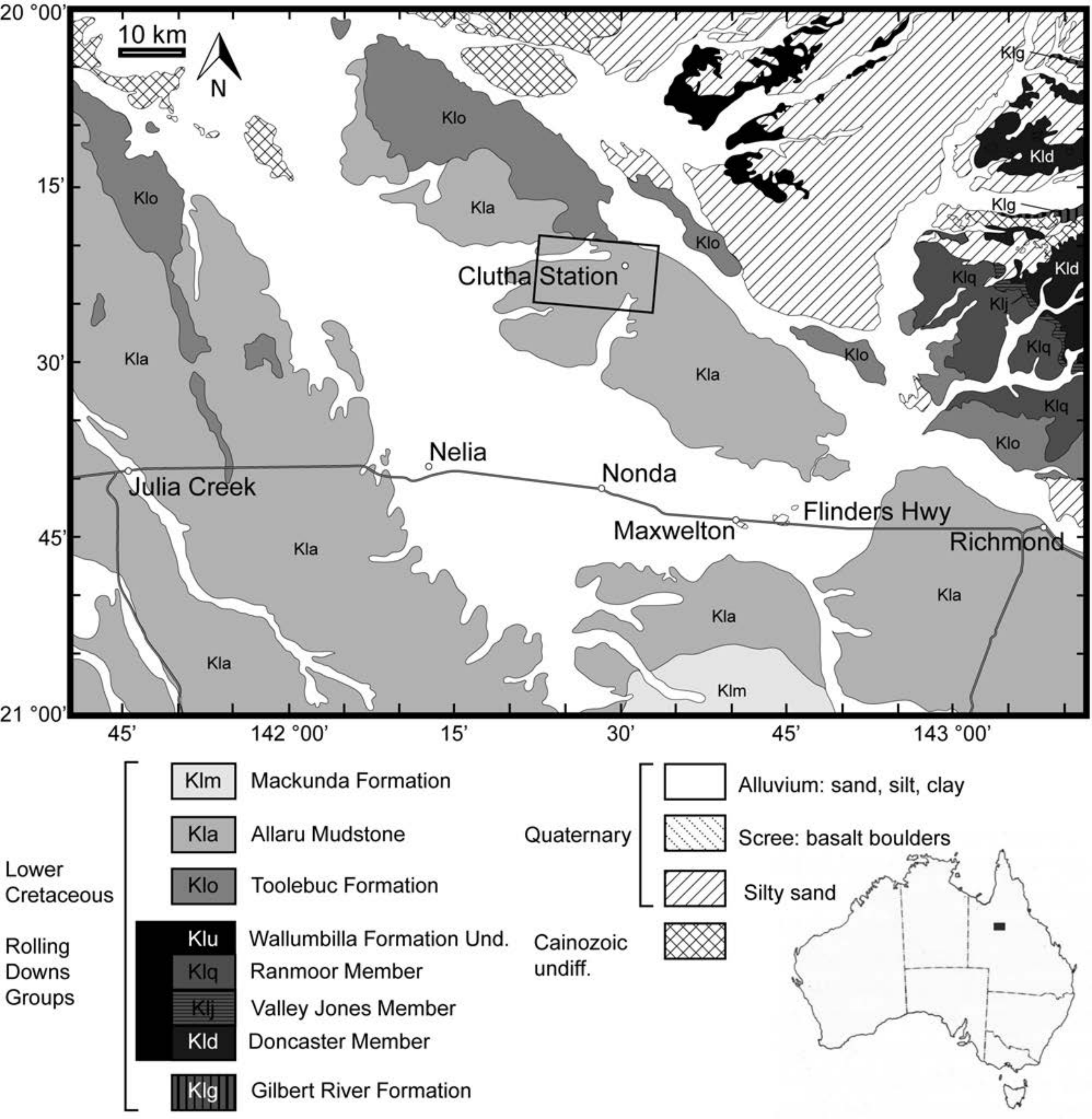
Appendix

List of specimens catalogued under QM F2316, the *Austrosaurus mckillopi* hypodigm. For the purposes of continuity, rather than convenience, the holotypic blocks initially described by Longman (1933) are referred to by their original letters.

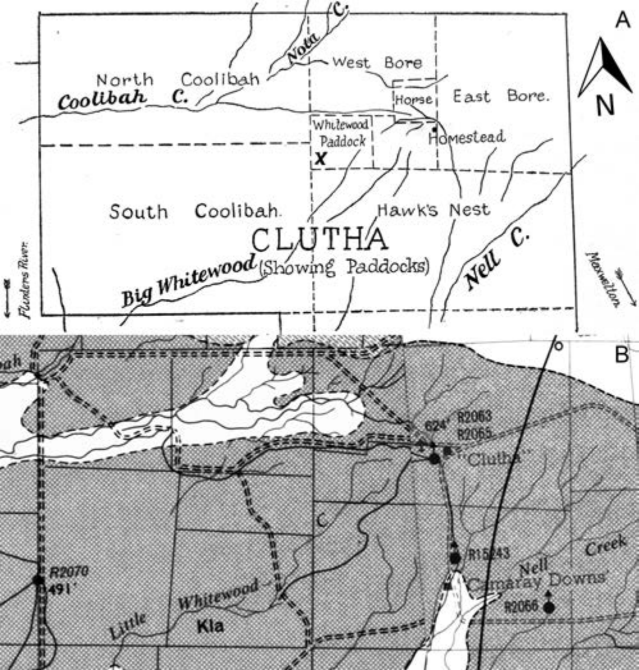
Specimen	Description	Previous references	Notes
A	Two incomplete yet articulated dorsal centra representing the posterior portion of dorsal vertebra II (**a1**) and the anterior portion of dorsal vertebra III (**a2**). One fragment, which preserves portions of the neural arches of both dorsal vertebrae II and III (**a3**) keys into the dorsal surface of the combined **a1+a2** block and includes a rib fragment.	“Specimen A” in Longman (1933, fig. 3 and pls. XV and XVI); “Block A” in Molnar (2001b, fig. 1); “Longman’s specimen A” in Molnar & Salisbury (2005, fig. 20.1A).	Sequentially posterior to specimen B and anterior to specimen H. Large block (~255 mm long) with a large detachable fragment comprising mostly matrix.
B	Two incomplete yet articulated dorsal centra representing the posterior portion of dorsal vertebra I (**b1**) and the anterior portion of dorsal vertebra II (**b2**). A portion of matrix which preserves a small rib fragment (**b3**) keys into the left lateral pneumatic fossa of **b2**. A fourth fragment, comprising a neural canal cast (**b4**), keys into the dorsal margin of the intersection between **b1** and **b2**.	“Specimen B” in Longman (1933, pl. XVII).	Sequentially posterior to specimen C and anterior to specimen A. Large block (~300 mm long × ~280 mm high), with two smaller detachable fragments.
C	Two incomplete yet articulated presacral centra representing the posterior portion of the posteriormost cervical vertebra (**c1**) and the anterior portion of dorsal vertebra I (**c2**).	“Specimen C” in Longman (1933).	Sequentially anterior to specimen B. Large block (280 mm wide × 204 mm high)
D	Mid-section of dorsal vertebra IV	Molnar & Salisbury (2005, fig. 20.1B–C); note that “Longman’s (1933) Specimen C” in Molnar (2011a, fig.	Sequentially posterior to specimen E and anterior to specimen F. Large block.

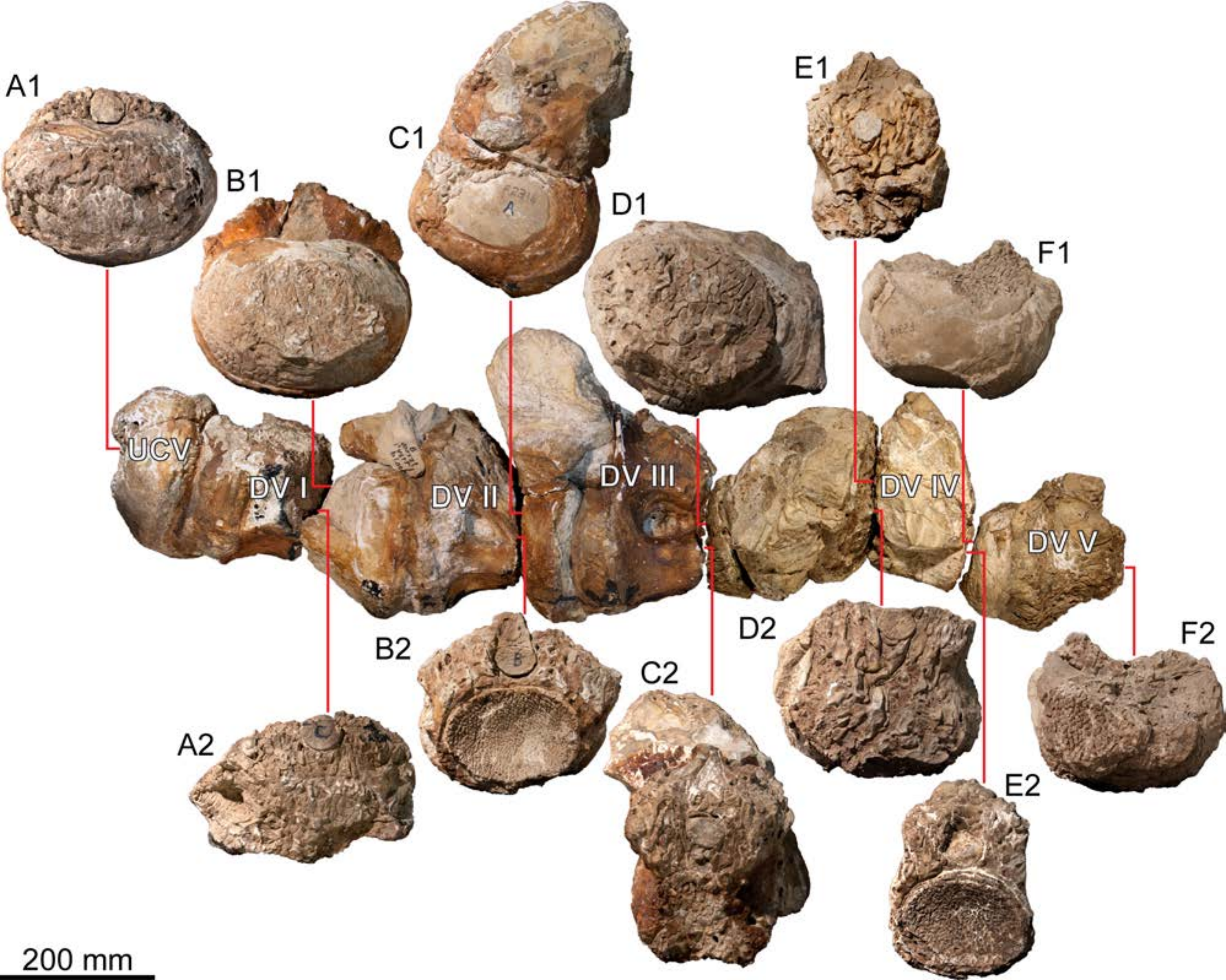
		1H) is *not* Longman's Specimen C.	
E	Two incomplete yet articulated dorsal centra representing the posterior portion of dorsal vertebra III (**e1**) and the anterior portion of dorsal vertebra IV (**e2**).	Molnar & Salisbury (2005, fig. 20.7).	Sequentially posterior to specimen H and anterior to specimen D. Large block.
F	Two incomplete yet articulated dorsal centra representing the posteriormost portion of dorsal vertebra IV (**f1**) and the anterior portion of dorsal vertebra V (**f2**).		Sequentially posterior to specimen D. Large block.
G	A fragment of mostly internal tissue around presumed neural canal infill.		Keys into specimens N and W. Large block.
H	Thin centrum portion from dorsal vertebra III.		Sequentially posterior to specimen A and anterior to specimen E. Small fragment.
I	Indeterminate fragment of internal tissue, containing possible laminae.		Small fragment (145 mm × 102 mm).
J	Right posterior section of a dorsal vertebra.		Small fragment (119 mm × 88 mm).
K	Neural canal cast with indeterminate internal tissue		Small fragment (70 mm × 50 mm).
L	Rib fragment		Small fragment.
M	Vertebral transverse process		Small fragment (90 mm × ~110 mm–140 mm).
N	Indeterminate vertebral fragment		Keys into specimen G. Small fragment (135 mm × 200 mm).
O	Vertebral centrum fragment		Small fragment (98 mm × 150 mm long.
P	Vertebral inter-zygapophyseal components of adjoining vertebrae.		Small fragment (120 mm × 107 mm × 100 mm).
Q	Vertebral inter-centrum components of adjoining vertebrae.		Small fragment (109 mm × 68 mm).
R	Vertebral inter-centrum components of adjoining vertebrae.		Small fragment (102 mm × 63 mm).

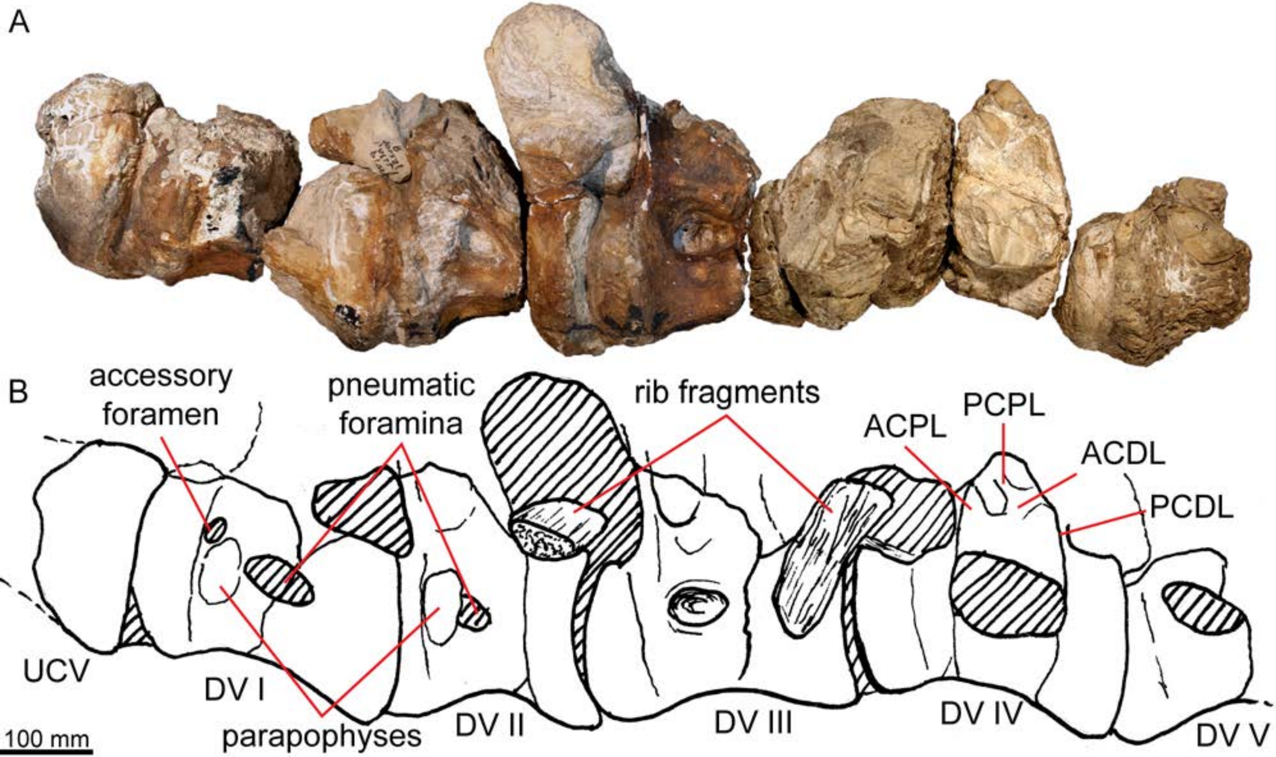
S	Matrix with two indeterminate fragments.		Small fragment (64 mm × 22 mm; 101 mm × 51 mm).
T	Matrix with two indeterminate fragments.		Small fragment (83 mm × 28 mm; 130 mm × 18 mm).
U	Indeterminate presacral vertebral fragment.		Small fragment (120 mm × 112 mm).
V	Indeterminate fragment, possibly of a rib.		Small fragment.
W	Indeterminate fragment, mostly comprising internal issue.		Keys into specimen G. Small fragment (133 mm × 150 mm).
X	Fragment of a neural arch, containing a section of neural canal cast.		Small fragment.
Y	Condylar fragment of a centrum.	Molnar (2011a, fig. 1I)	Small fragment (181 mm × 106 mm).

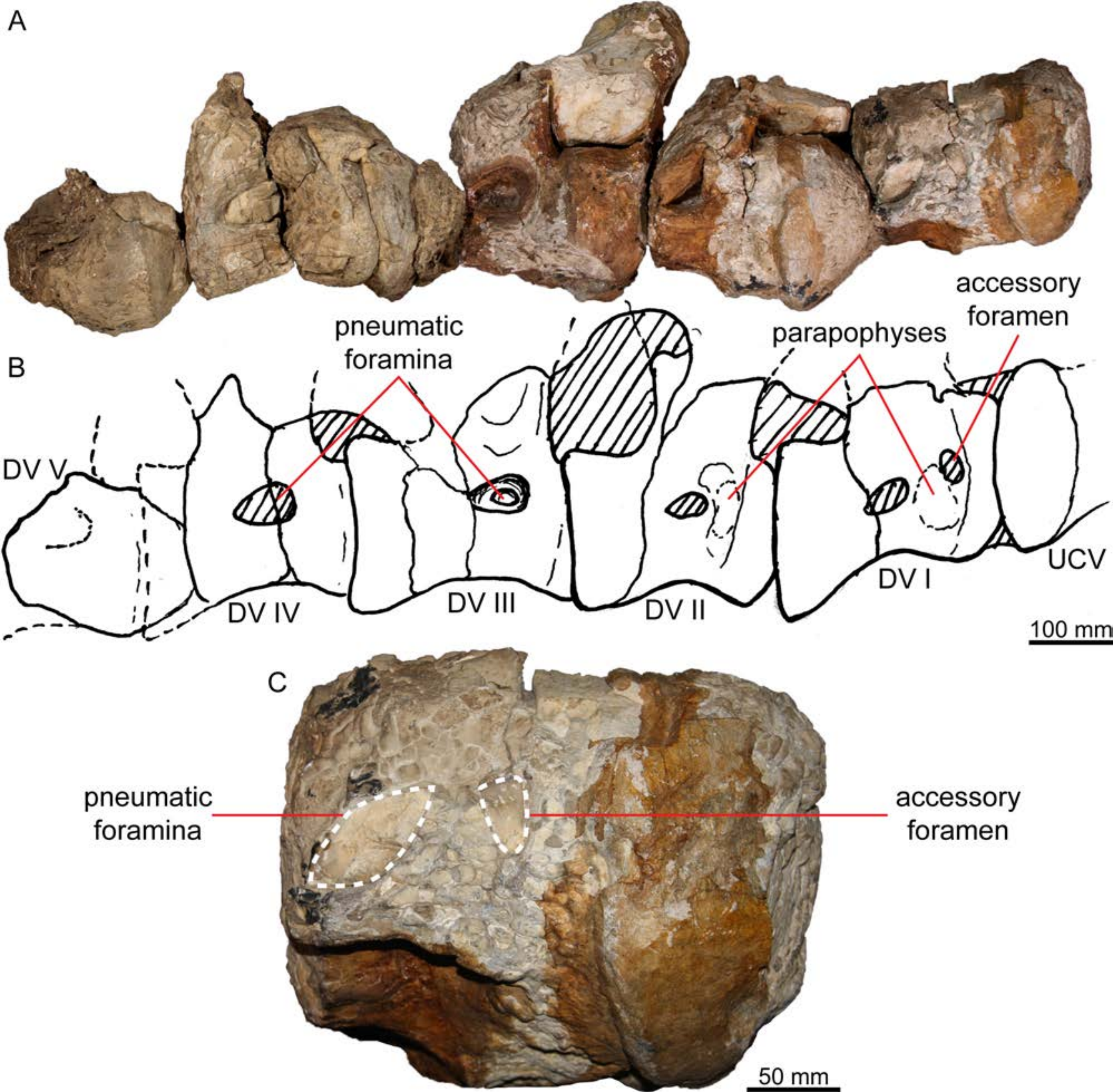

20 °00'
15'
30'
45'
21 °00'
45'
142 °00'
15'
30'
45'
143 °00'
10 km
N
Klo
Kla
Klg
Kld
Klq
Klj
Klm
Clutha Station
Nelia
Julia Creek
Nonda
Maxwelton
Flinders Hwy
Richmond
Klm Mackunda Formation
Kla Allaru Mudstone
Klo Toolebuc Formation
Klu Wallumbilla Formation Und.
Klq Ranmoor Member
Klj Valley Jones Member
Kld Doncaster Member
Klg Gilbert River Formation
Lower Cretaceous
Rolling Downs Groups
Quaternary
Alluvium: sand, silt, clay
Scree: basalt boulders
Silty sand
Cainozoic undiff.

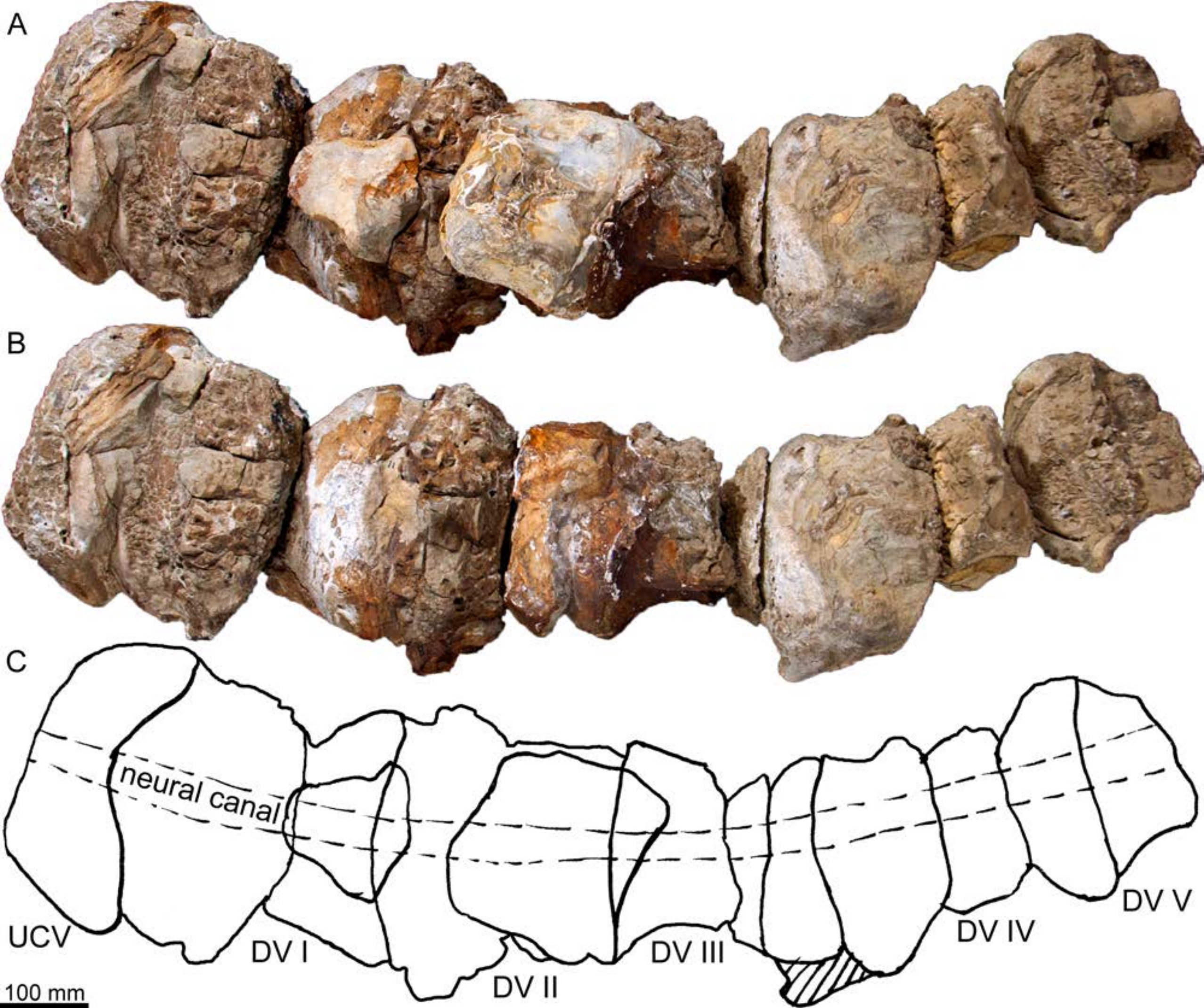

A
B
C
D
E
AUSTROSAURUS McKILLOPI DISCOVERED BY H.B.WADE IN 1932
FOSSILS of this GIANT MARINE ANIMAL [illegible] ARE IN BRISBANE MUSEUM.

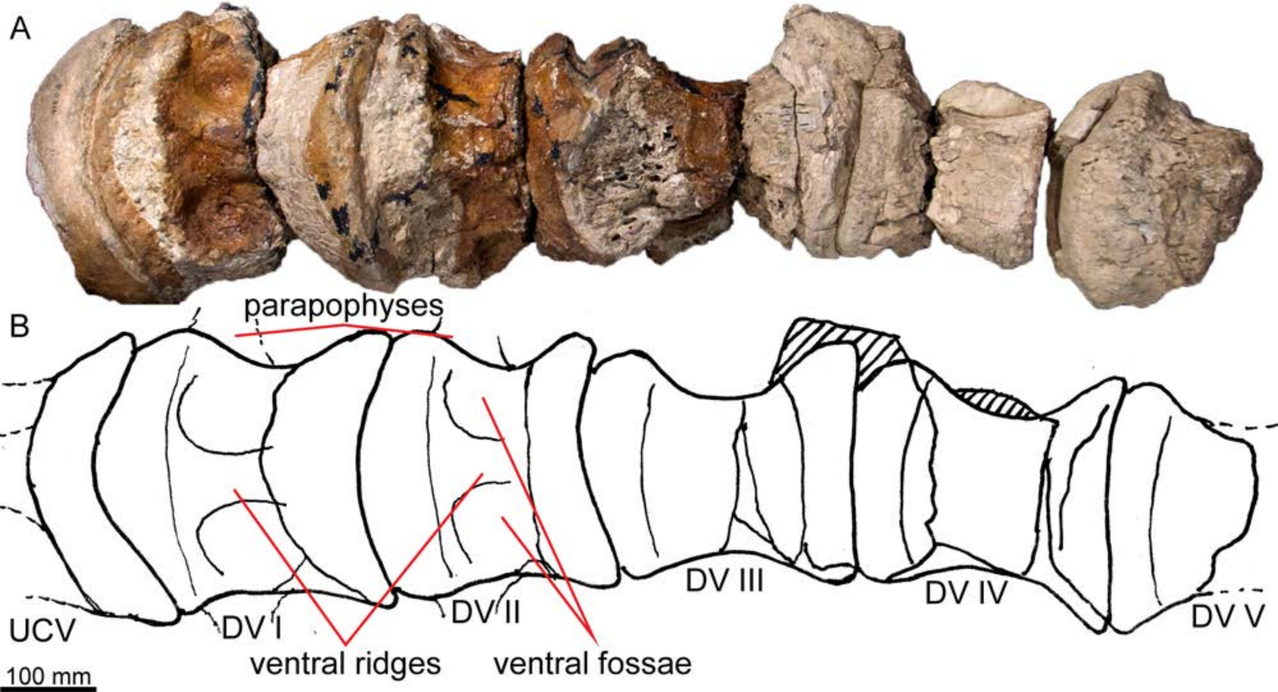

A
N
Nota C.
West Bore
North Coolibah
Coolibah C.
Horse
East Bore.
Whitewood Paddock
X
Homestead
South Coolibah.
Hawk's Nest
CLUTHA
(Showing Paddocks)
Big Whitewood
Nell C.
Flinders River
Maxwelton
B
ah
624'
R2063
R2065
"Clutha"
C
R15243
Nell
Creek
Camaray Downs'
R2066
R2070
491'
Little
Whitewood
Kla

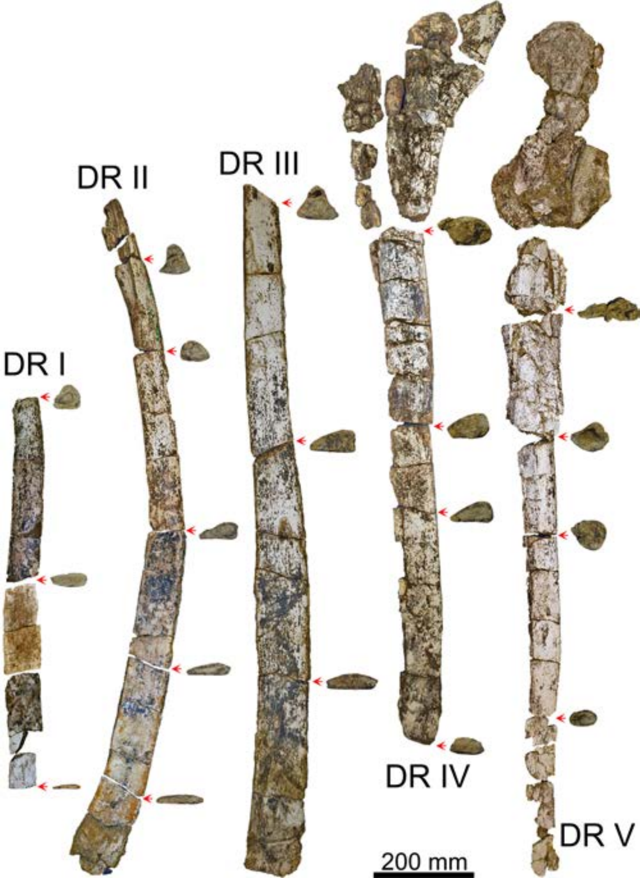

A1
C1
E1
B1
D1
F1
UCV
DV I
DV II
DV III
DV IV
DV V
B2
D2
F2
C2
A2
E2
200 mm


A
B
accessory foramen
pneumatic foramina
rib fragments
PCPL
ACPL
ACDL
PCDL
UCV
DV I
parapophyses
DV II
DV III
DV IV
DV V
100 mm

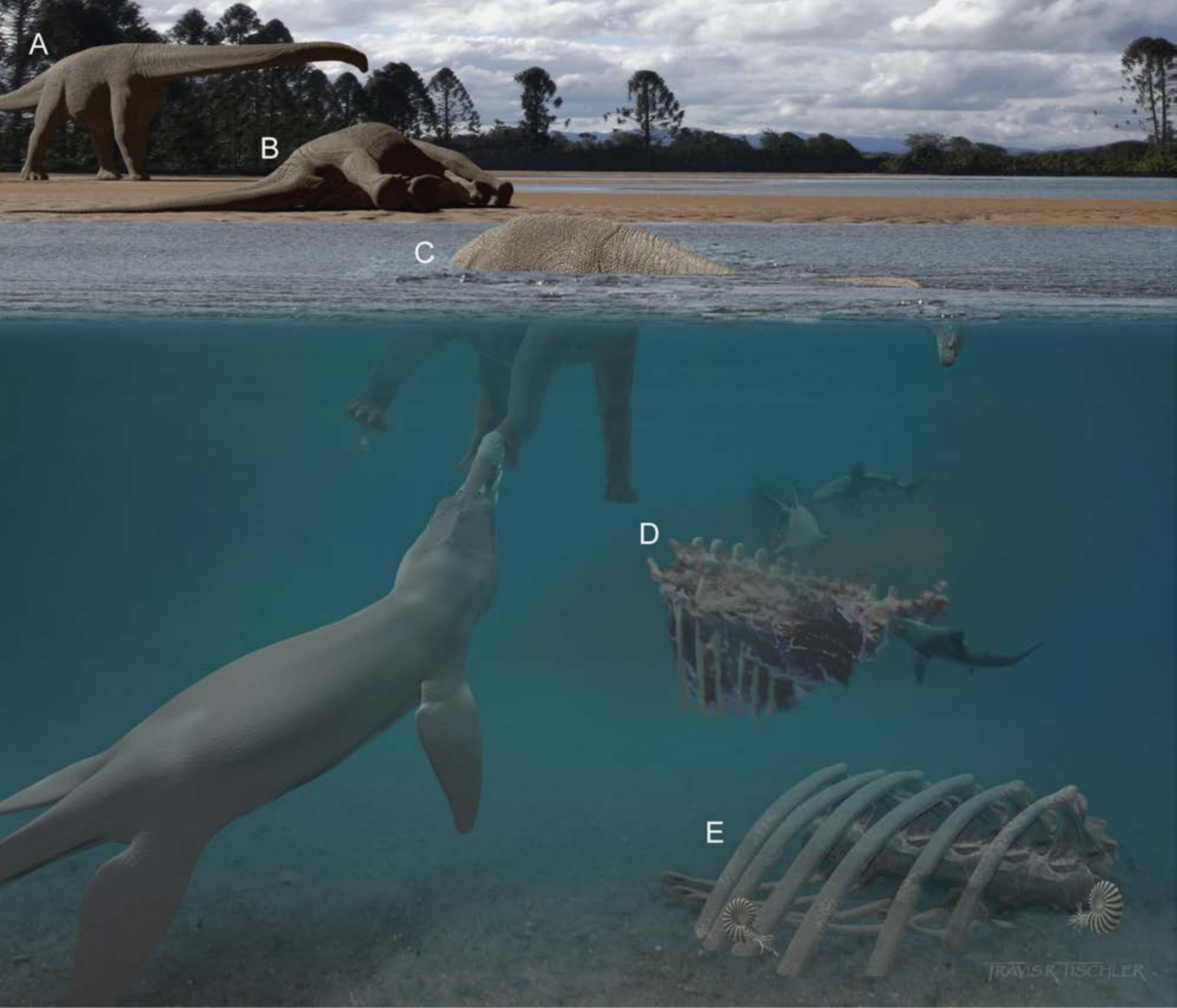

A
B
pneumatic foramina
parapophyses
accessory foramen
DV V
DV IV
DV III
DV II
DV I
UCV
100 mm
C
pneumatic foramina
accessory foramen
50 mm

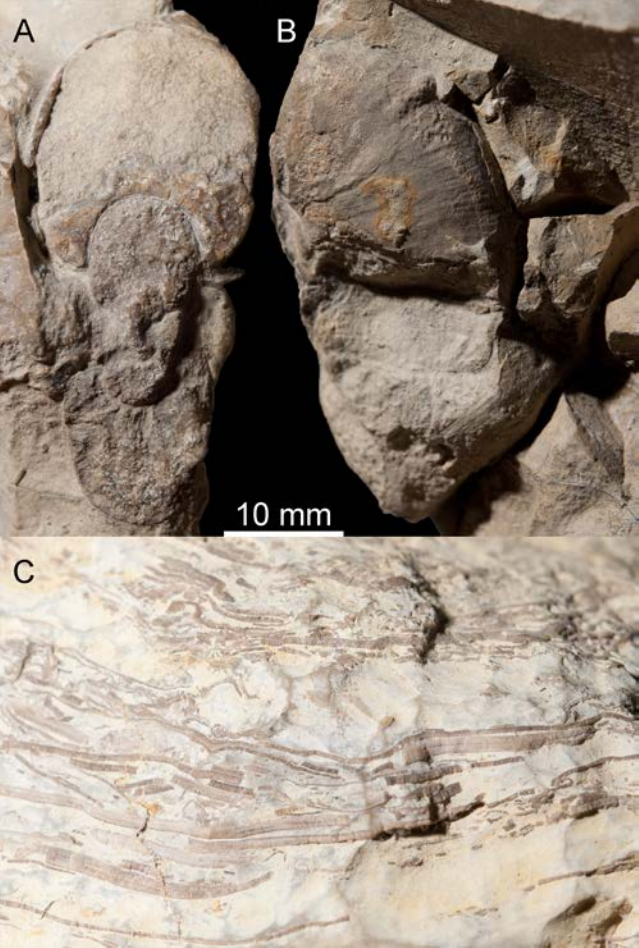

A
B
C
neural canal
UCV
DV I
DV II
DV III
DV IV
DV V
100 mm

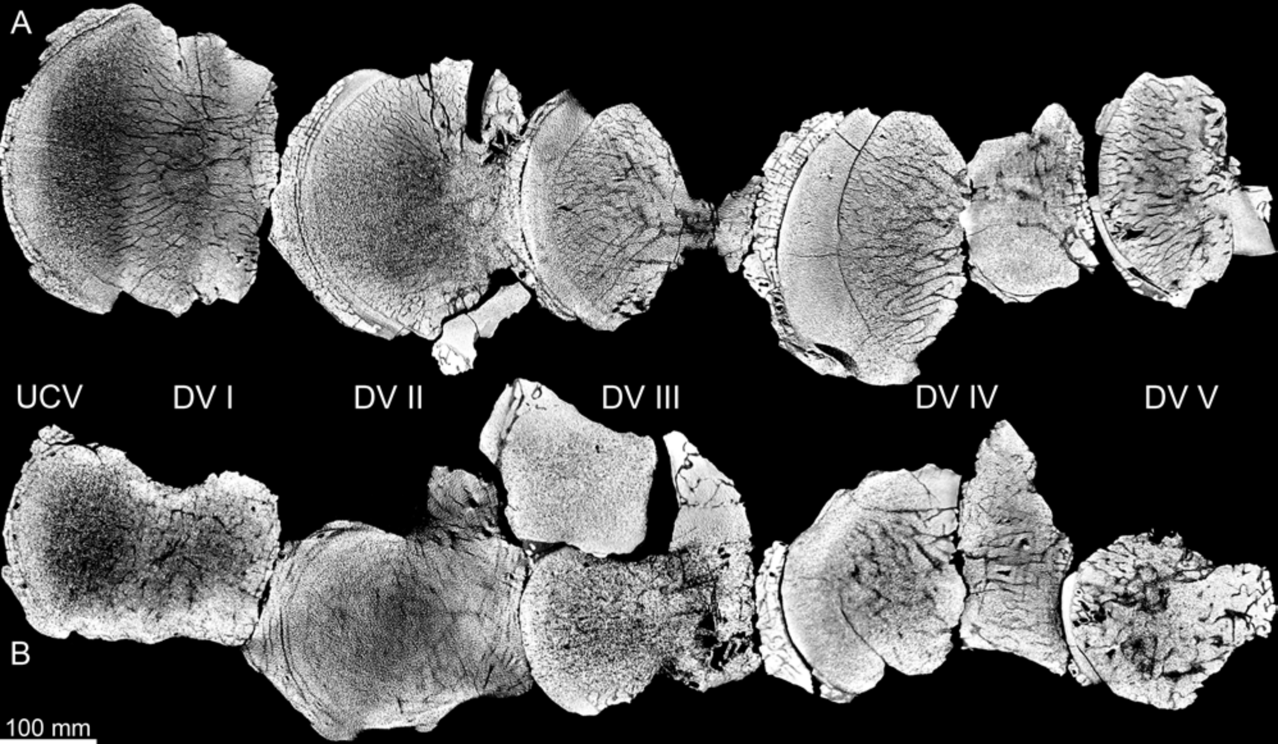

A
B
parapophyses
UCV
DV I
DV II
DV III
DV IV
DV V
ventral ridges
ventral fossae
100 mm

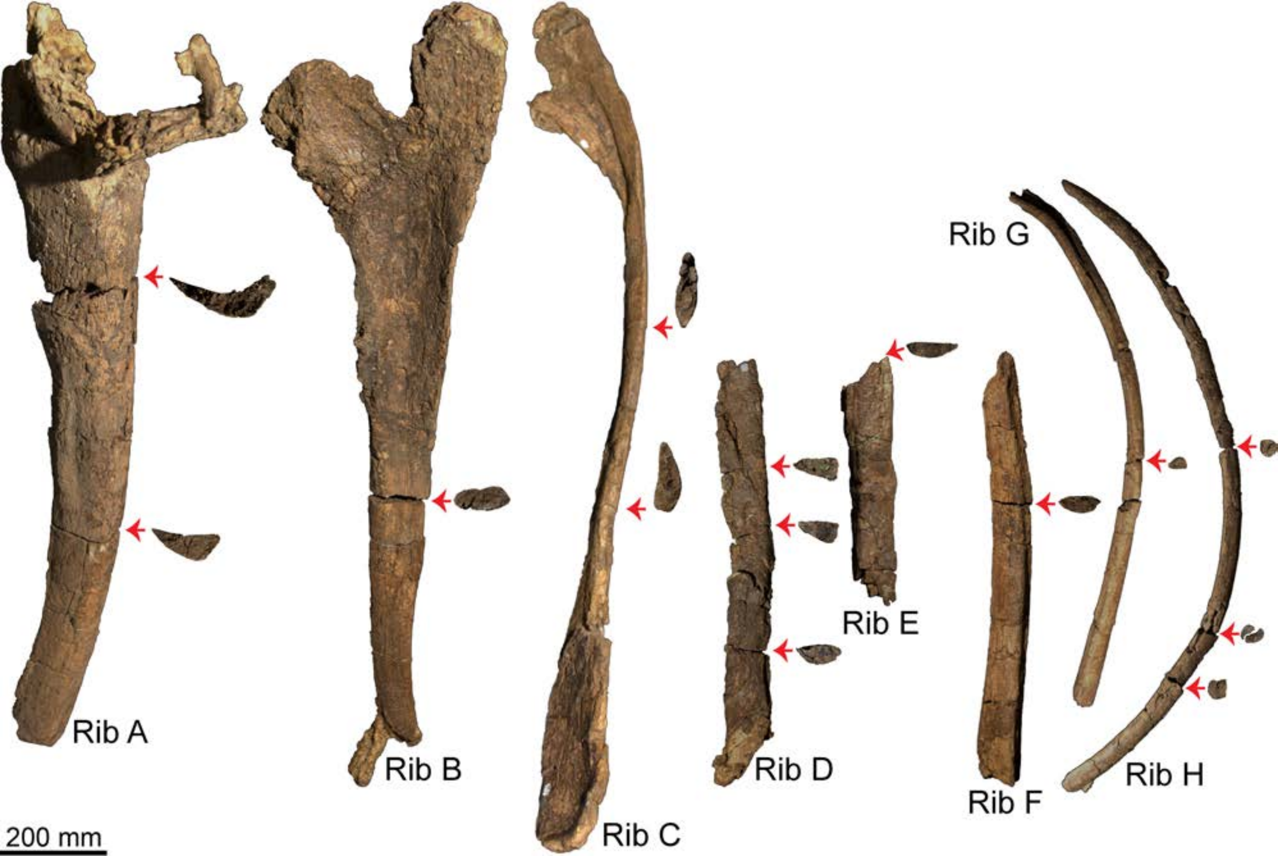

DR I
DR II
DR III
DR IV
DR V
200 mm

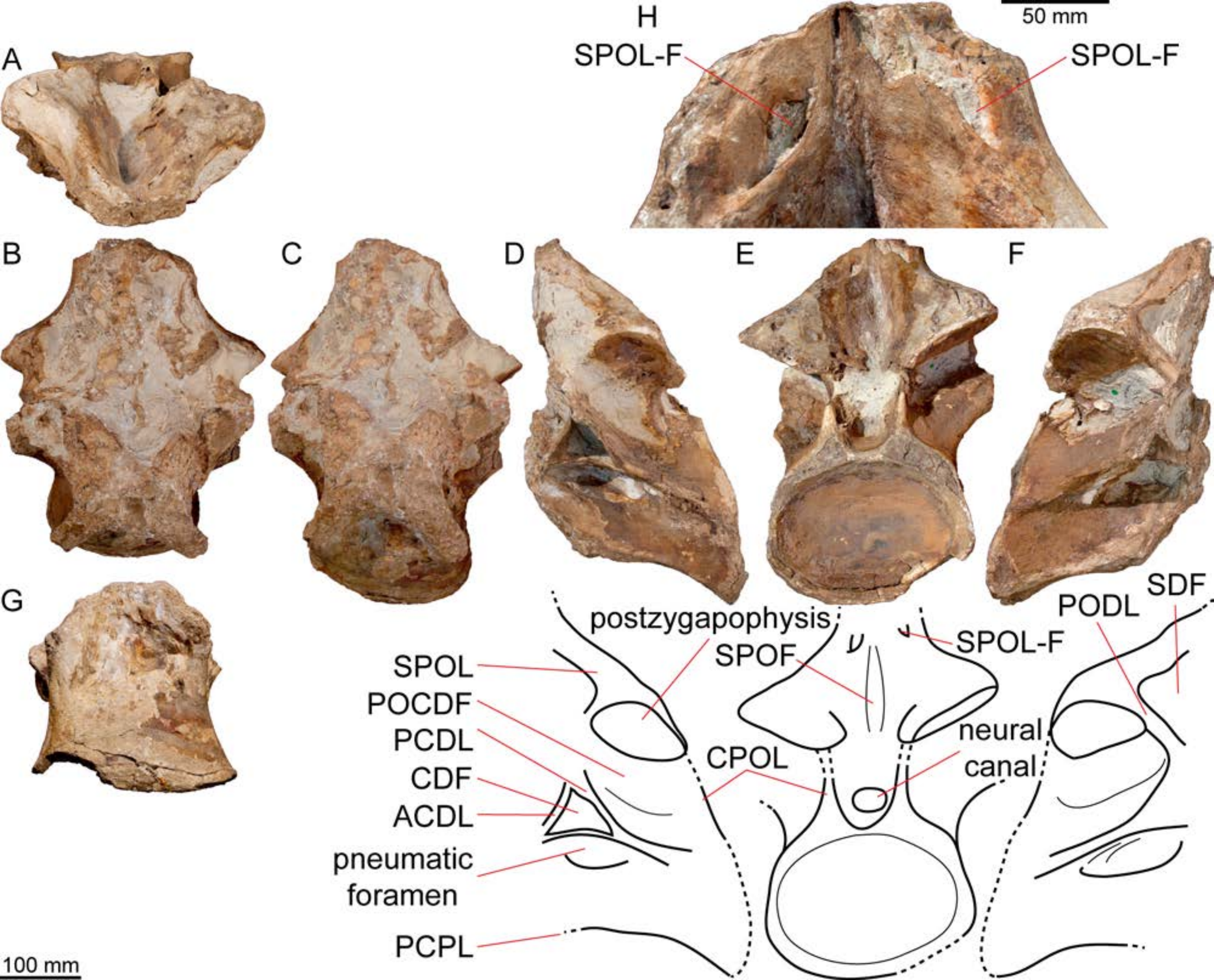

200 mm
N


A
B
C
D
E
TRAVIS R. TISCHLER


A
B
10 mm
C


A
UCV
DV I
DV II
DV III
DV IV
DV V
B
100 mm


Rib A
Rib B
Rib C
Rib D
Rib E
Rib F
Rib G
Rib H
200 mm


H
50 mm
A
SPOL-F
SPOL-F
B
C
D
E
F
G
SDF
PODL
postzygapophysis
SPOL-F
SPOF
SPOL
POCDF
PCDL
CDF
ACDL
pneumatic foramen
PCPL
CPOL
neural canal
100 mm