

## THE DINOSAURIAN ICHNOFAUNA OF THE LOWER CRETACEOUS (VALANGINIAN–BARREMIAN) BROOME SANDSTONE OF THE WALMADANY AREA (JAMES PRICE POINT), DAMPIER PENINSULA, WESTERN AUSTRALIA

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**ABSTRACT**—Extensive and well-preserved tracksites in the coastally exposed Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Dampier Peninsula provide almost the entire fossil record of dinosaurs from the western half of the Australian continent. Tracks near the town of Broome were described in the late 1960s as *Megalosauropus broomensis* and attributed to a medium-sized theropod trackmaker. Brief reports in the early 1990s suggested the occurrence of at least another nine types of tracks, referable to theropod, sauropod, ornithopod, and thyreophoran trackmakers, at scattered tracksites spread over more than 80 km of coastline north of Broome, potentially representing one of the world’s most diverse dinosaurian ichnofaunas. More recently, it has been proposed that this number could be as high as 16 and that the sites are spread over more than 200 km. However, the only substantial research that has been published on these more recent discoveries is a preliminary study of the sauropod tracks and an account of the ways in which the heavy passage of sauropod trackmakers may have shaped the Dampier Peninsula’s Early Cretaceous landscape. With the other types of dinosaurian tracks in the Broome Sandstone remaining undescribed, and the full extent and nature of the Dampier Peninsula’s dinosaurian tracksites yet to be adequately addressed, the overall scientific significance of the ichnofauna has remained enigmatic.

At the request of the area’s Goolarabooloo Traditional Custodians, 400+ hours of ichnological survey work was undertaken from 2011 to 2016 on the 25 km stretch of coastline in the Yanijarri–Lurujarri section of the Dampier Peninsula, inclusive of the coastline at Walmadany (James Price Point). Forty-eight discrete dinosaurian tracksites were identified in this area, and thousands of tracks were examined and measured in situ and using three-dimensional photogrammetry. Tracksites were concentrated in three main areas along the coast: Yanijarri in the north, Walmadany in the middle, and Kardilakan–Jajal Buru in the south. Lithofacies analysis revealed 16 repeated facies types that occurred in three distinctive lithofacies associations, indicative of an environmental transgression between the distal fluvial to deltaic portions of a large braid plain, with migrating sand bodies and periodic sheet floods. The main dinosaurian track-bearing horizons seem to have been generated between periodic sheet floods that blanketed the preexisting sand bodies within the braid plain portion of a tidally influenced delta, with much of the original, gently undulating topography now preserved over large expanses of the present day intertidal reef system. Of the tracks examined, 150 could be identified and are assignable to a least eleven and possibly as many as 21 different track types: five different types of theropod tracks, at least six types of sauropod tracks, four types of ornithopod tracks, and six types of thyreophoran tracks. Eleven of these track types can formally be assigned or compared to existing or new ichnotaxa, whereas the remaining ten represent morphotypes that, although distinct, are currently too poorly represented to confidently assign to existing or new ichnotaxa. Among the ichnotaxa that we have recognized, only two (*Megalosauropus broomensis* and *Wintonopus latomorum*) belong to existing ichnotaxa, and two compare to existing ichnotaxa but display a suite of morphological features suggesting that they may be distinct in their own right and are therefore placed in open nomenclature. Six of the ichnotaxa that we have identified are new: one theropod ichnotaxon, *Yangtzeplus clarkei*, ichnosp. nov.; one sauropod ichnotaxon, *Oobardjidama foulkesi*, ichnogen. et ichnosp. nov.; two ornithopod ichnotaxa, *Wintonopus middletonae*, ichnosp. nov., and *Walmadanyichnus hunteri*, ichnogen. et ichnosp. nov.; and two thyreophoran ichnotaxa, *Garbina roeorum*, ichnogen. et ichnosp. nov., and *Luluichnus mueckeii*, ichnogen. et ichnosp. nov. The level of diversity of the main track types is comparable across areas where tracksites are concentrated: Kardilakan–Jajal Buru (12), Walmadany (11), and Yanijarri (10).

The overall diversity of the dinosaurian ichnofauna of the Broome Sandstone in the Yanijarri–Lurujarri section of the Dampier Peninsula is unparalleled in Australia, and even globally. In addition to being the primary record of non-avian dinosaurs in the western half of Australia, this ichnofauna provides our only detailed glimpse of Australia’s dinosaurian fauna during the first half of the Early Cretaceous. It indicates that the general composition of Australia’s mid-Cretaceous dinosaurian fauna was already in place by the Valanginian–Barremian. Both sauropods and ornithopods were diverse and abundant, and thyreophorans were the only type of quadrupedal ornithischians. Important aspects of the fauna that are not seen in the Australian mid-Cretaceous body fossil record are the presence of stegosaurians, an overall higher diversity of thyreophorans and theropods, and the presence of large-bodied hadrosauroid-like ornithopods and very large-bodied sauropods. In many respects, these differences suggest a holdover from the Late Jurassic, when the majority of dinosaurian clades had a more cosmopolitan distribution prior to the fragmentation of Pangea. Although the record for the Lower Cretaceous of Gondwana is sparse, a similar mix of taxa occurs in the Barremian–lower Aptian La Amarga Formation of Argentina and the Berriasian–Hauterivian Kirkwood Formation of South Africa. The persistence of this fauna across the Jurassic–Cretaceous boundary in South America, Africa, and Australia might be characteristic of Gondwanan dinosaurian faunas more broadly. It suggests that the extinction event that affected Laurasian dinosaurian faunas across the Jurassic–

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Cretaceous boundary may not have been as extreme in Gondwana, and this difference may have foreshadowed the onset of Laurasian-Eurogondwanan provincialism. The disappearance of stegosaurians and the apparent drop in diversity of theropods by the mid-Cretaceous suggests that, similar to South America, Australia passed through a period of faunal turnover between the Valanginian and Aptian.

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

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## INTRODUCTION

The Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Dampier Peninsula, in the Kimberley region of Western Australia (Fig. 1), contains potentially one of the world's most diverse dinosaurian ichnofaunas, preserved in discontinuous tracksites scattered over at least 100 km of coastline from Roebuck Bay east of Broome north to Minarriny (Coloumb Point) and possibly as far north as Cape Leveque (Glauert, 1952; Colbert and Merrilees, 1967; Long, 1990, 1992a, 1993, 1998, 2002; Thulborn et al., 1994, 2002, 2009; Rich and Vickers-Rich, 2003a; Willis and Thomas, 2005; Commonwealth of Australia, 2011; Thulborn, 2012). With the exception of a few fragments of bone from other fossil localities in Western Australia (Long, 1992b, 1995; Long and Cruickshank, 1996; Long and Molnar, 1998; Agnolín et al., 2010), this ichnofauna constitutes the primary record of dinosaurs for the western half of Australia, with many of the tracks having no obvious counterpart among described body fossils from other parts of the continent. The ichnofauna therefore provides valuable insight into the composition and paleoecology of Early Cretaceous dinosaurian faunas in eastern Gondwana, at a key time during the fragmentation of the supercontinent. In recognition of these and other outstanding heritage values, the intertidal zone along the Dampier Peninsula coastline from Roebuck Bay to Cape Leveque (excluding the area from Dampier Creek to Yinara [Entrance Point]) was recently included in the West Kimberley National Heritage List (Place ID 106063; Commonwealth of Australia, 2011).

### Indigenous Knowledge of Dinosaurian Tracks in the Broome Sandstone

*“The Country now comes from Bugarri-Garri [sic] (dreamtime). It was made by all the dreamtime ancestors, who left their tracks and statues behind and gave us our law, we still follow that law, which tells us how to look after this country and how to keep it alive.”*

—Paddy Roe OAM (Parliament of the Commonwealth of Australia, 1991)

Dinosaurian tracks in the Broome Sandstone form an important part of the cultural heritage of the indigenous people of the Dampier Peninsula and greater west Kimberley (Anonymous, 1999; Major and Sarjeant, 2001) and have likely been known to them for thousands of years. The tracks are integral to a song cycle that extends along the coast from Bunginygun (Swan Point, Cape Leveque) to Wabana (Cape Bossut, near La Grange) and then inland to the southeast over a total distance of approximately 450 km (Anonymous, 1999; Major and Sarjeant, 2001). Across Australia, song cycles (also called ‘songlines’ or ‘dreaming tracks’) delineate both a physical and a spiritual geography (together referred to as ‘country’), tracing, song by song, the paths taken by supernatural beings who sang songs for everything (places, animals, plants, stars, etc.) as they went, thereby singing the world into existence and conferring the spiritual essence of traditional law into the land (Stanner, 1979; Chatwin,

1987; Benterrak et al., 1996). On the Dampier Peninsula, this Creation Time (also referred to as the ‘Dreamtime’ or ‘The Dreaming’ by Stanner, 1979) is known as Bugarrigarra [bugarrigara]. Through song cycles, the creation stories, ceremonies, laws, rituals, language, and codes of conduct fundamental to sustaining the well-being of the land and its people are passed from one generation to the next (Roe, 1983; Chatwin, 1987; Bradshaw and Fry, 1989; Benterrak et al., 1996). Custodial care of song cycles and country is the job of men known as Maja (Law Bosses), who are typically chosen on the basis of personal qualities rather than bloodline.

The song cycle that extends along the Dampier Peninsula coastline is referred to locally as Ululong [ululuŋ] (hereafter referred to as the Song Cycle). Three other song cycles emanate from Minyirr Djugun Buru (the greater Broome area): Dabber dabber goon, which travels east, cutting through Uluru (Ayers Rock, Northern Territory) until it reaches the Pacific Ocean; Billungun, which follows the same path as Dabber dabber goon until it reaches Uluru where it splits three ways (see Crane, 2013: pl. 27); and Nunnungurugoon, which travels along its own path northeast, through the Kimberley.

**Marala, The Emu Man**—One of the important Bugarrigarra beings within the Song Cycle is called Marala [marala] (Mountford, 1973; Anonymous, 1999; Major and Sarjeant, 2001) (Fig. 2A). Marala, also referred to as ‘Emu Man,’ was the ‘lawgiver,’ and instilled in country the codes of conduct for behavior needed to help ensure its well-being, and there are numerous Bugarrigarra stories and parts of stories in which he features. In the process of moving through the Song Cycle from south to north, as well as in and out of the sea, Marala left behind three-toed tracks. He also left behind the grooved impressions of his tail feathers (his ‘ramu’ or ceremonial engravings) when he sat down to rest and create his law ground. Today, three-toed dinosaur tracks (typically those assigned to *Megalosauropus broomensis*) and impressions of cycad-like bennettitaleans (Marala’s tail feather impressions and ramu) are seen as testimony to Marala’s journey as narrated in the Song Cycle. A concentration of *M. broomensis* tracks at a Song Cycle place on Cable Beach is also known as Maralagun [place of Marala]. Marala’s tracks at Minyirr (Gantheaume Point) and Reddell Beach are referred to in a number of Bugarrigarra stories, some of which are publicly known, others of which are known only to a restricted number of people. The most notable of the publicly known stories involves Marala and the Ngadjayi [ngajayi] (female sea spirits) (Fig. 2). In part of another story, Marala encounters Warragunna (or Warakarna), the ‘Eagle Man’ or ‘Eagle-hawk’ (see Bates, 1929), who spears him (K. Akerman, pers. comm. 25 November 2015). When Walter ‘Snowy’ Jones relayed his discovery of tridactyl dinosaurian tracks at Minyirr in 1945 to Ludwig Glauert at the Western Australian Museum, he stated that “The tracks are known as Warragunna...” (Jones and Glauert, 1945–1946:6; Anonymous, 1946; see below). Presumably Jones did not realize that in this particular story Warragunna was the Bugarrigarra hero who found the tracks, not the one who made them (Marala). In Jones’ 1945 recount of the story, a ‘native’ tracks the giant footprints of a big bird who is traveling south, trying to cross the deep waters

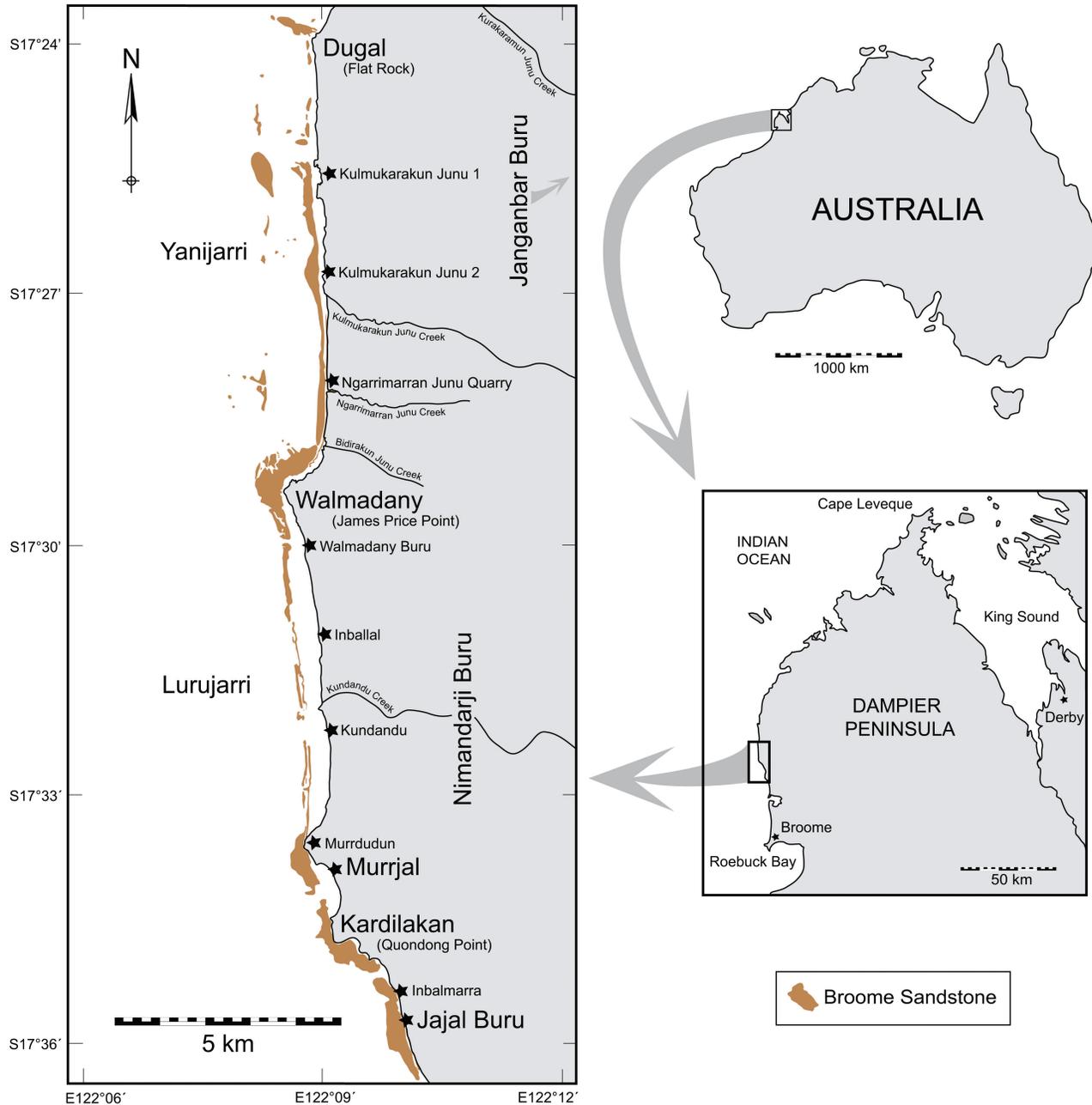


FIGURE 1. Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Dinosaur tracksites are scattered all along this stretch of coast, intermittently exposed at low tide on shore platforms and reefs of the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone. The extent of intertidal shore platforms and associated exposures of the Broome Sandstone is based on beach conditions during 2011–2012. Place names correspond to ethnographic sites on the Lurujarri Heritage Trail and include mythological and ceremonial places relating to the Song Cycle and its associated traditional law and culture, camping areas of historical significance, and numerous burials (modified and updated from those listed in Worms, 1944; Akerman, 1975, 1976; Bradshaw and Fry, 1989).

of Roebuck Bay. Turning back, the giant bird chases the man to Willie Creek. Elaboration of this story in 1946 indicates that the footprints created by the giant bird (Marala) during the chase created Roebuck Bay (Durack, 1946; Gardello, 1946; see Frontispiece). Another Bugarrigarra story that involves a giant ‘monster bird’ or giant eagle is that of Djaringgalong [dja:ɪŋgaluŋ] (Nangan and Edwards, 1976; Roe, 1983:29).

Because of their significance to the Song Cycle, many of the dinosaurian tracks and plant fossils described herein are

well known to certain indigenous people of the Dampier Peninsula. Knowledge of the Song Cycle and the dinosaurian tracks and associated fossils is thought to provide insight into Bugarrigarra. As such, much of this knowledge is considered sacred. Although some locations along the Song Cycle where dinosaurian tracks and plant fossils occur are law grounds, more broadly it is the presence of these trace fossils in the country through which the Song Cycle passes that is the most important thing. The disappearance of some tracks through

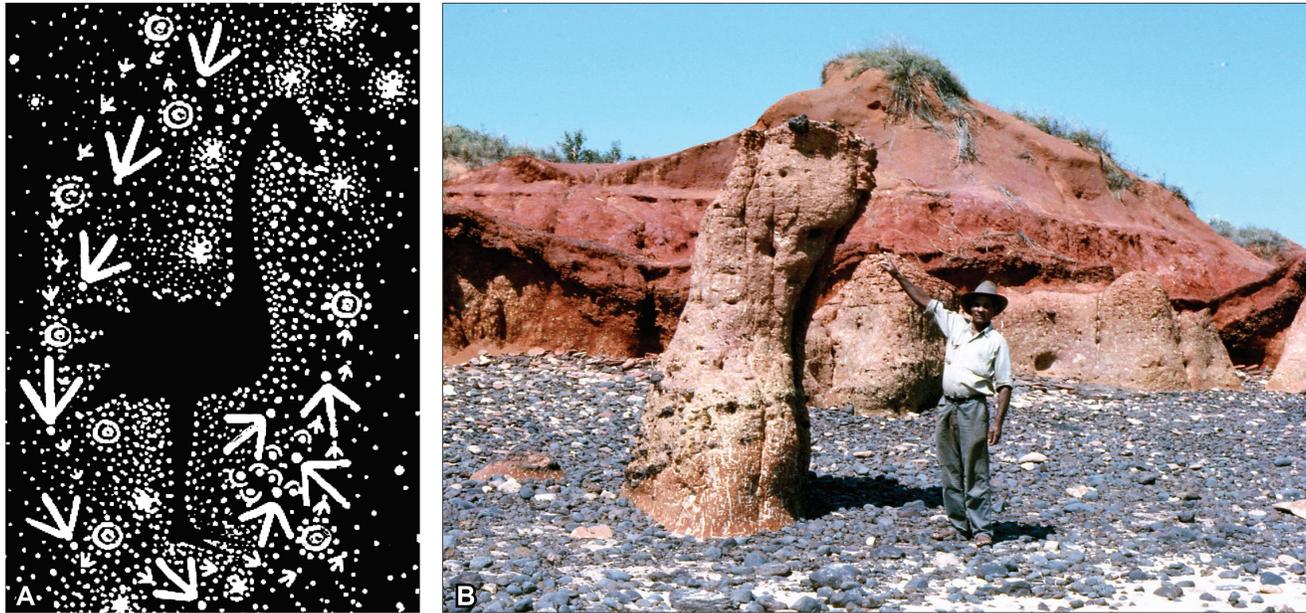


FIGURE 2. The Bugarrigarra story of Marala and the Ngadjayi [ngajayi] ('spirit women of the sea'). Marala, also known as 'Emu Man,' is one of the creator beings associated with the Song Cycle. **A**, Marala's emu-like form persists today as a shadow of dark nebulae running virtually the length of the Milky Way, his head (the Coalsack) near Jina (eagle's claw prints; the Southern Cross) and his neck along Gwuraarra (naala, or 'hitting stick'; the Pointers). Marala is surrounded by his giant three-toed tracks, which are preserved in the rocks of the Broome Sandstone and trace his journey along the coast of the Dampier Peninsula as narrated in the Song Cycle. Typically it is tracks assigned to *Megalosauropus broomensis* (see Figs. 19 and 20) that are linked to Marala, along with the impressions of cycad-like bennettitaleans (Fig. 17F), which are regarded as the mark of his tail feathers or ramu (ceremonial engravings). South of Minyirr (Gantheaume Point), Marala encountered a group of Ngadjayi (depicted as partially circled dots at his feet)—spirit women from the sea who had come out of the water to harden their skin in the sun and delouse each other with jungkur (lice sticks). When Yinara [jinaara], the most senior woman in the group, sensed that Marala was coming, she told the younger women to turn towards the land and not look at him. Marala saw the women and walked over to them. Although Yinara positioned herself between Marala and the others, the Emu Man was still able to get very close. Curious to see him, some of the women turned to watch Marala as he walked past. Yinara was able to drive Marala away, but she was angry with the younger women and shamed them for disobeying her. The spirits of Yinara and the other Ngadjayi moved into the sky and can be seen today as the constellation known as Pleiades. **B**, stone pillars representing the Ngadjayi occur at Bungurunan, a small beach west of Entrance Point, south of the township of Broome. In this photo from August 1976, Paddy Roe points to Yinara, the tallest of the pillars. Artwork courtesy and copyright Jo Manjun; photo courtesy and copyright Kim Akerman.

natural processes is seen as part of ongoing unfolding of Bugarrigarra, as is the appearance of new ones. It is accepted that tracks will come and go as knowledge of them is needed. For these reasons, the removal or desecration of tracks from country for any reason is considered a great offence, in most instances punishable by spearing (J. Roe, quoted in Anonymous, 1996). It can also bring illness and misfortune, not only to the perpetrators but also to the Maja under whose custodianship the crime occurred. (See Appendix 2 for further information on previous instance of theft and removal of dinosaurian tracks from the Dampier Peninsula.)

**Custodianship of the Song Cycle and Dinosaurian Tracks**—The Song Cycle passes through the country (from north to south) of the Bardi-Jawi, Nyulnyul, Jabirrabirr, Ngumbarl, Djukun, Yawuru, and Karajarri language groups (Tindale, 1974; McGregor, 1988; Bradshaw and Fry, 1989; Stokes and McGregor, 2003)—collectively referred to as the Nyulnyulan languages (Stokes and McGregor, 2003)—and is divided into a Northern Tradition and a Southern Tradition (Roe and Shaw, 2008; Botsman, 2012). Custodianship of the Song Cycle and the land through which it passes originally lay with Maja from each respective language area. But with dispossession of much of their traditional lands following the commencement of white settlement in 1865, and the displacement of many of the younger Jabirrabirr, Ngumbarl, Djukun, and Yawuru men and women to government-run missions, ongoing custodianship of both the

Northern and Southern traditions of the Song Cycle became increasingly tenuous moving into the 20th century.

Paddy Roe (Figs. 2B, 3A) was born around 1912 on Roebuck Station, east of Broome (Benterrak et al., 1996). Although this meant that he was born in Yawuru country, Paddy Roe grew up to become a fully initiated Njikina man (Benterrak et al., 1996). Njikina country covers a large area that lies to the east of Yawuru country (Tindale, 1974). When Paddy Roe and Pegallily, his woman, entered Jabirrabirr country in the early 1930s (Bradshaw and Fry, 1989; Benterrak et al., 1996; Roe and Shaw, 2008; Botsman, 2012), no young people remained and custodianship of not only Jabirrabirr but also Ngumbarl and Djukun countries sat with a powerful old Maja named Walmadany. Paddy and Pegallily were taken under the wing of the aging Jabirrabirr clan. Before he became too old, Walmadany chose Paddy Roe to become the new Maja for the Northern and Southern traditions of the Song Cycle, as well as the custodian of Jabirrabirr, Ngumbarl, and Djukun countries (Bradshaw and Fry, 1989; Roe and Shaw, 2008; Botsman, 2012; Goolarabooloo Lawmen, pers. comm., 2014). Paddy Roe subsequently settled his family north of Broome, initially at Willie Creek, then Buckley's Plain, the Native Hospital, and finally at Coconut Wells in 1979, where he established the Goolarabooloo Millibinyarri Community, with the goal of fulfilling the responsibility that had been entrusted to him by old Walmadany. When he died, Paddy Roe buried Walmadany alongside the other elders in the dunes above the point that bears his name.



FIGURE 3. Goolarabooloo Traditional Custodians and Maja (Law Bosses) for Jabirrjabirr, Ngumbarl, and Djugun countries, and the Northern Tradition of the Song Cycle and the dinosaur tracks of the Broome Sandstone. **A**, The late Paddy Roe, also known as Lulu, who was chosen to be Maja for this area by Walmadany, the last great Jabirrjabirr Maja, sometime in the mid-20th century. Paddy Roe is shown here with the Order of Australia Medal that was awarded to him in 1990. The original caption to the photo says, “This is my Gulbinna [shield]. The government gave me this medal. This Gulbinna is asking the medal, you going to break up this country or keep it the same since Bugarre Garre [Dreamtime]” (source unknown). **B**, Paddy Roe’s grandsons, who continued as Goolarabooloo Maja after his death in 2001. From left to right: Phillip Roe, the late Joseph Roe, and Richard Hunter. Photograph courtesy and copyright Damian Kelly, 2012.

Paddy Roe passed away in 2001. Before he died he made three of his grandsons—Richard Hunter, Phillip Roe, and Joseph Roe—Traditional Custodians and Maja for Jabirrjabirr, Ngumbarl, and Djugun countries, and the Northern Tradition of the Song Cycle (Roe and Shaw, 2008; Botsman, 2012) (Fig. 3B). Joseph Roe passed away in February 2014, but Richard Hunter and Phillip Roe are the Maja who currently have responsibility for maintaining, sharing and passing on the Song Cycle with other Maja of the Northern Tradition.

Because the land through which it passes has remained largely undisturbed and its custodianship maintained, the traditional law and culture encoded in the Song Cycle remains an important part of the way of life for many indigenous people across the Dampier Peninsula (e.g., Roe, 1983; Bradshaw and Fry, 1989; Benterrak et al., 1996; Botsman, 2012). Traditional ceremonial activities are still maintained, attended by people who travel hundreds of kilometers to participate.

On account of their cultural significance, access to the dinosaurian tracksites of the Dampier Peninsula coastline for research and related purposes requires the consent of the Goolarabooloo Traditional Custodians, particularly in Jabirrjabirr and Ngumbarl countries (Tindale, 1974; McGregor, 1988; Bradshaw and Fry, 1989; Stokes and McGregor, 2003). For tracksites in the greater Broome area (Minyirr Djugun Buru) that sit within traditional Djukun and Yawuru countries (Tindale, 1974; McGregor, 1988; Bradshaw and Fry, 1989; Stokes and McGregor, 2003), the consent of the Yawuru Community and Yawuru Traditional Owners is also appreciated.

#### Non-indigenous Knowledge of Dinosaurian Tracks in the Broome Sandstone and Previous Scientific Research

The earliest account of dinosaurian tracks on the Dampier Peninsula by a non-indigenous person that we are aware of comes from around the turn of the 20th century. Daisy Bates, an

Irish-Australian immigrant, became enthralled by indigenous culture during a three-month visit to Beagle Bay Mission in 1900. Bates subsequently returned to Broome during 1901–02. Based at Roebuck Plains Station with her husband Jack and son Arthur, Bates immersed herself in the study of ‘the saltwater tribes’ in the area. In her personal memoir of Bates, writer Ernestine Hill recalls Bates’ reaction to seeing a dinosaurian track preserved in rocks at Willie Creek, approximately 22 km north of Broome (Hill, 1973:44). Hill ascribes no specific date to Bates’ sighting of the track. Some of the cultural material collected by Bates aligns closely with information gathered decades later by others. Bates’ recount of the story of Warruganna, collected during her 1901–02 sojourn, and not published until 1929 (Bates, 1929), appeared well before later versions of this story involving the dinosaurian tracks at Minyirr—shared with Glauert via Walter Jones (see below)—emerged publicly (e.g., Anonymous 1946). At the time of publication, no dinosaurian tracks could be located at Willie Creek.

Thirty-four years later, two young girls and their mother stumbled across some of the three-toed theropod tracks at Minyirr that form part of the Marala and Warragunna stories (see above). Sheila Turnbull (nee Milner), her twin Flora Thyer (nee Milner) and their mother, Catherine, spent several days exploring the rock platforms around Minyirr in 1935 as part of a Girl Guides camp that was based at the abandoned lighthouse cottage (Anonymous, 1935) (Fig. 4A). Flora recounts the story as follows:

*“The most exciting thing for Mother, Sheila and me was the morning we were all down on the sea bed . . . very early at the time the tide was at its lowest, and we stumbled across the dinosaur footprints. It was quite scary—it looked as if whatever had made them had just passed by, so clear and perfect they were”* (Norman and Norman, 2007:232).

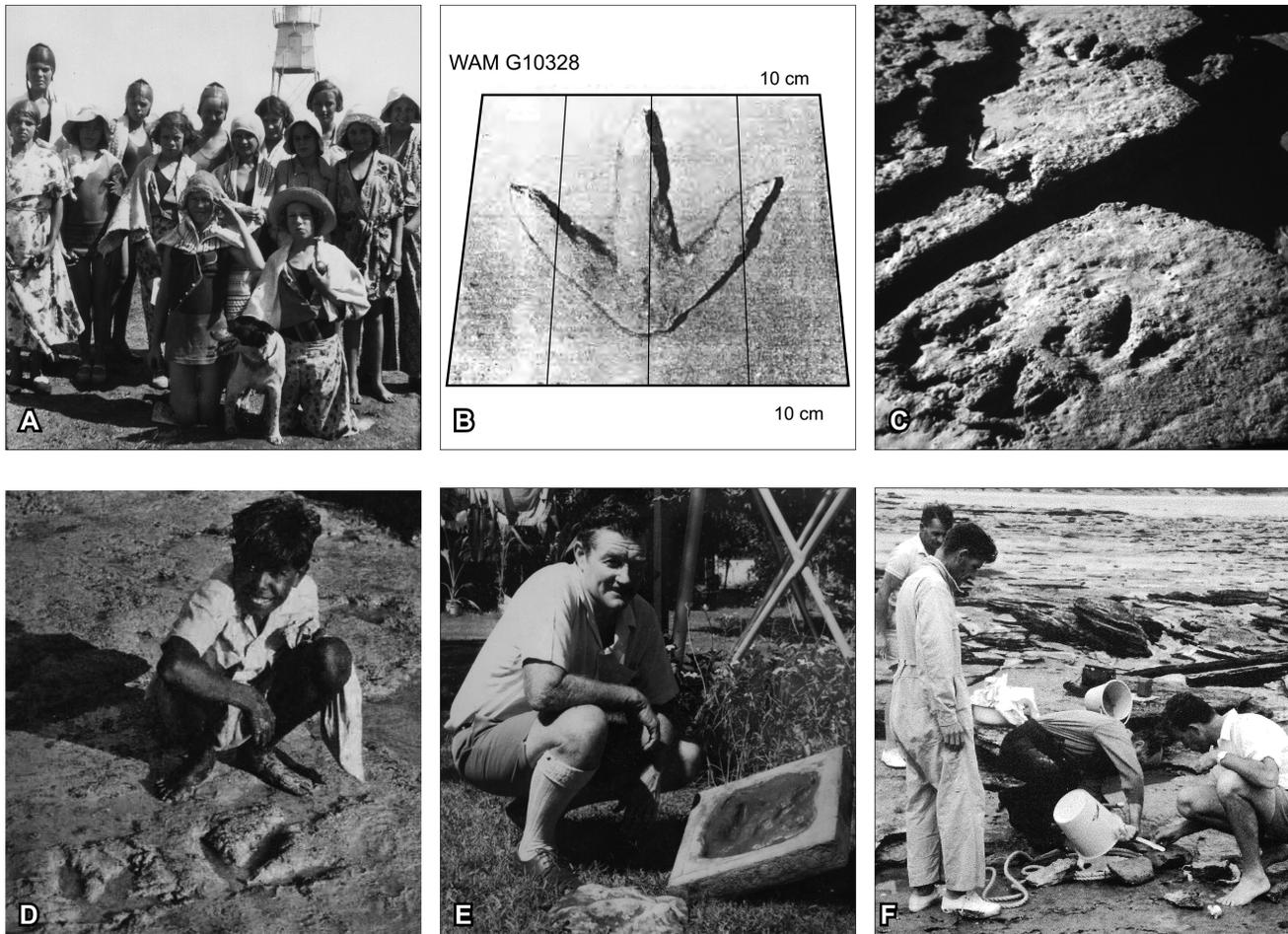


FIGURE 4. Broome dinosaur trackers 1935–1964. **A**, girls from the 1935 Guides Camp at Minyirr (Gantheaume Point lighthouse in the background). Flora Milner (centre row, fourth from right), Sheila Milner (front row, first from right, holding the Milner’s dog, Dixie) (photo courtesy Broome Historical Society); **B**, concrete replica (WAM G10328) of an in situ *Megalosauropus broomensis* track at Minyirr, created in 1945 by Walter Jones (adapted from Baird, 1989:fig. 7B); **C**, in situ *M. broomensis* tracks at Minyirr circa 1964, later described and figured by Colbert and Merrilees (1967) (courtesy and copyright M. Gower); **D**, Mervyn Hunter alongside in situ *M. broomensis* tracks at Minyirr in 1953 (the same tracks as in C) (from Serventy, 1964); **E**, Mo Gower with a replica and plaster cast of the holotype of *M. broomensis* (WAM 66.2.51) (courtesy and copyright M. Gower); **F**, members of the 1964 AMNH and WAM team led by Ned Colbert (center with bucket) casting an in situ *M. broomensis* track (RB 3–2; replica specimen WAM 64.6.10) at Reddell Beach (from Colbert, 1968).

The theropod tracks at Minyirr that were first noticed by the Milner girls—or some similar tracks nearby—were rediscovered on 23 September 1945 by Broome resident Walter ‘Snowy’ Jones, who was collecting shells on the reefs (Jones and Glauert, 1945–1946; Anonymous, 1946). Jones was unaware that the 13 tracks he found had been noticed previously and notified Ludwig Glauert from the Western Australian Museum. Jones later sent a map, drawings, and some measurements of the tracks to Glauert (Jones and Glauert, 1945–1946; Glauert, 1952:83) and in December 1945 provided him with a concrete replica (i.e., concave/negative epirelief) of one of them (WAM G10328; Fig. 4B) (Baird, 1989). A photograph of the tracks, taken by a US serviceman who happened to be at the scene during one of Jones’ visits, was also forwarded to Glauert. Jones’ replica was displayed in the Fossil Room at the Western Australian Museum in January 1946 (Anonymous, 1946). In acquiring information for Glauert, Jones discovered that local indigenous people were very familiar with these tracks, and one of the publicly known stories of Warragunna (see above) was shared with him. Jones’

discovery, and the material that he shared with Glauert, later formed the basis of the first scientific account of the Minyirr tracks (Glauert, 1952; see below).

Not long after their rediscovery by Jones, the theropod tracks at Minyirr came to the attention of Elizabeth Durack, who arrived in Broome in October 1945 and spent time at the lighthouse keeper’s cottage. Over the next 8 months, Durack painted a series of 93 artworks for her first solo exhibition, entitled *Time and Tide—The Story in Pictures of Roebuck Bay N. W. Australia* (Durack, 1946). The first painting in this series was *Legend*, which depicted the dinosaur tracks at Minyirr and the story of Warragunna (see Frontispiece). The paintings were exhibited in 1946 at the Museum and Art Gallery of Western Australia and the Athenaeum in Melbourne, and in 1947 at the David Jones Gallery in Sydney. Elizabeth’s sister, Mary, was equally inspired by the tracks made by these ‘prehistoric wanderers’ and penned the verse *Down there my Dinosaur* for the Bulletin in 1958 (Olsen, 1984).

The scientific and broader community gained greater awareness of the Dampier Peninsula’s dinosaurian tracks in 1953 when

Ludwig Glauert provided the first scientific account of the Minyirr theropod tracks. Although he was not able to see the tracks first hand, Glauert (1952) based his description on the concrete replica, map, drawings, photographs, and some measurements that were sent to him by Walter ‘Snowy’ Jones in 1945 (Jones and Glauert, 1945–1946; Glauert, 1952:83). He also included an account of the Warragunna story that had been shared with Jones.

Following the publication of Glauert (1952), the tridactyl tracks at Minyirr were again relocated in 1953 by Maurice ‘Mo’ Gower, a local wharfinger, Archie Whitworth, the Broome Clerk of Courts, and John Tapper, the local port manager (Rabbitt, 1989; M. Gower, pers. comm., 4 April 2014). In addition to the tracks described by Glauert (1952), Whitworth, Gower, and Tapper found upward of 13 new ones (Fig. 4C). Photographs of two of these tracks were taken by Vincent Serventy during the North-West Camp School in 1954 and were published on several occasions (e.g., Serventy 1954; 1955; 1964) (Fig. 4D). In addition, a cast of one of the tracks was made by camp school staff and later displayed at the Perth Wildlife Show (Serventy, 1964). Three sets of these new tracks were located approximately 1.5 km to the southwest of Minyirr at Reddell Beach (Rabbitt, 1989; M. Gower, pers. comm., 4 April 2014). Tapper and Gower began to carefully document the tracks and in the early 1960s started sending maps, detailed track and trackway measurements, casts, and replicas (made from various materials; see Fig. 4E) to the new curator at the Western Australian Museum, Duncan Merrilees (M. Gower, pers. comm., 4 April 2014). On a return trip to Broome in 1965, Serventy made casts of some of the tracks with Gower and a young naturalist named Harry Butler and noted that many of the tracks that he had seen in 1953 had since been lost to erosion (Serventy, 1967).

Although not speculating on what type of dinosaur may have made the tracks at Minyirr, Glauert (1952) noted their similarity to those of emus (*Dromaius novaehollandiae*) and, based on associated fossils of the bennettitalean *Ptilophyllum pectin* (now a junior synonym of *P. cutchense* Morris, emend.; Bose and Kasat, 1972; McLoughlin, 1996) sent to him by Capt. BE Bardwell, considered them to be Jurassic–Cretaceous in age. In subsequent accounts of the geology of the Broome Sandstone (see below), McWhae et al. (1956:107) and also Veevers and Wells (1961) attributed the Minyirr dinosaurian tracks to an ‘iguano-dont’. Both sets of authors gave no reason for their interpretation of the tracks as having been made by an ornithopod, but presumably it was because of their size and superficial similarity to broadly coeval ‘iguano-dont’ tracks from western Europe, now mostly assigned to *Iguanodontipus burreyi* (see Sarjeant et al., 1998, and references therein).

The first detailed study of the dinosaurian tracks at Minyirr and Reddell Beach commenced in the mid-1960s. Edwin ‘Ned’ Colbert from the American Museum of Natural History joined Merrilees in Broome for two days during May 1964 to investigate the tracks that had been documented by Tapper and Gower. Additional casts of four of the best tracks (three at Minyirr and one at Reddell Beach) were made with the assistance of Tapper, his brother Edgar, and Edgar Truslove (Colbert and Merrilees, 1967; Colbert, 1968; Akerman, 1981) (Fig. 1G). Merrilees returned for one day in August, with confirmation of various measurements being made subsequently by Tapper and Gower (Colbert, 1968). The results of this study were published in Colbert and Merrilees (1967).

The best-preserved tracks described by Colbert and Merrilees (1967) had a maximum length of 325 mm, with clear impressions of digits, individual digital pads, and sometimes unguals/claws. Colbert and Merrilees (1967) considered these tracks to be distinct enough to warrant the establishment of a new ichnotaxon and, based on comparisons that indicated that they might have been made by a ‘megalosaurian carnosaur,’ named them

*Megalosauropus broomensis*. In addition to the earlier photographs of Vincent Serventy, photographs of some of the *M. broomensis* tracks at Minyirr described by Colbert and Merrilees (1967) appeared in Playford et al. (1975:351). *Megalosauropus broomensis* remains a valid ichnotaxon (Baird, 1989; Lockley et al., 1996a; Lockley, 2000b; Thulborn, 2001, 2009) and, although long shrouded in nomenclatural issues (see Lockley et al., 1996a; Lockley, 2000b; Lockley et al., 2000; Thulborn, 2001, 2009), is the best known of the dinosaurian tracks from the Dampier Peninsula.

Subsequent to the description of *M. broomensis* by Colbert and Merrilees (1967), there was a hiatus of 23 years before any new reports on Dampier Peninsula dinosaurian tracks were published. In February 1987, the late Paul Foulkes (Fig. 52D), a resident of Broome and keen naturalist, discovered a series of large round tracks close to Broome at Reddell Beach (Kenneally et al., 1996; K. Foulkes, pers. comm., April 2014). Foulkes subsequently identified these tracks as pertaining to sauropods; the first time that the tracks of these dinosaurs had been recognized in Australia. This discovery prompted him to begin searching more widely along the Dampier Peninsula coastline, working closely with local indigenous groups for whom the tracks held special significance (Kenneally et al., 1996) (see above). Foulkes began to recognize numerous types of tracks preserved in similar settings to those at Minyirr and Reddell Beach, intermittently exposed at low tide on rocky shore platforms and oyster-encrusted reefs as far north as Walmadany (James Price Point), approximately 50 km from Broome (Thulborn et al., 1994; Long, 2002). Together with his then partner Louise Middleton (Fig. 46A), Foulkes began to compile a collection of photos and other data on the new tracksites.

In late 1989, Foulkes and Middleton contacted John Long, then at the Western Australian Museum. Long visited Broome in mid-1990, and, in addition to more theropod tracks similar to *M. broomensis*, he was able to confirm the presence of numerous other tracks and trackways referable to sauropods, large and small ornithopods, and quadrupedal ornithischians, at tracksites he was taken to by Foulkes, Middleton, and another Broome local, John Martin (Long, 1990; Rich and Vickers-Rich, 2003a). Long (1990:67) published a photograph (taken by Foulkes) of what he regarded to be a likely pentadactyl stegosaurian manual track (republished in Long, 1998:130; Willis and Thomas, 2005:216) (see Fig. 63), along with outlines of some of the other main morphotypes (republished in Long, 1998:127; Scanlon, 2006:fig. 5D). A photograph of what was regarded as a tridactyl stegosaurian pedal track later appeared in Rich and Vickers-Rich (2003a:89), Rich (2007:24), and Kear and Hamilton-Bruce (2011:120) (see Fig. 52). Long (1990) assigned some of the smaller ornithopod tracks that he was shown by Foulkes, Middleton, and Martin to *Wintonopus*, an ichnogenus best known from the Upper Cretaceous portion (Cenomanian–Turonian; Tucker et al., 2013) of the Winton Formation at Lark Quarry, central-western Queensland (Thulborn and Wade, 1979, 1984). Long subsequently enlisted the help of Tony Thulborn and the late Tim Hamley, then at The University of Queensland, both of whom first visited the area with Long in July 1991 as part of the ‘Great Dinosaur Hunt’ (Dayton, 1991; Long, 2002; Rich and Vickers-Rich, 2003a; Willis and Thomas, 2005), footage from which was first aired in on Australian news channels in August 1991, with the completed documentary coming out in 1992 (Beaton, 1992). Thulborn confirmed the earlier identifications made by Foulkes and Long (Long, 1992a, 1998, 2002; Thulborn et al., 1994; Thulborn, 1998; Henderson et al., 2000; Rich and Vickers-Rich, 2003a; Willis and Thomas, 2005), and he also proposed that the quadrupedal ornithischian tracks mentioned in Long (1990, 1992a) were made by a thyreophoran, provisionally identifying them as pertaining to a stegosaurian based on their similarity to schematics of conjectural stegosaurian tracks published in

Thulborn (1990:fig. 6.39) (Thulborn, 1998). Latex casts of some of the purported stegosaurian tracks were made by Long and Thulborn (see Dayton, 1991; Long, 1993; Rich and Vickers-Rich, 2003a), and, with the assistance of the Perth Logistics Battalion of the Australian Army, the boulder containing the pentadactyl manual track and associated tridactyl pedal track was taken back to the Western Australian Museum for further study (Long, 2002:6; see Appendix 2 for further information on this and related events).

Thulborn et al. (1994) provided the first detailed account of the dinosaurian tracksites on the coast north of Broome. Although intended as a preliminary assessment of the sauropod tracks, their study focused primarily on the depositional settings directly associated with the dinosaurian ichnites. Thulborn et al. (1994) found that dinosaurian tracks in the Broome Sandstone occurred in what they regarded as two distinct paleoenvironmental settings: a 'lagoonal/tidal paleoenvironment' and a 'swamp/forest paleoenvironment'. They distinguished each of these paleoenvironmental settings based upon observed differences in sedimentary features, track preservation, and faunal and floral compositions. Confirming the earlier reports of Long (1990, 1992a), Thulborn et al. (1994) identified at least ten different types of dinosaurian tracks, referable to theropod, sauropod, ornithopod, and thyreophoran trackmakers. Only the sauropod tracks were described in any detail, with further information provided in Thulborn (2002). A more exhaustive account of the sauropod tracks and the sedimentary structures associated with them has been provided recently by Thulborn (2012), who indicated that the total number of dinosaurian ichnotaxa present in the Broome Sandstone could be as high as 16.

Thulborn et al. (1994) and Thulborn (2012) found that sauropod tracks were ubiquitous in the Broome Sandstone, documenting them in scattered, disconnected tracksites spread over at least 100 km of coastline from Roebuck Bay north to Minarriny (Coloumb Point). In the sediments described as being representative of a lagoonal/tidal paleoenvironment, Thulborn et al. (1994) found that subcircular, elliptical, or oval-shaped sauropod pedal tracks dominated, ranging in length from 45 to 120 cm and sometimes forming recognizable wide-gauge trackways (sensu Farlow, 1992) characterized by short strides. This size range was later expanded in Thulborn (2002) to include tracks as small as 21 cm in length through to five with a length between 150 and 175 cm. Medium-sized *Megalosauropus*-like theropod tracks and large ornithopod tracks were also recorded in the lagoonal/tidal paleoenvironment, but Thulborn et al. (1994) found these to be much less common than the sauropod tracks. Thulborn et al. (1994:89) and Thulborn (2012) described the tracks in the lagoon/tidal paleoenvironment as being preserved in a highly silicified, thinly bedded, dull yellow to gray-colored siltstone to fine-grained sandstone, with rare plant remains, no obvious signs of macro-invertebrate fossils, and little evidence of invertebrate bioturbation. Thulborn et al. (1994) and later Thulborn (2012) considered many of the sauropod tracks in the lagoonal/tidal paleoenvironment to be transmitted tracks, some forming 'onion ring'-like stacks in the bedding below tracks exposed on the surface, with many indurated by subsequent deposition. Thulborn (2002, 2012) described some of the sauropod trackway sequences in the lagoonal paleoenvironment as broad, zig-zagging channels, often several meters in width, formed where the pressure ridges from successive tracks had coalesced. Rare, steep-walled, and flat-bottomed basins up to 5 m in diameter containing remnants of collapsed sauropod tracks were interpreted by Thulborn (2002, 2012) as having formed as a result of repeated impacts of sauropod feet, liquefying the substrate such that it consequently slumped into gigantic pools or load casts. Despite their abundance, Thulborn et al. (1994) and Thulborn (2012) considered most of the sauropod tracks in their lagoonal/tidal paleoenvironment too indistinct for referral to named or new ichnotaxa.

Tracks attributed to large sauropods were also the most common dinosaurian ichnites in Thulborn et al.'s (1994) swamp/forest paleoenvironment. The tracks of large and small theropods and ornithopods were more common in this paleoenvironment than in the lagoonal/tidal paleoenvironments. Although well preserved, Thulborn et al. (1994) noted that the tracks of quadrupedal ornithischians were much rarer in the swamp/forest paleoenvironment than any of the former three track types. The sediments of the swamp/forest environment were also described as containing significant amounts of plant debris, along with the remains of unidentified cycads and ferns. Although also formed in thinly interbedded siltstone and sandstone, Thulborn et al. (1994) and Thulborn (2012) described the tracks in the swamp/forest environment as deeply impressed, well-delineated natural molds. In places, the substrate is described as having bulged and welled-up around the feet of the trackmakers.

Thulborn et al. (1994:92) described the majority of sauropod tracks in their swamp/forest paleoenvironment as having been made by moderately large animals with a pedal length typically ranging from 45 to 90 cm. They also claimed that there were some larger examples over 100 cm in length, but that these were rare (Thulborn et al., 1994). (It is worth mentioning that the track they show as an example [Thulborn et al., 1994:fig. 3D] is less than 100 cm long.) They suggested that trackways comprising 'kidney-' or 'bean'-shaped pedal tracks with definite marginal notches that were indicative of unguals, and associated with shallow or crescent-shaped manual tracks were probably referable to *Brontopodus* (Farlow et al., 1989). Henderson et al. (2000) and Thulborn (2002, 2009, 2012) have reiterated this assignment. Other sauropod tracks given a brief mention by Thulborn et al. (1994) included what they described as a 'bean'-shaped morphotype with clearly defined notches indicative of digits, with a maximum length of 150 cm (Thulborn et al., 1994:fig. 3D), and unusually long and subrectangular tracks with a well-defined impression of digit I (Thulborn et al., 1994:fig. 4A). (Again, it is worth mentioning that the track shown as an example [Thulborn et al., 1994:fig. 3D] of the former morphotype is not 'bean'-shaped and is only ~97 cm long). Thulborn (2012:fig. 1) provided generalized outlines of some of the sauropod tracks in the Broome Sandstone but gave no further details on their identification other than the assignment of one particular track (Thulborn, 2012:fig. 30) to cf. *Brontopodus*.

Subsequent accounts of dinosaurian tracks in the Broome Sandstone have mostly reiterated the findings of Colbert and Merrilees (1967), Long (1990, 1992a, 1998), Thulborn et al. (1994), and Thulborn (2002, 2009). These include sections of books and general reviews (e.g., Dettmann et al., 1992; Henderson et al., 2000; Weishampel et al., 2004; Scanlon, 2006; Rich, 2007; Kear and Hamilton-Bruce, 2011), popular articles, and media reports. Notes for a field excursion associated with the 7th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics were distributed in 1997 (cited in Thulborn, 1998), but these were not intended to be a proper scientific publication. Unpublished reports on the Broome dinosaurian tracks have also been submitted to the Australian Heritage Council as part of the West Kimberley Heritage Assessment, and aspects of the contents of these reports appears in a Commonwealth of Australia Gazette Notice (2011). Recently, the Western Australian Department of State Development commissioned a series of reports on the paleontological features (including dinosaurian ichnites) of the Walmadany area as part of the Browse Liquefied Natural Gas Precinct Strategic Assessment Report (Environmental Protection Authority, Western Australia, 2012), three of which have been published (Siversson, 2010a, 2010b; McCrea et al., 2012). Contrary to previous accounts (e.g., Long, 1990, 1992a; Thulborn et al., 1994; Long, 1998), Siversson (2010a, 2010b) found minimal evidence for dinosaurian ichnites in the Walmadany area, with the exception of subcircular structures identified as degraded sauropod 'underprints' (transmitted

tracks). McCrea et al. (2012) briefly documented the occurrence of theropod, sauropod, ornithopod, and possible thyreophoran tracks at various sites in the Broome Sandstone along the Dampier Peninsula coastline, including sites in the area around Walmadany that they were taken to by one of us (S.W.S.), confirming the majority of identifications and statements made in earlier studies (e.g., Long, 1990, 1992a; Thulborn et al., 1994; Long, 1998). Further details on the findings of McCrea et al. (2012) are discussed in Systematic Paleoichnology.

### Aim of This Study

The aim of this study was to document and identify as best possible the dinosaurian tracks of the Broome Sandstone in the intertidal zone of the Yanijjarri–Lurujarri section of the Dampier Peninsula, inclusive of Walmadany (James Price Point; Figs. 1, 5), covering approximately 25 km of coastline. This area corresponds to the Dugal–Jajal Buru section of the Song Cycle and northern half of the Lurujarri Heritage Trail (see Bradshaw and Fry, 1989; Benterrak et al., 1996; Anonymous, 1999; Botsman, 2012) and was undertaken at the request of its Traditional Custodians, Goolarabooloo. Despite now being part of the West Kimberley National Heritage List, in recent years this section of coastline has come under considerable threat from extensive industrialization. For this reason, it was deemed imperative that aspects of its rich dinosaurian ichnofauna be fully documented and made public.

For specific information concerning the study area, indigenous place names, documentation and data archiving, terminology, and nomenclatural acts, see Materials and Methods.

**Institutional Abbreviations**—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **MNHM**, Morrison Natural History Museum, Morrison, Colorado, U.S.A.; **NDM**, Nanxiong Dinosaur Museum, Shaoguan, China; **NMV**, Museum Victoria, Melbourne, Australia; **PMA**, Provincial Museum of Alberta, Edmonton, Alberta, Canada; **QM**, Queensland Museum, Brisbane, Australia; **SAM**, South Australian Museum, Adelaide, Australia; **UQ**, The University of Queensland, Brisbane, Australia; **USNM**, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C., U.S.A.; **WAM**, Western Australian Museum, Perth, Australia.

## MATERIALS AND METHODS

### Study Area

The study area covers approximately 25 km of coastline, extending from Dugal (Flat Rock) to just south of Jajal Buru, near Kardilakan (Quondong Point) (Figs. 1, 2). The field work was conducted with the support of Goolarabooloo Traditional Custodians, who directed the activities of the authors when working on or near sites of ceremonial significance to the Song Cycle and its associated traditional law and culture.

Tracksites were delineated arbitrarily as any discrete portion of coastline where there was a concentration of dinosaurian ichnites. As such, tracksites can range from clearly defined, unbroken rock platforms with multiple tracks, trackways, or both, to isolated boulders with single tracks. Oyster-encrusted boulder fields and shallow reefs separate multiple tracksites in areas such as Walmadany (Fig. 5). Given that the majority of tracks in areas such as this appear to derive from a single horizon (see Geological Setting), it is very likely that they were originally part of a single, much larger tracksite, covering an area of several square kilometers, as has also been proposed by Thulborn (2012). For the purposes of this study, we have focused specifically on tracks that could be confidently identified and assigned to particular ichnotaxa and/or track morphotypes, and the designation of tracksites corresponds to areas where this was possible.

Tracksites were given the locality prefix ‘DP’ (Dampier Peninsula) and numbered using Arabic numerals. For each site, individual tracks or trackways are also numbered using Arabic numerals. Within trackways, tracks are numbered from ‘1’ onwards in the direction of travel, with left (‘l’) and right (‘r’) tracks numbered separately. The manual and pedal tracks within quadrupedal trackways are further distinguished with ‘m’ and ‘p’ labels, respectively. In cases where the trackmaker made a double step with one foot without completing the step cycle of the alternate foot, the first track is given the suffix ‘a’ and the second is given ‘b.’ For example, UQL-DP9-2(rp3) denotes the third right pedal track in trackway 2 at The University of Queensland Dampier Peninsula Field Locality 9. The numbering of tracksites does not follow any particular order along the coastline. Information about the location of tracksites and specific tracks and trackways has been lodged with the Goolarabooloo Traditional Custodians.

The Dampier Peninsula coastline is subject to one of the highest tidal ranges anywhere in the world, and many of the tracksites can only be seen for short periods during very low tides. Seasonal cyclone and storm activity can also greatly affect the distribution of sands along this portion of coast, periodically exposing some rock platforms whilst burying others. Most of this study was conducted between July and October 2011 to coincide with large spring tides (0.12–10.31 m). Additional data were collected during February and April 2012 following the 2011–2012 cyclone season, and again during August and November 2012, March 2013, and July 2016 when suitably large tides occurred. In total, our team spent 400+ hours on the reefs, documenting the tracks and local geology. Although every effort was made to locate as many tracksites and tracks in the study area as possible, it is expected that some were not exposed at the time of our surveys. We also know that at least some of the tracksites that we documented in 2011 were buried by shifting sands following the 2011–2012 cyclone season, and it is not known when they will be exposed again (if ever). We also suspect that we were not able to locate all the tracksites and tracks in some areas due to time limitations with the tides and the large expanse of rock over which tracks could occur (e.g., approximately 2.5 km<sup>2</sup> at Walmadany; see Fig. 5).

### Indigenous Place Names

Place names used in this study (Fig. 1) correspond to ethnographic sites on the Lurujarri Heritage Trail and include mythological and ceremonial places (law grounds) relating to the Song Cycle, camping areas of historical significance, and numerous burial sites (modified and updated from those listed in Worms, 1944; Akerman, 1975, 1976; Bradshaw and Fry, 1989). The orthography used in this report follows that recommended by McGregor (1988) and Stokes and McGregor (2003) for the Nyulnyulan languages, unless stated otherwise. The first time a place name is used the non-indigenous equivalent (if one exists) is given in parentheses.

### Lithofacies Analysis

Detailed facies and architectural element analysis was performed following the conceptual framework established by Miall (1977, 1985), Allen and Fielding (2007), Roberts (2007), Tucker (2011), Pearson et al. (2012), and Tucker et al. (in review). For consistency, a uniform set of facies codes was used to describe sedimentary units, and sections were constructed at the decimeter scale in each of the key study areas using a Jacob’s staff, Brunton compass, and handheld Global Positioning System (GPS) unit. Particular emphasis was placed on understanding and correlating important vertebrate trace-fossil localities (‘dinoturbation’ platforms) in each study area. Many horizons were walked out in order to define the horizontal and lateral



FIGURE 5. Walmadany (James Price Point) at mid-low tide (approximately 3 m), looking south towards Kardilakan (Quondong Point). The retreat of the tide exposes reefs of Lower Cretaceous (Valanginian–Barremian) Broome Sandstone. The reef system in the foreground of this photo is approximately 400 m from the edge of the beach. Photograph courtesy and copyright N. Gaunt.

continuity of beds and facies. The following types of field data were collected for each area and section: (1) lithology; (2) the nature of the upper and lower bounding surfaces; (3) external unit geometry and lateral extent (i.e., architectural elements *sensu* Miall, 2014); (4) scale and thickness of units; and (5) sedimentary and biogenic structures. Weathered and unweathered color was recorded using the 2009 Munsell color chart. Lithofacies associations (LFAs) and related architectural elements were recorded for three stratigraphic sections: one for the Yanijarri area (Fig. 9), one for the Walmadany area (Figs. 5, 10), and one for the Kardilakan–Jajal Buru area (Fig. 11).

#### Documentation and Data Archiving

Photographs of tracks were taken using a tripod-mounted digital camera (a Nikon D80 or Nikon Df with a Nikkor AF 24 mm f/2.8D lens), with exposure and shutter speed set manually, illuminated either by natural light or a remotely activated Nikon Speedlight SB-600. Digital elevation models (DEMs) were created using the photogrammetric software Agisoft PhotoScan Professional Edition (version 1.16 build 2038, 64 bit). Ambient occlusion images of the DEMs were created in CloudCompare (version 6.0 Mac OS, 64 bit). Height ramp (i.e., blue to red with cool colors representing the lowermost parts of the track as in Romilio and Salisbury, 2014) and contour (i.e., 1 mm or 1 cm height increments) filters were applied to DEMs using Paraview (version 3.98.0, 64 bit).

Flexible peels (casts) of selected *in situ* tracks (natural molds) were made using Pinkysil (Barnes Products), a two-part molding silicon rubber. Prior to the application of silicon, any obvious cracks or holes in the track were filled with pottery clay. The first two layers of silicon were applied in thin coats to avoid air entrapment, and a brush was used to dab the silicon into all the preserved surface features within and immediately around the track. Subsequent layers were thicker. Layers of loose-woven cotton cloth and hessian were used to reinforce the thicker layers of silicon rubber of larger casts. Peels de-molded in approximately 20 minutes from the time of application. The completed peels are about 3–8 mm thick.

Replicas of the *in situ* tracks were made by imbedding silicon rubber peels face-down in a sand box, with the hollow side up, such that they could retain their natural shape. The shape of tracks was further checked against three-dimensional (3D) digital models. A plaster backing shell was molded onto the back of the silicon cast, using plastic wrap to cover the underlying sand. The plaster extended a few centimeters beyond the silicon rubber cast to add a border. The silicon rubber cast and plaster backing shell were then turned over and cleaned. A plasticine lip (~1 cm deep) was then applied to the plaster around the peel, and any imperfections in the peel or plaster border were filled with plasticine. A spray release was then applied to the exposed plaster and plasticine, but it was not necessary on the silicon rubber cast. Rigid polyurethane resin (either Trowel-On or Easy-cast, both from Barnes Products) was then applied in layers as

two part by equal weight brush on. The first two layers were applied in thin coats to avoid air entrapment, making sure the resin was dabbed on into all cracks and pockets. Subsequent layers were thicker. With larger replicas, a small amount of 20 mm chopped-strand fiberglass was added to the Trowel-On during mixing for the thicker backing coats. The completed polyurethane resin replicas are about 5–10 mm thick. The replica was removed from the peel; plasticine removed; flash on the edges removed with a plaster cutter and smoothed off; and any small bits of the rubber peel removed. All replicas were painted with a thin coat of Langridge Power Pigments mixed with water, water-based glue, and crushed pindan sand (sourced from Broome) to approximate the color of in situ tracks.

The majority of track and trackway parameters were measured in the field using a carpenter's power return tape measure and a 30-m open reel fiberglass tape measure. All tracks were photographed with a scale bar and north arrow aligned to magnetic north using a Brunton Compass (throughout the study area magnetic north is 2.3–2.5° east of true north). For tracks and trackway dimensions that could not be measured directly in the field, measurements were taken in silico using ImageJ (version 1.46r) on single photographs, and using Agisoft Photoscan Pro (version 1.1.6 build 2028, 64 bit) on DEMs, with distances scaled against scale bars or points in the image for which the distance was already known. Other measurements, including divarication angles, digital impression extension lengths, and pace angulation, were also determined in this manner.

Schematic representations of tracks were constructed using contour lines from DEMs, in combination with the examination of in situ tracks, photographs, silicon rubber peels, and rigid polyurethane resin replicas, such that extramorphological features, erosional features, and infilling sediment could be taken into account. Continuous black lines represent the best possible approximation of the internal track outline and features such as the margin of digital pad impressions; black-filled areas represent unguis impressions; faint (gray) dashed lines represent the external track outline and extramorphological features; and black dashed lines represent the crest of displacement rims (see Fig. 19). Minor erosional features, cracks, and infilling sediments (mainly Quaternary beach gravels) that disrupt the track surface are shown in pale gray.

## Terminology

Ichnological terms used in this paper follow definitions adapted from various authors (Leonardi, 1987; Lockley, 1991; Farlow and Chapman, 1997; Belvedere, 2009) and to avoid ambiguity are summarized as follows.

**Trackway Descriptors**—Track surface, the sedimentary surface which a trackmaker traversed; track horizon, the sedimentary horizon in which tracks occur; trackway, a series of two or more successive tracks made by one trackmaker; pace, the distance between two successive tracks made by opposite autopodia (e.g., left and right pedes); stride, the distance between two consecutive tracks made by the same autopodium (e.g., consecutive left pedal tracks); track rotation, the angle between the trackway midline and the principal axis of a track; trackway gauge, the width between left and right tracks relative to the trackway midline; narrow gauge, tracks close to, or intersecting the trackway midline; wide gauge, tracks distant to the trackway midline; ipsilateral, occurring on the same side relative to a trackway midline; contralateral, occurring on opposite sides of the trackway midline; couplet (Fig. 6B), paired and sequential footfalls of a quadrupedal trackmaker that in combination represent one manual and one pedal track—both from the same side (i.e., ipsilateral); heteropody, the difference in size (as a percentage) of the manual track relative to the pedal track of a quadrupedal trackmaker. High heteropody indicates that the manual track is small relative to the pedal track, and vice

versa for low heteropody. Whereas prior expressions of heteropody were typically reported as estimates of the manual to pedal track length ratio (such as '1:3'; e.g., Lockley et al., 1994a; Marty et al., 2010), here we derive heteropody values more precisely using the software ImageJ and report them as a unit-less percentage. We bin heteropody of sauropod track couplets as mild (manual to pedal track area  $\geq 40\%$ ), medium (30–40%), pronounced (20–30%), and exaggerated ( $< 20\%$ ); interautopodial distance, the distance between manual and pedal tracks within couplets made by quadrupedal trackmakers; glenoacetabular distance, the distance between the shoulder and hip joints (see Fig. 6C for how this can be estimated for a quadrupedal trackmaker from a trackway); ichnofauna, the faunal diversity represented by track diversity.

Within a trackway comprising at least three ipsilateral tracks made by a quadruped, two different arrangements of couplets are possible (Fig. 6B). The first is where a manual track is positioned cranial to a pedal track on the same side of the trackway, herein referred to as coupled manual and pedal tracks (MP couplet). This arrangement is the more typical style in which pairs of pedal and manual tracks in isolation are depicted (Lockley et al., 1994a; e.g., Wright, 2005). The second type is where a pedal track occurs cranial to a manual track, herein referred to as paired pedal and manual tracks (PM couplet). It is important to note that different couplet arrangements are merely portions of a trackway, and that our notation is intended to aid in the more precise description of isolated couplets.

**Track and Trackway Measurements**—Track and trackway measurements are based primarily on those used by Nouri et al. (2011): De, digital impression extension;  $I^{\wedge}II^{\wedge}III^{\wedge}IV^{\wedge}V^{\wedge}$ , digital impression divarications; L, track length; Pa, pace length; SL, stride length; W, track width (Fig. 6A).

Tracks were categorized into size classes modified from Marty (2008), using either track length (L) or width (W) (Table 1). Theropod and ornithopod pedal tracks were classified as either small ( $10 < L < 20$  cm), medium ( $20 < L < 30$  cm), large ( $30 < L < 50$  cm), or very large ( $L > 50$  cm). Similar categories were used for thyreophoran tracks: small ( $W < 10$  cm), medium ( $10 < W < 20$  cm), large ( $20 < W < 35$  cm), or very large ( $W > 35$  cm). Pedal tracks formed by sauropod trackmakers were classified as either small ( $L < 55$  cm), medium ( $55 < L < 80$  cm), large ( $80 < L < 110$  cm), or very large ( $L > 110$  cm).

**Estimations of Likely Trackmaker Hip Height and Body Size**—We estimated conservative body sizes of trackmakers based either on a prederived hip height (most cases) or on the glenoacetabular length (sauropods). For theropod and many ornithopod tracks, the calculation of trackmaker hip height (acetabulum height [h]) is based on formulae developed by Alexander (1976):  $h = 4 \times$  pedal track length for bipedal trackmakers. For ornithopod tracks that lack a metatarsodigital pad impression (e.g., *Wintonopus latomorum*)—necessary for use in Alexander's (1976) equation—we modified Alexander's (1976) equation using data for *Hadrosauropodus* ichnospp. as given in Vila et al. (2013b:fig. 7 and supplementary information). For this type of subunguligrade ornithopod trackmaker,  $h = 5$  ( $4.6\text{--}5.3$  [ $n = 15$ ; mean = 4.9])  $\times$  length of the digital portion of the pedal track.

Estimates of body size and hip heights of sauropod trackmakers are based on the glenoacetabular distance of the ichnotopotype trackway of *Oobardjidama foulkesi*, ichnogen. et ichnosp. nov.—the only in-study sauropod trackway reported herein—rather than on published ratios of hip height to pedal track length, which have varied from 4.0 to 5.9 (Alexander, 1976; Thulborn, 1989; Gonzalez Riga, 2011). In early sauropodomorphs, the glenoacetabular length typically exceeds osteological hip height, and although these two lengths converge in later sauropods (e.g., Paul, 2010), hip height rarely exceeds glenoacetabular distance.

Thus, glenoacetabular length, measured directly from trackways with at least three pairs of sequential ipsilateral couplets

TABLE 1. Track and trackmaker size categories for dinosaurian ichnites of the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone at Yanijarri, Walmadany, and Kardilakan–Jajal Buru, the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Trackmaker type	Size	Pedal track size, lower length (cm)	Pedal track size, upper length (cm)	Trackmaker hip height (lower–upper) (cm)	
		Length (L)	Length (L)	Hip height ( $4.0 \times L$ )	
Theropod	Small	—	<20	<80	
	Medium	>20	30	80–120	
	Large	>30	—	>120	
		Length (L)	Length (L)	Hip height ( $3.1 \times L$ )	
Sauropod	Small	—	<55	<170.5	
	Medium	>55	80	170.5–248	
	Large	>80	110	248–341	
	Very large	>110	—	>341	
		Length (L)	Length (L)	Hip height ( $4.0 \times L$ )	Hip height ( $5.0 \times L$ )
Ornithopod	Small	—	<20	<80	>100
	Medium	>20	30	80–120	100–150
	Large	>30	50	120–200	200–250
	Very large	>50	—	>200	>250
		Width (W)	Width (W)	Hip height ( $6.0 \times W$ )	
Thyreophoran	Medium	>10	20	60–120	
	Large	>20	35	120–210	
	Very large	>35	—	>210	

(Fig. 6C), is subject to less variation within trackways than measurements of ‘reverse-extrapolated’ hip heights (i.e., calculated from pedal track length), being based on a greater measured proportion of a trackway to commence with. Conversely, ‘reverse-extrapolated’ hip heights from tracks assume an osteological pes height based on tracks, but which ignore the likely posture of the sauropod pes (specifically, the angle of the metatarsus relative to the horizontal) and an amount of unquantifiable soft tissue both around and under the pedal plantar region, as well as within the tarsometatarsal joint. These parameters obviously partly determine the hip height of a moving animal. As an example, in a near-complete specimen of *Camarasaurus*, SMA 002 (Tschopp et al., 2015), we formulated minimum pes length as a proportion of osteological hip height as being 4.8 or 5.7, with metatarsal postures of 30° and 45° to the horizontal, respectively. Additionally, an osteological pes of a given length may produce tracks of varying lengths that marginally exceed this ‘base’ osteological length, depending on numerous factors too difficult to quantify simplistically (e.g., behavior, substrate, soft tissues). This is corroborated by the typical variation in pedal track lengths in well-preserved sauropod trackways (e.g., Farlow et al., 1989; González Riga and Calvo, 2009; Xing et al., 2015f), which would in turn produce a variety of reverse-extrapolated hip height estimates if using a uniform hip height to track length ratio.

In the topotype trackway of *Oobardjidama foulkesi* (see Fig. 25), the only two measureable glenoacetabular lengths were 2.38 m (within the quadrangle of impressions formed by lp3-rp2 +rm2-lm2; see Fig. 6C for calculation of glenoacetabular distance) and 2.15 m (within the quadrangle of impressions formed by rp2-lp2 + lm2-rm1). The difference between these two measurements is approximately 10%. Using the distance calculated from the first set of landmarks, because it is based on better-preserved tracks in the sequence, we make an assumption that maximum hip height in the trackmaker was 2.38 m. This yields a hip height to pedal track length ratio of 3.35 for the best-preserved pedal track (rp2, 71 cm), and a range 3.05–3.10 for the other pedal tracks in the trackway sequence. Although rp2 more clearly shows morphological details that are characteristic of *Oobardjidama* (see Systematic Paleoichnology), its caudal margin is not well defined, making the determination of its exact length difficult. The next best-preserved pedal track in the trackway is rp1. This track has a well-defined rim around the heel

region and a clearly demarcated TL of 77 cm. Using rp1 as a proxy for pedal track TL results in the trackmaker conveying pedal impressions that are 1/3.1 of its hip height (2.38 m). Notably, this ratio is specific to the track-forming conditions at the topotype locality when the tracks were made.

In choosing to standardize all inferred sauropod trackmaker sizes to maximum hip height =  $3.1 \times$  pes length (or pedal track length), we acknowledge that these extrapolations are based on few data points but find it preferable to use an existing in-study metric as a comparative reference (glenoacetabular distance) rather than a hip height ratio derived from unspecified external track data (e.g., Alexander, 1976) or based on an assumption (e.g., Thulborn, 1989:42). Although González Riga (2011) presented a rigorous method for estimating hip height in the trackmaker of the Upper Cretaceous *Titanopodus*, the resulting ratio of  $h = 4.58 \times$  pes length (based on the hindlimb skeleton of a latest Cretaceous titanosaur) still produces estimated hip heights that are fractionally less than the glenoacetabular lengths in the *Titanopodus* trackways.

The nearly matching dimensions of the measurable glenoacetabular distance and the inferred hip height for *Titanopodus* implies that hip height to foot length ratios are more specific to the taxon of trackmaker, with a single ratio likely to be inapplicable for all sauropods. Indeed, given that pronounced heteropody was an aspect of the original diagnosis of *Titanopodus* (González Riga and Calvo, 2009), it cannot be known if this heteropody is exclusively a reflection of the trackmaker bearing an unusually reduced pes length compared with other sauropod trackmakers. Such a putative trait would result in a higher hip height to foot length ratio that would be inapplicable to other taxa. Additionally, if *Titanopodus* was made by a derived lithostrotian titanosaur—as seems probable—some body proportion ratios and parameters taken from trackways might be reflective of a derived titanosaurian bauplan, subtly distinct from antecedent sauropod trackmakers. In an ideal scenario where different sauropod track morphotypes in the Broome Sandstone were each represented by trackways, we would seek to apply separate glenoacetabular measurements to infer trackmaker body size specific to each trackway.

In the estimation of thyreophoran trackmaker size, we employed the hip height formula devised by Cobos et al. (2010):  $h = 6 \times$  pedal track width. Where only a manual impression is present, as is the case for Broome thyreophoran morphotypes A

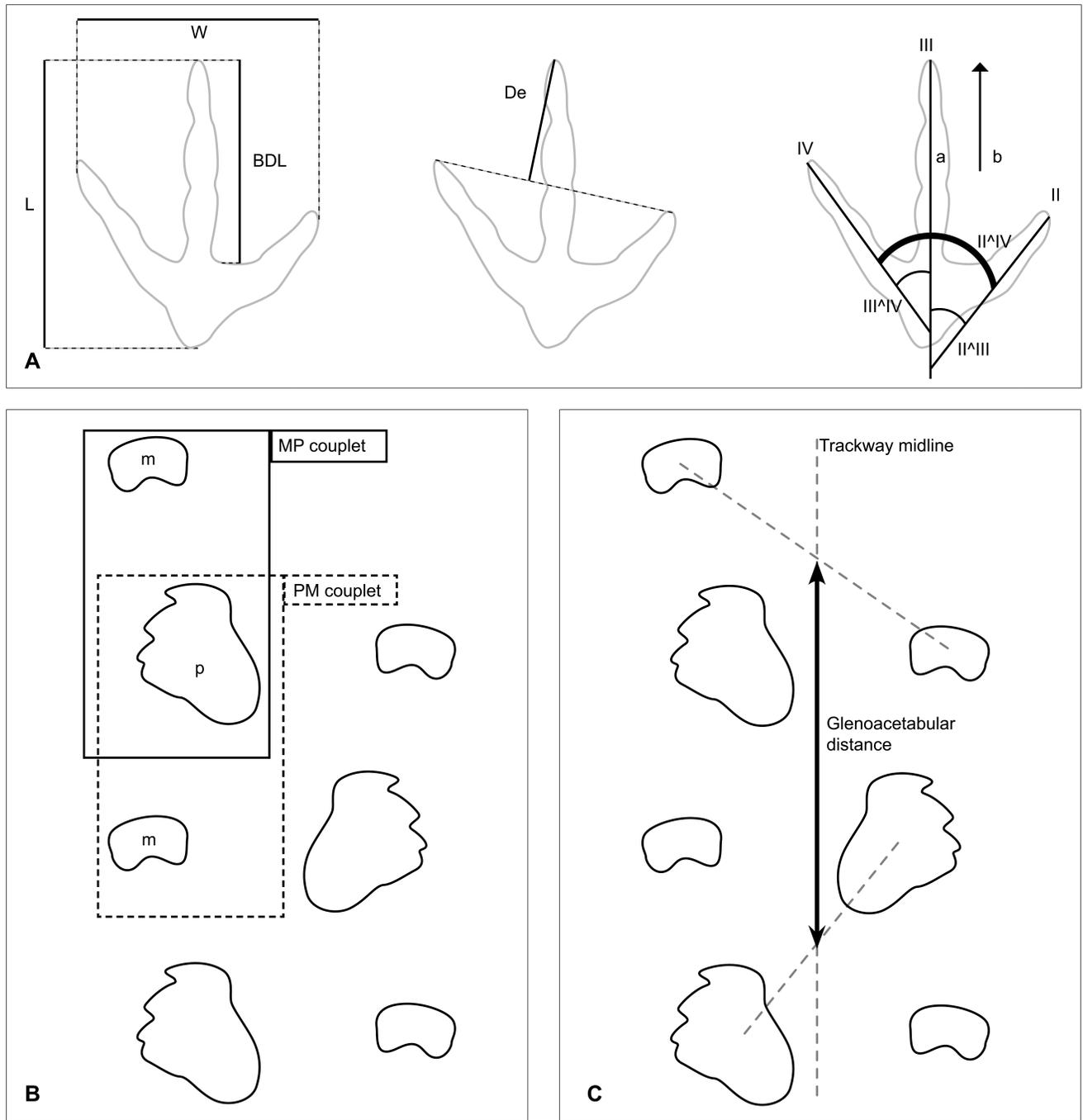


FIGURE 6. Measurements, parameters, and terminology associated with **A**, tridactyl tracks (track outline modified from Fig. 19); and **B**, segments of quadrupedal trackways. Coupled manual and pedal tracks (**MP couplet**) are those in which the manual track is positioned cranially relative to the pedal track in a normal tracking sequence, whereas coupled pedal and manual tracks (**PM couplet**) is where the pedal track is situated cranially to the manual track; **C**, illustration showing the calculation of the glenoacetabular distance from quadrupedal trackways. The midpoint between contralateral left and right manual impressions corresponds to a fixed cranial locus (mid-glenoid region), which is constrained in position relative to the moving limbs of an animal. Similarly, a fixed caudal locus (taken from the midpoint of contralateral left and right pedal impressions) corresponds to the acetabular region. Theoretically, the distance between the two loci along the trackway midline should correspond to the sagittal length of the animal's torso and ought not to vary greatly during locomotory progression—this distance equals the glenoacetabular distance. **Abbreviations:** **a**, axis of the digital impression (in this case for the axis of the impression of digit III); **b**, direction of principal track axis; **BDL**, basal digital impression length (in this case for the impression of digit III); **De**, digital impression extension;  $\text{II}^{\wedge}\text{III}$ , divarication angle between impressions of digits II and III;  $\text{III}^{\wedge}\text{IV}$ , divarication angle between impressions of digits III and IV;  $\text{II}^{\wedge}\text{IV}$ , total divarication angle; **L**, track length; **m** (or **M**), manual track; **p** (or **P**), pedal track; **W**, track width.

(Fig. 53) and B (Fig. 54), and in the absence of existing manual track formula or a possible candidate taxon, we inferred trackmaker size by scaling the glenoacetabular measurements from trackways assigned to ‘Tunasniyoj’ ichnotaxon B (Apesteguía and Gallina, 2011:fig. 2G) and ‘Tunasniyoj’ ichnotaxon C (Apesteguía and Gallina, 2011:fig. 4C). The manual impressions for both of the latter Bolivian ichnotaxa strongly resemble those assigned to Broome thyreophoran morphotypes A and B, respectively (although we note that the Broome morphotype is much larger than Tunasniyoj ichnotaxon B, with a width of 29 cm compared with 5–6 cm). Changes to the glenoacetabular distance due to differences in the possible ontogenetic stage of the trackmaker would likely be different between taxa and represent an important consideration to size scaling should an appropriate candidate be determined in the future. Until such time, the linear scaling employed here is used as a tentative guide to estimate the hip height of the Broome thyreophoran morphotype A and B trackmakers.

**Trackmaker Speed and Gait Estimates**—Hip height estimations for trackmakers were used in conjunction with Alexander’s (1976) equation  $speed \cong 0.25\sqrt{g} \times SL^{1.67} \times h^{-1.17} \cong 0.7826 \times SL^{1.67} \times h^{-1.17}$ .

## GEOLOGICAL SETTING

### Regional Tectonics

All the dinosaurian tracks described herein occur in the Broome Sandstone, a Lower Cretaceous unit within the Canning Basin of northwestern Western Australia. The Canning Basin sits atop the Archean Kimberley Block, covering a total area of 640,000 km<sup>2</sup>, with 530,000 km<sup>2</sup> of this onshore. The basin is divided into two northwest–southeast-trending troughs, separated by a mid-basin arch. This divide is thought to have developed in the early Paleozoic as an intracratonic sag between the Precambrian Pilbara and Kimberley basins (Smith, 1968; Plumb, 1979; Tapley, 1988; Drummond et al., 1991; Kennard et al., 1994; Haines and Wingate, 2007).

The stratigraphy within the Canning Basin extends from the Lower Ordovician through to the Holocene, with a depositional history that is interpreted as complex and multi-phased (Forman and Wales, 1981; Brown et al., 1984; Kennard et al., 1994; Haines and Wingate, 2007). The Paleozoic history of the Canning Basin includes the Ordovician Gogo reef complex, the Devonian/Carboniferous opening of the Fitzroy Graben, and the expansive Lower Permian glacial deposits. During the Mesozoic, through

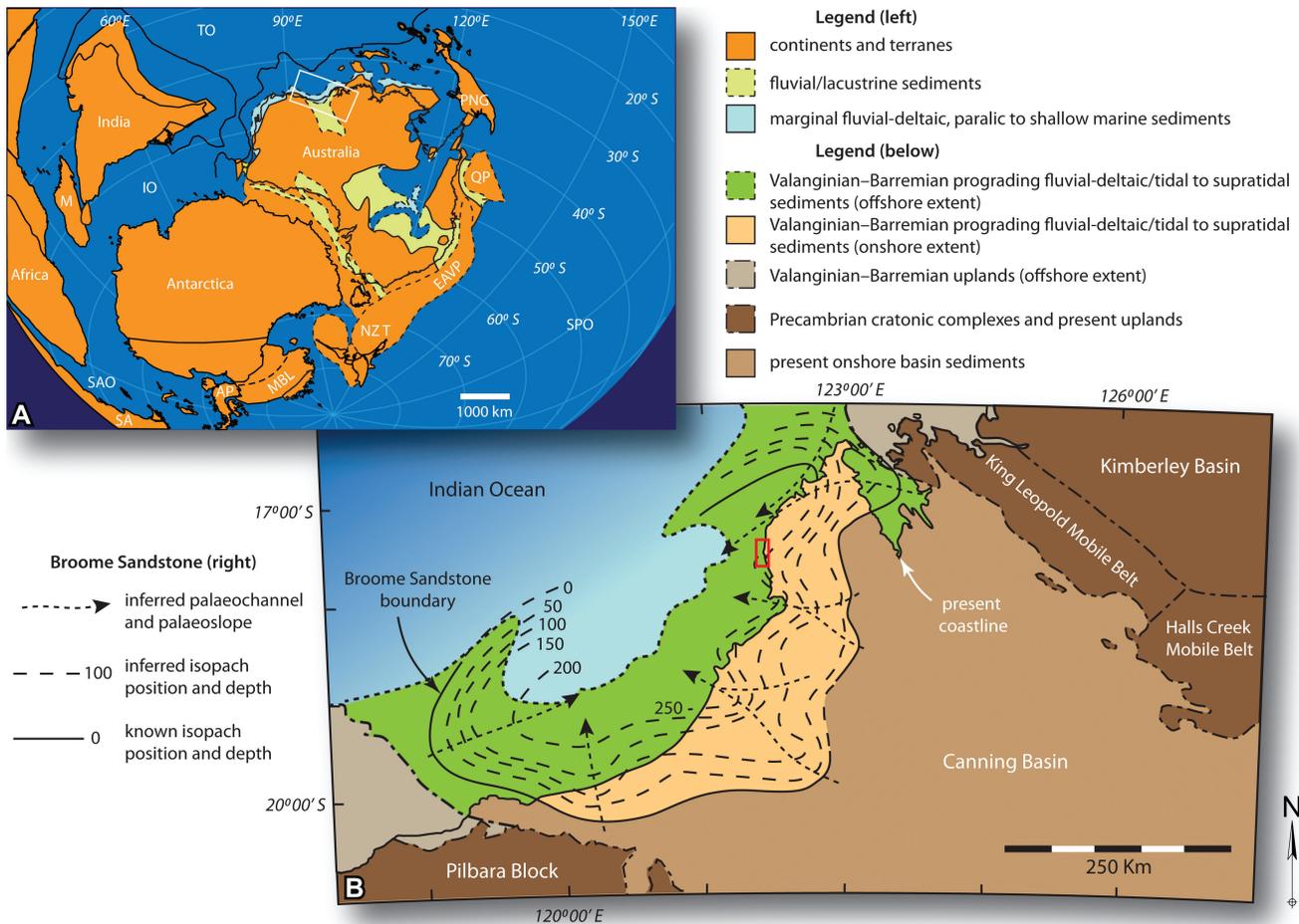


FIGURE 7. **A**, paleogeographic reconstruction of east Gondwana during the Early Cretaceous (~130 Ma) showing syndepositional basins within the Australian continental margins and the location of the west Kimberley–Pilbara portion of the Canning Basin (white box) (following Bradshaw et al., 1988; Dettmann et al., 1992; Bryan et al., 1997; Wanderes and Bradshaw, 2005; Muller et al., 2012). **B**, outcrop, subsurface extent, and inferred paleochannel directions of the Broome Sandstone relative to study area (red box) and surrounding regional geology (adapted from McWhae et al., 1956; Thom, 1975; Forman and Wales, 1981). **AP**, Antarctic Peninsula; **EAVP**, Eastern Australian Volcanic Province; **IO**, Indian Ocean; **M**, Madagascar; **MBL**, Marie Byrd Land; **NZT**, New Zealand Terrain; **PNG**, Papua New Guinea; **QP**, Queensland Plateau; **SA**, South America; **SAO**, southern Atlantic Ocean; **SPO**, southern Pacific Ocean; **TO**, Tethys Ocean.

much of Jurassic and into Early Cretaceous, the Canning Basin was covered by shallow marine shelves and marginal continental platforms that formed the eastern margin of the expanding rift system between Australia and India-Madagascar (Veevers and Wells, 1961; Veevers, 1967; Playford et al., 1975; Leslie et al., 1976; Plumb, 1979; Forman and Wales, 1981) (Fig. 7).

### Broome Sandstone

The Broome Sandstone forms a portion of the eighth depositional cycle within the Canning Basin, emplaced during three cycles of transgression and regression (Interval 8 of Forman and Wales, 1981). The base of the Broome Sandstone disconformably overlies the Upper Jurassic–Lower Cretaceous (Tithonian–Berriasian) sediments of the Baleine Formation and the Jarlemai Siltstone (Brunnschweiler, 1957; Yeates et al., 1984; Nicoll et al., 2009; Smith et al., 2013). Overlying the Broome Sandstone are the clastic sediments of the Lower Cretaceous (Aptian) Parla Formation and the Melligo, Frazier, and Leveque sandstones (Brunnschweiler, 1957; Veevers and Wells, 1961; Forman and

Wales, 1981), and the Upper Cretaceous–Neogene Emeriau Sandstone (Veevers and Wells, 1961; Forman and Wales, 1981) (Fig. 8).

Pervasive northwest–southeast-trending fault systems divide the Canning Basin into several subunits, greatly reducing the surficial exposure of many units. As a result, exposure of the Broome Sandstone is limited to the Broome Platform, the Jurgurra Terrace, and the Fitzroy Trough (Haines and Wingate, 2007). Onshore exposures of the Broome Sandstone are limited to discontinuous shore platforms and low rocky cliffs spread over approximately 200 km of the western coastline of the Dampier Peninsula, from Roebuck Bay north to Cape Leveque (Fig. 1) (Brunnschweiler, 1957). Exposures of Broome Sandstone along the coast rarely exceed a thickness of 11–15 m (during low tide). Boreholes, however, show that the preserved portion of the Broome Sandstone is at least 274 m thick (McWhae et al., 1956; Veevers and Wells, 1961; Playford et al., 1975; Forman and Wales, 1981; Gibson, 1983; Yeates et al., 1984; Haines, 2011). Paleogene–Quaternary coastal deposits also often unconformably overlay the more landward portions of the Broome Sandstone. These units typically include calcareous silts and silty sands (fluvial-estuarine deposits), consolidated and sometimes cross-bedded fine- to medium-grained calcareous sandstones (consolidated dune deposits), and coarsely sorted shell-rich breccias cemented with calcium carbonate to form calcarenites that dip towards the sea at low angles (beach deposits) (Brunnschweiler, 1957; Semeniuk, 2008; Nicoll et al., 2009; McCrea et al., 2012; Smith et al., 2013). Some of these Paleogene–Quaternary coastal deposits may be equivalent to the Pleistocene Tamala Limestone from the southwestern coast of Western Australia (see Lipar and Webb, 2014). In many parts of the Dampier Peninsula, the Broome Sandstone and the Palaeogene–Quaternary coastal deposits are also unconformably overlain by Quaternary–Recent red ‘pindan’ soils, which are primarily of aeolian and alluvial origin.

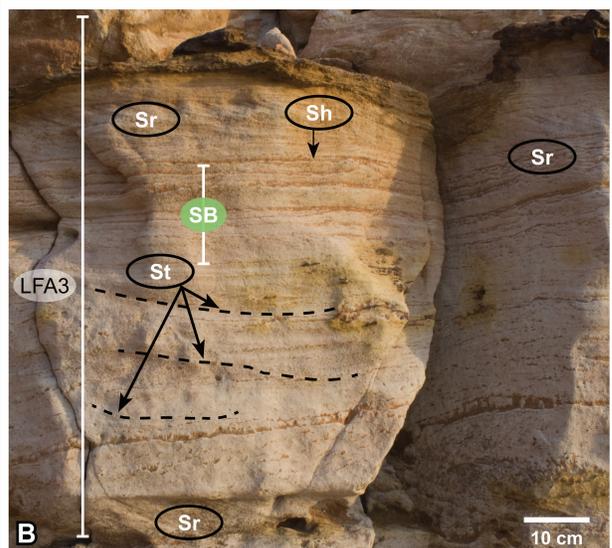
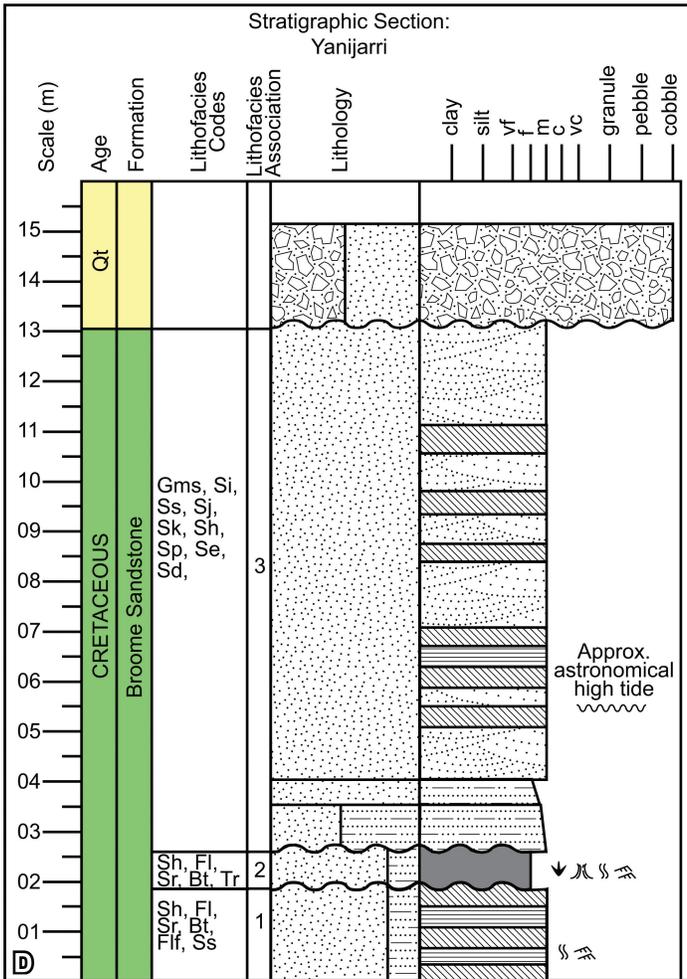
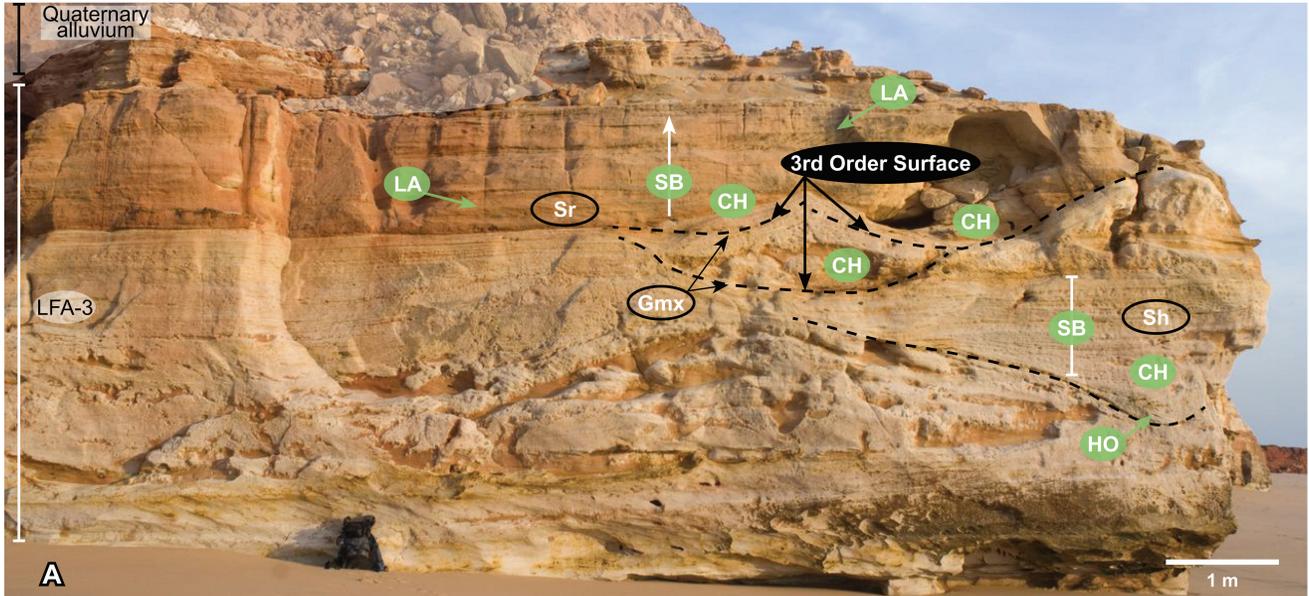
The Broome Sandstone is typically defined as alternating sequences of coarse-grained to fine micaceous sandstones, subordinate interbedded siltstones, conglomerates, and poorly preserved soil horizons, deposited in marginal coastal plain settings, typified by a series of prograding deltas (McWhae et al., 1956; Brunnschweiler, 1957; Veevers and Wells, 1961; Playford et al., 1975; Forman and Wales, 1981). Early studies of vertebrate ichnites (dinosaurian tracks) by Thulborn et al. (1994) indicated that these traces were emplaced and preserved within ‘lagoonal/tidal paleoenvironment’ and ‘swamp/forest paleoenvironment.’ Henderson et al. (2000) and Thulborn (2012) refined this interpretation to encompass a broader suite of paleoenvironments, spanning coastal plains, streams and channels, estuaries, deltas, and swamps, with ephemeral lakes and patches of forest.

In addition to dinosaurian tracks, the ichnofauna of the Broome Sandstone also comprises invertebrate trails and burrows with meniscate fillings (Brunnschweiler, 1957; Thulborn et al., 1994). Body fossils include arenaceous foraminiferans, microplankton, meiospores (Towner and Gibson, 1983), and rare bivalves (Yeates et al., 1984). Marine bivalves have been reported from outcrops exposed at or near Cape Leveque (Brunnschweiler, 1957; McCrea et al., 2012). Bennettitaleans, pteridosperms, and araucarian and podocarpacean conifers dominate the rich and diverse plant macrofossil assemblage. Other plant macrofossils include lycophytes, ferns, and pentoxylaleans (White, 1961; McLoughlin, 1996). Overall, the flora is thought to be indicative of fern-dominated coastal marshes and stream border communities, and *Ptilophyllum* swamp forests (Forman and Wales, 1981). McLoughlin (1996) suggested that the abundance of bennettitaleans was indicative of a relatively warm, but seasonal climate.

**Age**—Historically, a lack of marine invertebrate biostratigraphic indices and minimal palynological data (Balme, 1963)

Stage	Australian Dionocyst Zonation (HMP 2006)	Spore-Pollen Zonation SE Standard (HMP 2006)	Broome Platform (Includes Barbwire Terrace)
Early Cretaceous	A	<i>Diconodinium davidii</i>	Frazier Sandstone
			Parda Formation
	B	<i>Muderongia australis</i>	Melligo Sandstone
			Broome Sandstone
	H	<i>Muderongia testudinaria</i>	
	V	<i>Senoniasphaera tabulata</i>	
			Mowla Sst
	B	<i>Systematophora areolata</i>	
			<i>Ruffordiaspora australiensis</i>
<i>Egmontodinium tornyum</i>			
<i>Batioladinium lobispinosum</i>			
	<i>Cassiculosphaeridia delicata</i>		
<i>Kalyptea wisemaniae</i>			
	Late Jurassic	T	<i>Pseudoceratium iehiense</i>
<i>Retitriletes watheroensis</i>			
		<i>Dingodinium jurassicum</i>	
			<i>Omatia montgomeryi</i>
K		<i>Cribroperidinium perforans</i>	
	<i>Murospora florida</i>		

FIGURE 8. Jurassic–Early Cretaceous lithostratigraphic units in the Canning Basin, northwestern Western Australia, with ages and correlated stages following Smith et al. (2013). The Broome Sandstone can be constrained to the *Egmontodinium tornyum*–*Muderongia australis* Australian Dionocyst Zone (HMP 2006; Partridge, 2006) and the *Ruffordiaspora australiensis*–*Foraminisporis wonthaggiensis* Spore-Pollen Zone (SE Standard) (HMP 2006; Partridge, 2006), thereby making it middle Valanginian to middle Barremian (140–127 Ma; based on Gradstein et al., 2012).



- Legend**
- siltstone
  - sheet flood
  - plant remains
  - tracks/tracks
  - conglomerate
  - planar cross bedding
  - dewatering structures
  - sandstone
  - trough cross bedding
  - ripples
  - minor bioturbation
  - root traces
  - horizontal planar lamination

has meant that the age of the Broome Sandstone could only be broadly constrained. Initial phytostratigraphic assessments of the flora indicated an Upper Jurassic–Lower Cretaceous age (White, 1961). A review of the macrofossils by McLoughlin (1996) showed that the flora could be correlated with Douglas' (1969) *Ptilophyllum-Pachypteris austropapillosa* Zone (Zone B) of Victoria (the *Phyllopteroides laevis* Zone of Cantrill and Webb, 1987), thereby indicating a Neocomian–Barremian age (i.e., Berriasian–Barremian). Nicoll et al. (2009) and more recently Smith et al. (2013) further constrained the Broome Sandstone to the *Egmontodinium torynum–Mudergonia australis* Australian Dinocyst Zone and the *Ruffordiaspora australiensis–Foraminisporis wonthaggiensis* Spore-Pollen Zone (SE Standard), thereby making it mid-Valanginian to mid-Barremian (140 to ~127 Ma; Walker and Gradstein et al., 2012), a determination that is followed here (Fig. 8).

**Source**—From at least the Early Jurassic through to the present, the Kimberley Block has formed an enduring highland region to the northeast of the Canning Basin (Playford et al., 1975; Bradshaw et al., 1988) (Fig. 7B). The Kimberley Block forms the northern margin of Canning Basin and is therefore the most likely principal source of basin sediment (Yeates et al., 1984). The pre-Phanerozoic (1800–2000 Ma) King Leopold Mobile Belt (KLMB) to the northeast and west and the Halls Creek Mobile Belt (HCMB) to the west and southwest of the study area form the western margin of the Kimberley Block (Thom, 1975; Fig. 7B). The closest source for granitic and metamorphic lithics in some of the Broome Sandstone samples examined is likely to be the King Leopold Mobile Belt, ~160 km to the northeast of the study area, whereas the farthest source is the southwestern corner of the HCMB, ~500 km from the study area. Early and late granite intrusions, metamorphics, and other volcanics (welded ash flows, tuffs, and acid lavas) were formed in each of these two Mobile Belts (Thom, 1975). Thus, the closest highland source rocks during the Early Cretaceous is likely to have been the KLMB to the northeast of the Broome Sandstone.

## LITHOFACIES ANALYSIS

Detailed analysis of coastal exposures of the Broome Sandstone in the Yanijarri–Lurujarri section of the Dampier Peninsula revealed 16 repeated facies types that occurred in three distinctive lithofacies associations (LFAs) (Tables 1 and 2). Descriptions of the three LFAs and interpretations of their corresponding depositional environments are presented below and in Table 2. Following the approach and codes of Miall (1977, 1985, 2014), architectural elements were identified within each LFA based on their geometry, associated facies, and scale (Table 3).

All the strata in the study area are essentially flat lying with no appreciable dip except for localized uneven to undulating terrain (Figs. 16, 39D, 48A, B) interpreted here as the original land surface, along with sediment deformation associated with extensive bioturbation caused by heavy dinosaurian traffic (Figs. 9A, B, 15D, E) (also see Thulborn, 2012). The exposed sequence has been greatly eroded by surf action. As a result, the stratigraphically lowest units are more seaward. Dinosaurian ichnites typically occur in horizons within lithofacies association 2 (LFA-2),

many of which are laterally continuous over large areas (100–1000+ m<sup>2</sup>).

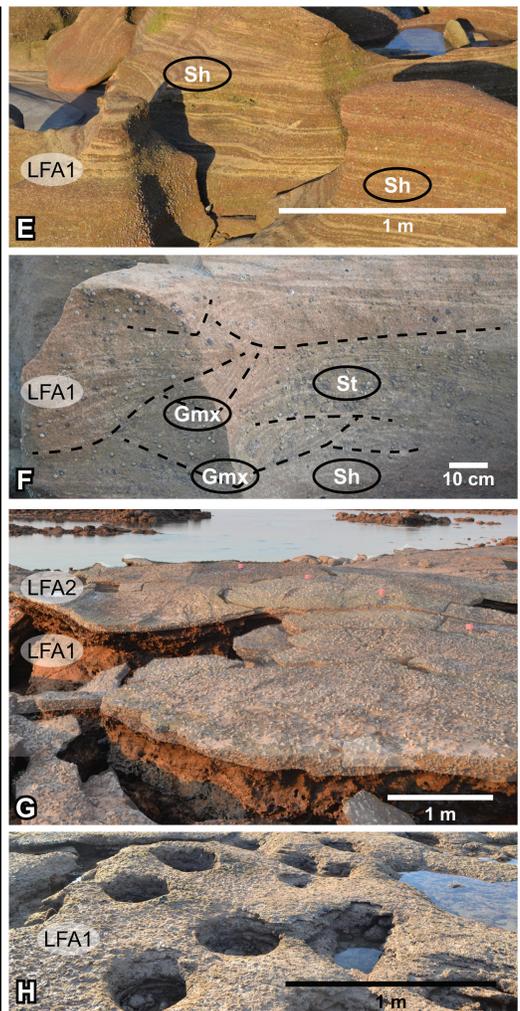
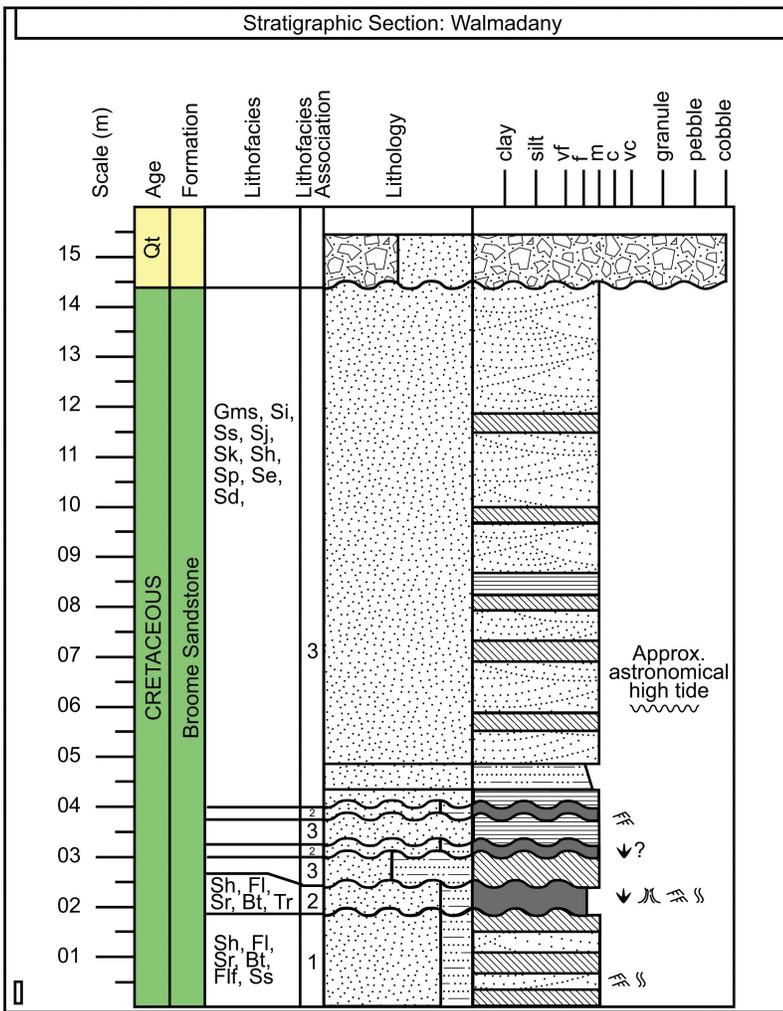
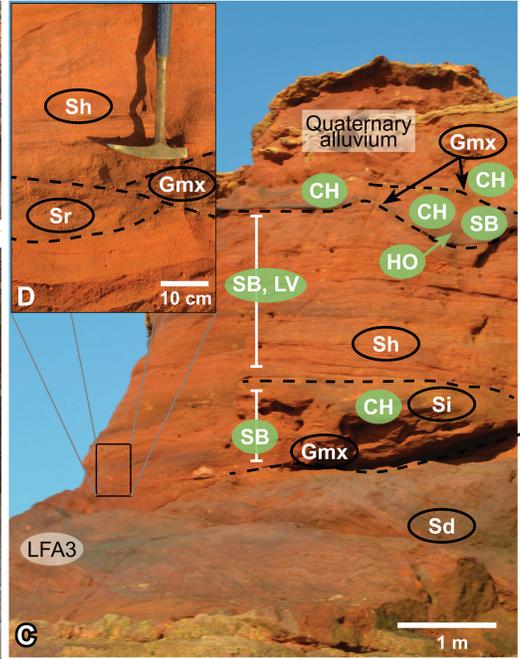
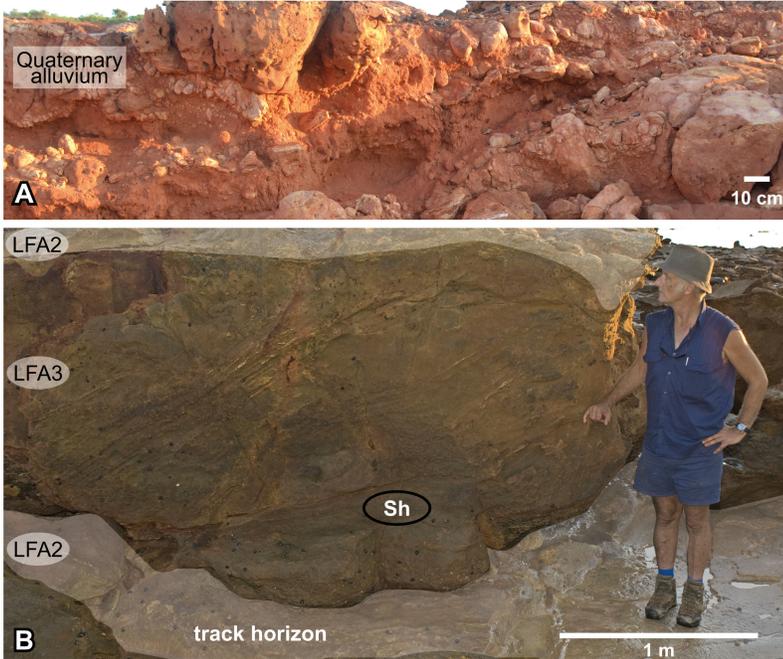
### Lithofacies Association 1 (LFA-1)

**Description**—Observations of LFA-1 are limited both by tide levels and by outcrop quality. Exposures typically comprise a thick, single unit that tapers into the underlying bedrock of the coastal platform. LFA-1 includes the following facies (in descending order of appearance): Sh, Sp, Ss, Se, Fl, Flf, and Sr (see Table 2). In heavily weathered sections, it occurs as a thinly interbedded sandstone and fine-grained siltstone (Sh, Sp, Se, Fl, Flf), with colors that range from light olive green (5GY 3/2) to very pale orange (10YR 8/2). Where exposures of LFA-1 are in close proximity to the overlying 'pindan' soils or Quaternary alluvium (Figs. 10A, 11D), they are often stained dark red (blood red, 10R 3/4). Unweathered sections are generally light gray (N9) to white (N8).

The uppermost sandstones of LFA-1 have a sharp and erosive contact (3rd–4th order) with the overlying LFA-2 (Fig. 9C). The lower bounding surfaces cannot be observed, being either submerged or, where exposed, covered in littoral zone invertebrates. Preserved structures in LFA-1 at Walmadany (Fig. 5) are best seen in rock platforms along the most seaward part of the reef system. These include Sh, Ss, Se, Fl, Flf, and Sr (Fig. 10E, F). These exposures often contain numerous, randomly positioned potholes, ranging in size from 10 to 150 cm in diameter (Fig. 10H; also see Siversson, 2010a:fig. 1, 2010b:fig. 5), and the architectural elements are difficult to determine. Sedimentary structures in outcrops of LFA-1 around Kardilakan–Jajal Buru are somewhat better preserved and include plain bed ripples (upper flow regime), 3rd-order scour marks, and very poorly preserved lenticular cross-bedding (Fig. 11B), along with similar sedimentary structures to those identified at Walmadany. Other sedimentary structures identified in sections of LFA-1 at Yanijarri and Kardilakan–Jajal Buru include asymmetric and symmetric ripple marks (Fig. 14A, B), along with very distinctive dewatering structures that range from convoluted laminae to poorly preserved flame structures (Fig. 9C; large and small scale; Fl and Sr). In many locations, the uppermost contact of LFA-1 is distorted due to localized vertical dewatering (Figs. 11A, 14C, D). These water escape features typically occur as raised, crater-like structures with a diameter of approximately 1–2 m, adjacent to or interspersed among large sauropod (Fig. 14C) and ornithopod (Fig. 14D) tracks or heavily trampled sauropod thoroughfares (see Figs. 11A, 15A, B) similar to those described by Thulborn (2002, 2012). Smaller (mm)-scale dewatering structures (convolute lamina flames) are also apparent in laminations at or just below the erosive contact between LFA-1 and LFA-2 (Fig. 9C). We interpret the majority of these dewatering structures to have formed as a result of compaction of the water-laden sediment, and in some instances this compaction may have been caused by the passage of heavy dinosaurs.

Generally, LFA-1 is dominantly characterized by quartz-rich, thick- to medium-bedded sandstones, consisting of medium-sized, moderately sorted, subangular to subrounded grains, exposed in a succession of overlying sandstone units. The lowermost outcropping bed(s) consists of a well-cemented, fine to coarse quartzarenite to subquartzarenite, with the best exposures at Walmadany (arenite Ss to sub-arenite; Qt 90–88%, L 10–12%:

←FIGURE 9. Lithofacies associations and architectural elements identified within the uppermost Broome Sandstone in the Yanijarri area of the Dampier Peninsula, Western Australia (see Fig. 1): **A**, uppermost exposed section of Broome Sandstone (LFA-3), capped by Quaternary alluvium; **B**, examples of sandy planar to ripple cross-lamination commonly observed within LFA-3; **C**, commonly observed 3rd-order surface between LFA-1 and LFA-2, with co-occurring dewatering structures preserved; **D**, lithostratigraphic illustration detailing the commonly occurring vertical profile observed in outcrop in the Yanijarri area. **Symbols: white oval/black text**, lithofacies association; **dashed black line**, bounding surface; **green oval/white text**, fluvial architectural element; **black circle/white text**, bounding surface order. See Tables 2, 3, and 4 for facies codes and architectural elements.



Qm 80% and Qp 30% [undulous to patchy extinctions; minor 1–2% possible microcrystalline quartz]; L 10–12%: chert 8–12% and heavy minerals 2–4%) (Fig. 13). Grains commonly exhibit minor embayments, contact suturing, and clay rims to marginal inclusions, with both secondary calcium cement and meniscus hematite. Grains are well to moderately rounded (larger grains seem to exhibit more rounding—several exhibit minor grain dissolution—than smaller grains and matrix), and for the most part it is well to moderately sorted. Secondary infill of cements (chert/calcite) and matrix (rock fragments) indicates that this unit was likely porous during deposition and shortly thereafter.

Isolated, poorly preserved evidence of invertebrate bioturbation (vertical and horizontal) was observed in exposures of LFA-1. Although some of the siltstones within this lithofacies do not fit the classic definition of a paleosol, they have characteristics (e.g., carbonate mud nodules) that are similar to the ‘soil horizons’ in ‘Unit C’ of Page (1998) from the type section at Minyirr (Gantheaume Point) (McWhae et al., 1956) and could be classified as a very poorly developed paleosol *sensu* Mack et al. (1993). Other poorly preserved types of bioturbation include *Ophiomorpha* (minor pellet development, vertical and horizontal criss-crossing of tube structures).

**Interpretation**—Lithofacies Association 1 is interpreted as having been deposited within a distal fluvial to distal and proximal delta portion of a prograding braid plain. The localized uneven to undulating topography associated with intertidal exposures of this lithofacies association (and overlying LFA-2) is interpreted as the original land surface, being an association of sand- to silt-dominated sand lobes with interlaced channels that discharged into the delta mouth under daily tidal influence. These lobes vary from rounded nulls to narrow and elongate ridge-like structures. Alternately, these ‘lobes’ could be interpreted as hummocky bedding (swale topography); however, these units distinctly lack muds (settling fines) characteristic of prodelta/delta front settings, which typically occur below the wave base. Furthermore, LFA-1 does not preserve any characteristics that would be associated with storm-like deposits. The distribution of these lobe structures and sedimentological characteristics with co-occurring moderate tidal influences are similar to that of a sandy fluvial- to tidal-dominated ‘Mahakam’ delta (more proximal to the alluvial delta plain). This idea is supported by the identification of large interference, ladderback, asymmetrical, and symmetrical ripples, and scour marks (Fig. 14A, B), all of which in association suggest that this area was influenced by tidal change and may have experienced minor beach or shore development in part. The identification of bioturbation structures (*Ophiomorpha*), which commonly occur in marginal sandy shore facies, between semi-consolidated substrates and the sublittoral zone (see Boggs, 2011), further supports the interpretation of LFA-1 as part of a prograding braid plain.

### Lithofacies Association 2 (LFA-2)

**Description**—LFA-2 comprises interbedded siltstones and sandstones, many of which have been subsequently silicified to form laterally continuous sheet-like horizons in many parts of the study area (Fl, Sh). Facies that were identified include Fl, Sh, Sp, Gmx, and Sr. Exposures of LFA-2 are best exhibited at Walmadany (Fig. 5). In weathered sections, LFA-2 ranges from light pink (5RP 8/2), to yellowish gray (5Y 8/1), pale red (10R 6/2),

and light gray (5G 7/4). Unweathered sections are generally light gray (N7). At Walmadany and Kardalikan–Jajal Buru, at least three of these horizons (multistory) were identified, indicating a repeated event (Figs. 10B, I, 11F).

LFA-2 commonly consists of a well-cemented, fine to coarse quartzarenite at Kardalikan to lithic sandstone at Walmadany (arenite Ss: Qt 97%, L 3; lithic Ss: Qm 82%, L 18%) (Fig. 13). The grains in LFA-2 are generally characterized by polycrystalline and monocrystalline recycled quartz grains (>97% of the total population). Individual grains are subangular to subrounded with minor inclusions, overgrowths, dissolution, and suturing present (Fig. 12). The dominant secondary cement is diagenetic iron or calcite.

The sandstone bed(s) range in thickness from ~15 to 50 cm (in agreement with similar beds described by Thulborn et al. (1994) and Thulborn (2012)). The sandstone sheets (Fl, Sh) are typically laterally extensive in all directions (e.g., approximately 2.5 km<sup>2</sup> in the case of Walmadany; Fig. 5) but are highly variable in terms of outcrop quality. Stratigraphically, platforms of LFA-2 can be readily correlated along the coastline for several kilometers (±2.5 km). Architecturally, LFA-2 is identified as LS, or a very extensive, laminated sand/silt sheet (blanket) (Miall, 1985) (Table 4). In some cases, the basal 3rd–4th-order surfaces of LFA-2 preserve rip-up clasts (Gmx); however, observable occurrences are directly related to outcrop quality. Preserved upper contacts are also rare, but if present they are identified as 3rd order. Ripple marks in LFA-2 were identified throughout the study area and included ladderback, interference, asymmetrical, and symmetrical ripples, ranging in scale from large to small and generally with an east–west-trending orientation (Sr).

Structurally, LFA-1 and LFA-2 together form a subtly uneven to undulating topography, augmented in parts by extensive ‘dinoturbation,’ principally caused by sauropods (Fig. 15; also see Thulborn, 2012). These surfaces range from flat lying, to undulating, to sloping, with a relative level variation of up to 1.2 m. A number of tracksites in the study area preserve evidence of dinosaurs that have had to negotiate this topography, with their feet causing the ejection of substrate on the down-slope side of the flanks of gently sloping ridges (Fig. 16A, B). In other areas, the trackways of single or multiple individuals traverse what was otherwise a smooth surface (Fig. 39D). The preservation of dinosaurian ichnites in LFA-2 is similar at all tracksites in the study area, varying primarily in terms of their density, the extent to which the sediments have been silicified, and the degree to which tracks are exposed or eroded. Manual and pedal impressions of upward of 20 distinct track types (see Systematic Paleoichnology) occur within LFA-2, many preserved as deep, detailed natural molds. Associated with some track-bearing surfaces in LFA-2 are well-preserved asymmetrical and symmetrical ripple marks and invertebrate trace fossils assignable to *Ophiomorpha*, *Planolites* (Fig. 17C) and *Skolithos* (Fig. 17D); similar structures are also apparent at Minyirr (Thulborn et al., 1994). In areas where the underlying planar cross-bedded sandstones of LFA-1 are not eroded, the most seaward exposures of LFA-2 are often littered with corals, oysters, and other littoral zone invertebrates, such that the better-preserved dinosaurian tracks and trace fossils are usually encountered closer to shore.

The impressions of complete and sometimes matted fronds of the bennettitalean *Ptilophyllum cutchense* are abundant in some

←FIGURE 10. Lithofacies associations and architectural elements identified within the Broome Sandstone in the Walmadany area of the Dampier Peninsula, Western Australia (see Fig. 1). **A**, capping (overlying) Quaternary conglomerates and ‘pindan’ soil horizons; **B**, multiple horizons of LFA-2, separated by horizontally laminated medium-grained sandstones of LFA-3, indicative of planar bed flow; Nigel Clarke for scale; **C**, co-occurring facies codes and architectural elements occurring within exposures of upper Broome Sandstone (LFA-3), with **D**, small-scale ripple cross-lamination to planar lamination identified; **E**, LFA-1 showing planar lamination with commonly co-occurring dewatering structures; **F**, LFA-1 showing ripple cross-lamination to small-scale trough cross-bedding with basal scour (granular) surfaces; **H**, LFA-1 with pervasive pothole weathering; **I**, lithostratigraphic illustration detailing the commonly occurring vertical profile observed in outcrops in the Walmadany area. See Figure 9 for explanations of symbols and Tables 2, 3, and 4 for facies codes and architectural elements.

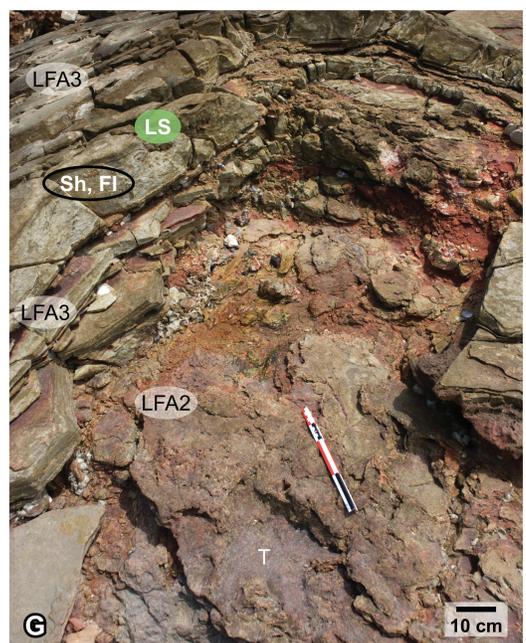
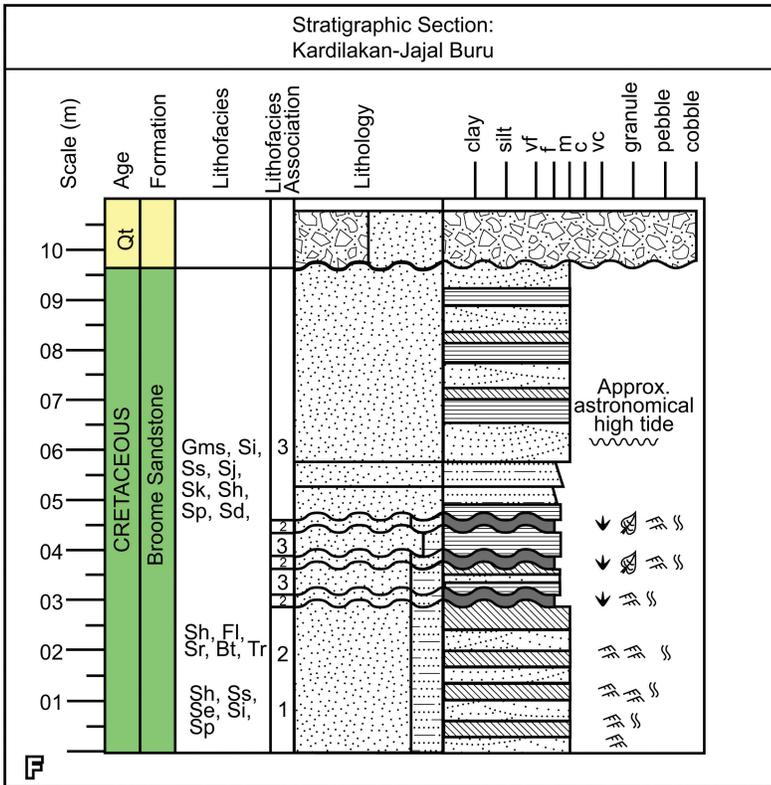
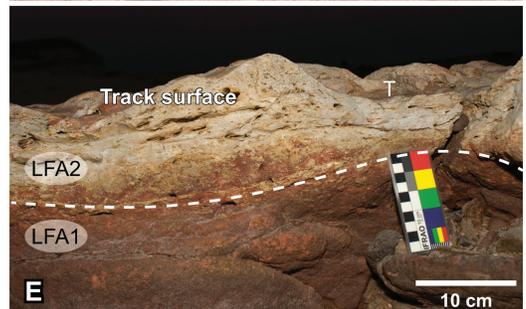
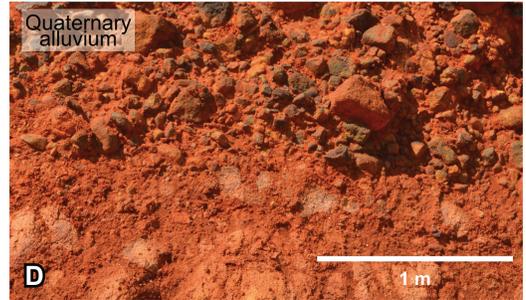
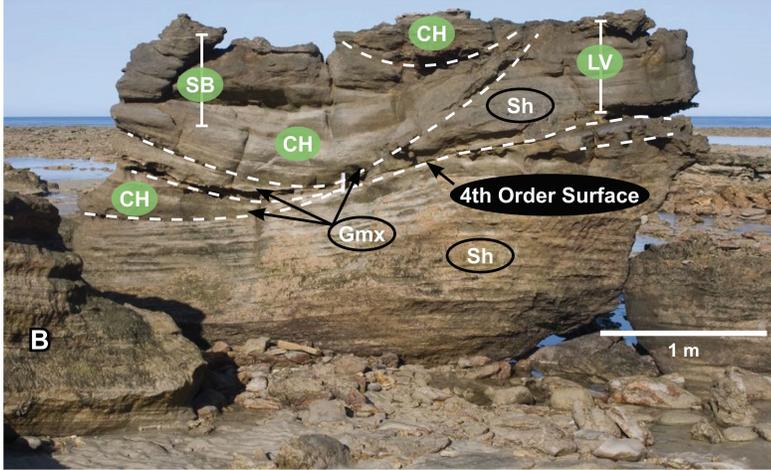
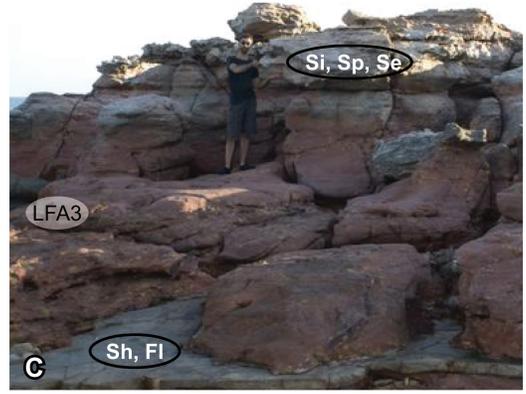


TABLE 2. Facies codes, lithofacies, sedimentary structures, and their associated interpretation in exposures of the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone at Yanijarri, Walmadany, and Kardilakan–Jajal Buru, the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Facies code	Lithofacies	Sedimentary structures	Interpretation
Gmm	Massive, matrix supported gravel	No grading	Alluvium
Gmx	Thin-lamina, matrix-supported gravel	Grading—erosional surface interlaminated conglomerate	Debris flow deposits—fine scale
Sm	Sand, very coarse, maybe pebbly	Massive bedded	Gravity flow
Sp	Sand, very coarse, maybe pebbly	Grouped planar cross-beds	Transverse bar (lower flow regime)
Sr	Sand, very fine to coarse	Ripple marks of all types	Lower flow regime ripples
Sh	Sand, very fine to very coarse, maybe pebbly	Horizontal lamination, parting or streaming lamination	Planar bed flow (laminar flow with minor upper flow possible)
Si	Sand, fine	Low-angle (<10°) cross-bedded	Scour fills, crevasse splays, antidunes
Ss	Sand, fine to coarse, maybe pebbly	Broad, shallow scours including eta cross-stratification	Scour fills
Se	Erosional scours with intraclasts	Crude cross-bedding	Scour fills
St	Sand, fine to very coarse, rare pebble inclusions	Solitary (theta) or grouped (pi) trough cross-beds	Dunes (lower flow regime)
Sd	Sand-silt with minor pebble inclusions	Cosets of low-angle (10–20°) tabular cross-bedding	Stacked channel fills
Fl	Sand, silt, mud	Fine lamination	Overbank or waning flood deposits
Flf	Sand, silt, mud, and fossils	Massive bedded	Overbank or waning flood deposits
Fm	Mud, silt	Massive, desiccation cracks	Overbank or drape deposits
Fsc	Silt, mud	Laminated to massive	Backswamp deposits
P	Paleosol	Pedogenic features (primitive)	Soil (primitive)

After Miall (2010).

TABLE 3. Lithofacies associations identified in exposures of the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone at Yanijarri, Walmadany, and Kardilakan–Jajal Buru, the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Lithofacies association	Facies code																Sediment size	Arch. elements	Bounding surfaces	Unweathered (UW) and weathered (W) color	Fossils	Interpretation of depositional environment
	Gmm	Gmx	Sm	Sp	Sr	Sh	Si	Ss	Se	St	Sd	Fl	Flf	Fm	p							
LFA-1																	vcL-fl (1000–125 μ)	CH, SB	4th–3rd	(UW) N9–N8 (W) 5GY(3/2), 10YR(8/2), 10R(3/4)	Y	Sediment-laden braid plain; distal fluvial to proximal deltaic
LFA-2																	mU-fl (350–177 μ)	LS	4th–3rd	(UW) N7 (W) 5RP(8/2), 5Y(8/1), 10R(6/2), 5G(7/4)	Y	Laterally expansive sheet flood
LFA-3																	vcL-mL (1000–250 μ)	CH, LA, HO, SB, LV, CS	4th–3rd	(UW) N7, N6 (W) 10YR(8/2), 10R(3/4), 10R(2/2), 10YR(8/6)	Y	Braid plain fluvial and alluvial (channel and adjacent to channel)

After Miall (2010), with sediment size classifications following Douglas (1968). See Table 2 for facies codes and Table 4 for explanation of symbols for architectural elements.

←FIGURE 11. Lithofacies associations and architectural elements identified within the Broome Sandstone in the Kardalakan–Jajal Buru area, Dampier Peninsula, Western Australia (see Fig. 1). **A**, Nigel Clarke examines a heavily (sauropod) trampled surface of sheet flooded sediments of LFA-2 (white overlay), overlain with horizontally laminated and medium- to fine-grained sandstones of LFA-3; **B**, weathered exposure (isolated outcrop) of LFA-3, exhibiting horizontally laminated sands (LV, Sh) incised by 3rd-order surface and channel-fill medium-grained sandstone (CH); **C**, Dr. Anthony Romilio in the uppermost exposed portion of LFA-3 at Kardalakan; **D**, Quaternary alluvium (polymictic paraconglomerate) cover overlying the uppermost Broome Sandstone (LFA-3); **E**, commonly observed contact between LFA-1 and track-bearing horizons of LFA-2, normally with co-occurring bioturbation or floral traces (see Fig. 17E, F); **F**, lithostratigraphic illustration detailing the commonly occurring vertical profile observed in outcrop in the Kardalakan–Jajal Buru area; **G**, onion-skin weathering of LFA-3, directly overlying a poorly exposed LFA-2 preserving an isolated right pedal track of *Megalosauropus broomensis* (UQL-DP45-10; Fig. 20F, G). See Figure 9 for explanations of symbols and Tables 2, 3, and 4 for facies codes and architectural elements.

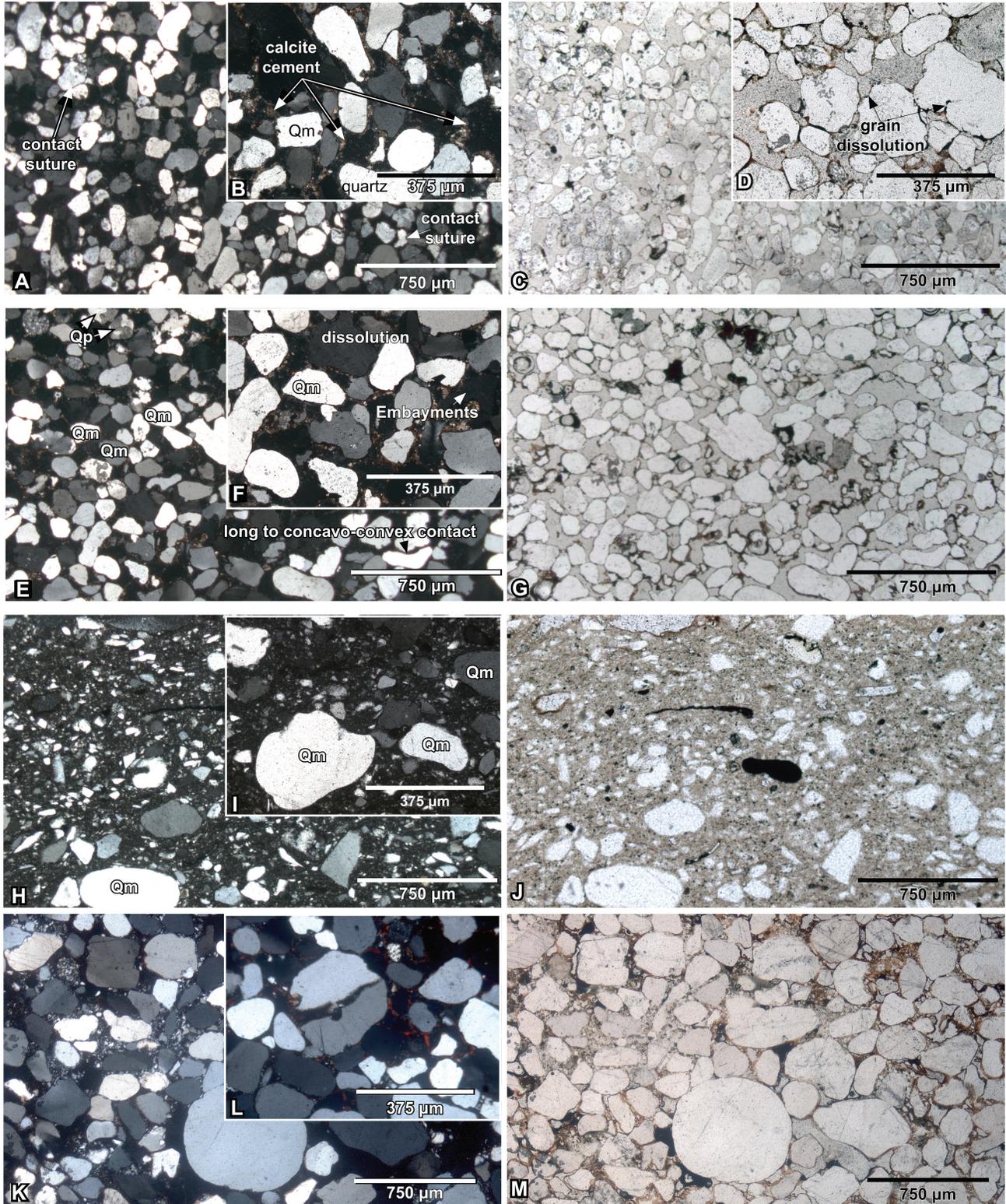


FIGURE 12. Petrographic thin-sections for representative horizons within each of the main lithofacies associations identified in exposures of the Broome Sandstone in the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Images display both cross-polarized (left column) and plane-polarized (right column) lights. **A, B, C, D**, uppermost exposed portions of LFA-3; **E, F, G**, lower-uppermost exposed portions of LFA-2; **H, I, J**, trackway horizon of LFA-2; **K, L, M**, uppermost part of LFA-1, directly beneath the track-bearing horizon of **H–J**. Abbreviations: **Qm**, monocrystalline quartz; **Qp**, polycrystalline quartz.

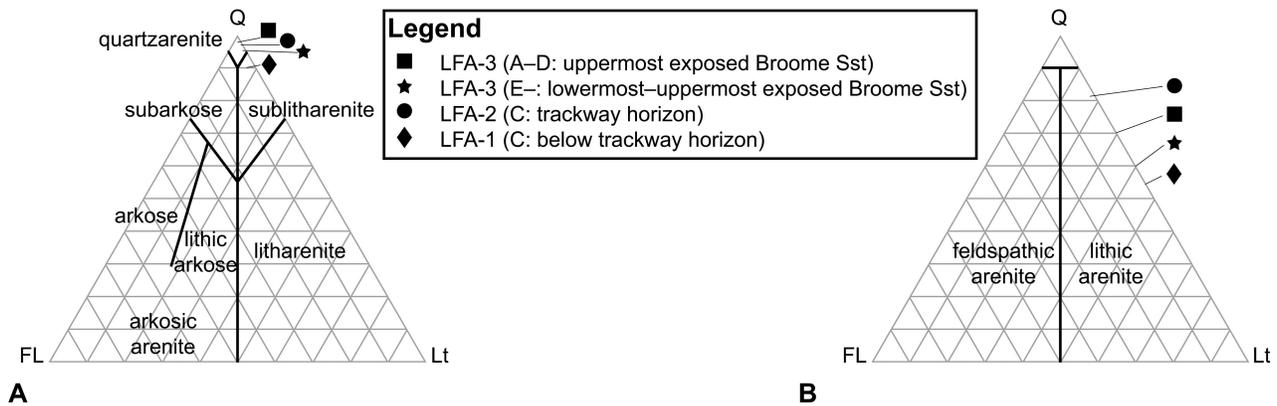


FIGURE 13. Classification of hand samples of representative Broome Sandstone lithofacies (see Fig. 12), based on the schemes of Folk et al. (1970) and Boggs (2009). All four samples plot between a sublitharenite and quartzite or lithic arenite. Point count data and sandstone classification for the Broome Sandstone is based on the 500-point count methodology of Gazzi-Dickinson (Ingersoll et al., 1984).

of the silicified track-bearing horizons of LFA-2 (Fig. 17E, F). Numerous and randomly oriented holes (ranging in diameter from 1 to 100 mm) also penetrate these horizons, which in places impart a vesicular appearance to the rock. In most instances, these holes appear consistent with voids left by plant stems, rather than invertebrate bioturbation features, which are typically infilled. The fact that the holes occur in the same horizons that also preserve numerous stem and frond impressions of *P. cutchense* supports this idea.

**Interpretation**—LFA-2 is interpreted as a thick sheet flood that extended outward from the distal fluvial braid plain to the proximal delta (delta plain), uniformly blanketing large areas in sediment. It should be noted that due to the undulating terrain, one would expect variability in the overall thickness of this flooding sediment, but due to erosion and lack of exposure in some areas the complete impact of these inferred flooding events is difficult to observe. We interpret the uneven topography of LFA-2 to be a direct result of the underlying topography associated with the depositional setting created by LFA-1: an actively migrating and uneven distal braid plain to proximal deltaic terrain, with sandy bar forms (SB) interlaced with active channels (CH). During the deposition of LFA-2, a sand sheet (of series of sand sheets) (LS) blanketed this topography. Inundation could have been either fluvial, such as flooding of the distributary channels, marine, from wave surges or tidal highs, or from excessive precipitation in the surrounding area farther upstream in the drainage basin. As water levels receded, sediment within and directly

adjacent to the still active channels was reworked by tidal and wave action.

The depth of some of the dinosaurian tracks that occur in LFA-2, combined with the nature of the upwellings around the larger tracks and the subsequent retention of the natural molds, suggests that the ground was boggy when dinosaurs traversed it, and that the sediment was sufficiently moist, cohesive, and plastic to retain and preserve tracks. If the sediment had been too water-laden, more slumping of the track margins would have occurred. At some tracksites, however, surfaces of LFA-2 lateral to heavily dinoturbated boggy ground appear to have been more resilient to penetration, despite still appearing to have been trampled by numerous dinosaurs. This suggests that the degree to which sediments were saturated was locally variable (SB or CH), that the water retaining capacity of the sediments was not homogenous, or that the depth of the water table and degree to which it kept the sediment moist was variable. Other bioturbation in LFA-2 includes *Orphiomorpha*, *Planolites*, and *Skolithos*, which commonly occur in marginal sandy shore facies, supporting the interpretation of this lithofacies association as a tidally influenced braid plain, post-sheet-flooding event. ‘Dinoturbation’ of LFA-2 at some tracksites appears to have caused little deformation of the tube-like plant stem voids within, suggesting that fresh plant debris was present at time the tracks were made. The ‘vesicular’ appearance of these beds very likely resulted from the inclusion of the plant debris within the sediment at the time of burial.

TABLE 4. Architectural elements (lithosomes) identified in exposures of the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone at Yanijjarri, Walmadany, and Kardilakan–Jajal Buru, Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Element	Symbol	Facies	Geometry and relationship
Channels	CH	Any combination	Sheet, concave-up erosional base, commonly bounded by 3rd–5th-order surfaces
Sandy bed forms	SB	St, Sp, Sh, Sl, Sr, Se, Ss	Lens, blanket, wedge, occurs as channel fills, crevasse splays, minor bars
Lateral-accretion macroform	LA	St, Sp, Sh, Sl, Se, Ss, Sr	Wedge, sheet; characterized by internal lateral accretion, 3rd–5th-order surfaces, flat-based erosion surface
Scour hollows	HO	St, Sl, Sr	Scoop-shaped hollow with asymmetric fill
Laminated sand sheet	LS	Sh, Sl, Sp, Sr	Laterally continuous sheets, blankets
Levee	LV	Fl, P, IvB, C, PB, Flf, Fm	Overbank flooding with pedogenic and soil development
Crevasse splay	CS	St, Sr, Fl, Gmx	Delta-like progradation from channel into adjacent floodplain

Modified from Miall (2010, 2014).



FIGURE 14. Examples of associated sedimentary structures within the Broome Sandstone in the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. **A**, ladderback ripples within outcrop of LFA-1, with two near subequal directions; **B**, interference ripples within outcrop of LFA-1, with one strong direction and two minor orientations; **C**, water escape structure (WES) in LFA-2 at UQL-DP9; **D**, Goolarabooloo Maja Richard Hunter alongside the topotype right pedal track of *Walmadanyichnus hunteri* (UQL-DP11-5) and a large water escape structure that perforates the uppermost part of LFA-1 and the track horizon of LFA-2. Numerous other *W. hunteri* tracks occur on this platform close to the raised water escape structure.

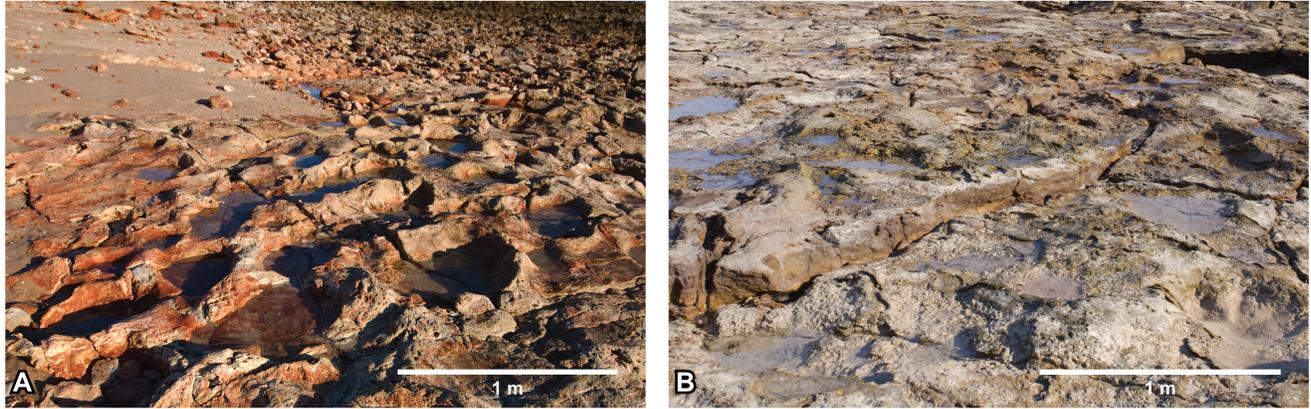


FIGURE 15. Exposures of LFA-2 preserving evidence of heavy ‘dinturbation.’ **A**, UQL-DP30, showing a likely sauropod thoroughfare; **B**, UQL-DP9, showing partly eroded tracks of large ornithopods and sauropods.



FIGURE 16. Examples of tracksites preserving evidence of dinosaurs that have had to negotiate the gently undulating topography of LFA-1 and LFA-2. **A**, Dr. Steve Salisbury with his right foot on one of several horizontally emplaced sauropod tracks (UQL-DP9-10) that traverse a gently sloping surface. The dinosaur’s feet have caused the ejection of substrate on the down-slope side of the slope; **B**, a second sauropod trackway (UQL-DP9-10) traversing a similar sloping surface at the same tracksite. The track in the foreground is approximately 70 cm long. **Abbreviation: T**, track. Photograph **A** courtesy and copyright Damian Kelly.

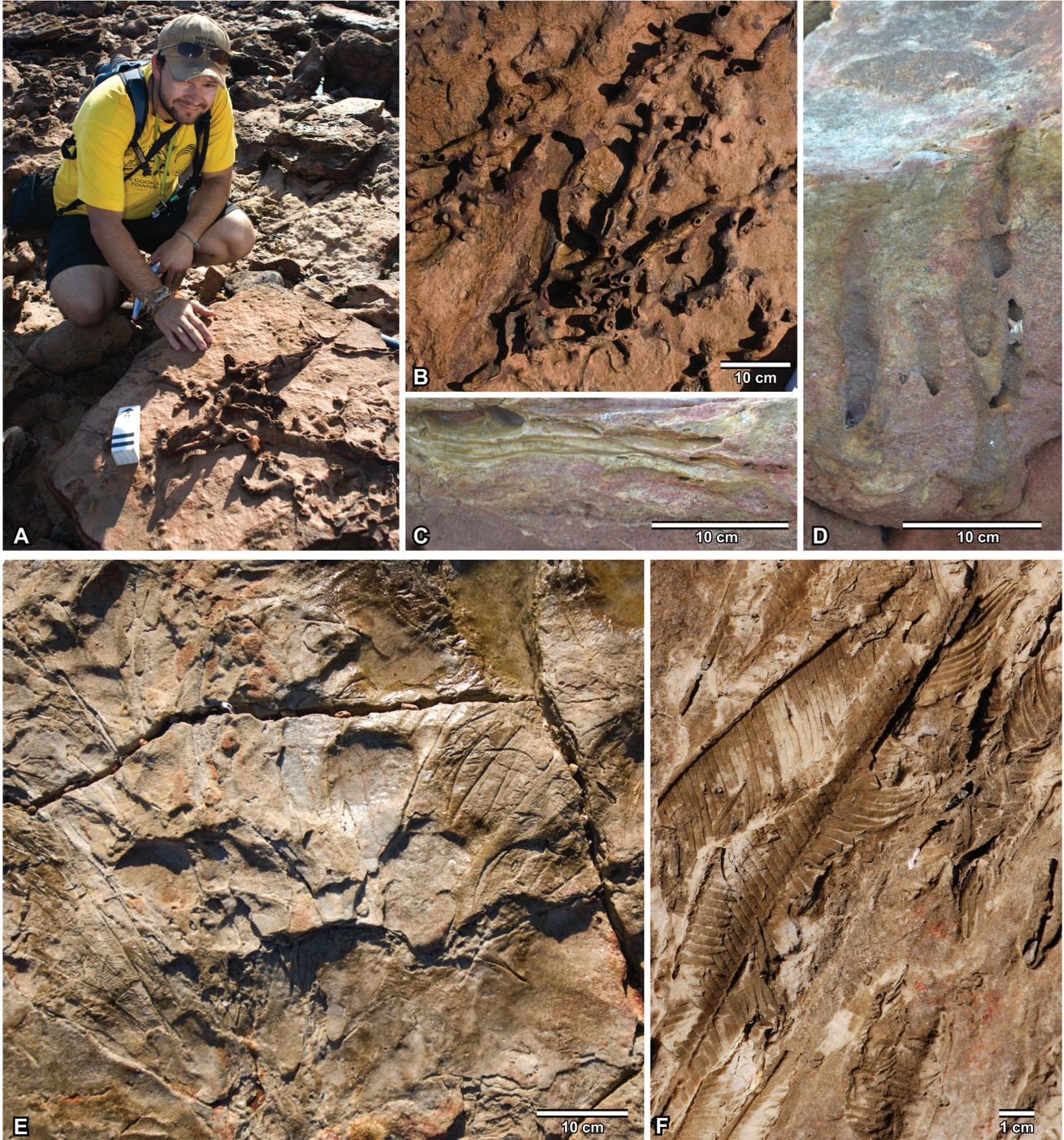


FIGURE 17. Examples of invertebrate trace and floral fossils within the Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. **A**, Dr. Ryan T. Tucker alongside a well-preserved example of a *Domichnia* or *Fodinichnia* complex of tubes and galleries. Preservation of these structures is rare and limited to LFA-2 (**B**, close up); **C**, an example of *Planolites*-type trace fossils, which commonly occur in the uppermost units of LFA-1, just below the track horizons of LFA-2; **D**, poorly preserved *Skolithos*-type trace fossils; **E**, **F**, matted fronds of the bennettitaleean *Pilophyllum cutchense* in the silicified track-bearing horizons of LFA-2.

### Lithofacies Association 3 (LFA-3)

**Description**—Lithofacies Association 3 includes the following facies codes in descending order: Sh, Sp, St, Si, Se, Sd, Sm, Fl, Flf, Fm, Sr, Gmx, Gmm, and P, and comprises thick to medium,

planar, tabular to ripple cross-laminated and tabular cross-bedded sandstones. Detailed description of this unit is limited both by tide levels and by outcrop quality. Horizons of LFA-3 form many of the low cliff lines and bouldery slopes that cap the littoral rock platforms and reefs of LFA-1 and LFA-2. All the

horizons in LFA-3 are predominantly cemented with iron and calcite, giving them a characteristic ‘blood red’ to black coloration. Rare unweathered sections are medium to light gray (N7–N6). Weathered sections exhibit a variety of oranges and red, with the blood red coloration associated with the iron of the overlying pindan sands being the most prominent (10YR 8/2, 10YR 8/6, 10R 3/4, 10R 2/2).

The erosive contact between LFA-2 and LAF-3 is distinctively sharp (3rd–4th-order surface) and easily identified in areas where LAF-3 occurs (Figs. 10B, 11A). The uppermost bounding surface is covered by near-modern alluvium (Figs. 9A, C, 11D). In the lower sections of some exposures in the Yanijarri area, north of Walmadany, and at Kardilakan, the lowermost preserved portions of this lithofacies association consist of minor interbedded units of a white coarse siltstone to granular sands (Gmx). In the northern part of Walmadany, these units are overlain by a distinctive assemblage of repeated facies, commencing with low- to medium-angle cross-bedded sandstones (0.4–0.8 m) (Sp, Si, Se, and Sd) that are truncated by a minor series of stacked horizontal sandstones (0.2–0.5 m) (Sh). In preserved outcrops at Yanijarri (Fig. 9A, B), channel structures (CH, HO; local cut and fill structures) dominate the outcrop. Channel structures laterally extend between 3.0 and 10.0 m, with a maximum thickness around 2.0 m. These are commonly accompanied by point bars (SB), levee (LV), and splay (CS) development surfaces (Allen, 1983; Miall, 1988). Stacked sandy bar forms (SB) are commonly tabular bodies, which extend laterally for tens of meters with a vertical thickness of 0.4–1.0 m. Levee and splay deposits (LV, CS) are less well preserved, yet commonly extend for approximately 10 m and then either pinch out or are weathered away. At Yanijarri and Walmadany, overlying the basal conglomerate horizon in LFA-3 is a thick sequence of incised and infilled multistory channel sets (CH, HO), with interbedded trough cross-cutting to tabular cross-cutting sandstones (Sh, Sp, Si, Se, and Sd) (2.0–4.0 m) (Figs. 9A, B, 10C). This uppermost part of LFA-3 is a repetition of structures and textures that are similar to those seen in the lower units of this lithofacies association. Beds alternate between planar, non-tangential tabular sandstone bodies (SB) and stacked trough cross-bedding (CH). Channel bodies extend laterally from 2 to 8 m, with a thickness ranging from 0.1 to 0.8 m. Lateral accretions (LA) were identified within these sections, but their preservation was poor. Channel troughs and scour hollows are better preserved and commonly exhibit a basal conglomerate (Gmx) lens, with subsequent infill grading normally.

In the Kardilakan–Jajal Buru area, the lowermost unit within LAF-3 appears to be a 3–10 cm layer of poorly sorted, subrounded to rounded, pebble to large cobble conglomerate (Gmx). Although it was identified at three separate localities immediately above track-bearing horizons of LFA-2, we are not entirely convinced that this ‘horizon’ forms an in situ part of the Broome Sandstone; it could easily be made from a more recent (Quaternary) amalgamation of eroded pebbles and cobbles that have become cemented to the seaward sections of the Broome Sandstone rock platforms. Similar lithified beach gravels were seen within potholes and rock pools throughout the study area. Without the benefit of fresh sections or cores, we are presently not able to confirm the true nature and source of this horizon.

The sandstones within lower sections of LFA-3 are best classified as a quartzarenite (Qt 97%, L 3%) or a sublitharenite (Qm 60%, L 40%) (Fig. 12E, G) (Fig. 13). Grains are subangular to subrounded and more uniform in overall grain size and sorting than those in LFA-1 (Fig. 12K, M) and LFA-2 (Fig. 12H, J). Grains commonly exhibit embayments, dissolution, contact suturing, clay rims to marginal inclusions, and both secondary calcium cement and meniscus hematite. The rock is also very porous and includes trace amounts of chert and heavy minerals. Page (1998) described the presence of rare, poorly developed

soil horizons with preserved root and carbonate mud nodules in a similar lithofacies at Minyirr. Strata in the uppermost section of LFA-3 are almost identical to the lower ones, with many grains exhibiting embayments, dissolution, contact suturing, marginal inclusions, and both secondary calcium and iron cement. However, clay rims seem to be less prominent (Fig. 12A–G). The sandstone is classified as quartzarenite (Qt 100%) and a sublitharenite (Qm 69%, L 31%) (Figs. 12A, B, 13).

**Interpretation**—LFA-3 is interpreted as preserving a diverse suite of fluvial, fluvial, and/or alluvial paleoenvironmental depocenters. The lowermost outcrop strata of LFA-3 range from tabular sandstones to interbedded tabular sandstones, siltstones, and thin mudstones, which are overlain by cross-bedded to trough cross-bedded sands. This increase in energies is interpreted to be the transgressive (seaward) extension of the distal fluvial braid plain and delta, with deposition transitioning from deltaic with tidal influence to braid plain and alluvial influence. The middle and upper sections of this lithofacies association comprise well-preserved, large, meandering/cross-cutting channel bodies with preserved bank/levee and medial channel infill. This interpretation is similar to that proposed by McLoughlin (1996) for a similar lithofacies association at Minyirr (approximately 50 km to the south), which he considered to be indicative of a meandering river in a humid environment.

#### Alluvium (Near-Modern Sedimentation)

Throughout the entire study area, the Broome Sandstone is unconformably capped by Quaternary conglomerates and aeolian ‘pindan’ soil horizons, along with Holocene–contemporary beach and coastal dune sediments (Brunnschweiler, 1957; Semeniuk, 2008; Nicoll et al., 2009; McCrea et al., 2012; Smith et al., 2013). There are extensive exposures of the Cable Beach Sand and its constituent members (the Cape Boileau Calcarenite Member and the Lombadina Conglomerate Member) (Semeniuk, 2008) at the southern end of Walmadany, extending south to Kardilakan. Deposition of these units likely occurred during the mid-Holocene highstand (Woodroffe and Horton, 2005; Semeniuk, 2008; Lipar and Webb, 2014) given their occurrence on the landward side of the current astronomical high-tide mark.

#### Paleoenvironmental Interpretation

The lithofacies associations that occur within the lower portions of the exposed Broome Sandstone in Yanijarri–Lurujarri section of the Dampier Peninsula are indicative of an environmental transgression between the distal fluvial to deltaic portions of a large braid plain, with migrating sand bodies and periodic sheet floods (Fig. 18). There are minor indications of tidal influence (very thin, mud drapes coupled with interference–ladderback ripples), but these are rare. The undulating surfaces commonly associated with LFA-1 and LFA-2 are interpreted as part of the original topography, supported by the fact that (1) both lithofacies associations consistently display the same gently undulating topographies; (2) the horizons associated with these surfaces do not cross-cut or disrupt the bedding plains; (3) the preserved plant remains curve to the contours of the surfaces; (4) dinosaurian tracks often follow the unevenness of the terrain. In this context, the lowermost coastically exposed strata (that of LFA-1) are interpreted as representing a distal braid plain, comprising actively migrating sand bodies (transverse and longitudinal bar forms) with incising channel forms (CH). The main dinosaurian track-bearing horizons in LFA-2 seem to have been generated between periodic sheet floods that blanketed the preexisting sand bodies within the braid plain portion of a tidally influenced delta. The onset of these thick sandy blankets would have been the main mechanism for the numerous dewatering structures that are identified between LFA-1 and LFA-2. This indicates that emplacement of these sheet floods was likely a rapid event. The upper parts of the outcropping Broome Sandstone (LFA-3) are

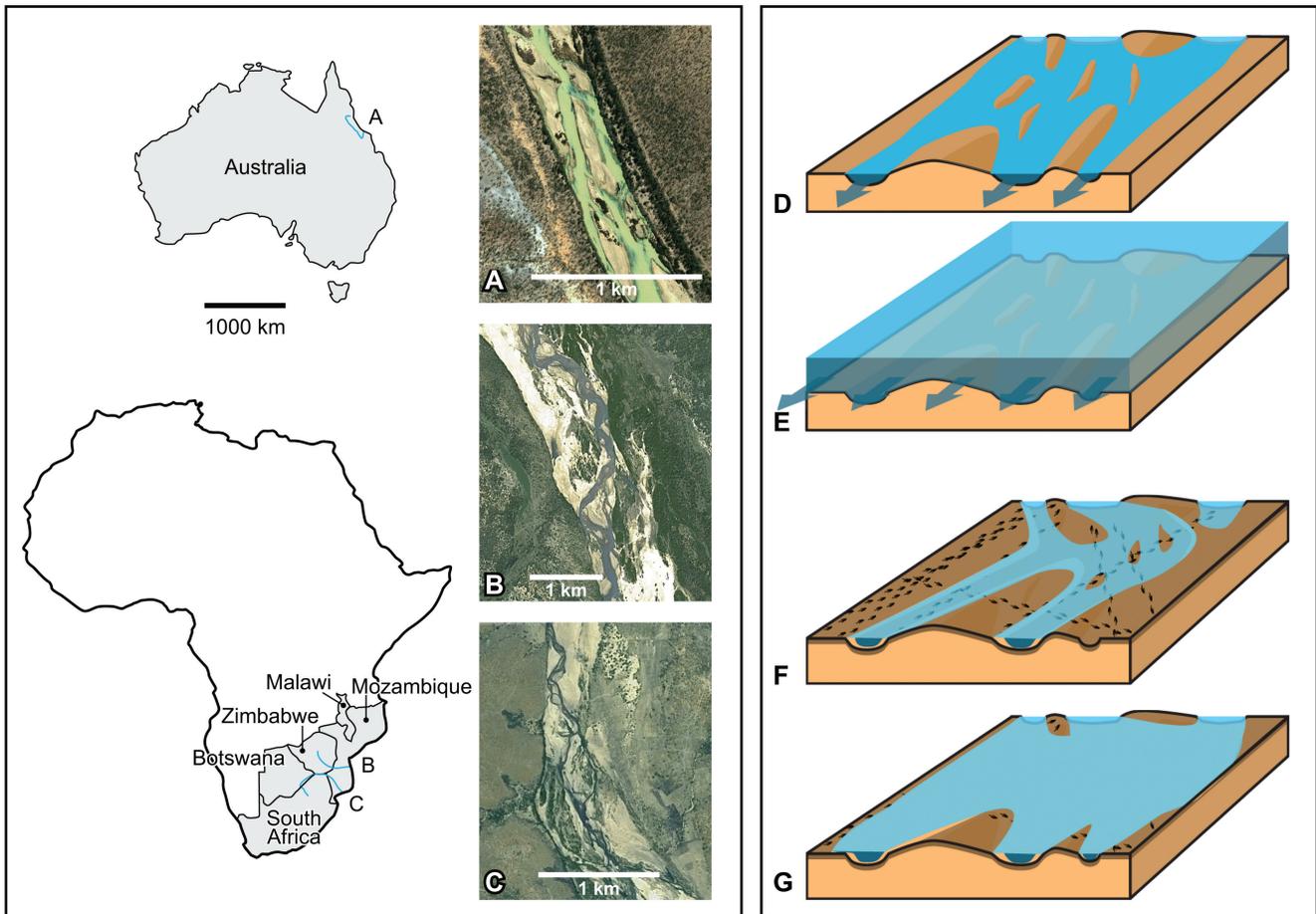


FIGURE 18. Bed-load-rich (sandy) braid plains. **A–C**, modern examples: very distal portions of the **A**, Burdekin River, Queensland, Australia, and **B**, Save (Sabi) and **C**, Limpopo rivers, sub-Saharan Africa; **D–G**, paleoenvironmental reconstruction of Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia, at the time of deposition of exposed portions of the Broome Sandstone: **D**, ‘normal-flow’ period within a sand-rich distal braid plain, which corresponds to LFA-1; **E**, waxing (sheet-flooding) period of high flow within the braid plain, with emplacement of sediments capping LFA-1. Deposition was likely rapid, with the common co-occurrence of dewatering structures between LFA-1 and LFA-2; **F**, sheet-like flood muds and silts get traversed by dinosaurs; **G**, continued evolution of the prograding delta seaward, with waxing and waning flow velocities in the braid plain. **A–C** copyright Google Earth.

interpreted to be interlaced migrating channels within a distal fluvial braid plain that is feeding a prograding delta.

On the balance of all observations, during the Valanginian–Barremian the Yanijjarri–Lurujarri section of the Dampier Peninsula most likely represented part of a distal braid plain associated with a large fluvial system, transitioning into the proximal or landward portion of a prograding delta (due to large geographic expanse that may also qualify as a ‘mega fan’), as has been suggested by previous authors for other parts of the Broome Sandstone (e.g., McWhae et al., 1956; Brunnschweiler, 1957; Veevers and Wells, 1961; Playford et al., 1975; Forman and Wales, 1981). This interpretation is also consistent with the overall coarsening upwards of sediments from LFA-1 to LFA-3 and the transition from the channel sands, point bars, and thinly interbedded sands and silts of LFA-1 and LFA-2, to the fluvial-dominated tabular/lenticular cross-bedded sandstones of LFA-3. The lack of any thick carbonate muds and obvious deep to marginal marine invertebrate fossils or macrofossils (shells or corals) indicates that the study area was not lagoonal or estuarine, although there is a lot of evidence to suggest that this area was tidally influenced in LFA-1 and LFA-2. Overall, the depositional environment could be considered broadly analogous to the distal fluvial to proximal alluvial delta plain portions of the modern Save (Sabi) and Limpopo rivers of Zimbabwe

and Mozambique, Africa, or the Burdekin River of northern Queensland, Australia (Fig. 18A–C). Each of these river systems has broad expansive distal braid plains, up to 1.5 km across in the case of the Save, characterized by a main channel set with interwoven secondary and tertiary channels, separated by migrating sandbars that together form undulating topographies. The fluvial system associated with the deposition of sediments in the study area seems to have alternated between high- and low-flow periods (particularly during the deposition of LFA-1 and LFA-2), possibly corresponding with seasonal changes in water levels. During what may have been a wet season, deposition of flooding sediments appears to have blanketed the sand lobes and, in the process, generated an ideal environment for dinosaurian tracks to be laid down and subsequently preserved. The textural difference between the finer-grained and more finely laminated track-bearing horizons of LFA-2 and the overlying sand deposits of LFA-1 and LFA-3 may have facilitated not only the preservation of the track surfaces but also the subsequent parting of the two horizons during erosion. It is worth noting that with the exception of some of the larger sauropod tracks (see Thulborn, 2012), natural casts of dinosaurian tracks are rare in the Broome Sandstone.

The abundance of well-preserved but allochthonous plant material in exposures of LFA-2 suggests that areas adjacent to

the river channels and sandbars were moderately to well vegetated. Several forms of bioturbation also indicate that a range of invertebrates inhabited the area. The tracksites in the study area probably represent areas where dinosaurs moved across or along portions of the tidally influenced braid plain. In the case of the herbivorous species, this was most likely to access feeding grounds on either side of the braid plain. Heavily trampled areas most likely represent thoroughfares that were used by multiple dinosaurs, possibly moving in herds or small groups over a period of several days.

The preservation of track-bearing horizons is only likely to have occurred under a particular set of depositional conditions. In the first instance, the sediments that make up the track-bearing horizons need to have been deposited. The finely laminated nature of the sand and silt that constitute the majority of track-bearing horizons indicates that their deposition occurred subsequent to episodic sediment-laden sheet floods that invaded proximal portions the braid plain. The water level in these areas then must have dropped, very likely resulting in changes to the course of the main channels, thereby exposing the sediments subaerially and making these areas accessible to dinosaurs, which then walked over them. It is possible that many of the track surfaces were still partly covered in water, or nearly so, when dinosaurs traversed them. The various track surfaces must have then become consolidated to some degree, sufficiently hard to remain intact during burial, but not to the extent that they started to dry out and deteriorate as a result of normal erosive processes. The silt in these horizons may have added to the cohesiveness of the wet sand, thereby facilitating track preservation. Nevertheless, given the high sand content of LFA-2, we suspect that these horizons may only have retained well-preserved tracks for a short period of time (days rather than weeks). Larger tracks probably persisted for longer periods, as would have the localized buckling of some beds that the passage of the larger dinosaurs appears to have caused. Burial of the track surface then occurred as a result of channel sand and overbank deposition, again mostly likely linked to changes in the course of the main river channels, but possibly also a result of additional flood events.

Most of the main areas where tracksites are concentrated (Yanijarri, Walmadany, and Kardilakan–Jajal Buru) contain multiple horizons that can be assigned to LFA-2, exposed across the intertidal platforms over a stratigraphic thickness of several meters. In most instances, however, the majority of tracksites in each of these areas occur in only one of these LFA-2 horizons. Although the extent of the track-bearing horizons is punctuated in parts by either rubbly, heavily eroded areas or stretches of sand, it is possible to see that the original track surfaces were quite extensive. It is also possible that many of the rubbly areas represent deeply trampled zones resulting from heavy sauropod traffic, as has been proposed in part by Thulborn (2012:fig. 26). In the case of Walmadany, the track-bearing horizon appears to cover an area of several square kilometers, a fact also observed by Thulborn (2012).

## SYSTEMATIC PALEOICHOLOGY

### THEROPOD TRACKS

#### *MEGALOSAUROPOUS BROOMENSIS* Colbert and Merrilees, 1967

(Figs. 19, 20, 57A, 58A, B, S1; Table 5)

**Holotype**—WAM 66.2.51, a rigid epoxy resin, fiberglass, and plaster cast (i.e., a convex/positive hyporelief) of topotype track G5-6 (Colbert and Merrilees, 1967:fig. 1), the natural mold of a left pes (Figs. 19A–C, 65A).

**Paratypes**—WAM 64.6.5 and WAM 64.6.7, plaster replicas of topotype tracks G5-7 (the natural mold of a right pes) and G6-1 (the natural mold of a right pes), respectively (Colbert and Merrilees, 1967:fig. 1).

**Topotypes**—Over 20 tracks, some of which were designated field numbers G5-1, G5-6, G5-8, G6-1, G6-2, G7-1, G7-3, G7-3, and G8-1 in Colbert and Merrilees (1967:fig. 1). The numbering of these tracks was later considered arbitrary, and among figured tracks only two sets formed trackways: G5-8 and G5-7 (two consecutive right pedal tracks) and G7-3, G7-2, G6-2, and G5-6 (four consecutive pedal tracks, commencing with a right). All these tracks were preserved as in situ natural molds.

**Type Locality, Horizon, and Age**—The topotype specimens were preserved in situ on discontinuous rock platforms in the intertidal zone at Minyirr (Gantheaume Point; 17°18′28.125S 122°10′40.20E), Broome, Dampier Peninsula, in the west Kimberley region of Western Australia (Colbert and Merrilees, 1967:fig. 1), and derive from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Referred Specimens**—WAM G10328, a concrete replica (concave/negative epirelief) of the natural mold of a left pes, one of a series of tracks on a rock platform in the intertidal zone west of the type locality, briefly described by Glauert (1952) and figured by Baird (1989:61); and WAM 64.6.10, a plaster replica of the natural mold of a left pes, one of three isolated in situ tracks in the Broome Sandstone on rock platforms in the intertidal zone at Reddell Beach, Broome, Dampier Peninsula, in the west Kimberley region of Western Australia (Colbert and Merrilees, 1967). Colbert and Merrilees (1967) considered the latter set of tracks to be stratigraphically lower in the Broome Sandstone than the topotype tracks. Two in situ tracks on rock platforms of the Broome Sandstone in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia: UQL-DP35-1, an isolated natural mold of a left pes (Figs. 20A–C, 57A, 58A, B, S1), preserved in situ at UQL-DP35; UQL-DP11-1, an isolated natural mold of a left pes (Fig. 20D, E) preserved in situ at UQL-DP11; and UQL-DP45-10, an isolated natural mold of a right pes (Fig. 20F, G) preserved in situ at UQL-DP45 (see Fig. 11G). (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Amended Diagnosis**—Pedal tracks: medium- to large-sized (proximodistal length 28.6–44.3 cm, mediolateral width 22.5–35.5 cm), tridactyl, mesaxonic (digital impression extension to track length ratio 0.30–0.47), longer than wide, with an average maximum length to maximum width ratio approximately 1.0–1.3; individual digital impressions proportionately elongated and narrow, and of similar width (the approximate width of each digital impression is approximately one-seventh the total track length), with the central digital impression (digit III) being the longest (basal digital impression length 42–72% the total length), and the impressions of digits II and IV often extending distally to approximately the same level relative to the principal track axis; on shallow tracks, the impression of digit II shortens proximally relative to the length of the impression of digit IV; axes of the impressions of digits III and IV typically intersect distal to the intersection of the axes of the impressions of digits II and III; total divarication angle between the axes of impressions of digits II and IV 66–81°; divarication of axes of impressions of digits III and IV (31–45°) typically greater than divarication of axes of impressions of digits II and III (27–39°); digital pad impressions may be present, with the formula 2/II, 3/III, 3/IV; a possible fourth pad impression may also be present proximally on the impression of digit III (visible only on the holotype); ungual impressions may be present distally on all digital impressions; a separate, circular metatarsodigital pad impression immediately proximal to the proximal end of the impression of digit IV and in

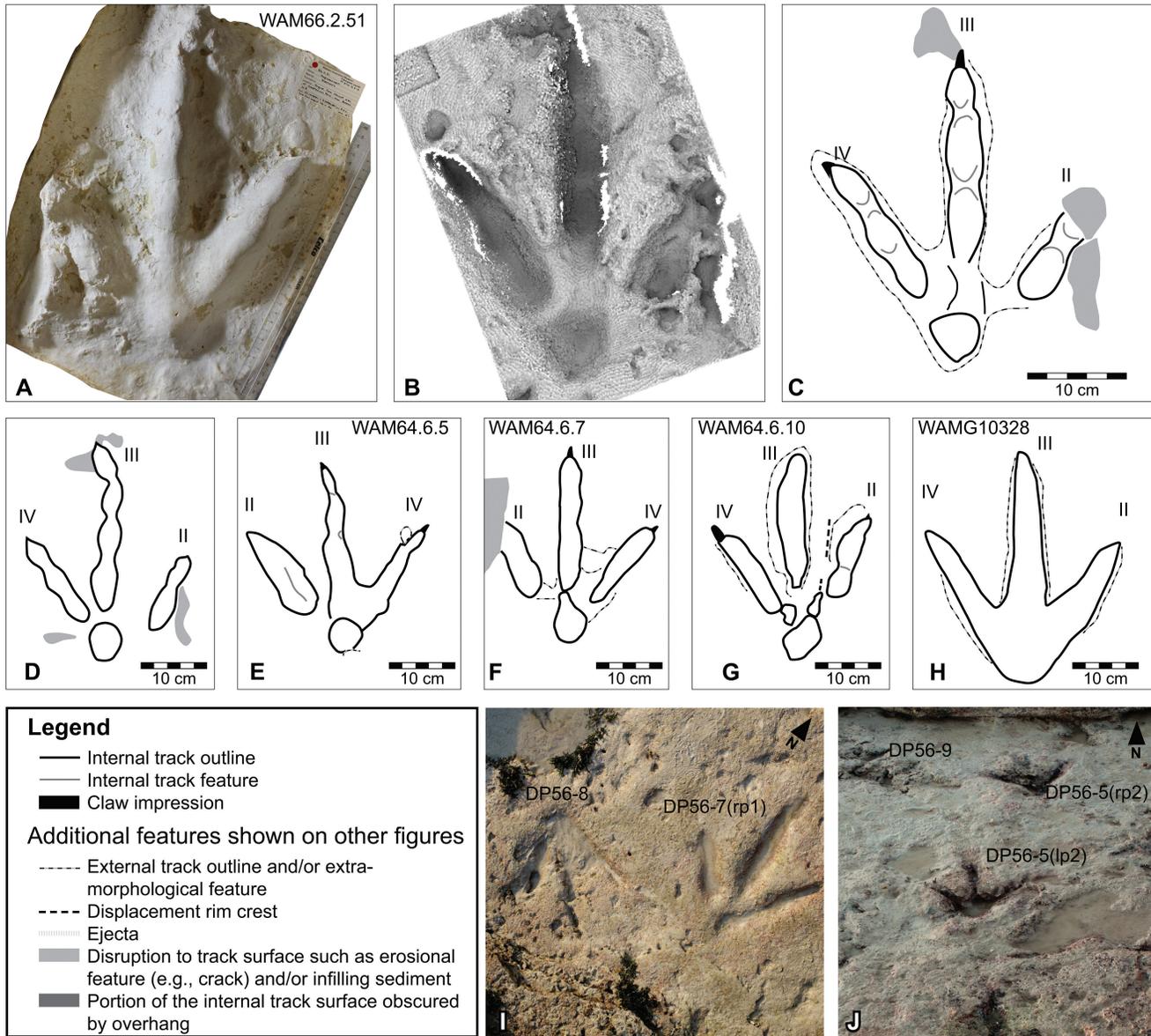


FIGURE 19. *Megalosauropus broomensis* Colbert and Merrilees, 1967, from Minyirr (Gantheaume Point), Broome, Western Australia. The holotype WAM 66.2.51, a fiberglass cast (convex hyporelief of topotype track G5-6) of a left pedal impression, as **A**, photograph; **B**, ambient occlusion image; **C**, schematic interpretation; and **D**, schematic interpretation of the same specimen by Merrilees that appeared in Haubold (1971:78, abb. 48.1). Fiberglass replicas of the paratypes (concave epireliefs of topotype tracks G5-7, G6-1, RB3-2, and unknown, respectively; see Colbert and Merrilees, 1967:fig. 1) as schematic interpretations: **E**, WAM 64.6.5, **F**, WAM 64.6.7, **G**, WAM 64.6.10, and **H**, WAM G10328. Photographs of the in situ specimens: **I**, UQL-DP56-8 and UQL-DP56-7(rp1); and **J**, UQL-DP56-9, UQL-DP56-5(lp2), and UQL-DP56-5(rp2).

line with the principal track axis on the majority of shallow tracks, with a maximum width that is slightly greater than that of each digital impression; on deeper tracks, the diameter of the single metatarsodigital pad impression increases, becoming contiguous with the proximal end of each digital impression; separation between the impression of digit II and that of the metatarsodigital pad results in proximomedial indentation on shallow tracks; proximolateral indentations between the impression of digit IV and the metatarsodigital pad shorter than the corresponding proximomedial indentations; hallucal impression absent on all tracks, irrespective of depth. Trackway: pace angulation 140–160°; typical stride length approximately 7 times the maximum

pedal track length; typical pace approximately 3 times the maximum pedal track length.

**Description**—DP35-1, DP11-1, and DP45-10 (Fig. 20) are the only three tracks in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula that can be confidently assigned to *Megalosauropus broomensis*. These are medium- to large-sized, tridactyl, mesaxonic pedal tracks, longer than they are wide, with a length to width ratio of 1.1–1.3 (possibly higher for DP35-1; see below), consistent with the proportions of the topotype tracks from Minyirr. The impression of digit III is the longest on each track, with the basal digital length constituting 42%, and 49% of the track length for tracks DP45-10 and

DP11-1, respectively. These values are less than those of the holotype (69%) and paratype (60%, 71%) specimens, perhaps due to the lack of internal details preserved in the DP45-10 and DP11-1 tracks. The impressions of digits II and IV are subequal in length, with digital impression extension to track length ratios of 0.42 and 0.30 on DP11-1 and DP45-10, respectively. On DP35-1 and DP45-10, the impressions for digits II and IV extend distally to approximately the same position relative to the principal track axis, either side of the impression for digit III, whereas on DP11-1, the impression of digit II extends slightly farther distally than does that of digit IV. Specimen DP35-1 is at least 25 cm long (the distal-most portion of the impression of digit III on this track is not defined) and 19 cm wide. Specimen DP45-10 is larger, being 33.8 cm long and 30 cm wide, whereas DP11-1 is considerably larger, being 42 cm long and 32 cm wide, making it one of the largest confirmed *M. broomensis* tracks so far described. The digital impressions on DP35-1 and DP45-10 are proportionately slender, with a width ranging from 10% to 21% of the total track length.

The impression of a single digital pad for digit II is apparent on DP35-1, and a circular metatarsodigital pad impression is continuous with the proximal end of the impression of digit IV and in line with the principal track axis. Specimen DP11-1 is a rather flat track and lacks internal detail. DP45-10 also lacks internal track details, and the proximal margins of individual digital impressions are contiguous with the metatarsodigital pad impression as they are on DP35-1. However, the overall morphology is consistent with those of other tracks assigned to *M. broomensis*. The divarication angle between the long axes of the impressions of digits II and IV on the three tracks averages 73.7° (72° on DP35-1, 68° on DP11-1, and 81° on DP45-10). The divarication angles between the axes of the other digital impressions are also similar: 39°, 38°, and 45° for III^IV and 33°, 30°, and 36° for II^III on DP35-1, DP11-1, and DP45-10, respectively. The preservational differences between these three tracks may be related to their size (and hence that of each trackmaker), differences in the way the substrate may have reacted to each pes, or both.

**Remarks**—The holotype and paratype materials of *M. broomensis* are housed in WAM, and it is primarily on the basis of these specimens that Colbert and Merrilees (1967) described the taxon. Although numerous tracks assignable to *M. broomensis* occur at Minyirr and Reddell Beach, the platform preserving the topotype tracks collapsed into the ocean sometime between 1989 and 1990 and has not been accessible since (L. Middleton, pers. comm., 2011). Additional, well-preserved tracks (also assignable to *M. broomensis*) were exposed nearby as a result of this collapse, and it is these tracks that are typically photographed (e.g., McCrea et al., 2012:fig. 20). The tracks described by Glauert (1952) were preserved on a platform to the west of the latter series of tracks, but they were poorly preserved and provided little in the way of detailed morphological information (Colbert and Merrilees, 1967). These tracks are also no longer accessible.

Colbert and Merrilees (1967) decided to name *M. broomensis* based on detailed comparisons of the tracks at Minyirr with the foot skeleton of *Allosaurus fragilis* (AMNH 5753) and ‘carnosaur’ tracks on display in the AMNH from the Albian Glen Rose Formation in the Paluxy River Valley near Lanham Mill, Texas (Bird, 1941). The latter set of tracks is most likely attributable to *Eubrontes? glenrosensis* Shuler, 1935 (Lockley, 2000a; Lockley et al., 2000; Adams et al., 2010; but see below for additional comments on the nomenclature of these tracks). Colbert and Merrilees (1967) also compared *M. broomensis* with several other theropod ichnotaxa, including *Irenesauripus mclearnii* and *I. occidentalis* from the Lower Cretaceous Gething Formation at Peace River, British Columbia (Sternberg, 1932; Currie and Sarjeant, 1979), and *Satapliasaurus dsotesenidze* and *S. kandelakii* from the Lower Cretaceous of Georgia (Gabuniya, 1951; Sarjeant, 1970).

The drawings of the *M. broomensis* tracks in Colbert and Merrilees (1967), although useful for ascertaining stride and pace measurements, lack sufficient morphological detail for comparisons with other theropod tracks. Subsequent published accounts of the morphology of *M. broomensis* (e.g., Lockley et al., 1996a, 2000) have therefore presumably been based on a schematic interpretation of the topotype track by Merrilees (Fig. 19D) that appeared in Haubold (1971:78, abb. 48.1). It is not known whether the schematic was based on a firsthand examination of the in situ track (Colbert and Merrilees, 1967:fig. 1, track G5-6), a photograph of it, or the holotype (WAM 66.2.51; Fig. 19A–C). Given that Merrilees’ sketch shows the track as it would be preserved in situ, we suspect that it is based on one or both of the former two options. Whatever the case may be, there are minor discrepancies between the morphology depicted in the Merrilees’ schematic and that displayed by the holotype—a fact also commented on (but not elaborated on) by Baird (1989) and Thulborn (2009).

Our own examination of the holotype and other tracks from Minyirr that are assignable to *M. broomensis* indicates that the digital pad formula for this ichnotaxon is 2/II, 3/III, 3/IV, not including unguis impressions, which may be present distally on each digital impression. This formula reflects the soft-tissue configuration of the plantar surface of the trackmaker’s pes rather than the number of phalanges present on the digits (see below). The proximal portion of the proximal-most pad on impression of digit III is constricted slightly, such that a case could be made for this digital impression comprising four pads, but this is only apparent on the holotype (Fig. 19A–C) and does not appear to be a consistent feature across all the tracks that we can assign to *M. broomensis*. A separate, well-defined, subcircular metatarsodigital pad impression occurs immediately proximal to the proximal end of the pad impression of digit IV and in line with the principal track axis. The pad impression for digit II is typically offset laterally from the metatarsodigital pad and the point of intersection of the long axes of the pad impressions of digits III and IV, with its long axis diverging at a smaller angle to the principal track axis than is the case for the pad impression of digit IV. As a consequence, the divarication of the long axes of the impressions of digits III and IV (35–40°) is typically greater than that for digits II and III (27–39°). In his illustration of the holotype specimen (Fig. 19D), Merrilees appears to have mistakenly interpreted a unguis drag or erosional feature at the proximal end of the impression of digit III as an additional digital pad impression, turned out laterally to the principal track axis. This additional impression is not apparent on any of the other *M. broomensis* tracks that we have examined, and for this reason we suspect that its inclusion by Merrilees was an error. Merrilees’ outline of the possible hallucal impression also seems to be in the wrong position and is not consistent with our interpretation of the specimen. Our interpreted outline of the holotype track is shown in Figure 19C.

In their diagnosis of *M. broomensis*, Colbert and Merrilees (1967) give the “rather extra-ordinary” (Lockley et al., 2000:321) phalangeal formula of 3/II, 4/III, and 5/IV. As is explained later in their paper, however, this is because they took the pad impressions within the impressions of digits II and III and the proximal pad impressions within the impression of digit IV to represent swellings between phalanges, following earlier studies by Peabody (1948, 1955) and Baird (1957). For the correspondence between the distal-most pad impressions on digit IV and the underlying phalanges, they followed the findings of Baird (1957). The ‘phalangeal formula’ that they propose is therefore not for *M. broomensis* *sensu stricto*, but for that of the trackmaker, and also includes unguis/claw phalanges. Not surprisingly, the formula that they propose is consistent with that of the majority of medium- to large-bodied theropod taxa for which a complete pedal skeleton is known (e.g., *Allosaurus fragilis* [Madsen, 1976],

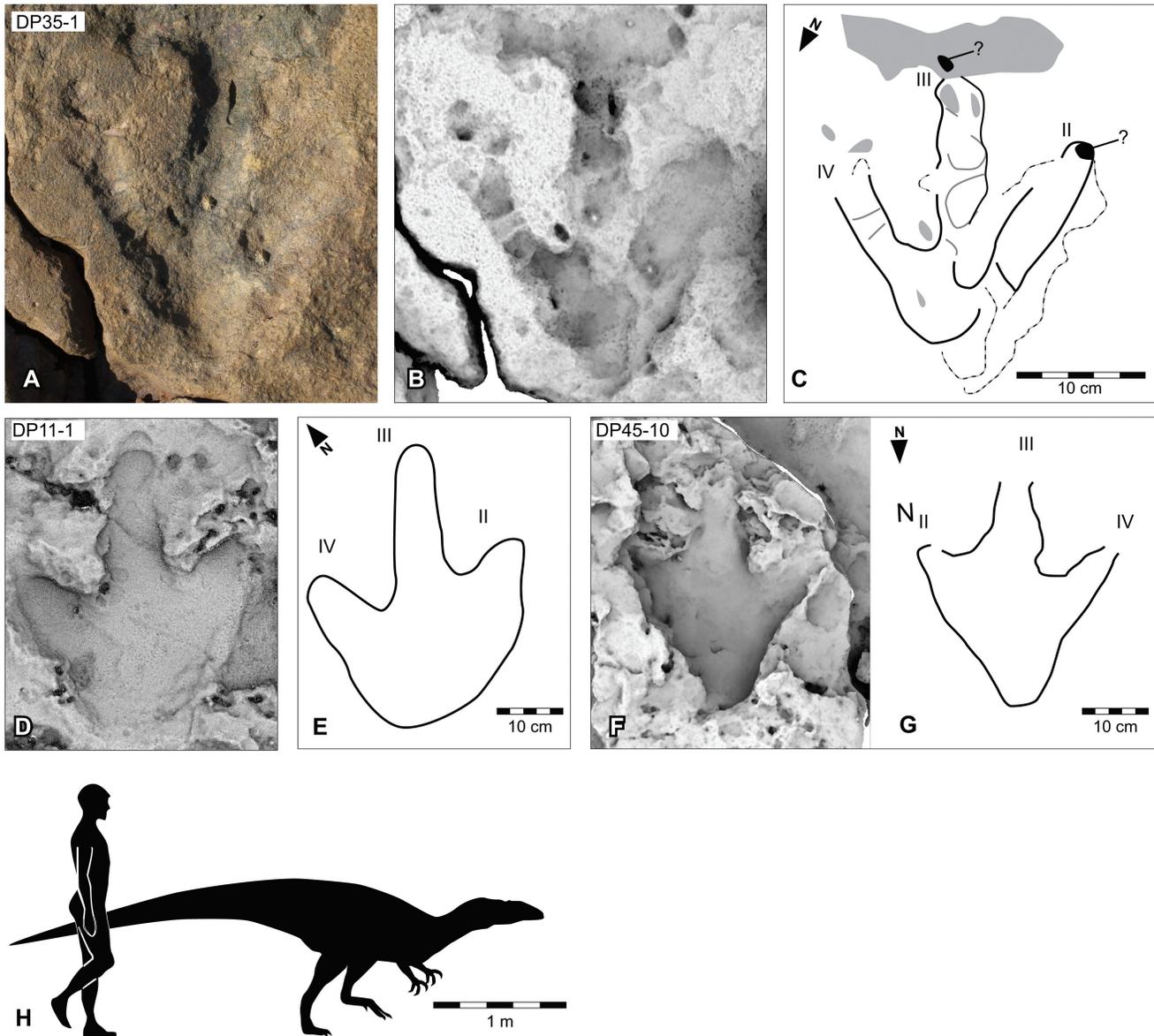


FIGURE 20. *Megalosauropus broomensis* Colbert and Merrilees, 1967, from the Yanijjarri–Lurujjarri section of the Dampier Peninsula, Western Australia. Left pedal impression, UQL-DP35-1, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Possible left pedal impression, UQL-DP11-1, preserved in situ as **D**, ambient occlusion image; and **E**, schematic interpretation. Possible right pedal impression, UQL-DP45-10, preserved in situ as **F**, ambient occlusion image; and **G**, schematic interpretation. **H**, silhouette of hypothetical *M. broomensis* track-maker based on UQL-DP35-1, compared with a human silhouette. See Figure 19 for legend.

comparisons with which formed part of their assessment of *M. broomensis*). Given that there are uncertainties concerning the precise relationship between the digital pad impressions seen in theropod tracks and the phalangeal skeleton in theropod body fossils (Heilmann, 1926; Bock, 1952; Lucas and Stettenheim, 1972; see Thulborn, 1990), in our amended diagnosis of *M. broomensis*, we have focused specifically on characteristics of the tracks and have not attempted to extrapolate these characteristics into skeletal features of the trackmaker, at least insofar as the diagnosis of the ichnotaxon goes.

None of the tracks assignable to *M. broomensis* that we have examined shows a hallucal impression (Fig. 19). Even deeply impressed tracks such as DP11-1 seem to lack this feature, although it is possible that it has been lost to weathering. The

absence of a hallucal impression on *M. broomensis* indicates that the hallux on the trackmaker was located high on the metatarsus relative to the pes and did not touch the substrate during walking.

Ever since Colbert and Merrilees (1967) established *Megalosauropus*, the ichnotaxon has been riddled with taxonomic issues. Tracks from the Upper Jurassic of Uzbekistan and Turkmenistan (*Megalosauropus uzbekistanicus*; Gabuniya and Kurbatov, 1982; Lockley et al., 1996c) and Germany (*M. teutonicus*; Kaefer and Lapparent, 1974) and the Lower Cretaceous of Portugal (*M. (?Eutynichnium) gomesi*; Antunes, 1976) have been assigned to this ichnotaxon, along with a vast sundry of unnamed tracks from Europe and North America (see Lockley et al., 1996a, 2000; Lockley, 2000b; Thulborn, 2001, 2009). Many of these

TABLE 5. Measurements of tracks assigned to *Megalosauropus broomensis* from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijjarri–Lurujjarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	II^III	III^IV	Total^	bdl II (II/L)	bdl III (III/L)	bdl IV (IV/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)
WAM 66.2.51 (holotype)	29.2	25.1	1.2	11.6 (0.47)	39	35	74	11.4 (0.39)	20.1 (0.69)	15.5 (0.53)	2.8 (0.10)	3.5 (0.12)	3.8 (0.13)
WAM 66.6.5	27.9	25.6	1.1	10.3 (0.37)	30	36	66	15.7 (0.56)	16.7 (0.60)	11.7 (0.42)	3.8 (0.14)	4.8 (0.17)	3.8 (0.14)
WAM 66.6.7	32.3	~25.7	1.3	13.1 (0.41)	27	40	67	12.7 (0.39)	23.0 (0.71)	15.8(0.49)	4.6 (0.14)	4.2 (0.13)	3.5 (0.11)
35-1	>25	22.5	>1.3	>6.5	33	39	72	13.1 (~0.52)	>15 (~0.6)	14.7 (~0.59)	5 (~0.22)	4 (~0.18)	2.5 (~0.11)
11-1	44.3	35.5	1.2	18.7 (0.42)	30	38	68	13.3 (0.30)	21.5 (0.49)	13.4 (0.30)	8.2 (0.19)	8.3 (0.19)	9.1 (0.21)
45-10	33.8	30	1.1	10.2 (0.30)	36	45	81	6.9 (0.20)	14.2 (0.42)	12.8 (0.38)	3.4 (0.10)	5.5 (0.16)	4.2 (0.12)

bdl = basal digital impression length; bdw = basal digital impression width; De = digital impression extension; II = impression of digit II; III = impression of digit III; IV = impression of digit IV; L = track length; W = track width. ^ denotes angle between respective digital impressions.

tracks show little if any resemblance to the type ichnospecies from the Broome Sandstone, and their assignments to the ichnogenus have involved minimal discussion of any similarities or differences with the type material. As has been discussed in a number of papers (Lockley et al., 1996a, 2000; Lockley, 2000b; Thulborn, 2001), the majority of assignments to *Megalosauropus* have been based on the idea these tracks should be linked to a particular type of trackmaker (see Peabody, 1948, 1955; Lapparent, 1951; Lessertisseur, 1955; Baird, 1957), in this instance a ‘megalosaur-like carnosaur.’ Consequently, the age, size, and provenance of certain theropod tracks has often been considered important when assigning tracks to *Megalosauropus*, sometimes in precedence to track morphology. As such, *Megalosauropus* has come to represent what many researchers consider an ichnotaxonomic ‘wastebasket’ (Lockley et al., 1996a), to the point where it has become so broadly defined morphologically as to be of little taxonomic utility. A suite of studies (Lockley et al., 1996a, 2000; Lockley, 2000b; Thulborn, 2001) have focused on the ‘megalosaur track issue,’ with the consensus being that *Megalosauropus* should be restricted to the type species from the Broome Sandstone. Many of the tracks previously assigned to *Megalosauropus* are now placed in *Megalosauripus* (spelt with an ‘i’), whereas others are considered distinct and in need of reassignment to new ichnotaxa (Lockley et al., 1996a, 2000; Lockley, 2000b; Thulborn, 2001). Surprisingly, much, if not all, of this work has been carried out with only minimal information presented on the morphology of *M. broomensis*, which, as outlined previously, has been limited to the description by Colbert and Merrillees (1967) and insufficient or inaccurate figures (e.g., Haubold, 1971:78, abb. 48.1).

A detailed review of the various nomenclatural issues surrounding ‘megalosaur tracks’ is beyond the scope of this study. Suffice it to say, we broadly support the findings of earlier studies (Lockley et al., 1996a, 2000; Lockley, 2000b; Thulborn, 2001), where it was agreed to restrict *Megalosauropus* to *M. broomensis*. We acknowledge that there are additional nomenclatural problems relating specifically to *Bückerburgichnus*/*Bueckerburgichnus* and *Megalosauripus* (see Thulborn, 2001), but we consider these to be largely tangential to *M. broomensis*.

Among other theropod tracks in the Broome Sandstone, *M. broomensis* most closely resembles *Yangtzeipus clarkei*, ichnogen. et ichnosp. nov. The two track types fall within a similar size range, and the digital impression extension to track length ratios are comparable (and average of 0.37 for *M. broomensis* and 0.34 for *Y. clarkei*). Both also have a separate, single, circular metatarsodigital pad impression immediately proximal to the impression of digit IV and in line with the principal track axis, and both lack a hallucal impression. *Megalosauropus broomensis* differs from *Y. clarkei* in that it has a lower track length to track width ratio, larger divarication angles, and much narrower digital impressions. Additionally, tracks assigned to *M. broomensis* typically display a digital pad impression formula of 2/II, 3/III, 3/IV, with the impressions of an ungual on all digital impressions,

whereas *Y. clarkei* has a digital impression pad formula of 2/II, 1/III, 2/IV, and the impression of an ungual is thus far only ever associated with the impression of digit II.

As has been pointed out recently by Thulborn (2009), *M. broomensis* is not, as formerly supposed (e.g., Lockley et al., 2000), a highly aberrant type of theropod track. As discussed previously, part of this perception probably stems from the problematic way that Colbert and Merrillees (1967) diagnosed *M. broomensis*, and the subsequent use of an erroneous schematic interpretation of the topotype track (1971:78, abb. 48.1) (Fig. 19D) that appears to have become the primary source of data for comparisons involving the track outline.

Colbert and Merrillees (1967) initially compared *M. broomensis* with *Eubrontes? glenrosensis* Shuler, 1935 (Lockley, 2000a; Lockley et al., 2000; Adams et al., 2010). Based on their close similarity to *M. broomensis*, Thulborn (2009) went so far as to propose that the Glen Rose tracks could be assigned to cf. *Megalosauropus*. Although we acknowledge the broad similarity of *Eubrontes? glenrosensis* to *M. broomensis* in terms of overall size, general proportions, and lack of a hallucal impression, the former can be distinguished from the latter based on its smaller divarication angles and much lower digital impression extension to track length ratio. Tracks assigned to *Eubrontes? glenrosensis* (see Shuler, 1935; Langston, 1974; Farlow, 1981, 1987; Pittman, 1989; Lockley et al., 2000; Farlow, 2001) lack the fine detail typically associated with shallower tracks assigned to *M. broomensis*, which show a clear and characteristic pattern of digital pads and a single metatarsodigital pad. The digital impressions of tracks typically assigned to *Eubrontes? glenrosensis* are proportionately shorter relative to those of *M. broomensis*, asymmetrical with a medially directed tip to the impression of digit III, and the hypices between the impressions of digits II and III and the impressions of digits III and IV are situated more distal to the proximal track margin (with the possible exception of DP11-1). As a consequence, there is a more elongated ‘heel’ region in *Eubrontes? glenrosensis* than in *M. broomensis*. Based on these differences, we do not think that there are sufficient grounds on which to assign the Glen Rose tracks to cf. *Megalosauropus*, and we echo the suggestion of Lockley et al. (2000) that the former tracks should be assigned to their own ichnogenus.

Other tracks that Colbert and Merrillees (1967) compared *M. broomensis* with included *Irenesauripus mclearnii* and *I. occidentalis* from the Lower Cretaceous Gething Formation at Peace River, British Columbia (Sternberg, 1932; Currie and Sarjeant, 1979), and *Satapliasaurus dsotesenidze* and *S. kandalakii* from the Lower Cretaceous of Georgia (Gabuniya, 1951; Sarjeant, 1970). Thulborn (2009) also stated that *M. broomensis* resembles theropod tracks of several other ichnogenera, including *Eubrontes*, *Anchisauripus*, and *Irenesauripus*. Differences between *M. broomensis* and *Irenesauripus mclearnii* and *I. occidentalis* and between *Satapliasaurus dsotesenidze* and *S. kandalakii* are similar to those outlined previously for *Eubrontes? glenrosensis* (see Langston, 1974, for comments on the similarity

between the Glen Rose tracks and *Irenesauripus*). Of these tracks, *Irenesauripus mclearnii* is probably the most similar to *M. broomensis*. However, it differs in that the digital impressions, although proportionately narrow, taper more distally, the rear of the track is proportionately broader, and there is a possible hallucal impression. The divarication angles between the digital impressions are also slightly smaller than those for *M. broomensis*. *Irenesauripus occidentalis* is much broader across the proximal end of the track. *Satapliasaurus dsotesenidze* has a much larger divarication angle between the impressions of digits II and III and a smaller angle between digits III and IV compared with the condition in *M. broomensis*, whereas *S. kandalakii* is very similar to *Eubrontes? glenrosensis* (see previous comments).

As with *Eubrontes? glenrosensis*, comparisons of *M. broomensis* with other species of *Eubrontes*, in particular *Eubrontes giganteus* (see Olsen et al., 1998, and references therein), indicate that the latter typically has smaller divarication angles (30–40°; Olsen et al., 1998), metatarsodigital pad impressions proximal to the impressions of digits II and IV, both of which are not in line with principal track axis, and proportionately broader digital impressions with a lower digital impression extension to track length ratio.

McCrea et al. (2012:45) introduced the concept that “*Megalosauripus* [misspelt with an ‘i’ rather than an ‘o’] *broomensis* was a synonym of *Irenesauripus acutus*,” but did not elaborate further. There are similarities between *M. broomensis* and the *I. acutus* holotype schematic (Sternberg, 1932:fig. 2), including the digital impressions being long and slender with a fairly uniform width along their length (the width of each digital impression is approximately 10% of the total track length on the *I. acutus* holotype), the divarication angle between the impressions of digits III and IV being greater than the divarication angle between the impressions of digits II and III, a high degree of mesaxony (digital impression extension is approximately 30% of the total track length in the *I. acutus* holotype), and the metatarsodigital pad impression being in line with the principal track axis. However, *I. acutus* differs in that the proximal margin of the track is very narrow, forming an acute region that forms a triangular overall outline to the track. In *M. broomensis*, the same region is more rounded, forming a circular metatarsodigital pad impression in shallow pedal tracks and a broader proximal track margin in deeper tracks. Other differences include the divarication angle between the impressions of digits II and III (18° in *I. acutus*) and total divarication angle between the impressions of digits II and IV below the range of those for *M. broomensis*. For these reasons and the reasons outlined in the discussion above, we do not consider *M. broomensis* to be synonymous with *I. acutus* or a junior synonym of *Irenesauripus*.

There are many differences between *M. broomensis* and *Anchisauripus sillimani* and *Grallator parallelus* (see Olsen et al., 1998, and references therein). Both *Anchisauripus sillimani* and *Grallator parallelus* have much smaller divarication angles, metatarsodigital pad impressions proximal to all digital impressions, and an impression of digit III that is situated much farther distally relative to the impressions of digits II and IV than in *M. broomensis*. Consequently, these tracks have a much higher track length to track width ratio than tracks assigned to *M. broomensis*.

In conclusion, we propose that *M. broomensis* is a valid ichnotaxon that can be distinguished from other theropod tracks on a well-defined suite of morphological features. The future referral of other tracks, either from Australia or elsewhere, to *Megalosauripus* should ideally take these characteristics into account.

Long (1990) extended the potential geographic range of *M. broomensis* within coastal exposures of the Broome Sandstone from Minyirr to as far north as Walmadany (‘Price’s Point’ in Long, 1990) and assigned much larger tracks (up to 53 cm) to this ichnotaxon (Long, 1990, 1998). Thulborn et al. (1994) and

Thulborn (2009) also noted the presence of *M. broomensis* in areas other than Minyirr and Reddell Beach, typically as isolated tracks or trackways of solitary animals, but did not elaborate any further, other than stating that they occur “sporadically through a range of environmental settings in the Broome Sandstone, typically as isolated footprints and the trackways of solitary animals” (Thulborn, 2009:90). We are not sure whether the tracks described herein (DP35-1, DP11-1, and DP45-10) are the same as those referred to in these earlier studies. The tracks illustrated by Long (1990, 1998) are different from DP35-1, DP11-1, and DP45-10. Our findings nevertheless confirm the presence of *M. broomensis* north of Minyirr and Reddell Beach. Significantly, the rarity of *M. broomensis* in the Yanijjarri–Lurujarri section of the Dampier Peninsula is in sharp contrast to the situation at Minyirr and Reddell Beach, where these tracks are much more abundant. Given that the two areas seem to preserve different lithofacies and track associations (see Discussion), it is tempting to speculate that this trackmaker had a preference for more coastal paleoenvironmental settings, as has been proposed by Thulborn (2009).

YANGTZEPUS Young, 1960

YANGTZEPUS CLARKEI, ichnosp. nov.  
(Figs. 21, 57B, 58C, S2; Table 6)

**Etymology**—The ichnospecies name honors Nigel Clarke (Fig. 10B), a Broome resident and keen dinosaur tracker, who provided invaluable assistance with many aspects of the fieldwork and data collection associated with this study.

**Holotype**—WAM 12.1.1, a rigid polyurethane resin replica of UQL-DP57-1, the natural mold of a right pes (Figs. 21A–C, 57B, 58C, S2).

**Topotype**—UQL-DP57-1, the natural mold of a right pes preserved in situ.

**Type Locality, Horizon, and Age**—The topotype specimen is preserved in situ at UQL-DP57, in the intertidal zone of the Yanijjarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Referred Material**—Other tracks that can be assigned to *Yangtzeopus clarkei* include UQL-DP9-8, the natural mold of a left pes (Fig. 21D, E), preserved in situ at UQL-DP3, in the intertidal zone of the Yanijjarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, in the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Diagnosis**—Pedal tracks: medium- to large-sized (proximodistal length 24–32.9 cm, mediolateral width 19.7–20.5 cm), tridactyl, mesaxonic (digital impression extension to track length ratio 0.36), longer than wide, with an average maximum length to maximum width ratio of approximately 1.2–1.6; individual digital impressions proportionately elongated and broad, with the impression of digit III being the broadest impression (maximum digital impression width to track length ratio 0.20–0.33), with similar widths for the impressions of digits II (0.16–0.23) and IV (0.16–0.18); impression of digit III is the longest (basal digital impression length 61–81% of total track length), and the impression of digit II extends farther distally than digit IV relative to the principal track axis; axes of the impressions of digits III and IV typically intersect distal to the intersection of the axes of the impressions of digits II and III; total divarication angle between the axes of the impressions of digits II and IV 30–34°; divarication of the axes of the impressions of digits III and IV (20–23°) greater than divarication of axes of the impressions of digits II and III (10–11°); the distance between the proximal margin of

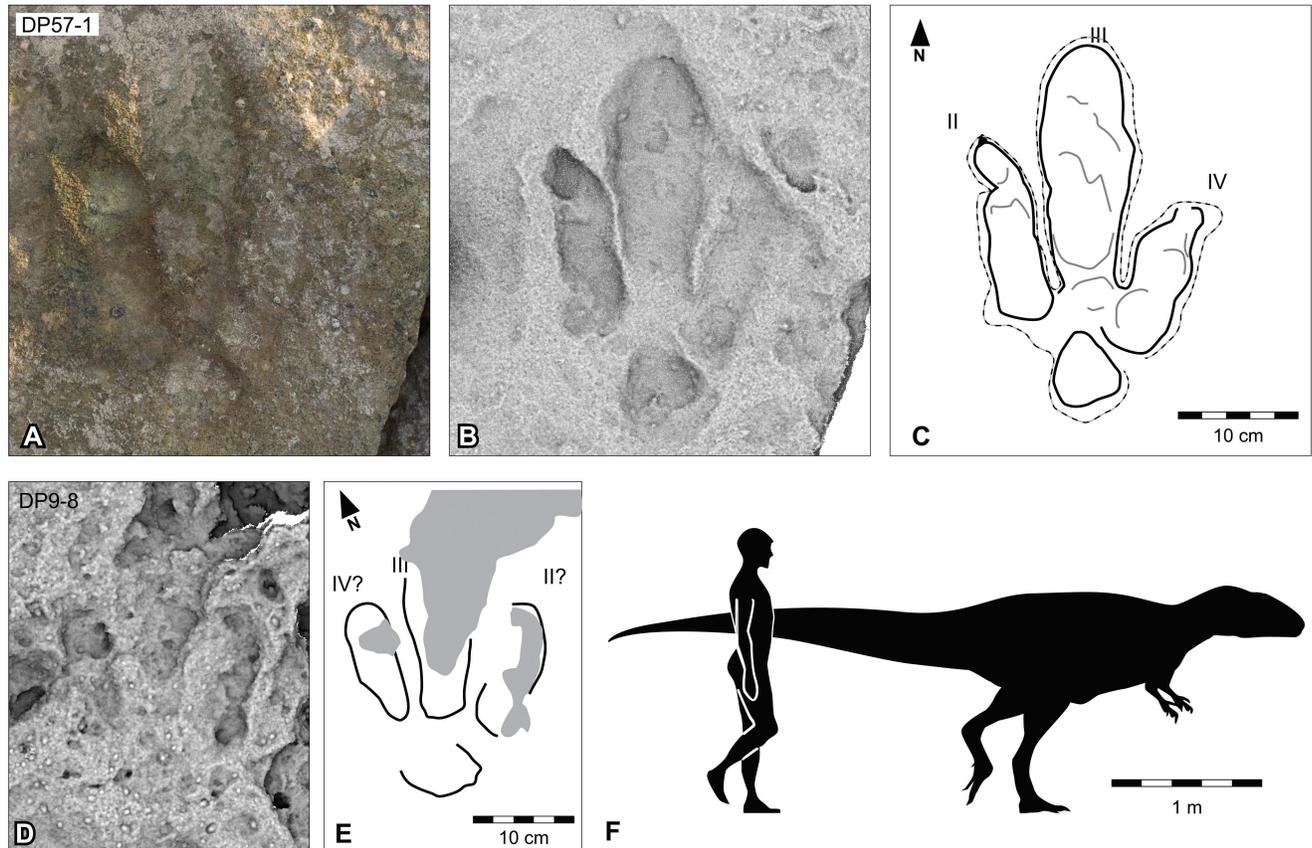


FIGURE 21. *Yangtzeopus clarkei*, ichnosp. nov., from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Right pedal impression, topotype UQL-DP57-1, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Possible right pedal impression, UQL-DP3-8, preserved in situ as **D**, ambient occlusion image; and **E**, schematic outline. **F**, silhouette of hypothetical *Yangtzeopus clarkei* trackmaker based on UQL-DP57-1, compared with a human silhouette. See Figure 19 for legend.

each digital impression and the metatarsodigital pad impression is greatest for the impression of digit III, then II, and the least for IV; possible digital pad formula 3/II, 2/III, 3/IV, with the pad impressions associated with the impression of digit IV being variably impressed; impression of unguis present distally on the impression of digit II; a separate, circular metatarsodigital pad impression occurs immediately proximal to the proximal end of the impression of digit IV and in line with the principal track axis, with a width that is approximately equivalent to the width of the impression of digit III; impression of the hallux absent.

**Description**—Although DP57-1 and DP9-8 are faintly impressed tracks, discernible in the field only under optimal lighting, both preserve fine details of the overall plantar morphology of the trackmaker. They are medium- to large-sized,

tridactyl, mesaxononic pedal tracks, longer than they are wide, with a length to width ratio of 1.6 for DP57-1 and one of at least 1.2 for DP9-8 (the distal portion of the impression of digit III on this track is not defined and appears to have been lost as a result of erosion). The impression of digit III is the longest on both tracks, followed by the impressions of digit II and then IV. The impression of digit II extends farther distally than that of digit IV relative to the principal track axis for both DP57-1 and DP9-8. Specimen DP57-1 has a digital impression extension to track length ratio of 0.36, with the basal length of the impression of digit III constituting 61% of the track length.

Specimen DP9-8 is at least 24.2 cm long (the distal-most portion of the impression of digit III on this track is not defined) and 19.7 cm wide, whereas DP57-1 is larger, being 32.9 cm long and

TABLE 6. Measurements of tracks assigned to *Yangtzeopus clarkei* ichnosp. nov., from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	II^III	III^IV	Total^	bdl II (II/L)	bdl III (III/L)	bdl IV (IV/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)
57-1	32.9	20.5	1.6	12 (0.36)	11	23	34	16.4 (0.50)	20.2 (0.61)	12.4 (0.38)	5.3 (0.16)	7.9 (0.24)	6.4 (0.19)
9-8	>24.2	19.7	>1.2	>8.6	10	20	30	16.7 (0.69)	19.7 (0.81)	13.8 (0.57)	5.5 (~0.23)	7.9 (~0.33)	4.4 (~0.18)

bdl = basal digital impression length; bdw = basal digit width; De = digit extension; II = digit II impression; III = digit III impression; IV = digit IV impression; L = track length; W = track width. ^ denotes angle between respective digital impressions.

20.5 cm wide. The digital impressions on DP57-1 are proportionately broad and of similar width along their lengths, with the impression of digit III being the widest and approximately 20% of the maximum track length, whereas those of digital impressions II and IV are both 16%. Although the digital impressions on DP9-8 are broad relative to length (digital impressions II, III, and IV have widths that are less than 23%, 33%, and 18% of the maximum track length, respectively), each digital impression narrows proximally. The impressions of digital pads faintly appear on the digital impressions of DP57-1 but are indistinct on DP9-8.

A single, circular metatarsodigital pad impression is present, separate from the proximal end of the impression of digit III, and in line with the principal track axis. On DP9-8, this is only faintly discernible. The divarication angles are very similar on both tracks, with an average of 21.5° for II<sup>^</sup>III (23° on DP57-1 and 20° on DP9-8), 10.5° for III<sup>^</sup>IV (11° on DP57-1 and 10° on DP9-8), and 32° for II<sup>^</sup>IV (34° on DP57-1 and 30° on DP9-8).

**Remarks**—Tracks assigned to *Y. clarkei* share a number of features with other Broome Sandstone tracks, including those assigned to *M. broomensis*. The range of track length and digital impression extension to track length ratios are similar, and the occurrence of the metatarsodigital pad impression immediately proximal to the proximal end of the impression of digit IV and in line with the principal track axis. The separate and circular impression of a metatarsodigital pad is also shared with some tracks attributable to *M. broomensis*. Also, both track types lack a hallucal impression. *Yangtzeopus clarkei* can nevertheless be distinguished from *M. broomensis* on account of the higher track length to track width ratio, smaller divarication angles, and much broader, subparallel digital impressions.

Published accounts of theropod tracks with blunt, broad digital impressions include the ichnogenus *Therangospodus* and *Eubrontes*. Tracks assigned to these ichnotaxa additionally resemble *Y. clarkei* on account of their small divarication angles (e.g., Lockley et al., 2000a:figs. 5, 6G; Mickelson et al., 2004:fig. 4; Xing et al., 2012:fig. 7a, e). The holotype of *T. oncalensis*, from the Berriasian(?) Oncala Group, Cameros Basin, Spain (Lockley et al., 2000a:fig. 7), shares similarities with *Y. clarkei* in terms of the impressions of digits II and IV being of subequal length and the impression of digit II extending farther distally than the impression of digit IV. However, *T. oncalensis* is distinct from *Y. clarkei*, with the former track having only minimal to no separation between the digital impressions proximally, larger divarication angles, a lack of a distinct metatarsodigital pad impression, a lack of digital pad impressions, and an acuminate distal outline to the impression of digit III. Although tracks assigned to *T. oncalensis* are highly variable with respect to these features (see Barco et al., 2006:figs. 5, 6), they are always distinguishable from *Y. clarkei*. Tracks assigned to *T. pandemicus* (Lockley et al., 2000a:figs. 5, 6G), as well as unnamed tracks associated with this ichnogenus (Mickelson et al., 2004:fig. 4; L.-D. Xing et al., 2012:fig. 7a, e), also resemble those of *Y. clarkei* in terms of their elongate, narrow track outline with broad blunt digital impressions. However, within this ichnospecies, there is also a large amount of variation in overall morphology, divarication angles, the degree of digital impression acumination, and the position of the impression of the metatarsodigital pad (e.g., shifting between a distolateral and a distomedial position). The elongate and broad digital impressions of both species of *Therangospodus* appear to be of similar width, which contrasts with both *Y. clarkei* and *Y. yipingensis*, where the width of digital impression is in the order III > II > IV. Because of this difference and the clear separation of the metatarsodigital pad and the digital impressions, and the impression of digit IV being more distally positioned relative to that of the impression of digit II, we regard *Y. clarkei* as being distinct from *Therangospodus*.

The large track size (i.e., >30 cm), digital impressions that are broad in proportion to their length, and small total divarication

angle (30–40°; Olsen et al., 1998) of *Eubrontes giganteus* are shared with the *Y. clarkei* track DP57-1. However, *Y. clarkei* differs in having a greater track length to track width ratio (1.6 compared with 1.4–1.5 for *Eubrontes*), and the single impression of the metatarsodigital pad that is in line and proximal to the impression of digit III as opposed to *Eubrontes*, which typically has two metatarsodigital pad impressions that align with the proximal portions of the impressions of digits II and IV.

A number of characteristics of *Y. clarkei* are much more consistent with the theropod ichnotaxon *Yangtzeopus yipingensis* from the Upper Jurassic or Cretaceous Lower Chiating Series (Jiading Group) of Sichuan Province, China (Xing et al., 2009b). These include the broad, distally rounded digital impressions all aligned subparallel, the digital impression length longest to smallest being III > II > IV, and the metatarsodigital pad impression being caudal to that of digit III.

*Yangtzeopus yipingensis* was initially interpreted as the tracks of a quadrupedal ornithischian (Young, 1960; Zhen et al., 1989). This was due to the close proximity of a small, tridactyl track with the larger pedal tracks. Young (1960) interpreted the former as a manual track, formed by the same, single trackmaker. Harris (1998) followed Young's (1960) interpretation when he identified an isolated, possible 'camptosaurid' pedal track from the Upper Jurassic Morrison Formation, Colorado, U.S.A., which he concluded closely resembled *Y. yipingensis*. However, in speculating on the possible identity of the trackmaker, Harris (1998) noted the track's theropod characteristics of high track length to track width ratio and small divarication angles. Xing et al. (2009b) reassessed the *Y. yipingensis* tracks, identifying them all as pedal tracks, the smaller track as made by a smaller bipedal theropod trackmaker, basing the evidence on the digital pad formula and the presence of ungal impressions.

We are in agreement with Xing et al. (2009b) that the *Y. yipingensis* trackmaker was most likely a theropod, and we also consider *Y. clarkei* of probable theropod affinity using the criteria of Wright (2004) of the high track length to track width ratio, overall track asymmetry, and the presence of narrow impressions of ungal. Additionally, a proximomedial indentation of the plantar surface is characteristic of theropods (Wright, 2004).

*Yangtzeopus clarkei* can be considered distinct from *Yangtzeopus yipingensis* based on the clear separation of the digital impressions and a well-defined metatarsodigital pad impression that is separate from the proximomedial and proximolateral portions of digital pad impressions. Additionally, most of the medial margins of the impressions of digits II and IV contact the impression of digit III to a lesser degree in *Y. clarkei* than in *Y. yipingensis*, and the divarication angle between the axes of the impressions of digits II and III is smaller than that of digits III and IV.

Similar to *M. broomensis*, tracks that can be assigned to *Y. clarkei* are rare within the study area (only two could be identified with certainty), and their occurrence was restricted to rock platforms at Walmadany. Long (1992b) mentioned the occurrence of a second kind of theropod track that was distinct from *M. broomensis* on account of its 'much larger central toe.' Although we were not able to locate this particular track in the study area, Long's comment on the size of the impression of digit III is reminiscent of *Y. clarkei*. Unfortunately, the precise location of the track described by Long (1992b) is not known.

#### BROOME THEROPOD MORPHOTYPE A (Figs. 22, 57C, 58C, S3; Table 7)

**Referred Material**—Four in situ tracks preserved in close association on a single isolated rock platform in the intertidal zone of the Yanijjarri–Lurujjarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia: UQL-DP25-1, the natural mold of a left? pes (Figs. 22A–E, 57C, 58C, S3) and additionally represented by WAM 12.1.2, a rigid polyurethane resin

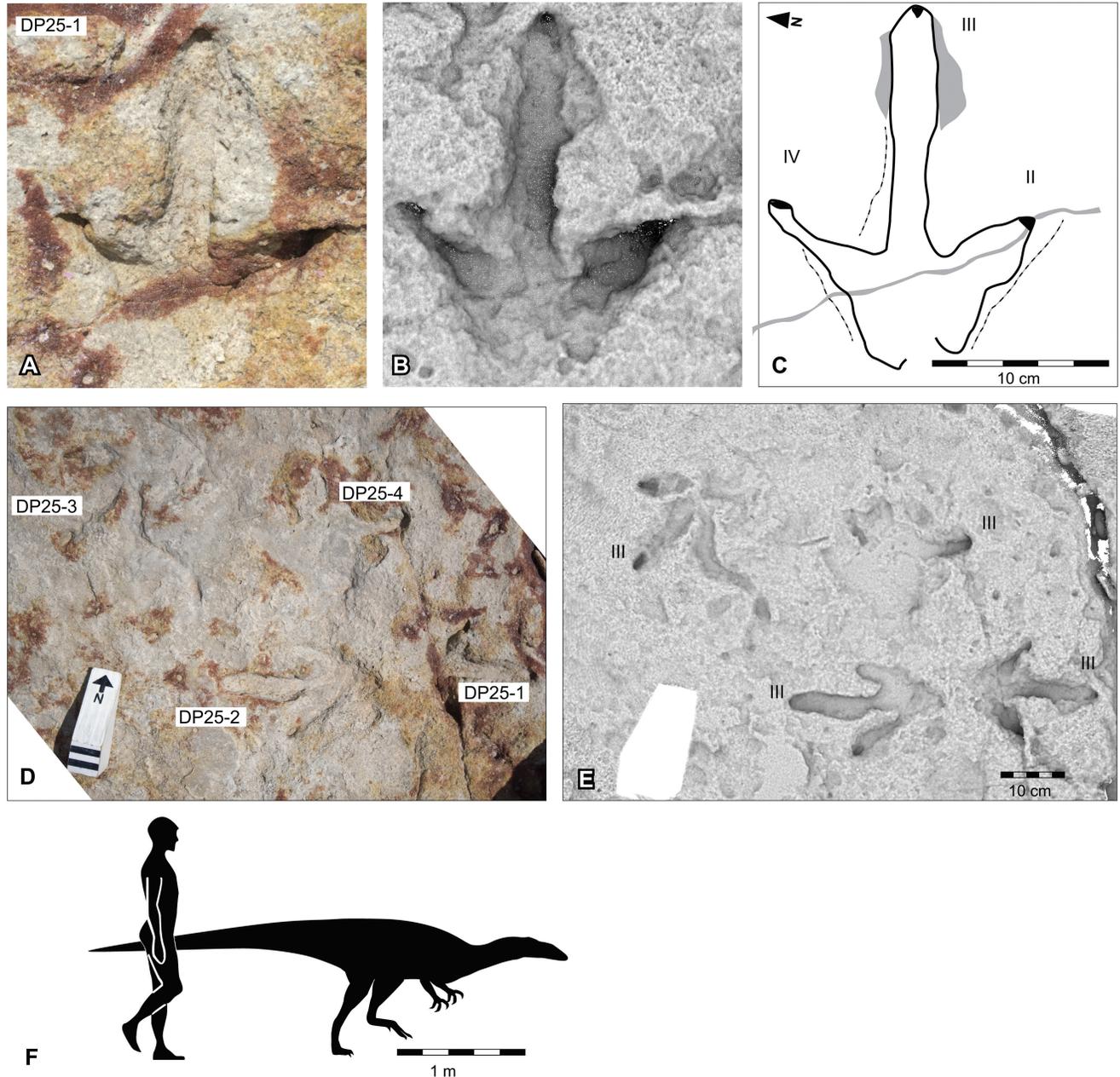


FIGURE 22. Broome theropod morphotype A, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Possible left pedal impression, UQL-DP25-1, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. The in situ platform containing four tracks as **D**, photograph; and **E**, ambient occlusion image. **F**, silhouette of hypothetical Broome theropod morphotype A trackmaker based on UQL-DP25-1, compared with a human silhouette. See Figure 19 for legend.

replica; UQL-DP25-2, the natural mold of a left? pes (Figs. 22D–E, 58C, S3) and additionally represented by WAM 12.1.2, a rigid polyurethane resin replica; UQL-DP25-3, the natural mold of a left? pes (Fig. 22D–E); UQL-DP25-4, the natural mold of a right? pes (Fig. 22D–E). (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality, Horizon, and Age**—The referred specimens are preserved in situ at DP25, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derive from

the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—Specimens DP25-1, DP25-2, DP25-3, and DP25-4 are all preserved on a single rock platform and, although weakly impressed and slightly weathered, display a suite of morphological features that allow them to be distinguished from all the other theropod tracks documented within the study area. All these tracks represent tridactyl and mesaxonic (digital impression extension to track length ratio between 0.43 and 0.63) left pedal tracks. All of the tracks border on our category of small to medium size (maximum proximodistal length

TABLE 7. Measurements of tracks assigned to Broome theropod morphotypes A and B, from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	II^III	III^IV	Total^	bdl II (II/L)	bdl III (III/L)	bdl IV (IV/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)
25-1	20.3	15.3	1.3	11 (0.54)	51	36	87	5.7 (0.28)	13.2 (0.65)	6.2 (0.31)	2.5 (0.12)	2.6 (0.13)	2.8 (0.14)
25-2	20.1	14.1	1.4	10.5 (0.52)	41	33	74	6.5 (0.32)	15.5 (0.77)	8.4 (0.42)	2.1 (0.10)	3.6 (0.18)	1.9 (0.09)
25-3	19	16	1.2	8.2 (0.43)	48	49	97	7.7 (0.41)	14 (0.74)	10.3 (0.54)	2.3 (0.12)	3.5 (0.18)	3.9 (0.21)
25-4	17.9	16	1.1	11.2 (0.63)	67	49	116	6.7 (0.37)	12.1 (0.68)	8.7 (0.49)	3.8 (0.21)	3.5 (0.20)	3.0 (0.17)
52-1	47	44	1.1	13.5 (0.29)	31	52	83	4.5 (0.10)	12.5 (0.27)	12 (0.26)	6.6 (0.14)	16.5 (0.35)	15 (0.32)

bdl = basal digital impression length; bdw = basal digital impression width; De = digital impression extension; II = digit II impression; III = digit III impression; IV = digit IV impression; L = track length; W = track width. ^ denotes angle between respective digital impressions.

20.3 cm, mediolateral width 16 cm), with three of the tracks (DP25-1, DP25-2, and DP25-3) showing a slight proximomedial indentation. The tracks are longer than wide, with a maximum length to maximum width ratio of approximately 1.1–1.4. The individual digital impressions are proportionately elongated and narrow, being 10–21% (II), 13–20% (III), and 8–21% (IV) of the digital impression width to track length ratio. The central digital impression (III) is the longest, with the basal digital impression length constituting approximately 65–77% of the track length. On tracks DP25-1 and DP25-4, the impression of digit II extends slightly farther distally than does that of digit IV, whereas the distal portion of digit II extends farther distally than that of digit IV in DP25-1 and DP25-4, and the opposite is the case for DP25-2 and DP25-3. The axes of the impressions of digits II and III intersect distal to the intersection of the axes of the impressions of digits III and IV for DP25-2, DP25-3, and DP25-4. The total divarication angle between the axes of the impressions of digits II and IV ranges from 33° to 67°, with the divarication of the axes of the impressions of digits III and IV of a narrower range (41–51°), yet overlapping the range of the divarication of the axes of impressions of digits II and III (33–67°). The metatarsodigital pad impression may be continuous with the proximal ends of the digit III and IV impressions and is more in line with the axis of the impression of digit IV than that of the principal track axis. Each track has one or more deeply impressed areas at the distal end of each digital impression that may represent impressions of unguals. The impression of a hallux is absent.

**Remarks**—These tracks represent the smallest theropod tracks thus far described from the Broome Sandstone. Broome theropod morphotype A differs from *Y. clarkei* and Broome theropod morphotype B on account of the narrow digital impressions. Of all the theropod tracks in the Broome Sandstone, they are most similar to *M. broomensis*. The elongate, narrow digital impressions, and the positional alignment of the metatarsodigital pad impression with the proximal ends of the impressions of digits III and IV are similar. The relative digital impression to track length ratio is variable yet overlapping between Broome theropod morphotype A and *M. broomensis* (II: 28–41% vs. 20–53%; III: 65–77% vs. 42–72%; IV: 31–54% vs. 30–56%, respectively). These tracks may potentially represent different sizes of the same ichnotaxon. However, Broome theropod morphotype A differs from *Megalosauropus* not only in smaller absolute size but also in the digital impression extension to track length ratio (43–63% vs. 34–47%, respectively) and total divarication angle (33–67° vs. 66–81°, respectively), although overlap in measurements does not make the two track types necessarily exclusive. Considering this, Broome theropod morphotype A may potentially represent tracks made by an earlier ontogenetic stage of the *M. broomensis* trackmaker.

We compared DP25-1, DP25-2, DP25-3, and DP25-4 with a suite of other theropod tracks from Australia and elsewhere in the world. Among described Australian theropod tracks outside of the Broome Sandstone, similarities are shared with

indeterminate theropod tracks from the Lower Jurassic Razorback Beds of the Fitzroy region in Queensland (Cook et al., 2010:fig. 7b) and unnamed theropod tracks from the Lower Cretaceous (middle–upper Aptian to lower–middle Albian; Wagstaff and McEwen Mason, 1989; Partridge, 2006) Eumeralla Formation of southern Victoria (Martin et al., 2012).

The slight track asymmetry and long extension of the impression of digit III beyond those of digits II and IV on DP25-1, DP25-2, DP25-3, and DP25-4 are similar to those of some of the indeterminate theropod tracks from the Razorback Beds (e.g., Cook et al., 2010:fig. 7b), as is the large divarication angle. The Razorback tracks have an impression along their proximal margin that is in line with the principal track axis and that Cook et al. (2010) refer to as a possible hallucal impression. A similar feature is displayed by *Irenesauripus mclearnii* (Sternberg, 1932) and *Grallator (Anchisauripus) madseni* (Irby, 1995), but it is not seen on DP25-1, DP25-2, DP25-3, and DP25-4.

Of all the described Australian theropod tracks, DP25-1, DP25-2, DP25-3, and DP25-4 compare best with the unnamed Aptian–Albian theropod tracks of the Eumeralla Formation, Victoria (Martin et al., 2012). The elongate, narrow digital impressions that lack digital pad impressions and the total digital divarication are similar, as is the digital impression extension to track length ratio (based on our own estimates from the published data and illustrations (Martin et al., 2012)). The two sets of tracks also overlap in terms of the relative narrowness of the digital impressions and the track length to track width ratio, but it is only upper values for the Eumeralla tracks that overlap with the lower values of the Broome tracks. Other differences include the smaller absolute size of the Eumeralla tracks, with a less variable total divarication angle.

Specimens DP25-1, DP25-2, DP25-3, and DP25-4 are distinct from '*Skartopus australis*' tracks (Thulborn and Wade, 1984) from the Upper Cretaceous portion (Cenomanian–Turonian; Tucker et al., 2013) of the Winton Formation, Queensland. This is due to their larger absolute size, the longer digital impression extension for the impression of digit III to track length ratio, and the greater angle of divarication. Of note, however, is the fact that Romilio et al. (2013) have provided evidence indicating that '*S. australis*' does not represent tracks of a theropod trackmaker but is instead a morphological variant of the ornithopod ichnotaxon *Wintonopus latomorum* (see below).

Specimens DP25-1, DP25-2, DP25-3, and DP25-4 share several features with *Zhengichnus jinningensis* (Zhen et al., 1986, 1989) of the Lower Jurassic lower Fengjiahe Formation of Jinning, Yunnan Province, China. The elongated, narrow digital impressions and relatively long impression of digit III impression and digital impression extension to track length ratio are similar, as is the wide total divarication. However, we consider DP25-1, DP25-2, DP25-3, and DP25-4 distinct from *Z. jinningensis* due to the less extreme digital extension extension to track length ratio and much smaller total divarication angle.

The track outlines of DP25-1 and DP25-2 show strong similarities to Middle Jurassic tridactyl tracks assigned to 'morphotype

Bvii' by Whyte and Romano (2003) and Whyte et al. (2007) from the Bathonian Scalby Formation and the Aalenian Lower Saltwich Formation of Yorkshire, U.K. Whyte and Romano (Romano and Whyte, 2003:fig. 20) do not specify the size of the illustrated track or whether it is a left or right imprint, but based on the linear proximolateral track margin, we suspect that the track pertains to a left pes. Our measurements of this track outline show that many of its features are consistent with Broome theropod morphotype A. These include being tridactyl and strongly mesaxonic (digital impression extension to proximodistal length approximately 0.53 compared with 0.52 and 0.54 in DP25-2 and DP25-1, respectively) and proportionately long and narrow (maximum proximodistal length to mediolateral width of approximately 1.56 compared with 1.4 in DP25-2). The impression of digit III on 'morphotype Bvii' is also very long relative to the total track length (75% of the proximodistal length [Romano and Whyte, 2003:212] compared with 77% in DP25-2), and all the digital impressions are proportionately narrow (width to track length ratios of II, III, and IV being 0.10, 0.14, and 0.17, respectively, based on our measurements of the schematic presented by Romano and Whyte, 2003:fig. 20). The Yorkshire track can be distinguished from Broome theropod morphotype A on account of a smaller divarication angle between the impressions of digits III and IV ( $15^\circ$  compared with  $41\text{--}67^\circ$  in Broome theropod morphotype A). Whyte and Romano (2003) and Whyte et al. (2007) suggest that the trackmakers responsible for these tracks were small gracile dinosaurs but do not specify if they were likely to have been theropods or ornithopods. We suspect that a theropod affinity for the Broome morphotype A trackmaker is more likely.

The only other ichnotaxon that we have found to resemble DP25-1, DP25-2, DP25-3, and DP25-4 is *Magnoavipes* (Lee, 1997; Lockley et al., 2001a) from the Lower Cretaceous (Cenomanian) Dakota Group, U.S.A. Shared features include the elongate digital impressions that have large divarication angles. The Broome tracks can be distinguished from *Magnoavipes* on account of their higher track length to track width ratio and a higher relative digital impression extension to track length ratio, from *M. lowei* due to the wider digital impressions, and from *M. caneeri* by lacking well-defined digital pad impressions (although this may be a function of the preservational condition of these traces).

To conclude, although DP25-1, DP25-2, DP25-3, and DP25-4 can be distinguished from other theropod ichnotaxa, we do not consider them well enough preserved to allow a sufficient number track features to be described. For these reasons we are hesitant to refer these tracks to a new ichnotaxon and instead assign them to Broome theropod morphotype A. As with other track morphotypes within the Broome Sandstone, it is hoped that future research will allow us to refine our understanding of the morphology of these tracks and potentially name them.

As with *M. broomensis* and *Y. clarkei*, tracks assignable to Broome theropod morphotype A were very rare within the study area, only occurring at one tracksite (DP25). We are not aware of these tracks occurring elsewhere along the Dampier Peninsula coastline within the Broome Sandstone. This may indicate that their trackmakers had a preference for a particular habitat type or, more likely, they were a rare component of the dinosaurian fauna. Additionally, the small size of these tracks may make them more difficult to find relative to other dinosaur ichnites, less likely to be preserved, and more likely to be lost to erosion.

#### BROOME THEROPOD MORPHOTYPE B (Figs. 23, 57D, 58E, S4; Table 7)

**Referred Material**—UQL-DP52-1, the natural mold of a left pes (Figs. 23A–C, 57D, 58E, S4; additionally represented by WAM 12.1.3, a rigid polyurethane resin replica). (From this

point onwards, excluding figures and tables, the UQL portion of the specimen number will be excluded in reference to these specimens.)

**Locality and Horizon**—The referred specimens are preserved in situ at DP52, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derive from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—Specimen DP52-1 is potential left pedal track of large size (proximodistal length 47 cm, mediolateral width 44 cm), tridactyl and mesaxonic (digital impression extension to track length ratio 0.29). The track is longer than wide, with a maximum length to maximum width ratio approximately 1.1. The digital impressions are triangular in outline, with the widest position for each at the hypex (the approximate maximum digital impression width to track length ratios of 0.14, 0.35, and 0.32 for the impressions of digits II, III, and IV respectively); the determination of digital impression numbering follows that for DP45-18 (see above). The impression of digit III is the widest digital impression, being moderately elongate, and the widths of II and IV are subequal, although II is short in length and IV is moderately elongated. The central digital impression (digit III) is the longest and extends over a quarter of the total track length, and the distal extension of the impression of digit IV is slightly greater than that of II relative to the principal track axis, although the impression of digit IV is much longer than that of digit II (26% and 10% of track total length, respectively). The axes of the impressions of digits III and II intersect distal to the intersection of the axes of the impressions of digits IV and III, and the total divarication angle between the axes of the impressions of digits II and IV is  $82^\circ$ , with the divarication of the axes of the impressions of digits IV and III ( $52^\circ$ ) greater than the divarication of the axes of the impressions of digits III and II ( $31^\circ$ ). The track outline is more indented proximomedially than proximolaterally. The proximal margin of the track is sublinear, broadening distally to form an overall subtriangular-shaped outline, with the rear part of the track presumably representing the impression of the metatarsodigital pad. Specimen DP52-1 has a fine sediment infill lining the entire bottom of the track, and as such digital pad impressions are not evident. Ungual and hallucal impressions are also absent. Much of DP52-1 is currently infilled with a thin layer of sand grains.

**Remarks**—There are a number of features of DP52-1 that lead us to consider the track to represent a distinct track morphotype. Among other tracks from the study area and the Broome Sandstone in general, DP52-1 resembles the theropod track of Broome theropod morphotype C (e.g., DP8-18[lp1]; see Fig. 24A–C), as well as a large ornithopod track, specifically one that is herein assigned to *Amblydactylus* cf. *A. kortmeyeri* (DP9-3; Figs. 44A–C, 61D, 62E, S15).

The overall size of DP52-1 is very similar to that of Broome theropod morphotype C (DP8-18[lp1]), with the length to width ratios being 1.1 and 1.04, respectively. These tracks have a distinct disparity between the shape and length of the impression of digit II (short, triangular-shaped) and that of digit IV (much more elongated with a more rounded distal end). The ratio of digital impression extension to maximum proximodistal length in DP52-1 is also similar to, but lower than, in DP8-18(lp1) (0.29 and 0.4, respectively). Specimen DP52-1 can be distinguished from Broome theropod morphotype C (DP8-18[lp1]) on account of the former having a less pronounced impression of digit III, a more caudally elongated proximal track margin, and differences to the overall shape of the digital impressions (particularly those of digit II and III).

Specimen DP52-1 is similar to *Amblydactylus* cf. *A. kortmeyeri* (DP9-3; Fig. 44A–C) on account of its similar length to width ratio (0.99 for DP9-3 and 1.1 for DP52-1; but see comments below on the extent of the heel region on these tracks),

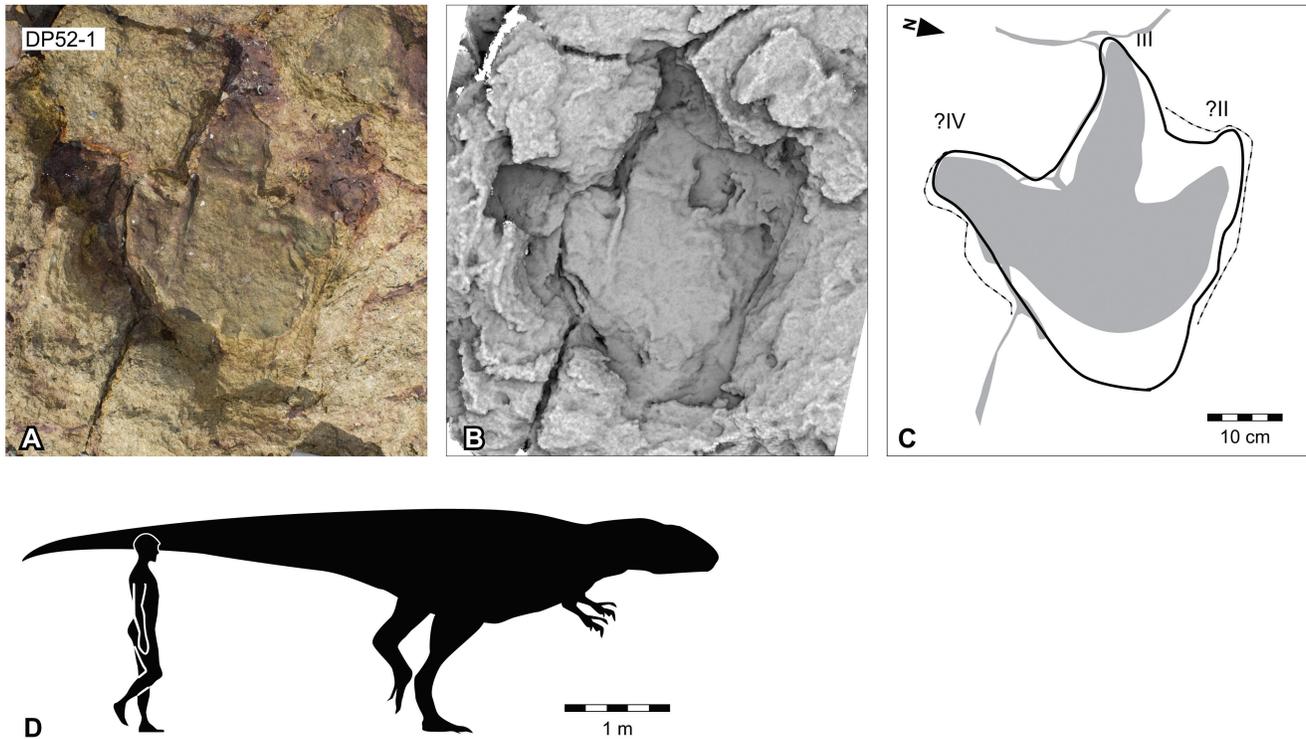


FIGURE 23. Broome theropod morphotype B, from Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Possible left pedal impression, UQL-DP52-1, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, silhouette of hypothetical Broome theropod morphotype B trackmaker based on UQL-DP52-1, compared with a human silhouette. See Figure 19 for legend.

triangular impression of digit III and the absence of digital pad impressions. At least two of the digital impressions on both sets of tracks have rounded distal tips (III and IV on DP52-1; II and III on DP9-3), with the other being more tapered, but we acknowledge that the numbering of the digital impressions on these tracks is tentative. The total divarication angle for DP52-1 ( $82^\circ$ ) is also similar to that for DP9-3 ( $80^\circ$ ). The digital impression extension to maximum proximodistal track length ratio for DP9-3 (0.34) is similar to that for DP52-1 (0.29). Despite these similarities, DP52-1 can be distinguished from DP9-3 by the proportionately much more elongated impression of digit IV and proportionately much longer heel region. The proximal margin of DP9-3 is also much more convex than the subtriangular outline displayed by DP52-1. On DP9-3, the impression of digit II extends farther distally than that of digit IV, whereas on DP52-1 the impressions of digits II and IV extend distally to approximately the same point. Thus, although there are some similarities, we consider DP52-1 to represent a morphotype that is distinct from that of the former tracks.

The broad-based, triangular impression of digit III of DP52-1 is reminiscent of the holotype of *Amblydactylus gethingi*, as is the elongation of the metatarsodigital pad impression shown as part of the external track outline (see Sternberg, 1932:fig. 8), although with regard to this latter feature, it cannot be determined if the track margin of DP52-1 represents the interior or exterior track margin due to it being partially infilled. Specimen DP52-1 differs from the *A. gethingi* holotype track with regard to the blunt impressions of digits II and IV, and large divarication of the impression of digit IV, but this may be a function of the

mobility of the trackmaker's pedal digits at the time of track preservation.

To conclude, although DP52-1 can be distinguished from other theropod ichnotaxa and shows some characteristics typically associated with theropod tracks, we do not consider it well enough preserved to allow a sufficient number track features to be described. For these reasons, we are hesitant to refer this track to a new ichnotaxon and instead assign it to Broome theropod morphotype B. As with other track morphotypes within the Broome Sandstone, it is hoped that future research will allow us to refine our understanding of the morphology of these tracks and potentially name them.

Tracks assignable to Broome theropod morphotype B are rare within the study area, with only one confirmed occurrence (DP52). We are not aware of these tracks occurring elsewhere along the Dampier Peninsula coastline within the Broome Sandstone Formation. This may indicate that their trackmakers had a preference for a particular habitat type or, more likely, they were a rare component of the dinosaurian fauna.

#### BROOME THEROPOD MORPHOTYPE C (Figs. 24, 57D, E, 58F, S5; Table 8)

**Referred Material**—UQL-DP6-3, the natural mold of a left pes preserved in situ (Figs. 24A–C, 57E, 58F), additionally represented by WAM 12.1.4, a rigid polyurethane resin replica; UQL-DP8-18, a partial trackway comprising the natural molds of two, or possibly three, consecutive tracks (Fig. 24G–I), including a left pes (UQL-DP8-18[lp1]) and at least one right pes

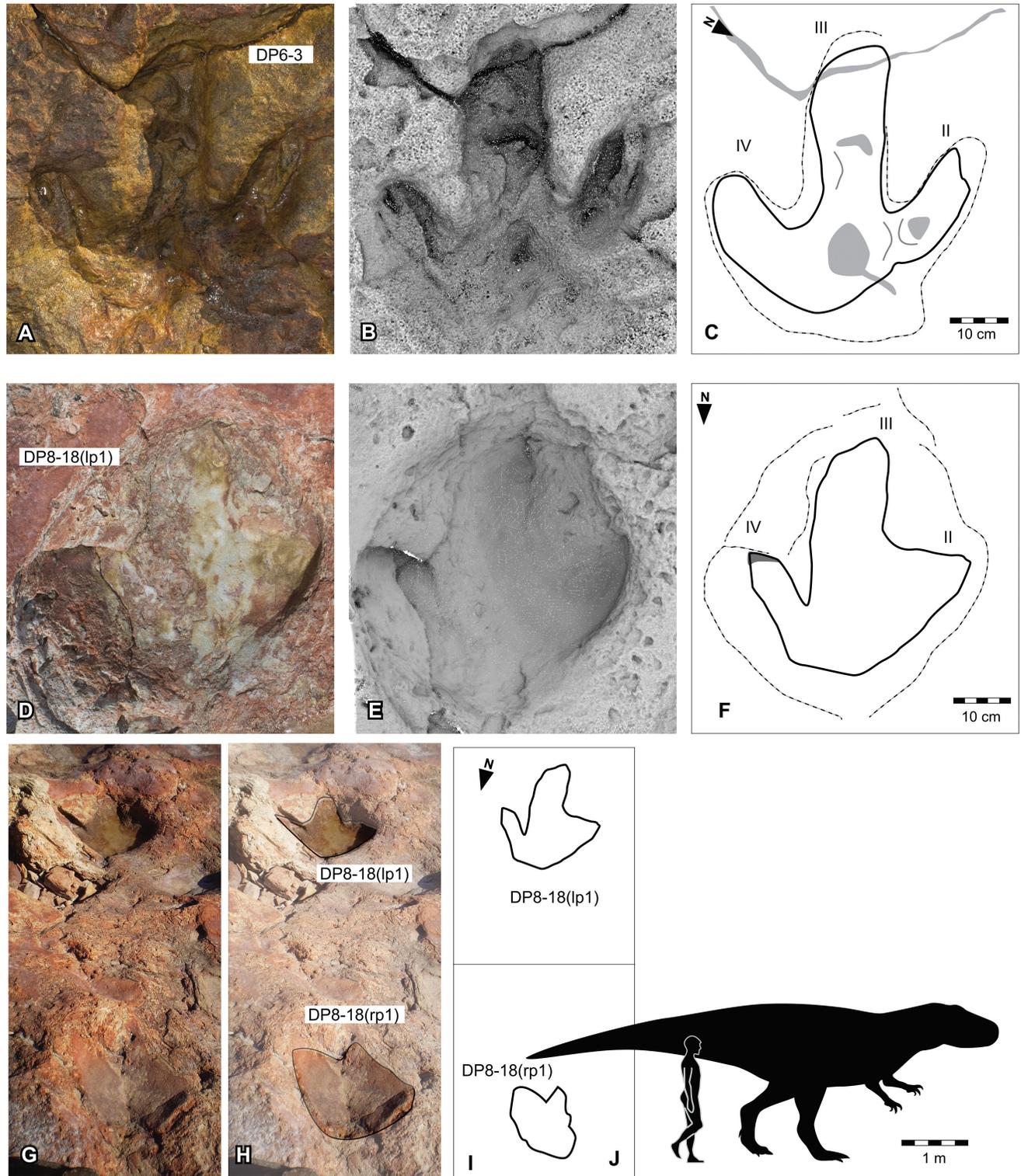


FIGURE 24. Broome theropod morphotype C, from the Yanijjarri-Lurujjarri section of the Dampier Peninsula, Western Australia. Left pedal impression, UQL-DP6-3, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Possible left pedal impression, UQL-DP8-18(lp1), preserved in situ as **D**, photograph; **E**, ambient occlusion image; and **F**, schematic interpretation. Trackway UQL-DP8-18, in **G**, oblique view photograph; **H**, with two tracks highlighted; and **I**, as a schematic map. **J**, silhouette of hypothetical Broome theropod morphotype C trackmaker based on UQL-DP6-3, compared with a human silhouette. See Figure 19 for legend.

TABLE 8. Measurements of tracks assigned to Broome theropod morphotype C, from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	II <sup>^</sup> III	III <sup>^</sup> IV	Total <sup>^</sup>	bdI II (II/L)	bdI III (III/L)	bdI IV (IV/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)	Pace (cm)	Stride (cm)
6-3	46.8	47.9	1.0	18.2 (0.39)	26	35	61	22.1 (0.47)	29.2 (0.62)	16.2 (0.35)	8.4 (0.18)	13.7 (0.29)	9.3 (0.20)	—	—
8-18(rp1)	—	—	—	—	—	—	—	—	—	—	—	—	—	140	295
8-18(lp1)	42	40.5	1.0	17 (0.40)	52	45	97	6.5 (0.15)	18.9 (0.45)	10 (0.24)	6.5 (0.15)	18.9 (0.45)	10 (0.24)	165	—
8-18(rp2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

bdI = basal digital impression length; bdw = basal digital impression width; De = digital impression extension; II = impression of digit II; III = impression of digit III; IV = impression of digit IV; L = track length; W = track width. <sup>^</sup> denotes angle between respective digital impressions.

(UQL-DP8-18[rp1]); UQL-DP8-18(lp1) is additionally represented by WAM 12.1.5, a rigid polyurethane resin replica. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality, Horizon, and Age**—The referred specimens are preserved in situ at DP6 and DP8, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derive from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—Specimen DP6-3 is a left pedal track of large size (proximodistal length 46.8 cm, mediolateral width 47.9 cm), tridactyl and mesaxonic (digital impression extension to track length ratio 0.39), with a pronounced proximomedial indentation. The track is slightly wider than long, with a maximum length to maximum width ratio of approximately 1.0. The individual digital impressions are proportionately elongated and robust, with the impressions of digits II and IV of similar width (approximate maximum digital impression width to track length ratios of 0.18 and 0.20) and the impression of digit III impression (approximate maximum width to track length ratio of 0.27) wider than the impressions of digit II and IV. The central digital impression (digit III) is the longest, with a basal length constituting 62% of the track length, and the impression of digit II extends distally farther than digit IV relative to the principal track axis. The axes of the impressions of digits II and III intersect distal to the intersection of the axes of the impressions of digits III and IV. The total divarication angle between the axes of the impressions of digits II and IV is 61°, with the divarication of axes of the impressions of digits III and IV (35°) greater than divarication of axes of impressions of digits II and III (26°). Although the fine details of the track appear to have been lost due to weathering, a digital pad formula of 1/II, 1/III, 1/IV can be discerned, with the proximal pad impression on digit II being smaller than the distal one. A metatarsodigital pad impression is also apparent, being continuous with the proximal ends of the impressions of digits III and IV more in line with the axis of the impression of digit IV than the principal track axis. The proximal end of the impression of digit II is separated from the metatarsodigital pad impression, creating a well-defined proximomedial indentation. Impressions of unguals and the hallux are absent.

Specimen DP8-18 is a trackway with two or possibly three consecutive pedal tracks. Of these, only DP6-18(rp1) is moderately well preserved and resembles DP6-3 in overall track morphology.

The overall track outline of DP8-18(rp1) is slightly longer than wide, with a maximum length to maximum width ratio of approximately 1.0. The impression of digit III is elongated and broad relative to the other digital impressions, and it is distally acuminate with a possible (eroded) impression of an ungual. The impression of digit III is broader when compared with DP6-3, and the hypex between the impressions of digits II and III of DP8-18(lp1) is less indented than in DP6-3, likely due to

preservational and/or erosional factors. On DP8-18(lp1), the total divarication angle between the axes of the impressions of digits II and IV is 97°, with the divarication of the axes of the impressions of digits III and IV (45°) greater than the divarication of the axes of the impressions of digits II and III (52°). The impression of digit IV of DP8-18(rp1) resembles that of DP6-3. On DP8-18(rp1), the approximate maximum digital impression width to track length ratios are 0.24, 0.15, and 0.45 for the impressions of digits II, III, and IV, respectively. The size of the impression of digit II appears much larger externally than it does internally, but part of the digital impression most likely represents a drag mark created as the toe slid through the sediment immediately prior to flattening out at the base of the track where its true outline is apparent. No impression of a hallux exists for this track, even though DP8-18(rp1) is approximately 10 cm deep.

Specimen DP8-18(lp1) precedes the above-described track but is only poorly preserved. It is revealed by an indentation of the track surface and has undefined track margins. The third potential track is very poorly defined, no more than a shallow amorphous depression, and may not be part of the trackway sequence. If, however, these collectively represent three tracks of a single trackway, then the pace measurements are 1.40 and 1.65 m, and the stride length is 2.95 m.

**Remarks**—Specimen DP6-3 bears a strong resemblance to tracks referred to as the ‘*Hispanosauropus*’ morphotype from the Upper Jurassic Lastres Formation of Asturias, Spain, by Avanzini et al. (2012:fig. 1C). These tracks share similarities in terms of their overall size, degree of mesaxony, proportionately elongated and broad digital impressions of unguals, and prominence of the proximomedial indentation. Specimen DP6-3 differs from tracks assigned to the ‘*Hispanosauropus*’ morphotype in Avanzini et al. (2012) in that it lacks impressions of unguals, and the impression of digit II extends farther distally relative to the principal track axis than does that of digit IV.

Although DP6-3 appears very similar to the ‘*Hispanosauropus*’ morphotype tracks shown by Avanzini et al. (2012), we are hesitant to assign the Broome track to this ichnotaxon on account of some of the differences that occur between it and illustrations of the holotype and paralectotype of the single *Hispanosauropus* ichnospecies, *H. hauboldi*. The holotype of *H. hauboldi* (Mensink and Mertmann, 1984) is a proportionately narrow track, with a maximum length to maximum width ratio of approximately 1.4, with only a slight degree of asymmetry, and the impression of digit II is longer than that of digit IV. The holotype of *H. hauboldi*, a topotype, is now considered lost, perhaps due to erosion (see Lockley et al., 2007), and the overall tridactyl appearance of the paratype specimen for this ichnospecies shown by Mensink and Mertmann (1984) is a result of cracks at the base of trace that form the third pedal track of an adjacent sauropod trackway (Lires et al., 2001). As such, the referral of the paratype specimen to *H. hauboldi*, and its bearing on the diagnosis of *Hispanosauropus*, is questionable. Consequently, Lockley et al. (2007) designated a new

paralectotype specimen for *H. hauboldi*. The DP6-3 track is distinct from the latter track in having impression of digits II and IV of unequal length, the distal portions of the digital impressions not acuminate, and the position of the metatarsodigital pad impression being placed more proximolaterally.

*Hispanosauropus* appears to be quite variable within the Lastres Formation in Asturias, Spain, and a reevaluation of this ichnogenus may be worthwhile in the future. The occurrence of specimens that are morphologically similar to DP6-3 (e.g., Lockley et al., 2007:fig. 5D, 2008a:fig. 7B; Avanzini et al., 2012:fig. 1C) indicates that the name *Hispanosauropus* could potentially be applied to the Broome tracks and it possibly represents the first record of a *Hispanosauropus*-like theropod track in Australia. However, until more specimens come to light to determine if the variability of the Australian tracks matches that of *Hispanosauropus*, we assign these tracks to Broome theropod morphotype C.

Specimen DP6-3 is potentially the largest theropod track thus far described from the Cretaceous of Australia. In the Jurassic (Bajocian–Bathonian)-aged Walloon Coal Measures of the Clarence–Moreton Basin, Queensland, theropod tracks of large size are known. This includes a photographed tetradactyl track that is stated to have a proximodistal length of about 2 feet (~61 cm) (Anonymous, 1952). Although this specimen was collected from the Balgowan Colliery and its current whereabouts are unknown, a second tetradactyl theropod specimen (QM F3702) from the same coalmine is of an equivalent proximodistal length (i.e., 60 cm). However, an even larger track (QM F12221) from the Westvale No. 5 Colliery, referred to the ichnospecies ‘*Changpeipus bartholomaii*’ by (Haubold, 1971), has a proximodistal length of approximately 70 cm and mediolateral width of approximately 57.5 cm. Although the latter track awaits a detailed analyses, and is currently considered a nomen nudum on account of lacking a formal description (Xing et al., 2009a:18), the overall track morphology differs from that of DP6-3.

Alongside other described Australian tracks, aspects of DP8-18(rp1) superficially resemble the schematics of several large tridactyl tracks that form a single trackway at Lark Quarry, southwest of Winton, central-western Queensland, in the Upper Cretaceous portion of the Winton Formation, initially referred to as cf. *Tyranosauropus* by (Thulborn and Wade, 1984). Although tracks within the Lark Quarry trackway are highly variable in terms of their overall shape, DP8-18(rp1) shares features with previously published outlines of tracks 1, 6, and 8 in terms of the strong degree of mesaxony as a result of an elongated impression of digit III (see Romilio and Salisbury, 2011; Thulborn, 2013). However, the highly simplified and stylized two-dimensional outlines of these tracks provided by Thulborn and Wade (1984) are a poor representation of their three-dimensional structure. A reevaluation of this trackway has shown that the best preserved tracks have rounded distal digital impressions and when combined with other traits are now referable to the ornithomimid ichnotaxon cf. *Iguanodontipus* (Romilio et al., 2014), making them markedly different from DP8-18(rp1).

McCrea et al. (2012:fig. 19e) illustrated DP6-3 and along with another large tridactyl track (located outside the current study area) identified it as pertaining to a large theropod trackmaker. Their figure was captioned as “cf. *Megalosauropus* or *Buckeburgichnus*” (see McCrea et al., 2012:table 6), but they did not state which tracks the assignments pertained to, nor did they elaborate on the reasons for these assignments.

Among other theropod tracks in the Broome Sandstone, DP6-3 shares some features with *Y. clarkei*. The elongate, broad digital impressions and the metatarsodigital pad impression that is aligned with the proximal end of the impression of digit IV are similar, as is the more distal positioning of the distal portion of impression of digit II relative to digit IV. However, DP6-3 can

be distinguished from *Y. clarkei* on account of the greater total divarication angle, the union of all digital and metatarsodigital pad impressions, and the proximolateral position of the metatarsodigital pad. Apart from their much larger overall size, DP6-3 and DP68-18(lp1) are similar to tracks assigned to Broome theropod morphotype A (e.g., DP25-1) in terms of their overall shape. However, DP6-3 and DP8-18(lp1) are absolutely larger, having proportionately broader digital impressions and a lower digital impression extension to track length ratio (0.39 and 0.4 for DP6-3 and DP8-18(lp1), respectively, compared with 0.43–0.63 for Broome theropod morphotype A).

Specimen DP8-18(lp1) also resembles theropod tracks in the Broome Sandstone assigned to *M. broomensis* (e.g., DP11-1; Fig. 20D). The digital impression extension to track length ratio displayed by DP68-18(lp1) is very similar to *M. broomensis* tracks (e.g., DP11-1: 0.42). Specimen DP8-18(lp1) also compares favorably with the majority of *M. broomensis* tracks in terms of overall size, and is similar to DP11-1 in that the metatarsodigital pad impression forms a large proportion of the track impression, and internal track details are absent. However, given that other tracks assigned to *M. broomensis* preserve well-defined digital pad impressions, the absence of this feature in DP11-1 is likely a preservational artifact and, as with DP11-18(lp1), may relate to the track having formed in heavily water-saturated sediment or subsequent erosional processes. This issue aside, DP8-18(lp1) and DP6-3 can be distinguished from *M. broomensis* on account of their proportionately much broader digital impressions.

Specimens DP6-3 and DP8-18 are the only tracks in the Yanijarri–Lurujarri section of the Dampier Peninsula that can be assigned to Broome theropod morphotype C, and we are not aware of any other tracks like them in other exposures of the Broome Sandstone. As such, we regard the trackmaker to be an extremely rare component of the area’s dinosaurian fauna.

## SAUROPOD TRACKS

*OOBARDJIDAMA FOULKESI*, ichnogen. et ichnosp. nov.  
(Figs. 25, 59A, 60A, S6; Table 9)

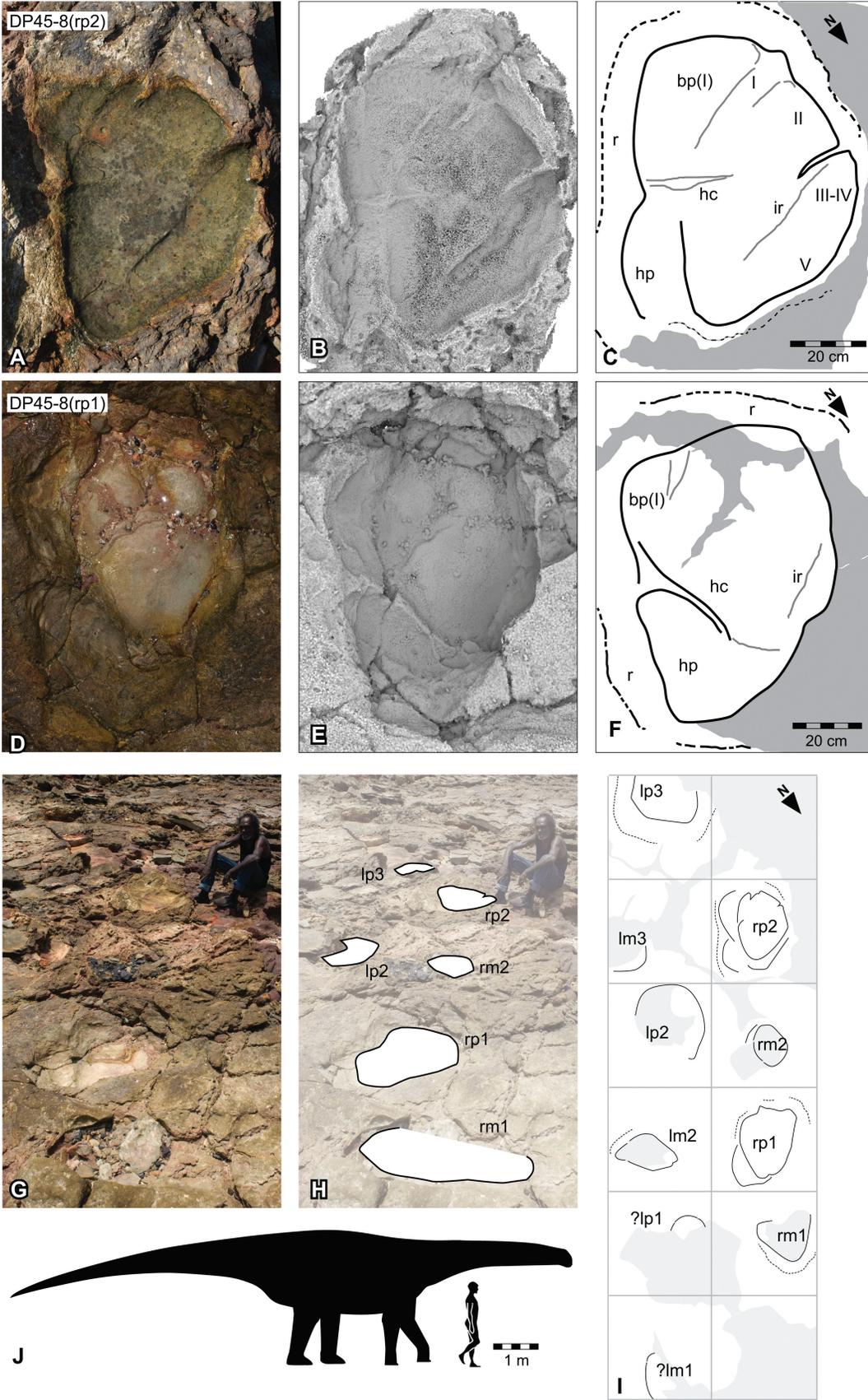
**Etymology**—‘Oobar’ [u: baɹ] and ‘djidama’ [dʲidama] are Nyulnyulan words for ‘little’ and ‘thunder,’ respectively, and are used in reference to the small size of the pedal impression relative to some of the larger sauropod tracks that occur in the Broome Sandstone. The ichnospecies name honors the late Paul Foulkes one of the Dampier Peninsula’s pioneering dinosaur trackers and the first person to recognize sauropod tracks in the Broome Sandstone.

**Holotype**—WAM 12.1.6, a rigid polyurethane resin replica of the natural mold of a right pedal impression (UQL-DP45-8 [rp2]; Fig. 25A–C).

**Topotype Material**—UQL-DP45-8, a single continuous trackway comprising 10 consecutive manual and pedal impressions. All tracks are preserved in situ as natural molds. (From this point onwards, excluding figures and tables, the UQL portion of the specimen number will not be included in reference to these specimens.)

**Locality, Horizon, and Age**—The topotype trackway is preserved at DP45 in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Diagnosis**—Trackway: weakly heteropodous (30–45%), variably medium- to wide-gauge trackways (sensu Romano et al., 2007), with inner trackway width of 30–50 cm; manual tracks positioned midway between fore and aft pedal tracks, and in line with the rear half of contralateral pedal tracks; manual tracks situated relatively medially, within pedal trackway width. Pedal impressions: large-sized (craniocaudal length: 70–85 cm), near-



piriform shape, but broadest across mid-track region, and with a lobed medial margin due to intersection of an asymmetrical heel pad crease; hallucal imprint widened medially by a bulbous cranial pad callosity; external outline of heel region semicircular as a result of occupation by a mediocaudal heel pad callosity; heel pad callosity medially offset and partitioned from fore-heel region of track by well-defined oblique ridge (~45–75° to the horizontal); acute fore-heel caudal margin of internal track exclusive of heel pad; pedal track angulation between 90° and 100°. Manual impressions: marginally wider than long (~115%); manual track angulation between 69° and 74°.

**Description**—*Oobardjidama foulkesi* is based on DP45-8, a southwest trending trackway that comprises eight consecutive distinct impressions and at least two other partial, somewhat ambiguous, indications of track positions (Fig. 25). In total, there are five pedal and five manual tracks, with each kind commencing and concluding with left impressions. Trackway DP45-8 is at least 6 m long. It is widest (2.1 m) between the second left manual impression (lm2) and the holotypic second right pedal impression (rp2), coinciding with a slight southward curvature in the trackway. Generally, DP45-8 is approximately 1.5 m wide at most other transverse chords along the trackway. The trackway occurs near the eroding margin of a ‘platform’ (an approximately level, large area of exposed tracking horizon), about midway along the littoral column within the intertidal zone. The presence of numerous mobile small boulders and pebbles and patches of lithified Quaternary beach gravel that blanket depressions at the site render some of the track impressions difficult to discern. Although the morphology of DP45-8 is well exemplified by two right pedal impressions (rp1 and rp2), the first, third, and last pedal impressions (lp1, lp2, and lp3, respectively) are only partially emarginated and exposed. Of the manual impressions, none are well exposed, with only rm2 being fully emarginated. With the exception of rp2, most impressions of DP45-8 are concealed by lithified beach gravel, eroded at their margins, or truncated by breakage and cracks; or impacted by a combination of these issues. This is especially true for the manual impressions, which, apart from their general size and placement relative to other impressions, show little in the way of discernible morphology.

The best-preserved single track of *Oobardjidama foulkesi* is DP45-8 (rp2), the holotypic impression (Fig. 25A–C), which has a maximum craniocaudal length of 71 cm and a mediolateral mid-width of 56 cm. The impression is situated flush against the southwestern ledge of the preserved platform of the tracking horizon, with the surface area just external to the northern track margin already showing erosion (Fig. 25A, B). Internally, rp2 is exceptionally well preserved, with the floor of the impression being appreciably smooth compared with the surface of the substrate outside of the pressure rims. As is often the case with bowl-shaped depressions found in the medium to high elevations within the intertidal zone of the study area, discoloration occurs along the inner rim walls of rp2, which mirrors some of the contours of the internal shape (Fig. S6). This is probably due to episodic pooling and drying of saltwater within the impression (Fig. 25A, showing the impression partially filled with water).

Among sauropod pedal impressions, DP45-8 (rp2) seems unusual in its morphology of the internal track floor. It comprises a well-delineated, triangular sub-impression, which contains

about 75% of the track area, nested within a larger near-piriform impression bounded by an almost enclosed expulsion/pressure rim (Fig. 25). The inner sub-impression is broadest cranially (along the western margin), where traces of the digital arcade are apparent, and tapers to an acute heel end caudally. The eastern margin of the central impression is not completely emarginated, because rp2 extends medially as paired lobed impressions, which have been shallowly impressed relative to the central inner impression.

A continuation of the cranial pressure rim medially, up to the damaged caudal margin, demonstrates that these medial lobed impressions represent part of the principal step trace of the trackmaker, rather than being extramorphological traces (Thulborn, 2004). The bulbous medial extensions represent medialward bulging of discrete zones of the plantar padding, formed during the trackmaker’s in-step. Their atypical form in rp2 is corroborated by analogous morphology in rp1, and the cranial-most of the paired bulges also occurs less prominently in other unnamed sauropod pedal impressions from the study area (see Broome sauropod morphotype E for comparative remarks). There may be multiple rationales for the manufacture of such an atypical trace as rp2, including biomechanical elaborations, but these are outside the present descriptive scope (see additional remarks for Broome Sauropod Morphotype E). In the descriptions below, the medial lobed impressions are considered bulged pad or callosity impressions of the digitometatarsal and heel pads, respectively.

The medial margin of the inner sub-impression is convex and is traversed mid-length by a short ridge that extends inwardly from the portion of rim defining the cranial-most bulged impression. Craniomedially, a short ridge extending from the cranial margin distinguishes a narrow area within the bounds of the inner sub-impression. This area probably represents an impression of digit I. The narrow shape, with cranial acuity, perhaps indicates an extended posture for the hallucal digit. Although the overall impression for rp2 is cranially convex, the inner sub-impression exhibits a distinctly straight cranial margin, which partly encloses a box-like internal area. The latter is interpreted as the impression of digit II, which might have been flexed laterally during the step of rp2 (on account of the straight margin being the lateral side of the flexed digit).

A second interdigital-separating ridge extends caudally from the craniolateral margin of rp2. This appears to distinguish the impression of digit II from the lateral digits (III–V), traces of which cannot be clearly segregated. The undulating lateral margin of rp2 is mostly convex, with a slightly concave profile close to the caudal end (Fig. 25C). On the floor of the inner impression, a craniocaudally trending elongate crease is present, which seems to have its origin at the terminal end of the prominent interdigital-defining ridge. The crease approximately bifurcates much of the inner impression into medial and lateral components, and the floor of the inner impression is deepest surrounding the caudal termination of the crease.

Of the two medial shallower sub-impressions in rp2, the cranial-most one—an impression of a bulged pad of the plantomedial surface of digit I in the trackmaker—occupies a greater area. It is strongly convex, approximately 50–55% of the craniocaudal length of the entire impression, and is medially bracketed by an elevated wall of pressure rim. The caudal limit of the bulged pad

← FIGURE 25. *Oobardjidama foulkesi*, ichnogen. et ichnosp. nov., from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Right pedal impression, UQL-DP45-8(rp2), preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Right pedal impression, UQL-DP45-8(rp1), preserved in situ as **D**, photograph; **E**, ambient occlusion image; and **F**, schematic interpretation. **G** and **H**, Goolarabooloo Maja Richard Hunter alongside the topotype trackway, UQL-DP45-8, viewed facing towards the south, with position of selected tracks indicated. **I**, schematic map. **J**, silhouette of hypothetical *Oobardjidama foulkesi* trackmaker based on UQL-DP45-8, compared with a human silhouette. **Abbreviations:** **bp(I)**, bulged pad/callosity associated with digit I; **hc**, heel-demarcating crease; **hp**, caudal heel pad/callosity; **I–V**, digital impressions I, II, III, IV, and V, respectively; **ir**, internal ridge; **r**, expulsion rim. See Figure 19 for legend.

TABLE 9. Measurements of *Oobardjidama foulkesi* ichnogen. et ichnosp. nov., from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	P length (cm)	P width (cm)	P L/W	M length (cm)	M width (cm)	M L/W	MID (cm)	HR (%)	P track rotation	P pace (cm)	P stride (cm)	M pace (cm)	M stride (cm)	P PA
45-8(lm1 + lp1)							—	—	—	—	—	—	—	—
45-8(rm1 + rp1)	77	59	1.31	40	53	0.75	(38) 35	40.5 (33.6)	10.9°	>116	—	<170	—	~105°
45-8(lm2 + lp2)	78	68	1.15	42	44	0.95	(~40–50) ~68	~35	—	156	195–230	160	195–220	99.6°
45-8(lm2 + rp2)	71	56	1.27	41	47	0.87	(23) 67	29.9	11.6°	~137	219	156	190	104°
45-8(lm3 + lp3)							(—) ~80–90	—	~0°	167	230	163	193	—
							(—)							

HR = heteropody ratio—calculated from MP couplets in the sequence, with corresponding PM couplet ratios listed in parentheses; M = manual impression MID = minimal interautopodial distance (as PM couplets, with corresponding MP couplets [pedal impression of that data row + succeeding manual impression] listed in parentheses); P = pedal impression; PA = pace angulation. Pace distances are between the track of the same data row and the preceding track; stride distances are between the track listed in the same data row and the preceding track of the same autopodium (i.e., two data rows before it); pace angulation at a given data row is the angle between the track listed in that row, and of the tracks listed in preceding and succeeding data rows.

impression is defined by both a notched constriction along the external pressure rim and a laterally extending internal transverse crease.

Although the sub-impression simply represents a functional extension of digit I, it is also separately defined in rp2 via a sub-parallel internal ridge on the floor of the impression, which is concomitantly the medial edge of the inner central impression. The equivalent demarcating feature in rp1 occurs in a more typical format—as a shorter ridge extending caudally from the cranial margin. In this respect, rp2 is more similar to isolated pedal impressions DP14-9 (Fig. 34A–C) and DP30-1 (Fig. 34D–F), both of which are referred to Broome sauropod morphotype E (see below). The presence of the internal partition defining the bulged impression in rp2 (and these other impressions), and the change in depth either side of it, suggests that the in-step of the trackmaker produced discrete, phased traces of a dynamically composed in vivo autopodium. The main difference in the shape of the digit I-attending bulged impression of *Oobardjidama* (DP45-8[rp1, rp2]) and that displayed by DP14-9 and DP30-1 is that in the former, the impression is craniocaudally asymmetrical and projects more medially, whereas in the latter it is narrower and more caudally extensive.

The most unusual and defining feature of *Oobardjidama* is the form of the caudal-most medial bulged sub-impression, which seems different between rp1 and rp2 (Fig. 25), but in fact shares parallel features of shape and definition. In both rp1 and rp2, the craniomedial origin of the sub-impression is defined by an inward kink (an acute concavity) of the external medial pressure rim; this extends on the internal track floor of rp1 as a continuous ridge that links obliquely to the lateral margin, whereas in rp2 the internal ridge is disconnected from the notch of the outer medial pressure rim. The sub-impression in both tracks is elongate (about 40% of total pedal impression length) and is aligned (long axially) at about 20–30° relative to the long axis of the entire impression.

Without drawing upon comparative specimens, an explanation for the formation of the caudal oblique sub-impression in *Oobardjidama* is not readily apparent. A similar internal crease-like partition occurs within the caudal area of pedal impressions referred to Broome sauropod morphotype A, below. However, the structure in morphotype A is transversely aligned, not obliquely as in *Oobardjidama*. In other specimens (referred to morphotypes C and E), lateral and medial constrictions of the impressions occur caudally (as inward notches of the pressure rim). All these specimens demonstrate, in one way or another, the presence of a compartmentalized ‘heel’ impression, which reflects the morphology of the plantar surface of the pes (see

respective remarks on other morphotypes). Uniquely, the impression for the heel pad in *Oobardjidama* appears to be markedly offset medially.

Whereas the form of the heel sub-impression in rp1 is closer to a more typical shape and alignment (e.g., Broome sauropod morphotype A; *Brontopodus birdi* [Farlow et al., 1989]), that of rp2 appears to be exaggerated further medially. However, both impressions rp1 and rp2 are rotated laterally (the rotation in each is ~30° relative to the trackway alignment), which thus overemphasizes the medially fixated form of the sub-impression. Another factor acting on the shape of the sub-impression in rp2 is that the tracking surface is slightly eroded caudal to the impression, with a segment of caudal pressure rim being incomplete (Fig. 25).

The first right pedal track of DP45-8, rp1 (Fig. 25A–C), is preserved as a topographically deeper impression than rp2 and is also present marginally downslope upon a shallowly undulated tracking horizon (Fig. 25G, H). As a result of rp1 being more regularly inundated with water and debris, it is a comparatively more eroded impression than rp2 both on the internal track floor and externally. The pressure rim is broad and weathered cranially and medially, but it is missing laterally due to damage (at a shallow level) of the substrate surface (Fig. 25E, F).

Track DP45-8 (rp1) is piriform in outline, as is typical for sauropod pedal tracks. The cranial margin is convex, with a cranial-most prominence occurring centrally, rather than medially as in rp2. The cranial half of the impression is rhomboidal in shape, due to the parallel medial and lateral margins. In the caudal half, the impression tapers to produce a semi-acute caudal heel. The heel pad sub-impression in rp1 is fully enclosed within a continuous caudal rim, fully separated from the cranial digitometatarsal sub-impression by an initially prominent medially originating ridge that weakens laterocaudally. The overall narrowing shape of the heel region of rp1 is suggestive of a similar shape in rp2 where that specimen completely rimmed.

Few traces of the digits are evident in rp1, unlike in rp2. Although the shallow craniomedial pad bulge/callosity of digit I is discernible by a short ridge on the track floor, signs of demarcation of other digits are absent. Laterally, a short axially aligned ridge is present upon the floor of the impression. This appears to be the equivalent structure to the much more extensive ridge in rp2. In both impressions, the internal ridge terminates cranial to the heel-demarcating ridge. In rp1, it is relatively closer to the lateral margin and appears to mirror a slight prominence in the mid-lateral margin of the impression. The bulge most likely represents an indication of the position of digit V in rp1, where it lies just cranial to a notch defining the beginning of

the heel region (Fig. 25F). This follows very similar morphology in many other sauropod pedal impressions, which often have a subtle lateral prominence as the impression of digit V (Farlow et al., 1989:380; as illustrated in Meyer et al., 1994).

The remaining pedal and manual impressions of DP45-8 are useful only insofar as they provide trackway parameter information (Table 9; Fig. 25I), supporting the characterization of *Oobardjidama*. But, given the poor preservation of the remaining impressions, coupled with the short sequence of tracks (i.e., few data points), most of the determinable parameters of the topotype trackway should be interpreted prudently, and as being supplementary towards diagnosing *Oobardjidama* (which is instead primarily based on a distinct pedal impression morphology).

Trackway DP45-8 is a wide-gauge form (Farlow, 1992). The internal margins of the left and right pedal impressions do not overlap the trackway midline and are separated by 10–20 cm. The pedal trackway ratio (Romano et al., 2007) varies between 34% and 45%, where it can be calculated; thus, DP45-8 can also be considered as either ‘medium’ or ‘wide’ in the gauge categories suggested by Romano et al. (2007).

The measurable pedal stride lengths could only be ascertained twice: between lp2–lp3 and rp1–rp2. They are relatively short (148 and 144 cm, respectively), approximately twice the average pedal impression length. Although this proportion is closest to *Polyonyx gomesi* when comparing with topotype trackways of other taxa (Santos et al., 2009), stride lengths are partially a function of the speed of progression (Alexander, 1976) and consequently have little bearing on ichnotaxon diagnosis.

With regard to pedal track alignment, rp1 and rp2 are orientated to face only slightly more westwards of the southwest tracking direction of the full trackway. The left pedal impressions are all preserved as incomplete subcircular rims, lacking finer details of digital or padding sub-impressions. Among them, only lp3 appears to indicate an orientation, being aligned southwards. Thus, at least three pedal impressions support a small degree of outward rotation of the pes in the *Oobardjidama* trackmaker. No information on inferred manual track alignment could be collected given the preservation.

The manual impressions, mostly indicated by positions of fragmentary borders, are variably ovate (either kidney-shaped: rm1, lm2, lm3; or circular: rm2). The manual tracks with intact outlines, rm1 and rm2, are relatively large with respect to rp1 and rp2 (43% and 28% heteropody). If the central (inner) impression of rp2 only is considered (as being an initial trace of an autopodium/substrate interaction), the ratio between it and rm2 is 53%, which is an exceedingly mild heteropody (but is common in some latest Cretaceous trackways, e.g., Lockley et al., 2002a). Because of the generally poor preservation of the manual tracks, these heteropody estimates should be interpreted cautiously.

With regard to position of the manual tracks, all impressions are well separated from the cranial and caudal margins of the pedal impressions—usually 23–38 cm cranial to, and 39–67 cm caudal to, sequential pedal impressions. In most instances, they are located slightly lateral relative to pedal impressions with respect to the trackway midline. Between rm1 and rp2, the fore and aft interautopodial gaps are approximately equal, which means that each manual impression is intermediately positioned between two pedal impressions. However, for short trackways such as lp2–lm3–lp3, variability interautopodial gap length is a useful diagnostic feature. In this segment, a short PM gap (lp2–lm3) is followed by a long MP space (lm3–lp3), which is the typical pattern in most sauropod trackways globally. Relative to an imaginary trackway midline, the manual impressions have variable contralateral positions. None appear medial relative to any immediately sequential pedal impression, but some are relatively laterally placed.

**Remarks**—As we have detailed, the holotypic pedal impression of *Oobardjidama foulkesi* (DP45-8[rp2]) presents a morphology that not only is unique among sauropod pedal tracks in

a global context but also provides some insight regarding the pedal surface anatomy of its trackmaker. The morphology and resultant interpretation of the second adequately preserved pedal impression in the topotype trackway, rp1, is largely consistent with that of the holotype. When coupled with the trackway pattern data, we conclude that DP45-8 characterizes a novel sauropod track type, one that is demonstrably unlike other well-diagnosed ichnotaxa and thus warrants a formal label.

*Oobardjidama* builds on the roster of sauropod ichnotaxa globally, many of which are augmented by referred specimens from an array of localities, depositional settings, and styles of preservation (Farlow, 1992; Lockley et al., 1994b; Mannion and Upchurch, 2010; Falkingham et al., 2012). However, some sauropod ichnotaxa in the past have been inadequately diagnosed, differentiated, or described, whereas other non-type track specimens have occasionally been referred to an ichnotaxon based on questionable justification (for previous systematic reviews, see Farlow et al., 1989; Lockley et al., 1994a). In light of this existing systematic framework, we compare *Oobardjidama* thoroughly with other sauropod tracks, providing an outline of differentiations, where present. Sauropod trackways have been recorded from the Late Triassic (Lockley et al., 2006a) to the latest Cretaceous (Lockley et al., 2002a; Vila et al., 2008). Hence, we segregate our comparisons into distinct temporal-morphological categories: (1) quadrupedal, purportedly sauropod Upper Triassic–Lower Jurassic trackways that may represent early and definite non-neosauropod sauropods (i.e., non-gravisaurian sauropods, or true gravisaurians [Allain and Aquesbi, 2008]); (2) narrow-gauge sauropod trackways from the Middle Jurassic onwards, including those considered *Breviparopus/Parabrontopodus*-like; (3) wide-gauge *Brontopodus*-type trackways; and (4) wide-gauge *Titanopodus*-type trackways). In the following remarks, no comparisons are made to the other sauropod tracks from the Yanijarri–Lurujarri study area (Broome sauropod morphotypes A–E)—because the subsequent descriptions of these specimens contain reference to *Oobardjidama*. We afterwards discuss the identity of the potential trackmaker of *Oobardjidama*-type tracks.

*Early Sauropod Tracks (Upper Triassic–Lower Jurassic)*. Among the quadrupedal ichnomorphs referred to early sauropodomorph trackmakers, it is not always clear which relate exclusively to non-sauropod or sauropod producers (Lockley et al., 2006a). This is expected given that the earliest sauropods that were contemporaneous with these tracks (non-gravisaurian taxa) presented a mélange of transitional autopodial characters, which would manifest in their track expressions (Avanzini et al., 2003; Xing et al., 2016b). Whereas quadrupedal trackways of *Navahopus falcipollex* and *N. coyoteensis* were evidently produced by non-sauropod sauropodomorphs based on a compatible manual track morphology (Baird, 1980; Milàn et al., 2008), those of *Eosauropus cimarronensis*, *Lavinipes cheminii*, and *Liujianpus shunan* (Avanzini et al., 2003; Lockley et al., 2006a; Xing et al., 2016b) may have had their origins amongst non-gravisaurian sauropod trackmakers.

*Tetrasauropus unguiferous* (Ellenberger, 1972; Lockley et al., 2001b; Wilson, 2005; Wright, 2005) seems to relate to a quadrupedal sauropodomorph trackmaker, but it is unknown if that specifically was a non-sauropod track. The manual and pedal digital impressions of *Tetrasauropus* include features that are similar to *Navahopus* (Milàn et al., 2008), suggesting a non-gravisaurian producer for them. *Lavinipes* and *Liujianpus* are well-diagnosed and illustrated ichnotaxa known from single Lower Jurassic localities in Italy and China (Avanzini et al., 2003; Xing et al., 2015c), but *Eosauropus* is the most abundantly represented potential early sauropod ichnomorph, with referable trackways from multiple localities in several Late Triassic units of the southwestern U.S.A. and Wales (Lockley et al., 1996b, 2001b, 2006a).

*Oobardjidama* differs from well-diagnosed quadrupedal sauropodomorph–early sauropod ichnotaxa (*Navahopus* spp., *Tetrasauropus*, *Lavinipes*, *Liujianpus*, and *Eosauropus*) of Upper Triassic–lowermost Jurassic outcrops (Hettangian–Sinemurian stages) in the following aspects:

- (1) Size. With a single exception (see below), the largest pedal impression of a Late Triassic–earliest Jurassic (pre-Pliensbachian) ichnomorph putatively formed by a basal sauropod does not exceed 50 cm in length. The pedal track length in the topotype of *Lavinipes* is 43 cm (Avanzini et al., 2003), with all tracks of *Navahopus* and *Eosauropus* being under 25 cm.
- (2) Morphology of pedal impressions. Pedal tracks of *Oobardjidama* exhibit a bulged extension attending the medial margin of the impression of digit I and an asymmetrically defined heel sub-impression. The combination of these features is lacking in the pedal tracks of *Navahopus* spp., *Tetrasauropus*, and *Lavinipes*. However, in *Liujianpus*, the digital impressions show comparatively shallow hypices and have an increased symmetry in length of extension, compared with the other early ichnotaxa. A notch in the medial pedal track margin, caudal to the impression of digit I, connects with a distinct transverse internal crease (Xing et al., 2016b) that compartmentalizes the pedal track into cranial (digital) and caudal (heel) sub-impressions (as also occurs in isolated pedal impressions from within our study area). These characteristics (Wilson, 2005:table 1), which lead to a piriform pedal track profile, reemphasize *Liujianpus* as a transitional sauropod ichnomorph—perhaps relating to a trackmaker with a ‘more gravisaurian-like’ body plan than those of the other mentioned ichnotaxa.
- (3) Gauge, pace angulation, heteropody, and individual pedal track axes. *Oobardjidama* is a wide-gauged ichnomorph, contrasting with the mainly narrow gauges in the aforesaid early sauropodomorph quadrupedal ichnotaxa, with the exception of *Liujianpus*. The Chinese form is partially narrow-gauged, but sections of both the holotype and paratype trackways show pedal impressions that do not cross the trackway midline (Xing et al., 2016b). Using the trackway ratio parameter of Romano et al. (Romano et al., 2007), *Liujianpus* is ‘medium-gauged’ (35–37%, approaching the ‘wide gauge’ threshold of <35%). Despite similar gauges, *Oobardjidama* and *Liujianpus* are different in pedal pace angulation (12–17° greater in *Liujianpus* [an even greater pedal pace angulation occurs in the other early ichnotaxa]) and in the degree of pedal track outward rotation (being more pronounced in *Liujianpus*). Unlike *Oobardjidama*, all early sauropodomorph ichnotaxa have pronounced to exaggerated heteropody, which is consistent with a predominantly hind limb–driven locomotion maintained over the sauropodomorph–sauropod transition (McPhee et al., 2014).

Beyond *Lavinipes* and *Liujianpus*, the majority of additional small and medium (pedal tracks <80 cm) sauropodomorph trackways or isolated tracks from the Lower Jurassic were most likely made by gravisaurian sauropods. Various isolated MP couplets and short trackway segments from the Holy Cross Mountains of southern Poland occur in Hettangian outcrops of the Zagaje and Skoby formations (Gierlinski, 1997; Gierlinski and Sawicki, 1998). These are small narrow-gauge tracks with pronounced heteropody (pedal length 24–42 cm). A single large tracksite (Sołyków tracksite) contains upwards of six parallel sauropod trackways, with a similar size range and morphology (Gierlinski and Pienkowski, 1999; Gierlinski et al., 2004). These tracks have either been likened to, or referred explicitly to, *Parabrontopodus*, on account of their narrow gauge and similar pedal track shapes (Gierlinski, 1997; Gierlinski

and Sawicki, 1998; Gierlinski and Pienkowski, 1999; Gierlinski et al., 2004).

From slightly stratigraphically higher at the site yielding the topotype of *Liujianpus*, Xing et al. (2016b) described a small trackway (‘JYS11’; pedal length 26 cm), which they likened to *Brontopodus*. This trackway is wide-gauge, but only marginally greater inner trackway swath that occurs in classical *B. birdi* trackways from the Gulf Coastal Plain of Texas (Farlow et al., 1989). The pronounced heteropody and consistently large MP interautopodial distances in JYS11 are unlike *Brontopodus*, whereas the position and orientation of the manual relative to pedal impressions are similar to topotype trackways of *Eosauropus* (Lockley et al., 2006a:fig. 3). Therefore, and comparable to the Polish Hettangian tracks, the pronounced heteropody (widespread among early sauropod trackways) with a lack of digital and heel impression detail in JYS11 warrants a general assignment for them. Elsewhere in the Lower Jurassic Ziliujing Formation of Sichuan, sauropod tracks likened to *Parabrontopodus* (Xing et al., 2014) also show many of the features common to *Eosauropus*-type early sauropod ichnomorphs.

In contrast to the lowermost Jurassic record (Hettangian–Sinemurian), occurrences of sauropod pedal track sizes greater than 50 cm in length become more prevalent in the upper half of the Lower Jurassic (Pliensbachian–Toarcian). A remarkably wide-gauge trackway (pedal track length 76 cm) from the Pliensbachian Aganane Formation of Morocco presents pronounced heteropody and shallow medial digital hypices (Jenny and Jossen, 1982:fig. 2; Ishigaki, 1986:fig. 26A, 1988:figs. 11, 23). In agreement with Xing et al. (2016b:889) that this trackway is reminiscent of *Liujianpus*, it further suggests a latent persistence of non-gravisaurian sauropod trackmakers into the latest Early Jurassic. Reiterating this inferred pattern is the continued presence of small (pedal track length 43 cm), narrow-gauge, and high-heteropody trackways ascribed to *Parabrontopodus* sp., from the Holy Cross Mountains, Poland, during the later part of the Early Jurassic (Gierlinski, 2009).

Amongst the richest Lower Jurassic dinosaurian track ichnoconoses are the tracksites of Lavini di Marco and peripheral localities, in the Hettangian–Sinemurian Monte Zugna Formation (Avanzini et al., 1997, 2006). In addition to the topotype of *Lavinipes*, other sauropod ichnomorphs from the megatracksite include several small trackways (pedal track length 40–50 cm) referred to *Parabrontopodus* isp., on account of their narrow gauge and high heteropody (Avanzini et al., 2006). At least one of the trackways, ‘ROLM 28’ (Dalla Vecchia, 1994:fig. 2; Avanzini et al., 2006:fig. 6C), actually has tighter pace angulation values, nearly moderate heteropody, intermediary gauge, and strongly laterally positioned manual tracks, when compared with *P. mcintoshi* (Lockley et al., 1994a). In these features, it is more like *Oobardjidama* and some early sauropodomorph ichnomorphs such as *Tetrasauropus* (Ellenberger, 1972; Lockley et al., 2001b) than *Parabrontopodus*, which alludes to a persistent and common Lower Jurassic morphotype.

A poorly preserved and moderately heteropodous MP couplet (Avanzini et al., 2006:fig. 6D) is the largest exemplar of a sauropod track (pes length 70 cm) before Pliensbachian times that we are aware of. Although Thulborn (1990:fig. 6.17a) illustrated an extremely large (pes length of 140 cm), highly heteropodous MP couplet as deriving from the Lower Jurassic of Morocco, we consider the listed age to be in error. The couplet constitutes part of the holotype trackway of *Breviparopus taghbaloutensis* (Ishigaki and Matsumoto, 2009:fig. 6, couplet 6 of section A of ‘Trackway Bre’), dated to Late Jurassic (Marty et al., 2010:112–113).

In summary, the overall trend among Early Jurassic sauropodomorph ichnomorphs suggests that medium to large (pes length >55 cm) tracks formed by definite gravisaurians occur mainly after the Sinemurian (Xing et al., 2011). Older, smaller,

and often relatively distinctive track types could have been formed variously among a paraphyletic array of increasingly derived track-producing taxa. Some Early Jurassic sauropodomorph trackways exhibit a widening of gauge and can be somewhat compared with *Oobardjidama* and *Brontopodus*-type trackways. It also seems apparent that many small Early Jurassic tracks/trackways are only superficially similar to *Parabrontopodus mcintoshii* (see below), which can be considered an explicitly definable ichnotaxon that is limited to upper Middle Jurassic occurrences onwards.

*Breviparopus/Parabrontopodus-Type Tracks (Middle Jurassic–?Upper Cretaceous)*. The recognition that sauropod trackways could be conveniently divided into ‘wide gauge’ and ‘narrow gauge’ categories (Farlow, 1992) led to the creation of *Parabrontopodus mcintoshii* for the latter (Lockley et al., 1994a). *Parabrontopodus*, exemplified by reference trackways from Purgatoire Valley dinosaur tracksite of the Morrison Formation, in southeastern Colorado, U.S.A. (Lockley et al., 1986; Schumacher and Lockley, 2014), was at first characterized by trackways with contralateral pedal tracks intercepting the trackway midline (producing a narrow gauge), and elongate pedal impressions of almost-medium to large sizes (50–90 cm) that are rotated outwards and which bear laterally directed digital sub-impressions (Lockley et al., 1994a:figs. 3, 4). The pronounced heteropody of small, semicircular manual impressions further diagnosed *Parabrontopodus* (Lockley et al., 1994a).

*Parabrontopodus* and *Parabrontopodus*-like couplets and trackways have been linked variously to non-neosauropod sauropods, diplodocoids, and basal macronarian trackmakers (Wilson and Carrano, 1999; Wright, 2005; Pascual Arribas et al., 2009; Marty et al., 2010). They are most abundantly known from various Upper Jurassic strata of Europe (Meyer, 1990; Lockley and Santos, 1993; Marty et al., 2003, 2010, 2013; Meyer and Thüring, 2003a; Le Loeuff et al., 2006; Santos et al., 2008).

Lockley et al. (1994a) reviewed other existing sauropod ichnotaxa, concluding that only *Rotundichnus munchehagensis* and *Breviparopus taghbaloutensis* were valid and were related to *Brontopodus* and *Parabrontopodus*, respectively, which is essentially a correspondence to the categories of gauge. With respect to this, the ichnosystematic supraspecific labels ‘brontopodidae’ and ‘parabrontopodidae’ were considered but not formalized (Lockley et al., 1994a; contra Apesteguía, 2005).

Lockley et al. (1994a) considered *Breviparopus* as a similar track type to *Parabrontopodus* but did not specify how they were distinguishable. Failing to find significant differences between these ichnotaxa, Wright (2005) suggested that they were synonymous and that the earlier named ichnotaxon, *Breviparopus taghbaloutensis* (Dutuit and Ouazzou, 1980), had priority for most narrow-gauge trackways, including those considered as *Parabrontopodus*. Belvedere (2009) and Marty et al. (2010) reviewed the holotype trackway of *Breviparopus* (Deio-D; = ‘Trackway Bre’ of Ishigaki and Matsumoto, 2009:fig. 6) from the Upper Jurassic Iouaridène Formation of Morocco, noting minor differences in the shape of the impressions and trackway pattern when compared with *Parabrontopodus mcintoshii*.

Hence, although it is clear that *Breviparopus* and *Parabrontopodus* are very similar, but differentiable when considered within the confines of an extremely specific framework of differentially diagnostic features (Marty et al., 2010), the two ichnotaxa as a collective are readily distinguishable from other sauropod ichnomorphs. This includes the differentiation from earlier-occurring narrow-gauged Late Triassic–Early Jurassic ichnotaxa (see preceding remarks). However, many narrow-gauge trackways from the Late Jurassic onwards are often sub-optimally preserved and, by not closely matching one of the two sets of diagnostic features, cannot be specifically assigned to either ichnotaxon. Such tracks have often been labeled *Parabrontopodus*-like (e.g., Moratalla, 2009) or assigned to a

broader *Breviparopus–Parabrontopodus* ichnosystematic nexus among narrow-gauge trackways (e.g., Avanzini et al., 2003; Santos et al., 2009; Castanera et al., 2014). For comparisons henceforth, we identify trackways as being of ‘*Breviparopus/Parabrontopodus*-type’ if they seem similar to both these ichnotaxa (relative to other others) but are indeterminate within this grouping.

*Oobardjidama* differs from *Breviparopus/Parabrontopodus*-type trackways principally in its relatively wider gauge condition and medium to mild heteropody. Although DP45-8 is not an extensive trackway, *Oobardjidama* also exhibits relatively large interautopodial gap spaces that regularly exceed manual track length. In contrast, most *Breviparopus/Parabrontopodus* trackways exhibit short MP interautopodial distances and correspondingly larger PM ones. Despite these differences, some Upper Jurassic megatracksites that contain multiple narrow-gauge trackways show variations in gauge proportions amongst parallel trackways, with a few occasionally being wide-gauge (Meyer, 1990; Moreno and Benton, 2005; Diedrich, 2011).

Infrequently, trackways assigned to *Parabrontopodus* do show much lower heteropody than the reference trackways of either *Breviparopus* or *Parabrontopodus* (e.g., Marty et al., 2010: trackway CTD-TCH-1055-S4, from Courtedoux Tchâfoué tracksite, Switzerland), or they exhibit moderate MP spacing that exceeds manual track length (Marty et al., 2010: trackway CTD-TCH-1055-S4; Marty et al., 2013: trackway S1, Rochefort–Les Grattes tracksite, Switzerland). For CTD-TCH-1055-S4 in particular, the combination of these features coupled with good preservation that includes pedal digital impressions (Marty et al., 2010) indicates that it ought not be referred to *Parabrontopodus*. This trackway shows similarity both in morphology and size to Lower Cretaceous trackways from China that have been likened to cf. *Brontopodus* (Xing et al., 2016a, 2016c).

*Breviparopus taghbaloutensis* specifically differs from *Oobardjidama* and other tracks within the *Breviparopus/Parabrontopodus* cohort of ichnomorphs by its more circular or bell-shaped pedal track outlines, a greater degree of manual and pedal track outward rotation in *Breviparopus*, and a more lateral positioning of the manual impressions with respect to the trackway midline (Marty et al., 2010). In addition, *Breviparopus* differs from *Parabrontopodus* by its slightly lower heteropody. The combination of these features is somewhat intermediate between *Parabrontopodus*- and *Brontopodus*-type tracks, but they are present in the holotype trackway (Deio-D; = ‘Trackway Bre’ in Ishigaki and Matsumoto, 2009) as well as a referred trackway, CTD-SCR-1000-S10 (Upper Jurassic, Courtedoux–Sur Combe Ronde tracksite, Switzerland; Marty et al., 2010).

Compared with the topotype of *Parabrontopodus mcintoshii*, *Oobardjidama* offers relatively wider manual impressions (relative to the pedal track width), which is closer to the condition of *Breviparopus*. The holotype of *P. mcintoshii* is a cast of a left MP couplet (hence mirrored as a ‘right’ in Lockley et al., 1994a: fig. 4), the pedal impression of which shows narrowly defined and partially laterally extended digital impressions. In this region, the holotype is not dissimilar to the holotype of *Oobardjidama*. However, the medial margin of the *P. mcintoshii* holotype is convex, rather than bilobed as in *Oobardjidama*. Both ichnomorphs terminate in a narrow caudal heel. The topotype trackway of *Parabrontopodus* shows the manual impressions close to alignment with the medial margins of the pedal tracks; hence, they are closer to the trackway midline than the manual impressions of *Oobardjidama* or *Breviparopus* (Lockley et al., 1994a; also present in referred trackway Deio Lav-A; Marty et al., 2010). Generally, most referred trackways of *Parabrontopodus* have pronounced to exaggerated heteropody, which is often due to the extremely craniocaudally narrow crescent forms of the manual impressions (e.g., Le Loeuff et al., 2006).

Several other formalized names have been applied to narrow-gauge trackways from the Upper Jurassic and Lower Cretaceous, although these are generally considered dubious applications of ichnotaxonomy (Farlow et al., 1989; Lockley et al., 1994a). Some of these trackways clearly belong to the *Breviparopus/Parabrontopodus* cohort of track types but are diagnostically indeterminate within this grouping with respect to *Breviparopus taghbaloutensis* and *Parabrontopodus mcintoshi* specifically. These include *Iguanodonichnus frenki*, from the Upper Jurassic of Chile (Moreno and Benton, 2005; Soto-Acuña et al., 2015), which, although regarded as being narrow-gauged, is also represented by some wide-gauge specimens (e.g., Moreno and Benton, 2005:fig. 2). Most *Iguanodonichnus* pedal impressions curiously tend to show an extended trace for the hallucal digit but are otherwise generally poorly preserved tracks lined with relatively thick pressure rims. The manual impressions are predominantly absent. Elsewhere, enormous pedal impressions (140–162 cm long) of the Lower Cretaceous *Parabrontopodus distercii* (Meijide Fuentes et al., 2001) were redescribed as smaller tracks (pedal track length 100 cm) infilled with sediment, with the individual track boundaries being indecipherable (Moratalla, 2009). Moratalla (2009) concluded that ‘*Parabrontopodus distercii*’ was *Parabrontopodus*-like while also being an unjustified new name. Other ichnotaxa, such as *Gigantosauropus asturiensis*, although narrow-gauged, are undiagnostic and should simply be considered indeterminate sauropod tracks (Lockley et al., 2007).

Some of the oldest sauropod tracks that have been considered *Breviparopus/Parabrontopodus*-like are from the earliest Middle Jurassic (Aalenian) Saltwick Formation of Yorkshire, U.K. (Romano et al., 1999; Romano and Whyte, 2003, 2012). Chiefly pedal only impressions, these specimens are difficult to comparatively assess without trackways. From strata of a similar age in Tibet, Xing et al. (2011:fig. 3) described a pair of large, contralaterally positioned MP couplets (pedal track length 80 cm), among other isolated track impressions, and considered them similar to *Brontopodus* on account of their wide gauge, high heteropody, and elongated pedal track shapes. Except for its gauge, this short segment of trackway is more like *Breviparopus/Parabrontopodus* in other characteristics. In the upper Middle Jurassic, *Breviparopus/Parabrontopodus*-type isolated tracks and trackways have been reported from Yorkshire and the Isle of Skye, northern U. K. (Romano and Whyte, 2012, and references therein; Brusatte et al., 2016) and from Morocco (Gierlinski et al., 2009). None of these records can be specifically referred to either *Breviparopus* or *Parabrontopodus* based on their preserved morphology, although the Isle of Skye trackways interestingly show moderate to low heteropodous track casts, with up to four cranially positioned digital nubbins (Brusatte et al., 2016).

Pascual Arribas et al. (2009) described ‘LCU-I-37,’ a long sauropod trackway with some excellently preserved associated natural casts from the Lower Cretaceous megatracksite Las Cuestas, in the Cameros Basin of Spain (Pascual Arribas and Hernández Medrano, 2010). This trackway was described as being similar to *Parabrontopodus* (Pascual Arribas et al., 2009), although it shows a minimally narrow gauge condition, with medium instead of pronounced heteropody, and strongly outturned couplets that result in the manual track being furthest from the trackway midline. These features conform well to the characterization of *Breviparopus* given by Marty et al. (2010). One of the pedal casts, LCU-I-37-12p, has indications of digits I–III with clear, three-dimensionally visible unguals, with two additional nubbins representing digits IV and V (Pascual Arribas et al., 2009:fig. 6). The medial area adjacent to the first ungual is slightly bulged in LCU-I-37-12p, although not as pronounced as the medial bulge in *Oobardjidama*. The corresponding manual cast bears an expression of the pollex ungual, somewhat similar to that characterizing *Polyonyx gomesi* (Santos et al., 2009). If we are correct

in considering the Las Cuestas trackway as being closer to *Breviparopus* than to *Parabrontopodus*, it provides a glimpse of fine plantar surface morphology of the *Breviparopus* trackmaker, presently lacking in Upper Jurassic *Breviparopus* exemplar trackways. Of relevance to the differential diagnosis between *Parabrontopodus* and *Breviparopus* (Marty et al., 2010) is that the outlines of the manual tracks in LCU-I-37 change from condensed semicircular crescents to deeper horseshoe-shaped profiles along the trackway; thus, LCU-I-37 exhibits a spectrum of manual track shape profiles, with extremes that are typical for *Parabrontopodus* and *Breviparopus*, respectively.

Castanera et al. (2010:fig. 1) documented a Late Jurassic trackway (‘71GR’) from the Iouaridène Formation, Morocco, with disproportionately large manual impressions. In addition to the exceedingly mild heteropody (>60%), 71GR differs from the coeval *Breviparopus taghbaloutensis* holotype trackway by the relatively medial positions of its manual impressions, coupled with a relatively greater equalization of fore and aft interautopodial spaces. Excluding the gauge, which is only minimally narrow in 71GR, the combination of the other characters is reminiscent of the condition in *Oobardjidama*. The Moroccan 71GR and the Chinese Jiefang trackways highlight the range of morphological diversity present among narrow gauge–type trackways.

In summary, discounting atypical referrals to *Parabrontopodus* (e.g., CTD-TCH-1055-S4; Marty et al., 2010), *Oobardjidama* is readily distinguished from the *Breviparopus/Parabrontopodus* nexus of ichnomorphs based on interautopodial spacing pattern, heteropody, and a generally wider gauge condition. *Oobardjidama* differs from pedal impressions of *Parabrontopodus* (the holotype) or *Breviparopus* (potentially LCU-I-37; Pascual Arribas et al., 2009) that display good preservation by the presence of a bulged medial digital sub-impression and demarcation of heel pad impression, but it is otherwise not closely comparable to most pedal impressions of *Breviparopus/Parabrontopodus* trackways with regard to clear track floor morphology. *Oobardjidama* does show some similarities to a few unnamed trackways of narrow gauge type (Castanera et al., 2010; Xing et al., 2015f), although additional work is needed to disentangle the trackway patterns these specimens show for future ichnosystematic comparisons.

*Brontopodus-Type Tracks (Middle Jurassic–Upper Cretaceous)*. Wide-gauged sauropod ichnotaxa that we consider diagnosable comprise, in order of their conception, *Brontopodus birdi*, *Titanopodus mendozensis*, *Polyonyx gomesi*, and *B. pentadactylus* (Farlow et al., 1989; González Riga and Calvo, 2009; Santos et al., 2009; Kim and Lockley, 2012), and *Oobardjidama foulkesi* herein. Within this grouping, *Polyonyx gomesi* (Middle Jurassic) and *Brontopodus* spp. (predominantly Lower Cretaceous) are communally united to the exclusion of *Titanopodus* (Upper Cretaceous) by a medium to mild heteropody (30–50%), relatively deep manual impressions (at least half as long as wide) that bear digital traces, manual impression trackway widths approximately equal to pedal trackway width, and outwardly rotated piriform pedal impressions, with three to four partially or entirely laterally directed digital impressions. The pedal trackway ratio is between 30% and 40% for most trackways of this grouping, equating to medium/wide gauges (Romano et al., 2007:table 1), although the holotypes of *Polyonyx* and *Brontopodus birdi* share a narrower range of 35–37%, whereas *Brontopodus pentadactylus* is estimated at 43% (medium). *Titanopodus*, in contrast, is much wider (the pedal trackway ratio is 26–31%; González Riga and Calvo, 2009).

To this cohort of track morphologies (i.e., *Polyonyx*, *Brontopodus*, various unnamed wide-gauge trackways), we apply the broad category label *Brontopodus*-type, contrasting with latest Cretaceous trackways that are *Titanopodus*-like. Previously, Santos et al. (2009) considered *Polyonyx* to represent a distinct ichnomorphotype (‘*Polyonyx*-like’) relative to *Brontopodus*-like

trackways (Santos et al., 2009:table 3). Although this idea is feasible, it should be noted that at the time of its proposal, three of the ichnotaxa that we consider herein were unknown to Santos et al. (2009). Moreover, *Polyonyx*-like is redundant in practice, given that it contains a single ichnotaxon, known from two trackways, 'G1' and 'G5,' both from the one tracksite, Galinha (Santos et al., 2008, 2009).

*Polyonyx gomesi* is from the Middle Jurassic Serra de Aire Formation of the Galinha tracksite, central Portugal, a site that contains at least 20 wide-gauge trackways, several of which are between 100 and 150 m in total length (Santos et al., 2008, 2009). Originally, the trackways of the Galinha tracksite were recognized as 'cf. *Brontopodus*' due to the wide gauge condition of the best-preserved exemplars (Santos et al., 1994). However, not all are equally well preserved, and subsequent research has focused on a smaller subset of the site, especially in regards to the two longest segments of trackway, 'G1' and 'G5' (Santos et al., 2009:fig. 3).

Galinha trackway G5, the holotype of *Polyonyx gomesi*, has large (average length 90 cm) piriform pedal impressions, which are a common shape for *Brontopodus*-type tracks but which differ from the holotypic pedal impression of *Oobardjidama* (DP45-8[rp2]) in its more elongate proportions, with a convex profile along the medial margin. The digital impressions in G5 are individually narrow with deep hypices, are either extended or flexed laterally, and each tends to occupy proportionally equal length of the cranial margin arc (Santos et al., 2009:fig. 4), whereas they are more prominent sub-impressions medially in *Oobardjidama*. Like all *Brontopodus*-type ichnomorphs, *Polyonyx* lacks the expansive medial bulged impression and longitudinal internal ridge present in the pedal impressions of *Oobardjidama*. The asymmetrical manual impressions of *Polyonyx* are unique among *Brontopodus*-type tracks due to the presence of a mid-caudally extending tapering sub-impression, which has been interpreted as a trace of the pollex unguis (Santos et al., 2009). In other *Brontopodus*-type manual impressions, the pollex unguis trace, if present, extends from the caudomedial margin. Unfortunately, the manual impressions in DP45-8 are too poorly preserved to decipher its morphology in *Oobardjidama*.

Among *Brontopodus*-type tracks, the low heteropody in G5 is comparable to that in DP45-8, although it should be noted that a larger sampling of heteropody values is required in *Oobardjidama* for this comparison to be meaningful. The very large, outwardly rotated manus impressions in Galinha trackway G1 results in an even milder heteropody (50%) than the holotype trackway G5, but due to a suboptimal preservation of the pedal impressions, which lack digital traces, G1 has been referred to *Polyonyx* sp. (Santos et al., 2009). Trackway G1, like *Oobardjidama*, has almost equal fore and aft interautopodial gap spaces, reminiscent of *Titanopodus*. Santos et al. (2009:418) inferred a non-neosauropod eusauropod trackmaker for *Polyonyx*, which links the age of the ichnotaxon, with an inferred pollex orientation and anatomy in contemporaneous sauropods, to the morphology of the manual impressions.

Compared with the *Breviparopus/Parabrontopodus* quandary, *Brontopodus birdi* is a well-defined ichnotaxon (Farlow et al., 1989), with reiterated instances of its track morphology coupled with a specific gauge and trackway pattern widespread globally, particularly in Lower Cretaceous formations (Meyer and Pittman, 1994; Lockley et al., 2014; Weems and Bachman, 2015; Xing et al., 2016c). Beginning in the late 1930s, and continuing to the present, a long history of field work and research on the reference tracksites of *Brontopodus* within the Glen Rose Formation of the Gulf Coastal plain of Texas has occurred, which readers should consult for further details (Bird, 1939, 1941, 1944, 1985; Langston, 1974; Farlow, 1987, 1992; Pittman, 1989; Pittman and Gillette, 1989; Hawthorne, 1990; Pittman and Lockley, 1994; Falkingham et al., 2014).

Among similar wide-gauged ichnotaxa, *Brontopodus birdi* is characterized by a combination of its piriform pedal tracks bearing short, narrow, laterally orientated digital impressions (digits I–IV), often with a nubbin-like protrusion of digit V in well-preserved impressions (Farlow et al., 1989; Marty et al., 2010). In contrast, impressions of the lateral unguis in *Oobardjidama* are not preserved (or were absent in its trackmaker). In *B. birdi*, a gently convex bulge is usually present along the cranial medial margin of the pedal impression, differing from the pronounced condition in *Oobardjidama*. The manual impressions of *B. birdi* have a bilobed caudal margin when fully preserved, indicating the regions of palmar impression of digits I and V in the manual track. However, *B. birdi* manual impressions do not show narrow unguis traces (Farlow, 1992), as seem to occur in *Polyonyx*. The manual impressions of *B. birdi* occur in line with the medial margins of the pedal impressions, whereas the pedal impressions are slightly rotated outwards.

Beyond superficial aspects of gauge and size, *Oobardjidama* and *B. birdi* do not share any unique features among the wide-gauged ichnomorphs. Aside from the plantar morphology of the pedal autopodium being distinctively expressed in *Oobardjidama* as large medial sub-impressions, the two ichnomorphs noticeably differ in the relative placement of the manual tracks. In reference trackways of *B. birdi* along the Paluxy River (Farlow et al., 2012; Falkingham et al., 2014), short MP interautopodial gaps are preceded by extremely long PM intracouplet spaces. This pattern, although seemingly typical in sauropod trackways, is actually unusual among other wide-gauged ichnotaxa (*Polyonyx*, *B. pentadactylus*, *Oobardjidama*, and *Titanopodus*), which instead tend to show a slight equalization of the interautopodial distances compared with *Breviparopus/Parabrontopodus*-type tracks.

The trackmaker of *Brontopodus birdi* has been speculated to be a brachiosaurid sauropod based on manual impression morphology (Farlow et al., 1989; Farlow, 1992) and has also been regularly linked to the finding of a pes skeleton from the stratigraphically higher Paluxy Formation. This pes, once attributed to '*Pleurocoelus*' (Gallup, 1989), is now referred to *Cedarosaurus weiskopfae*, a brachiosaurid titanosauriform (D'Emic, 2013). However, remains of other basal somphospondylians are also coevally present with *Cedarosaurus* in the Lower Cretaceous Trinity Group (D'Emic, 2013), which therefore constrains the suggested trackmaker no more specifically than to a basal titanosauriform identity.

The recently coined *Brontopodus pentadactylus* from the Lower Cretaceous Haman Formation of South Korea (Kim and Lockley, 2012) is a distinctive ichnotaxon founded upon two very small trackways (pedal track length less than 50 cm). The larger trackway, no. 1 (the holotype), has relatively large manual impressions (heteropody approximately 40–50%) that usually have three, but sometimes up to five, digital impressions along the cranial track margin. Uncommon among other wide-gauged morphotypes, the manual impressions appear to be fully laterally orientated (rotation 90°). The pedal impressions show an outward rotation of about 30°. The fore and aft interautopodial gap spaces are equal (Kim and Lockley, 2012:figs. 4, 5).

The smaller paratype trackway mainly repeats the morphology of the holotype trackway (Kim and Lockley, 2012:fig. 6C) but does show several minor differences. For instance, the manual impressions of the paratype are rotated outward at about 45°, whereas there are consistently five digital sub-impressions. Irrespective of the differences between the holotype and paratype, the combination of these traits in the holotype is unique among other wide-gauge track types. With respect to trackway pattern, *B. pentadactylus* and *Oobardjidama* are similar in interautopodial spacing, heteropody, and gauge (the pedal trackway ratio of *B. pentadactylus* is approximately 43%). The two differ in the morphology of the pedal impressions, however, where in *B.*

*pentadactylus* there is a more rounded caudal margin, presence of multiple well-defined digital impressions cranially, and gently convex lateral and medial flanks.

Despite the assignment of *B. pentadactylus* to *Brontopodus* (Kim and Lockley, 2012), the new ichnotaxon has multiple differences (many listed above) from *B. birdi*. For interautopodial spacing pattern, there is a close resemblance to *Oobardjidama* and *Titanopodus*, and less so to *Polyonyx*, than to *B. birdi*. The heteropody in *B. pentadactylus* is more similar to *Polyonyx* than other wide-gauged ichnotaxa, whereas the pedal trackway ratio as medium gauge is dissimilar enough to *B. birdi* to query it. Some of these features, coupled to a small track size, are reminiscent of tracks formed by probable juvenile sauropods (Xing et al., 2015d). For example, the strongly overturned manual impressions with straight caudal margins and five digital impressions closely match tracks from Nanguzhai, eastern China (Xing et al., 2010:fig. 4, 2015d). Given the differences between '*B. pentadactylus*' and other wide-gauged forms, we accept that it represents a unique track type, but warranting a new ichnogenus name rather than being referable to *Brontopodus*.

An unassigned trackway from the Cenomanian of Italy, 'Sezze Cava Petrianni I' (Nicosia et al., 2007), appears similar to '*B. pentadactylus*', *Polyonyx*, and *Oobardjidama* with regard to its low heteropody. Like *Oobardjidama*, Sezze Cava Petrianni I is similarly medium-gauge (i.e., a relatively narrow inner trackway width exists, sensu Meyer et al., 1994), has manual tracks ipsilaterally in line with the pedal impressions, and exhibits some large interautopodial gaps, although most manual impressions tend to lie closer to the cranial margin of the pedal impression. The occasional pedal digit marks are cranially projected (Nicosia et al., 2007:75, although some are depicted as more craniomedially orientated in Fig. 8). Despite these few similarities between *Oobardjidama* and Sezze Cava Petrianni I regarding trackway patterning, the detailed morphology of individual pedal tracks in the latter is poorly known (many are filled with sediment), and their greatly variable outlines hamper further comparisons.

Numerous other wide-gauge trackways that are classifiably *Brontopodus*-like are known. Some of these have received ichnotaxonomic names (e.g., Kaever and Lapparent, 1974; Hendricks, 1981; Dalla Vecchia and Tarlao, 2000; Meijide Fuentes et al., 2004; Diedrich, 2011) but should be considered dubious (for reviews, see Farlow et al., 1989; Lockley et al., 1994a; Kim and Lockley, 2012). Others are of comparative interest because they indicate morphologies outside the valid ichnotaxa that we have reviewed, but further documentation is required (e.g., wide-gauge *Breviparopus*-like trackway: Meyer, 1993; or disproportionate manual impressions: Lockley et al., 2002a). In summary, wide-gauged *Brontopodus*-type ichnotaxa, with the exception of *Polyonyx gomesi*, are most prevalent during the Early Cretaceous, comprising *Brontopodus birdi*, '*B. pentadactylus*', and *Oobardjidama foulkesi*.

**Titanopodus-Type Tracks (Upper Cretaceous).** *Titanopodus mendozensis*, from the Campanian–Maastrichtian Loncoche Formation (González Riga and Calvo, 2009), represents a wide-gauged morphotype different from the preceding *Brontopodus*-type ichnomorphs, and one with which *Oobardjidama* shares a similar autopodial track spacing pattern. As a Late Cretaceous ichnotaxon, *Titanopodus* has been linked to contemporaneous derived titanosaurian trackmakers (González Riga, 2011). Characterized by very-wide-gauge trackways (a pedal trackway ratio of 26–31% is relatively wider than the *Brontopodus*-type ichnotaxa), proportionately large and equally distant interautopodial gaps, pronounced heteropody, and outwardly rotated 'digit-less' manual impressions, *Titanopodus* appears to fit the trackway model of a derived titanosaurian trackmaker well (Wilson and Carrano, 1999; González Riga, 2011).

Other occurrences nearly identical to *Titanopodus* in trackway pattern comprise Late Cretaceous slightly more pronounced

heteropodous trackways from the Late Cretaceous of Fumanya, Spain (Vila et al., 2013a). A trackway referred to the dubious taxon *Sauropodichnus giganteus* (Lockley et al., 1994a), from the Albian–Cenomanian of the Rio Limay Formation (Calvo and Mazzetta, 2004:fig. 4), seems also to be referable to *Titanopodus*. If correct, this referral extends the range of titanosauriform trackways into the latest Early Cretaceous.

**Comparative Ichnosystematic Summary.** *Oobardjidama foulkesi* is part of an informal grouping of sauropod ichnotaxa that includes *Brontopodus birdi*, '*B. pentadactylus*', *Polyonyx gomesi*, and *Titanopodus mendozensis*, as well as many dubious ichnotaxa (e.g., *Rotundichnus munchehagensis*, *Elephantopoides barkhausensis*). This assemblage can be regarded as a wide-gauged 'ichnoclade' of sauropod tracks, although it is important to appreciate that gauge within a form ichnomorph is partially transmutable with ontogenetic size (Wright, 2005; Xing et al., 2015d) and/or behavior (Day et al., 2002; Castanera et al., 2012). *Oobardjidama* is transitional in morphology between *Brontopodus*-type forms (*B. birdi*, *Polyonyx*) and *Titanopodus*, and for this reason we have not explicitly assigned it to the former category. Like *Brontopodus*-type ichnotaxa, *Oobardjidama* has comparable heteropody and a moderate trackway gauge ratio range, whereas the greater symmetry in the fore and aft interautopodial gap distances renders *Oobardjidama* more similar to the extremely wide-gauged *Titanopodus*.

**Prospective Trackmaker.** Determining the identity of the trackmaker of *Oobardjidama* requires some delimited speculation. *Brontopodus*-type trackways are predominantly known from Upper Jurassic and Lower Cretaceous substrates globally (Lockley et al., 1994b), with only occasional records from the Middle Jurassic (e.g., Day et al., 2002; Santos et al., 2009) and Upper Cretaceous (e.g., Lockley et al., 2002a). The suggested trackmakers range from non-neosauropod eusauropods producing some of the Jurassic instances (Santos et al., 2009) to exclusively titanosauriform trackmakers (Wilson and Carrano, 1999; Day et al., 2002; Wright, 2005), although diplodocoids have been suggested to produce some wide-gauge trackways (McIntosh et al., 1992).

Despite a temporal association (Wright, 2005:261), a case against diplodocoids (as opposed to non-titanosauriform sauropods in general) biomechanically producing wide-gauge trackways is yet to be convincingly demonstrated. Farlow (1992) and others (Lockley et al., 2001b; Day et al., 2002) have rationalized that a particular manual track shape and/or low couplet heteropody in wide-gauge trackways contradicts their being made by a diplodocoid trackmaker. However, comparisons with osteology are often limited, with autopodial anatomy not well known beyond a handful of exemplar diplodocid specimens (e.g., *Apatosaurus*, *Diplodocus*; Farlow, 1992; Wright, 2005). Indeed, some diplodocids bore a relatively large manus (Gilmore, 1936; Wright, 2005:260), suggesting that their related trackways should show low heteropody. In this context, it is significant that the morphology of a complete autopodium, manus or pes, is unknown for any rebbachisaurid, which were the most common diplodocoids during the Cretaceous and which are known to have existed in the Lower Cretaceous of South America (La Negra Formation) and South Africa (Kirkwood Formation) (see Discussion).

Among Upper Cretaceous wide-gauge trackways, clear manual impressions can establish if the trackways were formed by contemporaneous saltasaurid or non-saltasaurid titanosauriforms. Because saltasaurids lack manual phalanges, including a large pollex unguis (González Riga and Calvo, 2009; as 'titanosaurids'), *Brontopodus*-type trackways with a medial digital trace as part of their manual track outlines were likely made by non-saltasaurid titanosauriforms (Day et al., 2002: but contrary to the Upper Jurassic trackway illustrated therein; González Riga and Calvo, 2009). Thus, *Titanopodus*-type

trackways (including trackways from Fumanya, Spain; Vila et al., 2013a) that lack manual digital traces can be confidently assigned to a saltasaurid trackmaker, whereas other Late Cretaceous tracks classifiable as *Brontopodus*-type (e.g., Lockley et al., 2002a) were made by non-saltasaurids—specifically, probably by other derived lithostrotian titanosauriform trackmakers.

Based on these trackmaker inferences for similar wide-gauged ichnotaxa, we exclude that *Oobardjidama* was made by a saltasaurid trackmaker with certainty and further propose it unlikely to have been produced by any form of lithostrotian titanosauriform either, because Lithostrotia lacks a pre-Barremian body fossil record (Mannion et al., 2013:156). Similarly, we discount a non-neosauropod sauropod trackmaker, because they failed to persist beyond the Berriasian of the Early Cretaceous (the geologically youngest are European turiasaurs; Royo-Torres et al., 2009). Thus, the trackmaker of *Oobardjidama* was either a macronarian, probably a non-lithostrotian titanosauriform, or a diplocoid, records of which exist in the Lower Cretaceous of other Gondwanan landmasses (Gallina et al., 2014; Wilson and Allain, 2015). Although it is tempting to assert the first choice to be more likely on account of titanosauriforms exclusively making up the Australian Cretaceous body fossil record (Agnolin et al., 2010), it should be recognized that the overall pre-Aptian record of Australian Cretaceous sauropods is barely in evidence (Poropat et al., 2015b). Therefore, both alternatives for the trackmaker of *Oobardjidama* are presently equally plausible.

#### BROOME SAUROPOD MORPHOTYPE A (Figs. 26–30, 59B, S7; Table 10)

**Referred Material**—UQL-DP8-30 and UQL-DP22-4, two isolated MP couplets; UQL-DP9-1, an isolated PM couplet. Provisionally assigned: UQL-DP8-1 and UQL-DP14-20, two isolated PM couplets; UQL-DP9-11, an isolated ?MP couplet; UQL-DP45-14, an isolated pedal track (see Thulborn et al., 1994: fig. 3D). All the specimens are preserved as natural molds. UQL-DP8-30 is additionally represented by WAM 12.1.7, a rigid polyurethane resin replica. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality, Horizon, and Age**—The specimens are preserved in situ at DP8, DP9, DP14, DP22, and DP45, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derive from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—Beyond DP45-8 (*Oobardjidama foulkesi*), all other sauropod tracks within the study area that we have surveyed are singular autopodial impressions or couplets (see Materials and Methods). None of these can be assigned to *Oobardjidama* or other existing ichnotaxa based exclusively on the diagnostic features of those taxa. Among the additional tracks in the study area, several present a unique combination of novel characteristics, so we are compelled to refer them to their own discrete categories (Broome sauropod morphotypes A–E, herein). The impressions that we consider as Broome sauropod morphotype A are generally united by a large to very large size of the pedal impression (Table 1), moderate heteropody (25–40%), and short to medium interautopodial distance (average pedal to manual track distance between 15% and 25% of couplet length). The pedal impressions are approximately piriform/keyhole-shaped outlines when well preserved, but they can assume an ovate shape in the largest impressions. Most contain a shallow and compartmentalized sub-impression for a heel pad (relative to the cranial region of the pedal impressions (see below).

There is considerable spread in the quality of preservation of specimens assigned to Broome sauropod morphotype A. The couplet DP8-30 is the best preserved and represents the main

exemplar for showcasing the typical key features of the morphotype. Conversely, DP8-30 is also atypical as one of the smaller specimens assigned to the morphotype. Specimens DP22-4 and DP9-1 reiterate most of the morphology of morphotype A, but at a larger scale. However, some of the largest specimens, which may be of interest to discussions of sauropod gigantism, are either marginally different in morphology compared with other impressions (e.g., DP8-1) or extremely poorly preserved (e.g., DP9-11 and DP14-20). Therefore, these latter specimens have only provisionally been assigned to Broome sauropod morphotype A.

**UQL-DP8-30.** The paired impressions of a keyhole-shaped pedal track and a semi-ovate manual track comprise a natural MP couplet, DP8-30, orientated in a northeasterly tracking direction (Fig. 26). The two impressions occur on a frequently sand-blanketed exposure (UQL-DP8) high along the littoral column, which also hosts other sauropod and non-sauropod track outlines of varying sizes. The additional sauropod impressions comprise at least four partial outlines, two of which are immediately adjacent to DP8-30 (Fig. 26C, tracks ‘t1–2’). Despite their positions, none of the other incomplete sauropod tracks can be presently demonstrated to extend with DP8-30 as part of a trackway.

Specimen DP8-30 appears to be a right ipsilateral couplet, based on the arrangement of the offset position of the manual impression relative to the pedal impression (i.e., occurring relatively laterally), the slightly deeper northern region of the pedal impression (equating to the medial internal section), the slight outward rotation of the pedal impression, and because scrutiny of morphological detail surrounding the manual impression indicates that a pollex trace occurred at its northwestern section (i.e., its caudomedial region; see below). The couplet has an elevated and craniocaudally broadly rounded interautopodial segment forming a bulged rim. This is somewhat reminiscent of the upheaved condition of the sediment that also occurs in DP9-11 (see below).

The manual impression is deep. Accordingly, the outlined profile of the manual impression changes with the depth of the track, partly related to the external shape of the trackmaker’s manus and partly to the locomotory dynamics of the forelimb (for further discussion on this, see Romano and Whyte, 2012:18–19). At the preserved top layer, the manual impression is nearly crescent-like in outline and, craniocaudally broad with a concave caudal margin. The cranial region is concentric, reflecting the colonnade arrangement of the metacarpus of the trackmaker, and is defined by a well-formed, 10-cm-thick rim. Compared with the outline of the top layer, the floor of the impression is a smaller trace in area, being bean-shaped with a narrow triangular extension mediocaudally (Fig. 26). The latter represents the trace for the ungual of digit I. The cranial margin at the floor of the track is slightly forward of the corresponding margin at the top layer. The external caudal margin and the deeper, cranial internal floor are linked via an inclined roller-like ramp, reflecting the shape of the palmar surface of the manus (see below). There is a narrow and increasingly shallower laterocaudal extension to the manual impression, extending somewhat towards the lateral margin of the pedal impression. The manual track morphology and arrangement in DP8-30 somewhat approaches the condition of *Titanopodus mendozensis* (González Riga and Calvo, 2009), in which the angled manual track is aligned at 45° relative to the tracking direction and occurs lateral to the pedal track.

The pedal impression is nearly keyhole-shaped, bearing a wide, convex cranial margin coupled with a relatively narrower, semicircular outlined heel region. The floor of the track along the cranial arc is the most deeply impressed. Shallow ridges, probably defining digital traces, occur on the internal surface of the adjacent cranial arc wall. At least one of these extends caudally on the floor of the impression and appears to demarcate the boundary between digits II and III

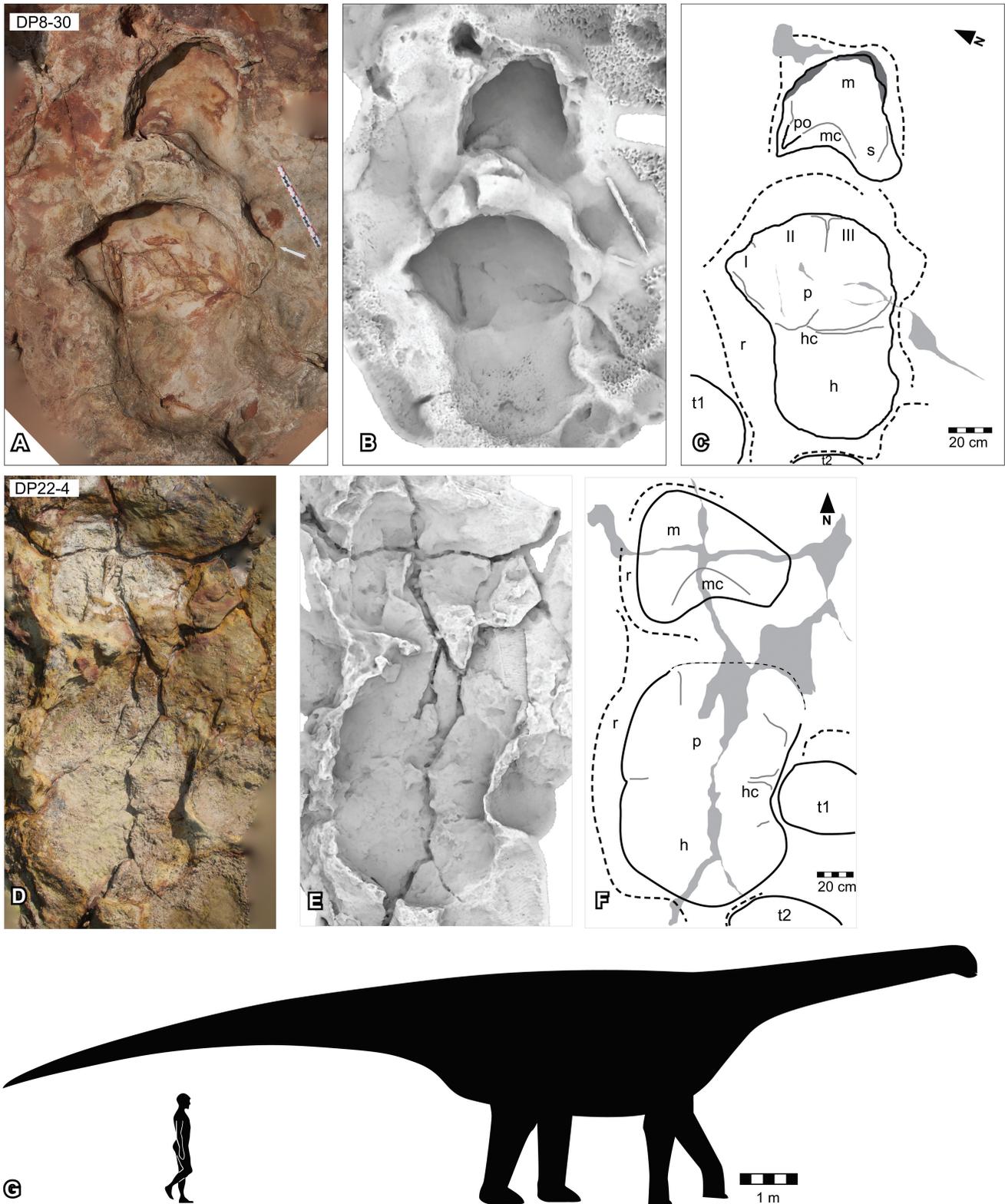


FIGURE 26. Broome sauropod morphotype A, from the Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia. Coupled right manual and pedal impressions, UQL-DP8-30, preserved in situ as **A**, orthophotograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Coupled right manual and pedal impressions, UQL-DP22-4, preserved in situ as **D**, orthophotograph; **E**, ambient occlusion image; and **F**, schematic interpretation. **G**, silhouette of hypothetical trackmaker of Broome sauropod morphotype A, based on UQL-DP8-30, compared with a human silhouette. **Abbreviations:** **h**, heel region; **hc**, heel-demarcating crease; **I–III**, selected areas of impressions by digits I, II, and III, respectively; **m**, manual impression; **mc**, molded ridge, representing a groove on the palmar-caudal surface of the trackmaker’s manus; **p**, pedal impression; **po**, deep trace of the pollex; **r**, expulsion rim; **s**, shallow lateral trace; **t1–2**, tracks extraneous to the described couplet specimens. See Figure 19 for legend.

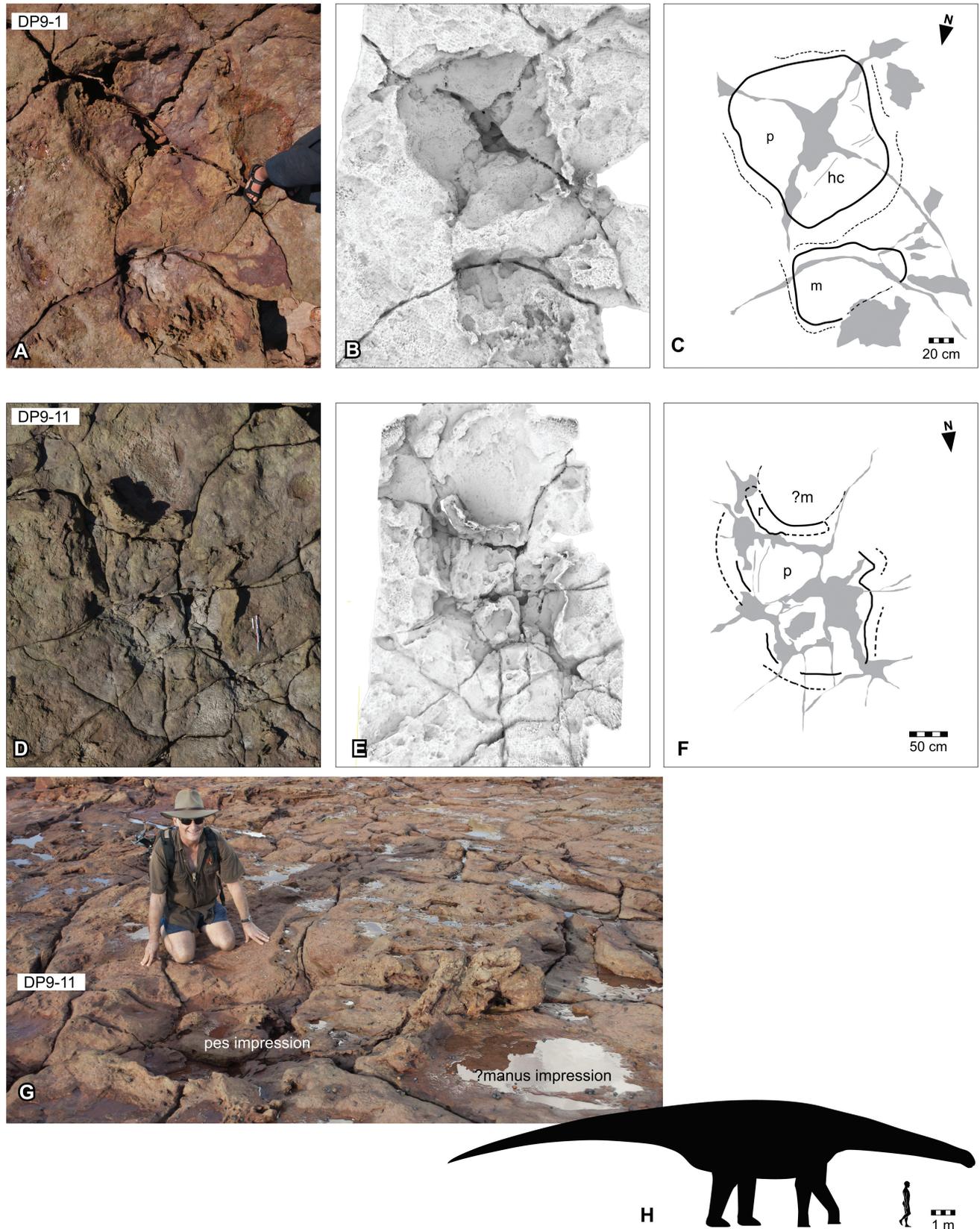


FIGURE 27. Broome sauropod morphotype A, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Coupled pedal and manual impressions, UQL-DP9-1, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Coupled manual and pedal impressions, UQL-DP9-11, preserved in situ as **D**, photograph; **E**, 3D image with ambient occlusion; and **F**, schematic interpretation; **G**, oblique photograph with Nigel Clarke for scale. **H**, silhouette of hypothetical trackmaker of Broome sauropod morphotype A, based on UQL-DP9-1, compared with a human silhouette. **Abbreviations:** h, heel region; hc, heel-demarcating crease; m, manual impression; p, pedal impression; r, expulsion rim. See Figure 19 for legend.

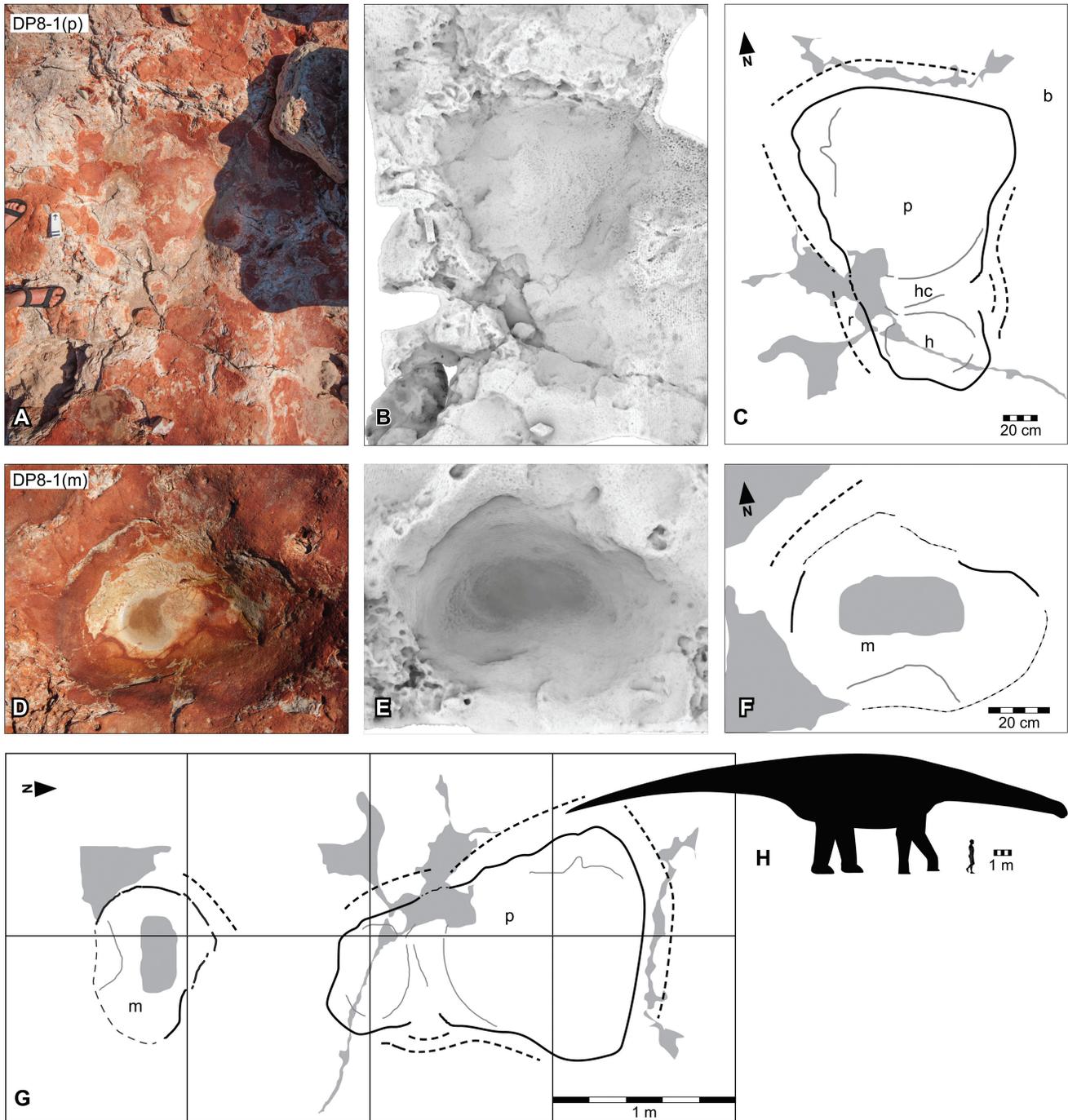


FIGURE 28. Broome sauropod morphotype A, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Pedal impression UQL-DP8-1(p), preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Manual impression UQL-DP8-1(m), preserved in situ as **D**, photograph; **E**, ambient occlusion image; and **F**, schematic interpretation. Coupled pedal and manual impressions, UQL-DP8-1, preserved in situ as **G**, schematic map. **H**, silhouette of hypothetical trackmaker of Broome sauropod morphotype A, based on UQL-DP8-1, compared with a human silhouette. **Abbreviations:** **b**, over-shadowing loose boulder; **h**, heel region; **hc**, heel-demarcating crease; **m**, manual impression; **p**, pedal impression; **r**, expulsion rim. See Figure 19 for legend.

(Fig. 26C). Although the probable medial area of the impression of digit I is deep and medially jutting, there is no apparent sub-impression for a bulged pad or plantar callosity as occurs in *Oobardjidama* or some of the other Broome sauropod morphotypes (see further remarks under ‘Broome Sauropod Morphotype E’). The heel

region, demarked by a semicircular caudal boundary plus parallel medial and lateral sides, is shallower than the digitometatarsal impression. The heel impression is plateaued relative to the cranial half of the impression, due to the presence of a ledge-like ridge on the floor of the track (Fig. 26).



FIGURE 29. Broome sauropod morphotype A, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Goolarabooloo Maja Richard Hunter alongside the pedal impression UQL-DP8-1(p). The scale bar Richard is holding is 40 cm long.

*UQL-DP22-4*. A second isolated MP couplet (DP22-4; Fig. 26D–F) is situated within a localized channel immediately surrounded by undulating topography. Several other extraneous sauropod tracks occur in immediate proximity to DP22-4, including an indeterminate manual impression ('t1' in Fig. 26F) that appears to overprint and distort the shape of the pedal track outline of DP22-4. The additional sauropod tracks cannot, at present, be demonstrated to extend DP22-4 into a trackway. Couplet DP22-4 was formed in a northerly tracking direction and shows medium heteropody with a short interautopodial distance.

The manual track is the best preserved and more sharply delineated of the two impressions of DP22-4. It is asymmetrically bean-shaped, with a strongly convex cranial margin and a slightly concave caudal margin. A dextral ipsilateral determination of DP22-4 is based primarily on the shape of the manual track, which is approximately similar to that in DP8-30 (Fig. 26A–C). The consistent aspect between these two manual impressions is that the craniocaudally longer and predominantly deeper left half—relative to tracking direction—represents the medial side. The lateral section is only marginally shallower in depth than the medial region. Although the DP22-4 couplet is very large (pedal track = 130 cm long), the manual impression is disproportionately larger compared with other couplet specimens of the study area. The width of the manual impression converges on the pedal track width, which reflects the weakest heteropody of any sauropod couplet in the study area.

The long axis of the manual impression is aligned approximately perpendicular to the tracking direction of the couplet, indicating that the manus of the trackmaker was not rotated (Xing et al., 2015d:478), unlike that of DP8-30, during its imprinting. Internally, the floor of the manual impression forms a shallow roller-like ramp onto the caudal margin, which is a form similar to what occurs in DP8-30 (Fig. 26A–C). This convex ramp appears to reflect the palmar morphology of the *in vivo* autopodium (see DP1-1 [Broome sauropod morphotype B] below, for further remarks on manual palmar morphology).

The bean-shaped pedal impression is imperfectly outlined cranially. The overall impression comprises two equal-sized semi-ovate depressions that are minimally defined by notches in the rim at the mid-track region laterally and medially (Fig. 26E, F). These constrictions of the outline extend inwardly as a transverse low ridge, which separates the sub-impressions of the digitometatarsal and heel pads. As in most pedal impressions, the medial region of the digitometatarsal pad impression is deepest in DP22-4. The caudal margin, unusually, is as transversely wide as the cranial end, and the overall area of the heel pad is also proportionately large, relative to other pedal tracks in the study area.

*UQL-DP9-1*. Couplet DP9-1 (Fig. 27A–C) is/was a very large one in close proximity to DP9-11 (Fig. 27D–G), another even larger but partial couplet (see below). Both occur on a jugged

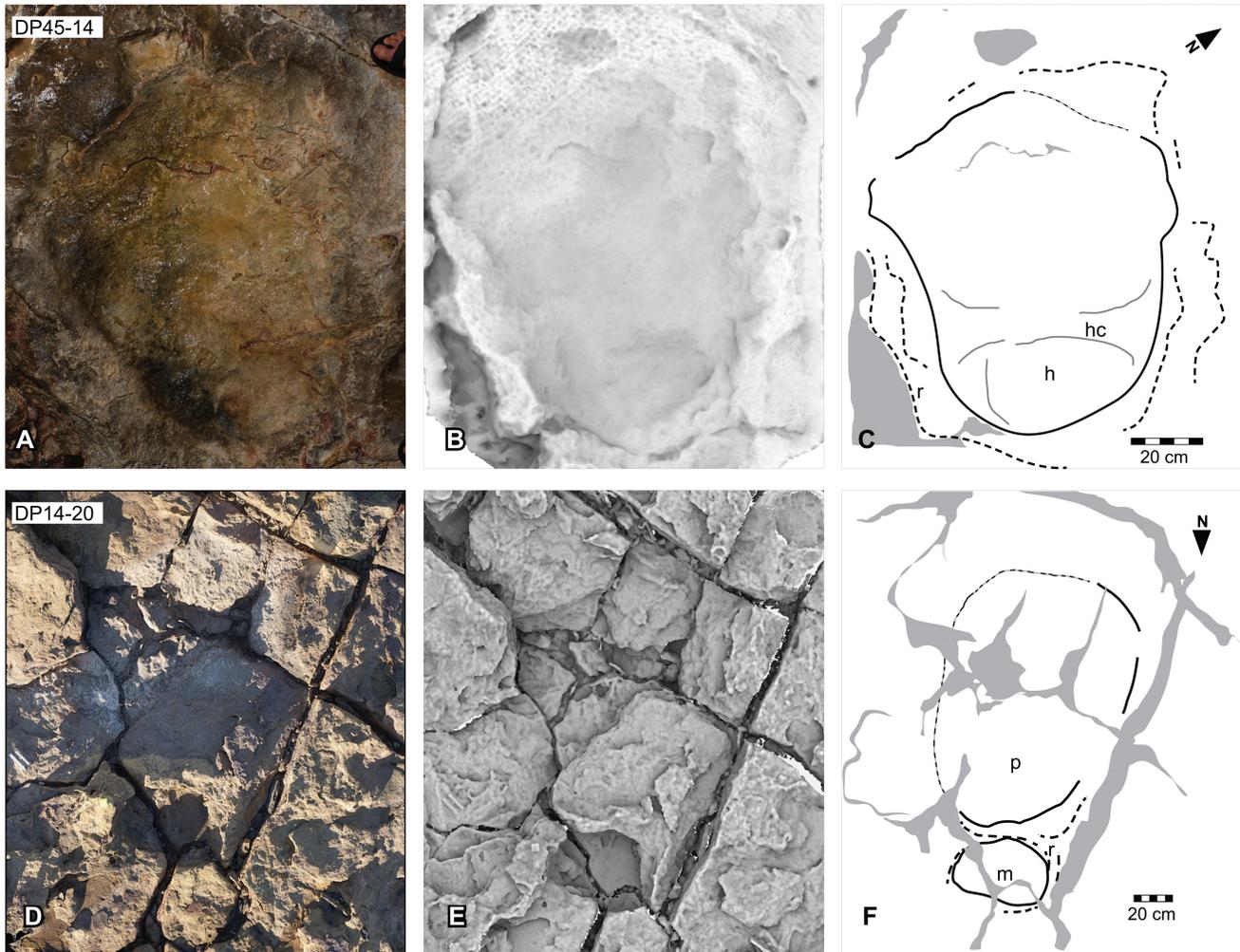


FIGURE 30. Broome sauropod morphotype A, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Pedal impression, UQL-DP45-14, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Coupled pedal and manual impressions, UQL-DP14-20, preserved in situ as **D**, orthophotograph; **E**, ambient occlusion image; and **F**, schematic interpretation. **Abbreviations:** **h**, heel region; **hc**, heel-demarcating crease; **m**, manual impression; **p**, pedal impression; **r**, expulsion rim. See Figure 19 for legend.

platform of the tracking horizon (UQL-DP9) that had been severely undercut by intertidal erosion prior to our study (in fact, DP9 is submerged at most times). Unfortunately, at some point during 2014–2015 the more distal western fragment of this platform containing most of the manual impression of DP9-1 broke off (along a crack, as per Fig. 27) and is now lost. The center of the pedal impression is also fractured through, ‘bottoming-out’ in the undercutting water column.

Both impressions are preserved chiefly as depressions outlined by continuous pressure rims, with most indicators of internal morphology of the track floor having been eroded. Specimen DP9-1 is a PM couplet (overall minimum length is 225 cm), which includes a pedal impression approximately 140 cm long, placing it among the largest sauropod track specimens from the study area. In the absence of unambiguous morphological details in both impressions, the ‘reverse’ (PM) couplet arrangement, perhaps dextral, is based on (1) the narrower western end of the pedal track, equating to the caudal heel region; (2) the convex-concave margins of the manual track equating to cranial/caudal sides; and (3) a wedge-shaped outline of the manual track, where the craniocaudally longer side is medial (as per DP22-4). The

trackmaker of DP9-1 was therefore heading southeast during its formation.

The pedal impression is trapezoid in shape, bearing an undulating northern medial side and a straighter southern lateral side. The caudal and cranial margins are nearly straight (Fig. 27). Assuming DP9-1 is a right couplet, the undulating medial side might relate to the presence of localized bulging of the medial plantar pad (see Broome sauropod morphotype E, for remarks). The few preserved internal details are shallow, probably eroded, buttresses that extend transversely from the medial and lateral margins. A short, broad, and extremely shallow transverse buttress occurs within the craniomedial region of the impression; this is presently indeterminate. Subparallel to the caudal margin, another weak but narrower ridge is nearly continuous across the transverse breadth. The second ridge seems to contour the barest indication of a sub-impression representing the heel pad.

The wedge-shaped manual impression is among the largest sauropod manual impressions from the study area (Table 10). As per DP22-4, the manual impression approaches the minimal width of the pedal impression, resulting in a medium heteropody ratio. Also similar to the above-described specimens, the surface

area inside the caudal margin is shallow compared with the cranial portion. The caudal margin itself is unclear, with the surface of the surficial substrate outside the manual impression being irregular in texture. This potentially represents extraneously displaced substrate (or, 'ejecta'), relating to sediment once adhering to palmar/plantar surfaces of the trackmaker's autopodia (Thulborn, 2004:297). The pressure rim circumnavigating the manual impression is about half as thick as the rim of the pedal track.

*UQL-DP9-11.* The immense specimen DP9-11 comprises a complete but internally fragmented pedal depression and a very incomplete outline of a manual impression (Fig. 27A–D). Tentatively considered a ?right ipsilaterally sided MP couplet, DP9-11 is at least 240 cm long and has a width range of 140–160 cm depending on the interpretation of the bounds of the fragmentary pressure rim. The couplet may have approached 290 cm in length, assuming an ovate manual impression shape. The trackmaker of the specimen was progressing towards the SSW during its formation.

The form and preservation of a steep wall of sediment in the interautopodial gap is central towards the identification of DP9-11 as an MP couplet arrangement. This distinctly high (~30–45 cm) rim of displacement substrate is convexo-concave in proximal outline and represents the preserved caudal margin (concave side) of the manual impression. The elevated form seems to indicate that it represents a mold of the caudal surface of the distal part of the trackmaker's manus, explicitly formed as the pes was planted into soft substrate in close proximity to an already in-place manus, therefore thrusting sediment up against it. The western section of the delicate interautopodial rim had been damaged prior to study, although the fresh nature of the broken surface attests both to this being recent and to the serendipitous retained preservation of such a feature in general.

In addition to the partial caudal margin, the manual track is only subtly impressed relative to the depression that forms the pedal track. It appears to be ovate, although its remaining margins are difficult to demark with clarity. The pedal impression is craniocaudally lozenge-shaped, with wavy lateral/medial rim margins. The pressure rim is discontinuous and is of variable topography (~0–10 cm high) around the depressed area of the track (~0–10 cm deep, relative to the external substrate level). The margins are best preserved caudally, and assumedly laterally (the western flank), as thin splayed sections of rim. The caudal margin is nearly straight (similar to the nearby couplet DP9-1). There is no rim craniomedially, but the general outline and position of this part of the impression suggest that it could pertain to the hallux. The pedal impression conservatively exceeds 165 cm in craniocaudal length, as measured along the western margin. However, inclusion of the craniomedial section of the impression (adjacent to the elevated steep wall) as a part of the track further extends the length to approximately 200 cm.

On the internal floor of DP9-11, a nearly transverse and narrow area in the center is disproportionately raised, but it does not exceed the elevation of the track rims. This may indicate a degree of substrate adhesion to the trackmaker's withdrawing autopodium, producing a raised plateau within the pedal impression, which is similar to sauropod tracks described from the Jurassic Iouaridène Syncline of Morocco (e.g., Boutakiout et al., 2012:fig. 5). It is important to acknowledge that the preservation of DP9-1 and DP9-11 is suboptimal, given that they represent somewhat weathered and eroded couplet impressions, rather than transmitted reliefs (sensu Thulborn, 2012). Accordingly, although there is a loss of morphological detail compared with other less-eroded impressions (e.g., DP8-30), the physical dimensions of the impressions remain immutable (but there is a reduced precision in measurements based on increasingly blurred landmarks; see further remarks on track sizes, below). The floor of the pedal impressions in DP9-1 and DP9-11 are heavily fractured, often in a semi-radial pattern. This could be

attributed to lines of weakness created in a slightly thinned zone of pliable tracking substrate during the passage of extremely colossal animals, subsequently enhanced by tidal erosive actions. The erosion at DP9 appears to be playing out both above and below the tracking horizon, accelerating the opening of the fissures in the center of the impressions.

The preservation of marginal rims of particularly low relief in both couplets at DP9 is likely due to erosion, with the discontinuous sections of rim in DP9-11 potentially being an additional facet of that. Cariou et al. (2014) described similar discontinuous track rims in sauropod tracks deposited in Upper Jurassic carbonate ramps, but these were attributed to sediment flow. Therefore, it is also feasible that the discontinuous splayed track rims in DP9-11 partly relate to localized conditions of the substrate.

*UQL-DP8-1.* The PM couplet DP8-1 is 300 cm long, indicating a trackmaker of immense size (Figs. 28, 29). With the pedal impression alone being 170–175 cm in length, any issues of preservation warrant addressing. The pedal and manual impressions of DP8-1 are not transmitted reliefs (sensu Thulborn, 2012), however, they certainly have been eroded by tidal action at the site. As we have already noted for DP9-11, weathering and erosion do not alter the original physical dimensions of the impressions but reduce the sharpness of any morphological feature impressed, including the prominence of the pressure rims. Couplet DP8-1 does have a slightly shallow depression for the pes, with the pressure rim being low in relief and showing weathering (similar to the condition of DP9-1). The manual impression has been eroded at its center. Only short segments of the manual track rim are weakly conserved, with the resultant perimeter being diffusely defined. However, DP8-1 differs from DP9-1 and DP9-11 in that any present-time continuous degradation only occurs top-down. Unfortunately, during the summer/wet season of 2013–2014, a section of the platform that included the entire manual impression and the caudal margin of the pedal impressions broke away as a result of the platform being undercut by erosion.

The trackmaker of DP8-1 was progressing northwards at the time of track formation, based on the profile of the pes and morphological features within the pedal and manual impressions (below). However, determination of ipsilateral placement (left or right side) is not possible. Given the erosion of the couplet, as well as minor differences in morphology compared with DP8-30/DP22-4, the referral of DP8-1 to Broome sauropod morphotype A is provisional, being based on the similarity of heteropody and a transverse heel-demarcating buttress (see below).

The relatively elongated pedal impression is triangular to piri-form in shape, vaguely approaching the form of the pedal track outline of DP8-30. The impression has a maximum cranial width of 130 cm, a mid-width of 105 cm, with the caudal margin of the heel narrowing to a minimum of 45 cm. The cranial margin is shallowly convex, as is also the case in DP8-30, but lacks unambiguous indications of digits. The western margin is convex, whereas the eastern margin, although undulating (like in DP9-11), is largely concave. A low relief, craniocaudally broad transverse ridge is present within the caudal area of the pedal impression, which appears to segregate the impressions for the heel region and the digitometatarsal section (Fig. 28B, C). Based on this, the impression for the heel pad was relatively small and circular compared with the more extensive pad impressions of DP8-30 and DP22-4.

The manual impression is situated south of the pedal impression and appears also to be positioned in alignment with the long axis of the pedal impression, rather than being offset lateromedially. The impression has a loosely ovate shape and is very large (Table 10), exceeding the width of the heel area of the pedal impression (Fig. 28), which thus differentiates DP8-1 from DP8-30, DP22-4, and DP9-1. Internal to the caudal margin, the wall of the impression appears to form a steep convex ramp, analogous to those observed in the manual impressions of DP8-30 and

DP22-4, which in turn reflect the palmar morphology of the trackmaker. This feature corroborates the southern margin being the caudal region of a manual impression and hence the association of the individual impressions as a PM couplet.

There is a large interautopodial gap (25% of couplet length) between the heel of the pedal impression and the cranial margin of the manual impression. However, in the absence of additional tracks cranial to the existing pedal impression, this length of PM interautopodial gap in DP8-1 is not comparable to those of other couplet specimens referred to Broome sauropod morphotype A (the others exclusively comprise MP gaps). In most sauropod trackways, the usual spacing arrangement is for short MP combined with long PM gaps (e.g., Santos et al., 2009; Falkingham et al., 2014), except in *Oobardjidama*, *Titanopodus*, and '*Brontopodus pentadactylus*' (González Riga and Calvo, 2009; Kim and Lockley, 2012), in which they are equidistant.

If DP8-1 is correctly assigned to morphotype A, the large PM gap relative to the total couplet length (if combined with the proportionally smaller MP gaps of the other specimens) rather weakly suggests that morphotype A also showed a typical interautopodial spacing arrangement. Conversely, the PM interautopodial gaps in the majority of sauropod trackways are at least the length of the pedal impressions, if not easily exceeding them, whereas the reverse appears to be the case in DP8-1. In this respect, DP8-1 is unusual compared with sauropod trackways globally, but it does corroborate the proportionately even shorter PM gaps present in DP9-1 (Fig. 27) and DP14-20 (Fig. 30) as perhaps being a defining feature of Broome sauropod morphotype A.

*UQL-DP45-14*. Specimen DP45-14 is an isolated sauropod pedal impression (Fig. 30A–C) and has been figured previously (Thulborn et al., 1994:fig. 3D). The elongate impression is piform to triangular in shape and, although large (length: 97 cm; transverse width cranially: 82 cm), is among the smaller pedal impressions referred to Broome sauropod morphotype A (Table 10).

Although DP45-14 appears moderately eroded, it is probably also a naturally shallow depression. The pressure rim is low but broad (5–15 cm thick) and is best preserved caudally around the heel region and along the caudal halves of the flanks. The pressure rim is not expressed clearly or entirely along the cranial margin, where the impression happens to be of shallowest relief. Thus, morphological details of the cranial half of the impression are poorly emphasized. Some patterned staining due to repeated pooling of water is present within the rim of the impression, particularly along the cranial margin (DP45-14 occurs reasonably high along the littoral column, so is dried regularly). The staining may highlight aspects of preservation not related to track morphology, which likely have been confused in previous interpretations (see below; also see description of DP8-16 under 'Other Sauropod Tracks'). Despite the limited preservation of DP45-14, articulated bennettitalean frond impressions in the tracking surface occur in close proximity.

Due to the overall symmetry of the impression, coupled with the absence of unambiguous morphology at the cranial end, DP45-14 cannot be identified as either a left or right pedal track. The trackmaker of DP45-14 was striking westwards at the time of its formation (Fig. 30). Within the clearer caudal half of the impression, a craniocaudally wide and low-relief transverse ridge is present, which defines the heel pad impression. The transverse width of DP45-14 along this buttress is 62 cm. The caudal margin is semicircular in profile, matching the heel outlines of the pedal impressions of other Broome sauropod morphotype A referrals (e.g., DP8-30 and DP22-4). Moreover, a continuous transverse heel-demarking ridge is a common feature of morphotype A, thus supporting the referral of DP45-14. Among these specimens, the form of the ridge is most similar to that of DP8-1. Cranially, the margin was likely convex in profile,

also conforming to the pedal track morphology of other referrals to morphotype A.

Specimen DP45-14 was originally briefly described by Thulborn et al. (1994:fig. 3), both as an example of a novel sauropod track, with most other study-site specimens being referable to *Brontopodus*, and as an impression exceeding 150 cm long: "For example, one very large form of pedal print, with bean-shaped outline and clearly-defined notches representing the digits, attains a maximum length greater than 150 cm (Fig. 3D)" (Thulborn et al., 1994:92). The dimensions reported for DP45-14 by these authors is an inconsistency in exceeding our measured length of the track by at least 150% (maximum length of 97 cm), and we are unable to provide conjecture explaining this discrepancy.

For reference, Thulborn et al.'s (1994:fig. 3D) photograph depicts DP45-14 obliquely at a low angle from the east, with a small, loose boulder lying adjacent to the heel of the print. Such boulders are frequently shifted about the rock platforms in the study area over time by wave action. The impression is also partly occupied by debris and sand in the earlier published photograph, with a thick band of water staining evident around the cranial margin (see above description of preservation). Although the poorly preserved cranial margin is slightly undulating in profile (Fig. 30), we fail to find clear evidence of the presence of notches representing digital impressions, as claimed by Thulborn et al. (1994:92 and caption for figure 3D as "...pes print with definite indications of digits [scalloped margin of print, towards kneeling figure]"). The alleged digital impressions appear to be a manifestation of the low-angle perspective of the image, coupled with water staining. Moreover, at least one of the cranial 'notches' equates to an area of shallow track-surface damage (shaded patch in Fig. 30C, compare with Fig. 30A).

*UQL-DP14-20*. The poorly preserved and heavily eroded couplet DP14-20 (Fig. 30D–F) is another provisional assignment to Broome sauropod morphotype A. It is a very large PM couplet (based on manual impression shape and orientation), of indeterminate ipsilateral position (i.e., left or right side). The enormous, 140-cm-long pedal impression (Table 10) is poorly defined because of the inconsistent distribution of its outlining pressure rim. It is essentially a shallow ovate-shaped depression crisscrossed by internal cracks. Although there is a partial rim present along the northern area, the flanks and wider southern end are not well delineated (Fig. 30F). Excluding the presence of the much clearer manual track outline, the large depression as representing an actual track impression is only substantiated by the profuse internal cracking, which seems to converge in the center of the depression. This is because an equivalent pattern and scale of cracks also occurs in the centers of the other pedal impressions that exceed 130 cm in length (i.e., DP9-1 and DP9-11).

The southern end of the pedal impression is broader and is therefore the likely cranial margin of the relief (in turn, indicating a southward progression by the trackmaker). The bean-shaped form of the manual impression exhibits convex southern and concave northern margins and conforms to the typical outline of many sauropod manual impressions. This morphology of the manual impression more compellingly supports the southerly tracking direction inferred from the pedal impression, given that the concave edge of a sauropod manual impression is typically its caudal margin. The outline of the manual impression, unlike that of the pedal impression is well delineated. Although the preserved segments of rim around the manual track have low relief, they do not extend far distally from the perimeter of the manual impression. The eastern ipsilateral side of the manual impression is slightly narrower (i.e., craniocaudally shorter) than the western side, suggesting that this would be its lateral margin (i.e., DP14-20 therefore represents a left couplet).

Of the 200 cm total length of the couplet, as little as 5% represents the interautopodial gap, which is unusual because DP14-20

represents a PM couplet (see description of DP8-1). Also unusual in DP14-20 is the exaggerated heteropody (see Materials and Methods), which is on par with that of DP1-1 (see Broome sauropod morphotype B). In contrast to DP14-20, the better-preserved couplets referred to morphotype A tend to exhibit pronounced to medium (usually medium) heteropody.

**Remarks**—Broome sauropod morphotype A comprises enormous isolated couplet and pedal-only impressions, here considered allied to a single ichnomorph based on a small set of shared morphological features. However, we caution that not every specimen exhibits all traits, nor demonstrates them in equal measure; this is an expected condition when dealing with disparate incomplete specimens. In these remarks, we briefly summarize the general morphology of the manual and pedal impressions of morphotype A, comparing them with other ichnomorphs, and comment on other occurrences of similar-sized gigantic sauropod track impressions.

The best-preserved manual impressions of the morphotype occur in DP8-30, DP22-4, and DP9-1. These are asymmetrically semicircular profiles that appear intermediate in shape between the manual tracks of *Titanopodus* (González Riga and Calvo, 2009) and those of *Breviparopus* (Marty et al., 2010). Whereas DP22-4 and DP9-1 are closer to the manual track profile of *Breviparopus* (Marty et al., 2010), DP8-30 exhibits an increasingly shallow laterocaudal ‘tail’ of the manual track (Fig. 26A). This is absent in the other manual impressions of morphotype A but occurs in the topotype of *Titanopodus mendozensis* (González Riga and Calvo, 2009). Specifically, the shallow laterocaudal extension of the manual track is recurved, appearing to ‘laterally wrap’ the pedal track in DP8-30. However, DP8-30 differs from the manual track of *Titanopodus* in its greater craniocaudal expansion. The manual tracks of DP8-30 and DP22-4 are lateromedially shorter than the corresponding pedal tracks, whereas in *Titanopodus* the manual track consistently is as broad or even exceeds the width of the cranial margin of the preceding pedal track in couplets.

The major distinction between the well-preserved manual impressions of morphotype A and those of *Titanopodus* concerns the retention of either a distinctive medial trace for the pollex (specifically in DP8-30) or some other form of caudomedial expansion of the manual track that may signify a digital trace (e.g., in DP22-4; less so in DP9-11). The presence of such zones of track extension along the edges of the manual impression could conform to manual phalanges being retained in the trackmaker’s manus, rather than precluding their absence. In contrast, short areas of medial or caudomedial expansion of the manual impression are absent in *Titanopodus*, for which the probable loss of manual phalanges has been inferred for the trackmaker of *Titanopodus* (González Riga and Calvo, 2009:638).

Pedal morphology is relatively poorly constrained in Broome sauropod morphotype A compared with that of the manus. The clearest exemplar is the keyhole/piriform profile in DP8-30, which is reminiscent of topotype tracks of *Brontopodus birdi* (Farlow et al., 1989) more than any other ichnotaxon. The increasingly circular profiles of the larger pedal impressions resemble ichnomorphs that are better informed by trackway pattern data than by the corresponding low-detail morphology of their respective tracks—including *Breviparopus* (Marty et al., 2010) and many instances of *Parabrontopodus* trackways that have weak morphology of the pedal impressions (Marty et al., 2003; Schumacher and Lockley, 2014). Despite the deregulated outlining of pedal tracks among other specimens of morphotype A, nearly all show some evidence of an internal heel pad partitioning via a buttress or narrow ridge on the track floor. When well preserved, this demarcation appears continuous and is generally perpendicular to the long axis of the impression (thus distinguishing morphotype A from the slanted condition in *Oobardjidama*). The nearest comparable morphology to this among sauropod pedal tracks globally is with large pedal impressions of *Brontopodus birdi*

from the Paluxy River site and other localities around southern U.S.A. (Farlow et al., 1989; Pittman and Gillette, 1989; Weems and Bachman, 2015). Overall, Broome sauropod morphotype A appears to be a *Brontopodus*-like ichnomorph, although the consistent lack of characters diagnosing various *Brontopodus*-type ichnospecies prevents an absolute assignment of these tracks. Also, although DP8-30 bears a well-defined pedal impression, it is not typical among the referrals of morphotype A given that it is among the smallest and hence might not represent its typical form.

If we are correct in grouping the couplet specimens DP8-1, DP8-30, DP9-1, and DP14-20 into the current single morphotype, the consolidation of incomplete trackway pattern measurements/ratios from various specimens can be used to predict what a hypothetical trackway of Broome sauropod morphotype A might appear like. Excluding the extremely incomplete DP8-11, the average MP and PM gaps are both approximately 14% of the total couple lengths (‘interautopodial ratio,’ Table 10), which implies that manual impressions were registered approximately equidistantly relative to fore and aft pedal impressions. This prospective trackway pattern appears to set morphotype A apart from the majority of *Brontopodus* and *Parabrontopodus* trackway referrals, which tend to have short MP gaps followed by relatively longer PM gaps (e.g., Farlow et al., 1989; Pittman and Gillette, 1989; Lockley et al., 1994a). Other trackways with comparable equidistant fore and aft interautopodial spacings include *Titanopodus* (González Riga and Calvo, 2009) and *Brontopodus pentadactylus* (Kim and Lockley, 2012). However, the consistently small interautopodial ratio in morphotype A also equates to short spacing between successive autopodial steps, which contrasts strongly with *Titanopodus* (González Riga and Calvo, 2009), which has long spaces between successive ipsilateral impressions. Overall, although the track outlines of morphotype A appear to show varying aspects of similarity to the major types of Cretaceous sauropod tracks (*Brontopodus*, *Titanopodus*, *Parabrontopodus*), the deduced trackway pattern based on present limited data is unique for this morphotype.

An obviously striking aspect of some of the pedal tracks assigned to morphotype A are the extremely large dimensions reported (Table 10; tracks regularly exceeding 140 cm). This may spur the perception that some or all of these are transmitted reliefs (i.e., undertracks or ghost tracks; Thulborn, 1990), with the corresponding true track outline (Milàn and Bromley, 2008) being relatively smaller in dimensions. The pedal tracks, however, lack the ‘onion ring’ marginal layering characteristic of deeply transmitted tracks (Thulborn, 2012) and sometimes include details of morphology that are consistent with the preservation of true tracks. The latter include digital creases apparent in the cranial portion of the pedal impression of DP8-30 and the steep interautopodial rim in DP9-11. The most weakly defined specimens (DP45-14 and DP8-1) tend to occur within areas high up on the littoral slope that are subject to frequent wave disturbance. Their diffuse margins are likely attributable to the greater degree of the erosion of the surface or near surface compared with other specimens (e.g., DP8-30 is protected by a deep layer of sand at most times, whereas the site DP9 lacks mobile fragments like pebbles that can easily abrade track margins).

Given the circumstance where the pedal tracks of Broome sauropod morphotype A (often 130–175 cm long) do not represent deep transmitted impressions, it is noteworthy that very few cases of pedal tracks exceeding 130 cm in length that are not transmitted have been reported globally. Thulborn (2002) reported non-transmitted tracks reaching 175 cm long, with others being 150–175 cm, from the Broome Sandstone. However, Thulborn (2002) did not specify details of individual track specimens (nor figure them), and as a result we cannot recognize if any of the dimensions reported therein relate to impressions we might have already described here.

Du et al. (2002) briefly reported Lower Cretaceous sauropod trackways from Gansu, China, as potentially the largest known

at the time. A photographed pedal track (Du et al., 2002:fig. 2) was stated to be “150 cm × 142 cm,” and corresponding manual tracks of “69 cm × 112 cm” (exceeding the size of that of DP8-1) were noted to be crescent-like. However, details of whether the Gansu tracksite includes true or transmitted tracks remain unknown. Similarly, the holotype trackway of *Parabrontopodus distercii*, from the Lower Cretaceous of Spain, comprises elongate pedal impressions with broad rims reported to be as long as 165 cm long, but with most being approximately 140 cm long (Meijide Fuentes et al., 2001:table 1 and fig. 1). Further appraisal of this tracksite is required to confirm both their dimensions and preservation. Lee and Lee (2006) documented the Lower Cretaceous ‘Jaegun Guhagpo’ *Parabrontopodus*-like trackway from South Korea, which comprises circular pedal tracks between 106 and 124 cm in length. The associated manual tracks of this trackway are relatively large and bean-shaped, appearing *Brontopodus*-like.

Until now, Late Jurassic trackways of the Moroccan *Breviparopus taghbaloutensis* (Dutuit and Ouazzou, 1980) and the undiagnostic Iberian *Gigantosauropus asturiensis* (Mensink and Mertmann, 1984) have been the most thoroughly documented sauropod tracks that exceed 100 cm. The average pedal track length in the holotype of *Breviparopus* is 110 cm (trackway Deio-D; Marty et al., 2010), whereas in ‘Trackway Tu’ it is 115 cm (Ishigaki and Matsumoto, 2009), with individual tracks of these sequences reported to be up to 140 cm long (Thulborn, 1990:fig. 6.17). Originally reported as 135 cm long (Mensink and Mertmann, 1984), the size of the *Gigantosauropus* tracks were

later revised down to average 110 cm, and to not exceed 125 cm in length (Lockley et al., 2007). For additional remarks concerning broad-level assessment of the distribution of Broome dinosaur track sizes, and its faunal implications, see Discussion.

#### BROOME SAUROPOD MORPHOTYPE B (Figs. 31, 59C, 60C, S8; Table 10)

**Referred Material**—UQL-DP1-1, an MP couplet set, preserved as natural molds, and also represented by WAM 12.1.8, a rigid polyurethane resin replica. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality, Horizon, and Age**—The referred specimens are preserved in situ at DP1 in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia; Early Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—An incomplete but well-preserved MP couplet, DP1-1, comprises a lenticular-outlined manual track (36 cm long, 52 cm wide) with a medium to large pedal track (~85 cm long), formed in a northerly tracking direction. The couplet has exaggerated heteropody (the manual impression is <20% of the area of the pes impression; see Materials and Methods). The ipsilateral side is presently indeterminate. The manual track occurs marginally west of the midline of the pedal track, suggestive of this being a left couplet. However, this very slight deviation is not sufficient basis to determine the ipsilateral side, given the typical variation of manual track position within sauropod

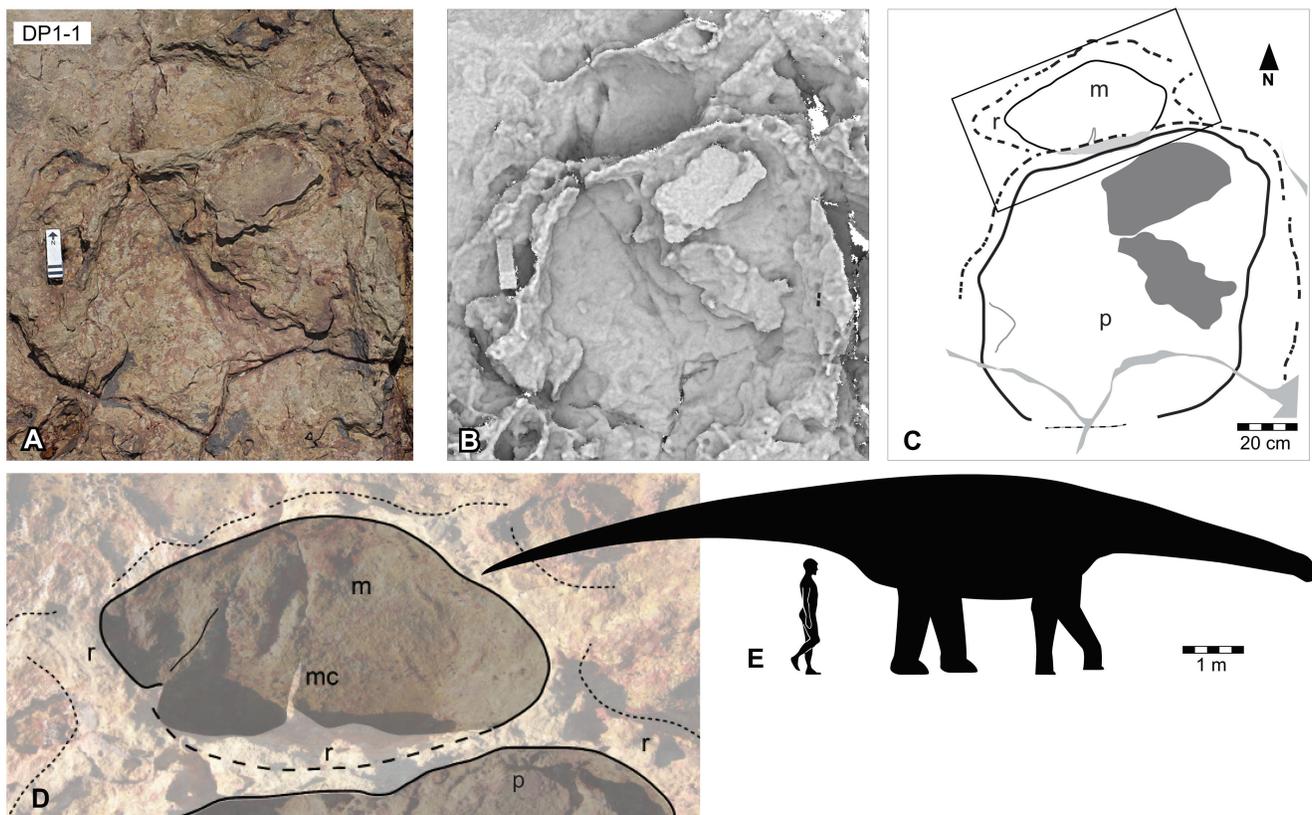


FIGURE 31. Broome sauropod morphotype B, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Coupled right manual and pedal impressions, UQL-DP1-1, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, close up of the manual impression and interautopodial region showing area within the box in **C**, as viewed from an oblique cranial aspect. **E**, silhouette of hypothetical trackmaker of Broome sauropod morphotype B, based on UQL-DP1-1, compared with a human silhouette. **Abbreviations:** **m**, manual impression; **mc**, molded ridge, representing a groove on the palmar-caudal surface of the trackmaker’s manus; **p**, pedal impression; **r**, expulsion rim. See Figure 19 for legend.

trackways (Xing et al., 2015d:478). The manual track combines a convex cranial margin with a straighter but bilobed caudal margin. Mainly visible from a cranial oblique aspect, the bilobed section of the mid-caudal margin is parted by a short cranially extending raised crease on the floor of the manual track. Viewed from above, the mid-caudal margin of the manus is obscured by the rim of the pedal track, which slopes forward and partly overhangs the internal area of the manus (Fig. 31).

The oblong pedal track bears little or no morphological detail of the pedal indenter and is chiefly identified based on the preserved portions of the raised rim of the track. This rim is built up to the sides of the cranial margin and the cranial flanks of the track but becomes diffuse caudally. Near the manual track, an area within the pedal impression is raised significantly above the floor of the rest of the track, being in-filled with medium- to fine-grained tabular sandstone of Lithofacies Association 3 (Tables 2 and 3). The western (lateral) track margin is mostly convex, whereas the opposing eastern edge is slightly concave (Fig. 31). The caudal margin is unclear, but the trajectories of the weathered lateral rims suggest that the track did not continue much beyond the intersection of two cracks in the substrate (Fig. 31C).

**Remarks**—Unique morphological aspects of DP1-1 among the sauropod tracks from the study area include the lenticular shape of the manual track with an unusually exaggerated heteropody of the couplet. The combination of these features renders it impractical to assign DP1-1 to Broome sauropod morphotypes A and C, whereas the couplet cannot be compared directly with the pedal track only Broome sauropod morphotypes D and E. And although one couplet referred to Broome sauropod morphotype A—DP14-20 (Fig. 30D–F)—also has exaggerated heteropody, the shapes of the manual impression are dissimilar in the two tracks. We applied a conservative estimate of the position of the caudal margin of the pedal track, so the heteropody of DP1-1 would be further exaggerated with a hypothesized longer pedal impression.

An additional potentially distinguishing aspect of DP1-1 is the negligible interautopodial distance between manual and pedal tracks, arising from the thrust pedal step. However, this dimension is only comparable in the subset of MP couplets from the study area (Table 10), limiting its usefulness. The MP couplets referred to Broome sauropod morphotype A all have an interautopodial distance of between 10% and 15% of total couplet length (Table 10), but it is problematic to conclude if these small differences taken from mostly imperfectly preserved tracks are significant. That being said, DP1-1 can be unambiguously distinguished from *Oobardjidama foulkesi* based on interautopodial distance and manual track position, additional to differences in heteropody. In *Oobardjidama*, the manual impressions are disparate from the cranial margin of the pedal impressions, resulting in a large interautopodial proportion (~25%) in MP couplets.

Worldwide, narrow-gauge trackways with pronounced heteropody are often referred to *Parabrontopodus mcintoshi*, or considered to be ‘*Parabrontopodus*-like’ (e.g., Marty et al., 2003, 2010; Le Loeuff et al., 2006; Xing et al., 2015d, 2015h). As argued in earlier remarks, we consider the second label essentially a broader-level classification for any narrow-gauge trackway with pronounced heteropody, which we informally label part of the ‘*Breviparopus/Parabrontopodus* nexus’ in order to indicate a broader (connected) grouping, and to avoid suggesting referral to a specific ichnotaxon beyond being loosely both ‘*Breviparopus*-like’ and ‘*Parabrontopodus*-like’ (see remarks under *Oobardjidama*). As discussed by Lockley et al. (1994a:140), we also consider it imprudent to formalize or endorse higher ichnotaxonomic names for sauropod tracks.

Although the manual/pedal track area percentage of DP1-1 is within the range of the pronounced to exaggerated heteropody typical of trackways assigned to the *Breviparopus/Parabrontopodus* nexus, the absence of gauge data in DP1-1 precludes

assignment to that group. Another issue precluding such a referral is that trackways of the wide-gauged *Titanopodus mendocensis* also exhibit pronounced heteropody (González Riga and Calvo, 2009; González Riga, 2011). *Titanopodus*, however, differs from DP1-1 because it consistently has equidistant MP and PM interautopodial gap spaces. Although some trackways recently referred to *Parabrontopodus* regularly show the pedal impression encroaching on the caudal margin of the manual impressions, as occurs in DP1-1 (e.g., Le Loeuff et al., 2006; Marty et al., 2010), couplets of *Breviparopus/Parabrontopodus* or *Titanopodus* conversely do not exhibit the extremely exaggerated heteropody that is present in DP1-1.

Although obviously different in manual track morphology, Broome sauropod morphotype B is not adequately comparable via pedal track morphology to other well-defined eusauropod ichnotaxa (e.g., *Brontopodus*, *Polyonyx*) to warrant further remarks. Within a global scheme, morphotype B should be considered ichnotaxonomically indeterminate and not assignable to other described, unnamed sauropod track morphotypes. However, within a more limited scope of the Yanijarri–Lurujarri study area, DP1-1 is uniquely differentiable from other tracks there, pending future data, and hence is considered a distinct morphotype.

The interface between the bilobed caudal margin of the manual track and the overhanging cranially extending rim of the pedal track is insightful regarding the morphology of the trackmaker’s manus. The forward-sloping pedal track rim is explainable if the pedal in-step of the trackmaker drove forward the displacement rim left previously by the manus. As a result, there is a negligible interautopodial distance (Table 10), differentiating DP1-1 from DP9-1. The short, slanted ridge on the floor of the manual track that extends to the bilobed portion of the caudal margin feasibly reflects the external palmar morphology of the trackmaker’s manus. Specifically, the bilobed subimpressions represent digits I and V in a colonnade manus. Well-preserved sauropod manual casts from the Middle and Upper Jurassic of Europe and North America corroborate the caudal crease in DP1-1 reflecting the soft anatomy of the trackmaker’s manus (Milàn et al., 2005; Platt and Hasiotis, 2006:fig. 5; Romano and Whyte, 2012:fig. 7A). In these examples, a median shallow groove on the caudal surface of the autopodium extends onto the caudal side of the palmar surface. This morphology would channel sediment expulsion during in-step of the autopodium or facilitate sediment uplift during autopodial withdrawal. In either case, a resulting median crease is formed.

#### BROOME SAUROPOD MORPHOTYPE C (Figs. 32, 59D, 60D, S9; Table 10)

**Referred Material**—UQL-DP14-17, a MP couplet set, preserved as natural molds. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality, Horizon, and Age**—The referred specimen is preserved in situ at DP14, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—DP14-17 comprises a large (Tables 1 and 10) right MP couplet, which is orientated in a westwardly tracking direction. The interautopodial distance is short, shifting from between under 20 cm (medially/centrally) to about 5 cm (laterally), where part of the pedal track rim slightly overhangs the manus track. The expulsion rim at the interautopodial gap is relatively steep, and despite some breakage, this is an aspect analogous to the condition in Broome sauropod morphotype A couplet DP9-11. Although the manual impression is incompletely emarginated medially, it probably was transversely broad

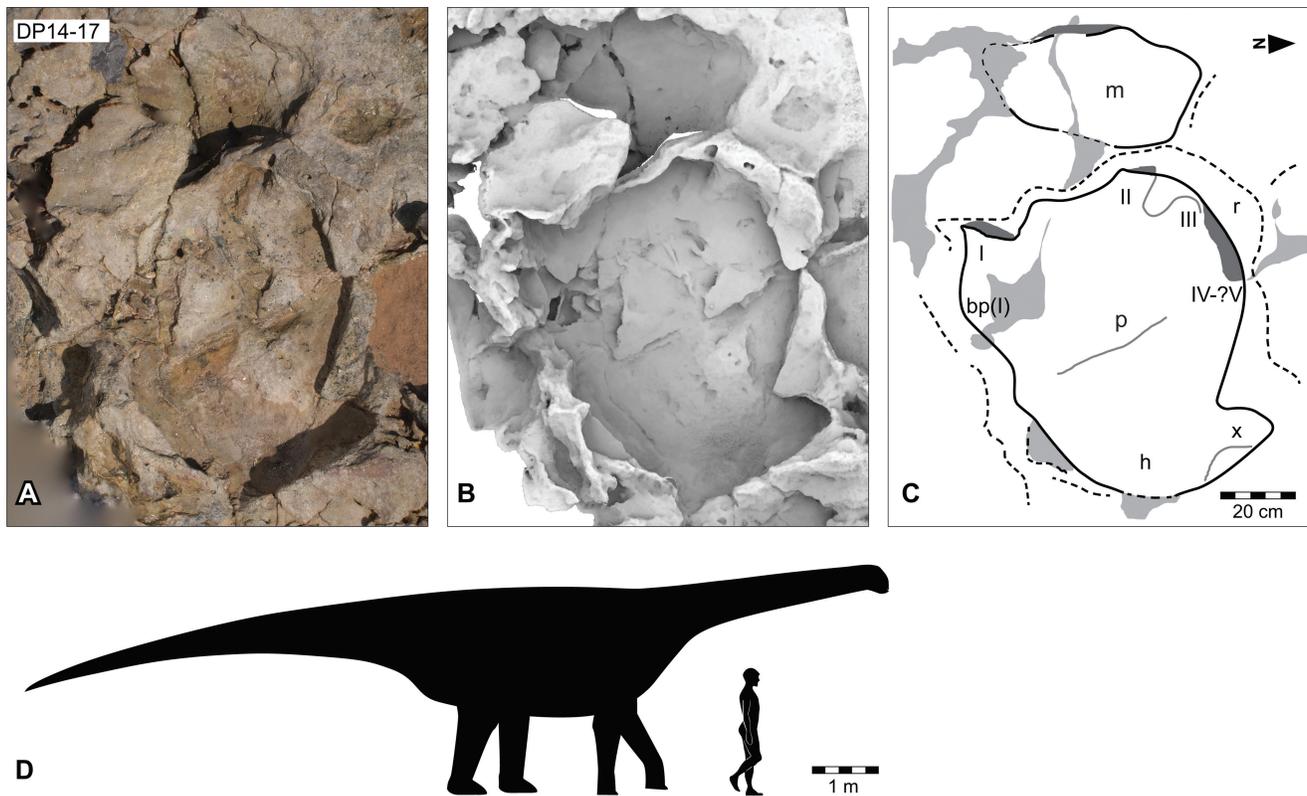


FIGURE 32. Broome sauropod morphotype C, from the Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia. Coupled right manual and pedal impressions, UQL-DP14-17, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, silhouette of hypothetical trackmaker of Broome sauropod morphotype C, based on UQL-DP14-17, compared with a human silhouette. **Abbreviations:** **bp(I)**, bulged pad associated with digit I; **h**, heel region; **I–V**, digital impressions I, II, III, IV and V; **m**, manual impression; **p**, pedal impression; **r**, expulsion rim; **x**, impression of unclear origin. See Figure 19 for legend.

compared with the pedal impression. The resulting heteropody ratio therefore is less than 30% (likely 25% assuming an extrapolation of the preserved manual track outline), which equates to pronounced heteropody (sensu Lockley et al., 1994a; see Materials and Methods).

The manual track is imprinted directly in front of the pedal track, rather than being offset laterally relative to the long axis of the pedal track. A wedge-like section of an interautopodial portion of the couplet between the southern margin of the manual impression and the cranial end of the pedal impression has broken away, presumably along cracks. Although the outline of the missing section makes it seem from above that the manual impression bears an acuminate extension toward the pedal impression (Fig. 32), the manual impression is relatively short craniocaudally (Table 10). The preserved segments of the discontinuous manual track margin indicate that the impression is longer laterally and slightly craniocaudally shorter in the midsection. The manual track is relatively deeply impressed compared with the pedal track, particularly where they are closest, although the floor of the track is now being undercut by tidal erosion. A small median section of the cranial expulsion rim overhangs the corresponding floor of the track; otherwise, the cranial margin of the manual track is convex. The lateral part of the floor of the track is shallow, and the adjoining rim here also weaker.

The well-preserved pedal track has an approximately ovate outline, and discounting the protruding digital impressions, it is transversely broader cranially. It is slightly pinched caudally. There are at least two distinct acuminate digital impressions

cranially, a single broader sub-impression along the lateral margin, and a third acuminate impression occurring caudally. Of the indentations in the cranial rim margin, the first two represent short impressions of digits I and II and occur along the craniomedial and mid-cranial margin of the track, respectively. The impression of digit I, which is mainly a trace of the ungual, extends cranially. Medial to this, a short bulge in the pedal track outline suggests an outward expansion in the metatarsodigital pad during the footfall and can be considered a pad callosity trace (Fig. 32). The impression of digit II is a laterally deflected (north-pointing) mark, documenting the trace of a laterally flexed ungual (Fig. 32). This is separated from the convex lateral border of the track by a broad, shallow crease. This larger rounded lateral area of the track could represent the impressions of any of digits III–V, either collectively or individually. Most likely, this space received digits IV and V, with digit III occupying an area adjacent to the broad internal ridge that delimited digit II.

The third and largest acuminate mark ('x' in Fig. 32) is a relatively deep, large, broad, laterally extending impression (15 cm long) that originates near the heel region of the track. The identity of this feature is unclear, although it may represent either an unusual trace of digit V, a result of extramorphological activity (sensu Thulborn, 1990), or a partial impression from an extraneous track-making activity. The cranial base of the mark forms an acute angle against the body of the track. The mark is straight, rather than being curved as is often the case for the terminal areas of sauropod digital traces. The internal track wall between the heel region of the track and the triangular impression slopes forward to form a steep decline to the floor of the pedal track

(Fig. 32). Inclusive of this ramp, the margin of the pedal impression between the apex of the triangular impression and the caudal-most extent of the heel impression is almost straight. If the triangular impression is not part of the pedal morphology of the trackmaker, the ramped part of the internal heel impression may additionally be a result of extramorphological activity such as autopodial withdrawal. Excluding the triangular impression in DP14-17, the heel region gradually narrows caudally to a gentle convexity. The cranial demarcation of the heel is denoted by a cleft in the medial mid-track margin, where the track narrows to less than 50 cm mediolaterally.

The expulsion rim is variably extended around the pedal track. A narrow ridge of the rim is particularly thin (2–5 cm thick) along much of the cranial margin of the track. The rim forms a thicker bulge both medially and laterally (approximately 15 cm thick around the impressions of digits III–V).

**Remarks**—Broome sauropod morphotype C is represented by a single MP couplet, DP14-17, which displays good preservation of the pedal impression cranially. Accordingly, mainly aspects of pedal track morphology differentiate this morphotype from other tracks, which therefore also limits comparisons during the assignment of DP14-17. If the triangular impression caudally ('x' in Fig. 32) does represent an impression of digit V, it would add to the characterization of the morphotype. In this scenario, morphotype C would further be characterized by its distinctly straight, elongate impression of digit V, with a strong divarication from the internal pedal heel impression area. This configuration in the pedal impression of DP14-17 would distinguish the morphotype from all other sauropod pedal tracks documented in the study area. Alternatively, as we have alluded to earlier, it is plausible that such a configuration is a product of extraneous or extramorphological activity. An alternative is that an unusual digital configuration represents momentary biomechanical variation in the pes of the trackmaker, which increases the likelihood that DP14-17 could be assignable to another sauropod track morphotype from the area. At the time of writing, we have no additional evidence to support this last possibility.

Aside from the peculiar impression near the heel area, two other unique aspects of DP14-17 are apparent that preclude referral to other sauropod morphotypes in the area. The relatively large breadth of the manual track with respect to the pedal track distinguishes DP14-17 from other track couplets in the area. The ratio of pedal to manual track width is 1.26 in DP14-17, a ratio that is the lowest among all non-overprinted couplets from the study area (which typically range from 1.5 to 1.8). Three couplets referred to Broome sauropod morphotype A have comparably low ratios: DP22-4, DP9-11, and DP8-30. However, the first (DP22-4) is partially overprinted by other tracks, affecting the measured pedal track width, the second (DP9-11) is poorly preserved, whereas the third (DP8-30) is among the better-preserved exemplars of morphotype A, but it is readily distinguished from DP14-9 based on manual and pedal track shapes.

Secondly, although the manual track is imperfectly preserved in DP14-17, the existing outline of the lateral half suggests a wedge-shaped form, at least toward the center of the track (Fig. 32), combined with a pronounced heteropody relative to the pedal track (Table 10). The wedge-shaped impression of the manus of DP14-17 renders it different from the few well-preserved manual tracks of other morphotypes in the area: in Broome sauropod morphotype A, the manual track is classically a deep bean- to crescent-shaped outline, as are many tracks globally (e.g., Farlow et al., 1989; González Riga and Calvo, 2009; Xing et al., 2015c); in Broome sauropod morphotype B (DP1-1), the manual track is lenticular, rather than being expanded laterally. Pronounced heteropody in DP14-17 distinguishes it from most of the couplets of *Oobardjidama foulkesi*, morphotype A (medium to mild heteropody), and morphotype B (exaggerated heteropody).

Besides the above three major points concerning unique morphology, DP14-17 is distinguishable from other sauropod track types within the study area in other aspects: DP14-17 has a relatively short interautopodial distance, differentiating it from *O. foulkesi*; DP14-17 has a pedal track that is longer craniocaudally than it is transversely wide, differentiating it from all specimens referred to Broome sauropod morphotype E (squat rounded tracks), whilst concomitantly not being as relatively elongate as tracks assigned to morphotype D; DP14-17 has divaricated digital impressions, differentiating it from all Broome sauropod morphotypes other than morphotype E; DP14-17 has a reduced cranial pad callosity impression associated with the impression of digit I, unlike the more extensive morphology seen in *O. foulkesi* and morphotype E; and, given the well-preserved pedal impression, DP14-17 apparently lacks a strong continuous heel partition or a heel-associated callosity, in contrast to *O. foulkesi* and morphotype A.

Broome sauropod morphotype C shares with the holotype track of *O. foulkesi* and Broome sauropod morphotype D a cranially directed impression of digit I, although in DP14-17 the impression probably only represents an ungual trace rather than a more extensive digit as occurs in morphotype D; also, the presence of digital impressions occurring along half of the perimeter of the pedal impression is a common aspect of both Broome sauropod morphotypes C and E.

The steep ramp at the laterocaudal margin of the track in DP14-17 is also present in morphotype E, but it occurs in a relatively more cranial position and is shallower in the latter form. A similar ramp occurs in a well-preserved right pedal track from Las Cerradicas tracksite (Lower Cretaceous, Spain), track 'LCR14.6p' (Castanera et al., 2011:figs. 5b [natural mold] and 6 [cast]). Castanera et al. (2013) draw attention to a prominent lateral indentation in purportedly right pedal impression, 'EMajS2.1,' from El Majadal tracksite (however, this specimen could be also interpreted as a left track with a medial bulge). In some pedal tracks from the Briar Plant tracksite (Lower Cretaceous, Arkansas; referred to *Brontopodus birdi* [Farlow et al., 1989], but see earlier comparative remarks on *Oobardjidama*), the lateral track margin is notched to varying magnitudes (Pittman and Gillette, 1989:fig. 34.17F–J).

Couplet DP14-17 is not readily referable to an established sauropod ichnogenus globally, foremost because of a lack of trackway parameter information. This precludes *Breviparopus taghbaloutensis/Parabrontopodus mcintoshi* (Ishigaki, 1989; Lockley et al., 1994a; Marty et al., 2010), despite their comparable heteropody to DP14-17. *Brontopodus birdi* (Farlow et al., 1989), *Polyonyx gomesi* (Santos et al., 2009), and '*B.*' *pentadactylus* (Kim and Lockley, 2012) typically have medium to mild heteropody associated with large, caudally concave manual tracks, with the latter ichnotaxon additionally showing strongly outwardly rotated manual tracks. The couplets of *Titanopodus mendozensis* have extremely long interautopodial distances relative to total couplet length (González Riga and Calvo, 2009; González Riga et al., 2015), which are not comparable to DP14-17 or any of the track morphotypes from the Yanijarri–Lurujarri study area (Table 10). The early sauropodomorph pedal tracks of *Eosauropus cimarronensis* (Lockley et al., 2006a; not considering referred trackways that lack pedal digit morphology [i.e., Lockley et al., 2011]) and *Liujiapus shunan* (Xing et al., 2016b) exhibit three or four parallel digital impressions along the cranial margin of the track, respectively, which differs from the spread condition in DP14-17.

#### BROOME SAUROPOD MORPHOTYPE D (Figs. 33, 59E, 60E, F, S10; Table 10)

**Referred Material**—UQL-DP11-4 and UQL-DP14-10, isolated right pedal tracks preserved as natural molds, and an

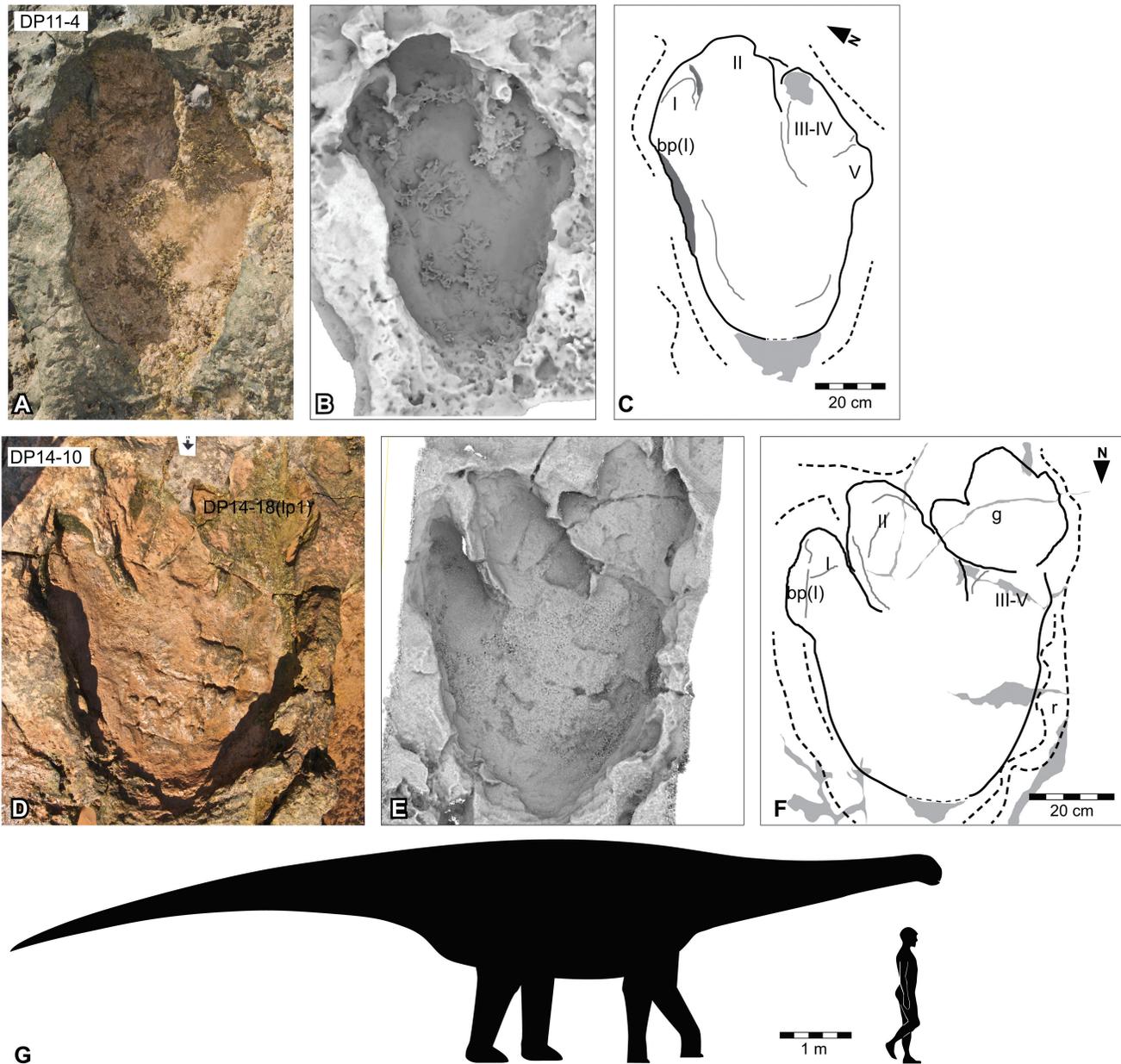


FIGURE 33. Broome sauropod morphotype D, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Right pedal impression, UQL-DP11-4, preserved in situ as **A**, photograph; **B**, ambient-occlusion shading; and **C**, schematic interpretation. Right pedal impression, UQL-DP14-10, preserved in situ as **D**, photograph; **E**, ambient occlusion image; and **F**, schematic interpretation. **G**, silhouette of hypothetical track-maker of Broome sauropod morphotype D, based on UQL-DP11-4, compared with a human silhouette. **Abbreviations:** **bp(I)**, bulged pad/callosity associated with digit I; **g**, overprinted pedal impression of *Garbina roeorum* (UQL-DP14-18[lp1]); **I–V**, digital impressions I, II, III+IV, and V, respectively; **p**, pedal impression; **r**, expulsion rim. See Figure 19 for legend.

isolated ?right pedal track (unnumbered) figured in Thulborn et al. (1994:fig. 4D). Rigid polyurethane resin replicas of UQL-DP14-10 and UQL-DP11-4 are deposited in the Western Australian Museum (as WAM 12.1.9A and WAM 12.1.10, respectively). (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Location, Horizon, and Age**—The referred specimens are preserved in situ at DP14 and DP11, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derive from

the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone; the unnumbered track figured in Thulborn et al. (1994: fig. 4D) is from an unknown locality on the Dampier Peninsula.

**Description**—Track DP11-4 is a large-category (Table 1) right piriform pedal impression, which was laid down in an eastwardly tracking direction. It is a relatively slender impression (Table 10), bearing traces of at least three major digital trace partitions. The first two are divaricated by an internal crease (i.e., an interdigital rim) and represent the impressions of extended digits I and II, respectively. The second digital impression is separated from the remaining lateral area of the track by

a well-formed deeply divaricated internal ridge, which extends caudally almost to the heel impression region. The third, lateral-most impression has a short intervening oblique ridge (Fig. 33), which likely represents the boundary either between the impressions of digits III and IV or between the impressions of digits IV and V.

Although extended, digit I of the trackmaker of DP11-4 appears to have been medially rounded, tapering to shallow apex, which might represent the unguis. Digit II appears to have been broad and also appears to preserve a transverse ridge that could represent a trace of a phalangeal boundary or an extramorphological product (sensu Thulborn, 1990), such as resulting from pedal withdrawal. Similar to DP14-10 below, the impression of digit I of DP11-4 is also relatively narrow, with the impression of digit II making up nearly 40% of the maximum width of the cranial portion of the track. Collectively the impressions of digits I and II constitute 66% of the transverse width of the digital arcade of DP11-4.

The expulsion rim is evenly prominent around the medial and lateral sides of the track but is slightly diffuse or eroded caudally. Along the medial margin, most of the rim forms a narrow overhang over the corresponding deep margin of the track. Cranially, the rim fluctuates between being narrow (5 cm thick) and being prominent between the impressions of digits I and II and digits II and III (up to 15 cm thick). As per DP14-10, DP11-4 gradually narrows in width caudal to the mid-length, to form a rounded heel impression.

Track DP14-10 is a medium to large (Tables 1 and 10) right sauropod pedal track that is partially overprinted by a thyreophoran track (DP14-18[lp1]) referred to *Garbina roeorum*, ichnogen. et sp. nov. (Fig. 33). The sauropod track is obovate in shape, with its broader cranial margin nearly 60 cm wide along the digital impressions, although this area has been deformed by the thyreophoran trackmaker in the southwest cranial portion of the track. Just caudal to the overprinted part of the track the width is under 55 cm, and this measurement declines caudally toward the heel. Both superimposed tracks are deeply impressed and well demarcated from the tracking surface substrate. However, the track is uniformly deeper (~20 cm) than the thyreophoran track (~7 cm), suggesting a considerably heavier trackmaker; DP14-10 is orientated in a southerly direction.

Track DP14-10 bears two large digital impressions, pertaining to digits I and II, which collectively form 70% of the track width. Both digital impressions are extended cranially, rather than being flexed laterally as typically occurs in other sauropod tracks. The impression of the hallux (digit I) is proportionately quite slender and is appended with a shallow pad bulge that is discriminated by an internal crease (Fig. 33). Half the length of the halluxal impression comprises a spoon-shaped indentation of the unguis. The impression of digit II is noticeably more shallowly impressed than the hallux and extends slightly farther cranially than the hallux. This impression is nearly 37% the length of the overall track. Although the remaining digital impressions, were they present, have been obliterated by the *Garbina* track, they would have been relatively small compared with those of digits I and II (given that the space lateral to the impression of digit II occupied 30% of the cranial track width). A broad expulsion rim delimits the lateral side of the track. The margin of the heel impression is rounded, and the internal surface corresponding to the heel pad appears rugose and slightly upwelled.

An unnumbered track (Thulborn et al., 1994:fig. 4D) was not observed firsthand during our surveys of the Yanijarri–Lurujarri section of the Dampier Coast, so we refer readers to the figure in Thulborn et al. (1994). This track is small (~40–45 cm long) and appears to have extended digits and an overall pedal shape similar to DP14-10 and DP11-4. The rim is evenly developed around the track and, as pointed out by Thulborn et al. (1994), bears concentric lamination that most likely relates to an eroded state of the rim

**Remarks**—The pedal only tracks DP11-4 and DP14-10 share several unique characteristics not found in other sauropod pedal tracks from the Yanijarri–Lurujarri section of the Dampier Peninsula, indicating that they represent impressions made by the same type of sauropod trackmaker. In the absence of intermediate track morphologies, this track type can easily be discriminated from other sauropod morphotypes in the study area, as well as from the majority of sauropod pedal track profiles in a global context. However, we refrain from establishing a new ichnogenus because of the absence of manual tracks and whole-trackway data associated with these two tracks, which would otherwise facilitate meaningful utility of a new ichnotaxic name.

The traits shared by DP11-4 and DP14-10 are large cranially orientated digital impressions; maximum length of digital impressions one-third length of whole pedal track (i.e., the digital impressions are deeply divaricated, particularly that of digit II); digital impressions I and II occupying the majority of cranial pedal width (between 60% and 75%); and a narrow length to width ratio and elongation index of the overall pedal impression (Table 10). With the exception of the elongated profile of the pedal impression, all the other features are absent in other sauropod track types from the study area. Although some impressions of Broome sauropod morphotype A may have comparable elongation in the pedal impression those of DP11-4 and DP14-10 lack the mid-track constriction in the profile that would yield a piriform outline with a demarcated internal heel region. Instead, these pedal tracks of morphotype D gradually taper from front to back, producing a generally subtriangular outline (the medial wall overhang in DP11-4 masks this form).

Aside from the unique combination of features presented by Broome sauropod morphotype D, there are additional similarities and differences between it and other unnamed pedal morphotypes from the study area. Morphotypes C and D both share minor pad bulge/callosity sub-impressions associated with the medial margin of the impression of digit I which is readily distinguishable from the broad and long sub-impression in morphotype E. In morphotypes A (when preserved) and D, the extent of the impressions for the digital arcade is limited to the cranial margin, whereas it is spread radially in morphotypes C and E. Morphotype D is not appropriately comparable to morphotype B, because of the poor preservation of the pedal track in the latter.

The shape of the track outline and proportions of the digital impressions in Broome sauropod morphotype D superficially resemble those of the Early Jurassic *Otozoum moodii* (Rainforth, 2003; Schumacher and Lockley, 2014; D’Orazi Porchetti et al., 2015). However, the much smaller tracks of *Otozoum* typically show additional sub-impressions of tarsometatarsal anatomy, located in the heel region of the impressions and considered to be made by non-sauropod sauropodomorphs (Rainforth, 2003). Broome sauropod morphotype D resembles the holotype of *Polyonyx gomesi* from the Middle Jurassic of Portugal (Santos et al., 2009), showing cranial extension of the impressions of digits I and II combined with a generally slender profile of the trackmaker’s pes. However, morphotype D differs from *Polyonyx* by its atypical relative width and extended length of those particular digital impressions. The outer digital impressions of *Polyonyx* are also curled laterally and not limited in space as in morphotype D. Some well-preserved pedal impressions of *Polyonyx*-like trackways from the Jurassic–Cretaceous interval of Spain (Torcida Fernández-Baldor et al., 2015) also demonstrate cranially projecting unguis impressions, as do a few of the topotype pedal tracks of *Brontopodus birdi* (e.g., Farlow et al., 1989:fig. 42.9). Nonetheless, Broome sauropod morphotype D differs from these tracks in the same features as noted for *Polyonyx*. Until future discoveries of morphotype D tracks within trackways are made, general comparisons with diagnosable and familiar ichnotaxa (i.e., *Brontopodus*, *Titanopodus*, or the *Breviparopus/Parabrontopodus* nexus) are not constructive.

Broome sauropod morphotype D is not the first occurrence of pedal tracks with a combination of the listed set of characteristics. In some respects, the tracks of Broome sauropod morphotype D converge on the morphology of some pedal tracks ascribed to stegosaurians, particularly *Deltapodus* spp. and *Deltapodus*-like tracks (Milàn and Chiappe, 2009; Mateus et al., 2011; Li et al., 2012: ‘trackway A’ therein; Xing et al., 2013a, 2015b). These similarities include the digital arcade arranged along the cranial margin into three major sub-impressions, with the impressions of digits I and II (digits II and III in stegosaurians) occupying 60–70% of the cranial track width, as well as the similar rounded shape of the heel impression following an elongated track profile. The main discriminating factors between morphotype D and these stegosaurian pedal tracks are (1) size, with stegosaurian pedal tracks rarely exceeding 50 cm in length; (2) the shallower divarication of digital impressions in stegosaurian tracks resulting in the hypices nearer the cranial track margin compared with the sauropod tracks; and (3) with the exception of *Deltapodus curriei* (Xing et al., 2013a), the more strongly caudally tapering outlines that result in a triangle-like pedal shape in stegosaurs. In *Deltapodus curriei*, which are large-sized stegosaurian impressions from the Lower Cretaceous of Central Asia (Xing et al., 2013a), the pedal track outlines are indented mid-length to result in a rounded heel that resembles sauropod tracks.

Like *Deltapodus curriei*, some notably small sauropod trackways and isolated tracks (pedal track length: 25–50 cm) have been described from eastern China in recent years that seem to blur the morphological distinction between sauropod and stegosaurian tracks (Xing et al., 2013b:126). Two tracksites are worth mentioning in comparison with Broome sauropod morphotype D because they exhibit a near-identical morphology in the pedal track alone: the narrow-gauge trackways LSV-S1 and LS1-S2 from the Jishan Provincial Geopark tracksite (Xing et al., 2013b) and the pedal only trackways BL-S1 and BL-S2 from the Beilin tracksite (Xing et al., 2015d). Both sites are from the Lower Cretaceous Dasheng Group. Indeed, consideration was initially given to whether the Jishan LS1-S2 pedal tracks were produced by a stegosaurian on account of their rounded and shallowly divaricated digital impressions (Xing et al., 2013b). Within both the Jishan and Beilin tracksites, the proportionately elongated pedal impressions regularly display two straight first two digital impressions (assumed to be digits I and II) occupying 65–80% of the cranial breadth, which is comparable to Broome sauropod morphotype D (i.e., Xing et al., 2013b:figs. 6 and 10, 2015d: fig. 3).

Although the sauropod affinities of the small pedal tracks from China were confirmed by attributes of the trackways as a whole, these and other small trackways were subsequently assigned to *Parabrontopodus* sp. based primarily on their pronounced heteropody (Xing et al., 2015d, 2015h). We feel that such nonspecific referrals based on few criteria further destabilizes the systematic distinction between sauropod ichnogenera and fosters a vaguer definition of what tracks any given ichnotaxic label should precisely refer to. In this particular case, pronounced heteropody also occurs in other tracks (*Breviparopus* and *Titanopodus*), whereas the unusual digital morphology described for Broome sauropod morphotype D and the small tracks from East Asia (as a convergence to stegosaurian digital morphology) is not an aspect of the holotype track of *Parabrontopodus mcintoshi* (Lockley et al., 1994a:figs. 3, 4).

Finally, Xing et al. (2015g) described a variety of taxonomically unassigned, very small to medium sauropod tracks/trackways (pedal lengths: 11–55 cm) from the Kimmeridgian–Valanginian Tuchengzi Formation. At least one of those pedal tracks, QJDILL-S1 (lp1; part of a mildly heteropodous trackway), shares with DP11-4 a similar shape and arrangement of tri-dactyl indentations (Xing et al., 2015g:figs. 4, 10). A second

isolated track, QJDIII-SI2, is close in shape to Broome sauropod morphotype D but contains shallow digital hypices reminiscent of stegosaur pedal tracks (Xing et al., 2015g:fig. 13). Xing et al. (2015g) referred both these Tuchengzi Formation tracks to the same morphotype of unnamed sauropod.

In summary, these comparisons indicate that East Asian occurrences of Broome sauropod morphotype D-like tracks tend to be rather diminutive, where recognized (also see miniature trackways in Lim et al., 1989; Lockley et al., 2002b). In relation to small sauropod tracks, Xing et al. (2015d) suggest that changes in gauge and heteropody with track size may be related to either, or both, ontogenetic or taxonomic differences among trackmakers. In addition to these, we propose that juvenile trackmakers underwent minor changes to the morphology of the autopodium during ontogeny (e.g., shape or flexibility of digits, or form of the plantar pad around the digits), which may explain the higher abundance of stegosaurian-like track morphologies specifically in small sauropod tracks. In contrast, the pedal tracks of Broome sauropod morphotype D were not formed by particularly small trackmakers, which further attests to its distinction as an ichnological track type.

#### BROOME SAUROPOD MORPHOTYPE E (Figs. 34, 59F, 60G, S11; Table 10)

**Referred Material**—DP14-9, an isolated left pedal track and DP30-1, an isolated right pedal track (Thulborn et al., 1994: fig. 4C). Both specimens are preserved as natural molds. DP14-9 is additionally represented by WAM 12.1.11, a rigid polyurethane resin replica. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality, Horizon, and Age**—The referred specimens are preserved in situ at DP14 and DP30, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia; Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—Track DP14-9 (Fig. 34A–C) is a left pedal track orientated in a near-northerly direction that represents one of the smaller sauropod tracks from the Yanijarri–Lurujarri study area (Table 10). The circular impression is noticeably deep—combined with the raised expulsion rim around the lateral margin, much of the internal cranial area, including sub-impressions of digits II and III, sits approximately 15 cm below the surrounding track surface. The track depth approaches 20 cm laterocaudally, at the heel. The expulsion rim is most pronounced and broadest (up to 15 cm) in an arc around the caudal half of the track.

Medially, cranially, and laterally, there are approximately three major sub-impressions, representing regions of digital presence. Adjacent to the medial margin, the first of these represents the trace of pedal digit I. The floor of this sub-impression is internally partitioned by a shallow cranially curving ridge, resulting in a deeper, broad lateral section and a shallower, narrow medial counterpart. The shallower (~5 cm depth) partition represents a bulged extension of a plantar pad/callosity that is typically attendant with digit I (as noted in several other sauropod pedal tracks from the study area). In DP14-9, the impression for the bulged pad is much narrower than in comparative tracks (e.g., DP14-17, DP30-1; Xing et al., 2010:452) and follows the full length of the impression of digit I, narrowing during this course; it thus terminates at the cranial track margin. The entire impression of digit I has a rounded medial margin and is slightly curved laterally.

The area of impression of digit II probably represents mostly the ungual, which is divaricated from the impression of digit I by a caudally extending (~15 cm) incursion of the bounding rim. The impression of digit II, although extending further cranially than the surrounding digital impressions, indicates that this digit

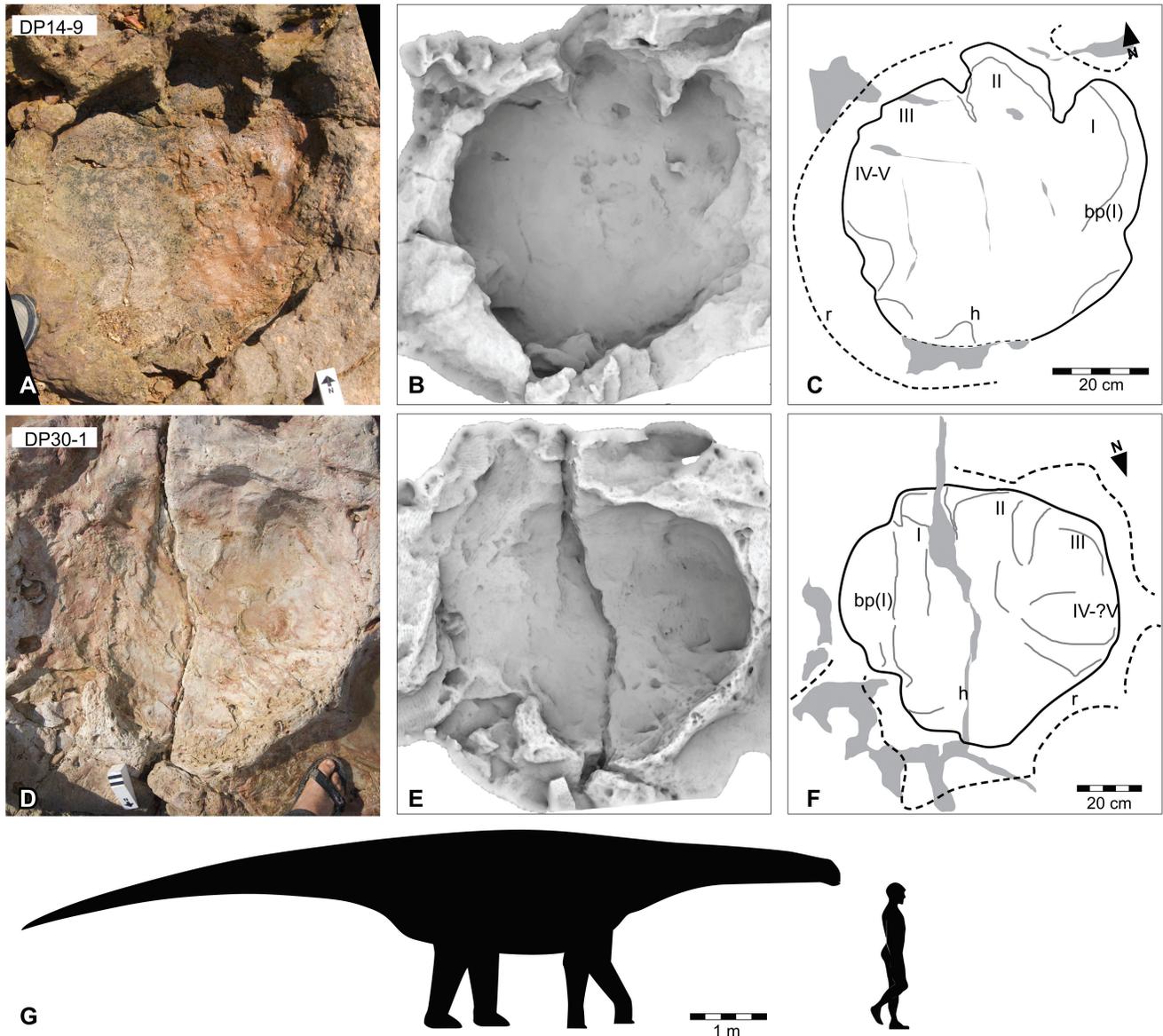


FIGURE 34. Broome sauropod morphotype E, from the Yanijjarri-Lurujarri section of the Dampier Peninsula, Western Australia. Left pedal impression, UQL-DP14-9, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Right pedal impression, UQL-DP30-1, preserved in situ as **D**, photograph; **E**, ambient-occlusion shading; and **F**, schematic interpretation. **G**, silhouette of hypothetical trackmaker of Broome sauropod morphotype E, based on UQL-DP14-9, compared with a human silhouette. **Abbreviations:** **bp(I)**, bulged pad/callosity associated with digit I; **h**, heel region; **I-V**, digital impressions I, II, III, IV, and V, respectively; **r**, expulsion rim. See Figure 19 for legend.

of the trackmaker was flexed laterally during the emplacement of DP14-9. The impression of digit II is approximately as broad as that of digit I, and collectively these impressions account for half the breadth of the track. Two areas of impression of digits III and IV-V are indicated by a subtle kink in the cranio-lateral rim, but otherwise this region forms a single large sub-impression. Constrictions in the track outline, laterally and medially, define the broad semicircular heel region. Whereas the lateral demarcation between the impressions of the heel and digit V is composed of a short well-defined ramp between the rim and track floor, the medial one is a subtle notch in the track outline at the caudal end of the shallow pad bulge of digit I (Fig. 34B, C).

Track DP30-1 (Fig. 34D-F) has been figured but not described previously (Thulborn et al., 1994:fig. 4C; the image in

Thulborn et al. [1994] shows the track obliquely at a low angle and can be somewhat equated with Fig. 34D-F if their image is rotated 110° clockwise. It is a rounded impression, approximately 80–85 cm long and wide, which we identify as a right pedal track orientated in a southerly tracking direction. The dextral identification is supported by the westward curvature of the phalangeal impressions attributed to the first two digits, which appear to flex laterally (Fig. 34F). The exposure of rock that contains DP30-1 is part of a dense accumulation of predominantly sauropod tracks, most of which are superimposed (Fig. 15A; DP30, a track-trampled area; Thulborn et al., 1994:92). Although many of the surrounding impressions were probably made by the same trackmaker, we cannot assign these other tracks to Broome sauropod morphotype E without

additional study of the site to establish associations between tracks at DP30.

There are approximately five short indentations of the rim around the medial, cranial, and lateral arcs of DP30-1, which define regions of impressions of digits and the heel pad (Fig. 34E, F). Although the inferred arrangement of the digital arcade is nearly identical to that of DP14-9, the individual digital impressions of DP30-1 are not as extended and distally diverged. The impression of digit I in DP30-1 is accompanied by a cranio-caudally narrow convex bulge occurring along the medial margin of the track, which is noticeably shallower than the rest of the impression (Fig. 34E). This sub-impression of the digit I attendant pad bulge is similar in general shape to that of DP14-9 but differs in being relatively cranio-caudally shorter, more symmetrical, and has an abrupt caudal termination. Cranio-medially, part of the trace of digit I is represented by a shallow sub-impression that is demarcated from the bulged impression of digit I and probably represents the impression of an unguis. This contrasts with DP14-9, in which the bulged pad sub-impression extends apically along the medial side of the impression of digit I to reach the cranial track margin.

The sub-impression of digit II is mostly broad (e.g., at its base), but distally, where it would represent the unguis, the sub-impression is acuminate and curved laterally, thus following the cranial margin of the track outline. The impression of digit II is laterally segregated from a deeper area within the lateral portion of the pedal impression by a broad, low ridge, representing a natural mold of the interdigital area. This latter sub-impression (lateral-most) represents the impression of digits III–V and encompasses an arc of approximately 25% of the pedal track outline. Similar to the track DP14-9, the deep sub-impression for digit V is caudally subtended by a broad, ramp-like ridge (Fig. 34B, E), which separates it from the heel region. The ridge only extends a short distance before dissipating on to the track floor. In contrast, an analogous heel-demarking ridge is more extensive in *Oobardjidama foulkesi* and Broome sauropod morphotype A. The heel impression is semicircular in outline.

The expulsion rim for DP30-1 constitutes an up to 15 cm thick raised ridge bounding the cranial, lateral, and caudal margins of the impression. It is generally lower and thicker cranially and cranio-laterally but is well formed and narrower caudally to add definition to the heel.

**Remarks**—Tracks DP14-9 and DP30-1 share a unique combination of characters, indicating that the same trackmaker, and perhaps one different from the producers of the other morphotypes in the study area, made these impressions. These features include a relatively rounded pedal impression with an almost 1:1 length to width ratio (Table 10); the radial spread of the digital impressions to occupy 45–55% of the track perimeter; the broad semicircular shape of the caudal heel margin; and the similar structure of the medial pad bulge accompanying the hallucal impression. Tracks DP14-9 and DP30-1 both have a distinct crease within the cranio-medial section of the track, which conforms to a medial delineation between a narrow plantar-surface callosity and the remaining surface of an *in vivo* pes (see further remarks below on the bulged pad/callosity). Other sauropod pedal tracks from Yanijarri–Lurujarri study area share some of these characteristics but exhibit other meaningful differences, thus precluding referral of DP14-9 and DP30-1 to one of the afore-described Broome sauropod morphotypes. We accordingly at present consider DP14-9 and DP30-1 to be a distinct sauropod track morphotype.

Pedal impressions of Broome sauropod morphotype E and *Oobardjidama foulkesi* (DP45-8[rp1, rp2]) not only have a relatively enlarged medially flanking pad bulge attending the impression of digit I, it is also segregated from the digital impression by the presence of a crease in the floor of the tracks. However, Broome sauropod morphotype E differs from *Oobardjidama* by its relatively lesser

medial-ward expansion and greater caudal-ward limit of the bulge impression. In the first of these proportions, Broome sauropod morphotype E is more similar to other well-preserved sauropod pedal impressions globally than to *Oobardjidama* (Farlow et al., 1989; e.g., *Brontopodus birdi*/B. isp.: Meyer and Pittman, 1994; Farlow et al., 2012), but in the second feature, the converse is true. Moreover, the round squat pedal outlines of Broome sauropod morphotype E with semicircular heel impressions differ from the piriform pedal shapes with strongly medial-positioned heels in *Oobardjidama*.

Although the solitary pedal impression referred to Broome sauropod morphotype B (DP1-1) is also circular, that track lacks the finer preservation of details of the autopodial plantar surface to be realistically compared with morphotype E herein. Broome sauropod morphotypes A, C, and D differ from morphotype E in bearing typically elongated pedal track profiles. The pedal impressions of morphotype A appear to lack a defined medial bulge, although these same tracks generally exhibit weaker internal preservation than morphotypes C, D, and E. Although an impression of the medial bulge of digit I is present in morphotypes C and D, they are limited in extent and unlike the well-defined counterparts in morphotypes E and *Oobardjidama* in also lacking a partitioning crease for a callosity (see discussion below on the bulge/callosity in sauropod pedal tracks). Additionally, the sub-impression in morphotype E is shallower than those of morphotypes C and D.

There is a divaricated separation between the impressions of digits II and III in Broome sauropod morphotype E, which is also present in morphotype D and the holotype impression of *Oobardjidama* (DP45-8[rp2]). However, the impressions of the outer digits III–V occupy a limited space along the track margin in morphotype D, while being caudally extensive in morphotype E and *Oobardjidama*. The segregation between the impressions of digits III–V is not clear in any of these tracks. However, the collective digits III–V in morphotype E are more deeply impressed than the heel section, compared with the other morphotypes. Although Broome sauropod morphotype E appears to have a delimited sub-impression for the heel, the region is distinguished simply via the form of the bounding caudal rim. In both specimens, contralateral constrictions in the track outline due to short internally extending sections of the rim define the heel. In contrast, morphotype A and *Oobardjidama* have well-defined heel sub-impressions on the internal track floor.

Despite the excellent preservation of track detail, Broome sauropod morphotype E is not referable to any well-established sauropod ichnogenus in a global context, due to the absence of trackway and couplet parameter information. Regardless, morphotype E lacks the elongate and piriform profile of the holotype/topotype exemplars of all currently diagnosable sauropod ichnotaxa, including *Brontopodus birdi* (Farlow et al., 1989), *B. pentadactylus* (Kim and Lockley, 2012), *Titanopodus mendozensis* (González Riga and Calvo, 2009), *Parabrontopodus mcintoshi* (Lockley et al., 1994a), and *Breviparopus taghbaloutensis* (Belvedere, 2009; Marty et al., 2010). The wide contour of the morphotype E pedal tracks contrasts with the elongated piriform to subtriangular outlines usually occurring in sauropod pedal tracks that show excellent textural preservation and morphological detail (e.g., photographs of pedal impressions in Farlow et al., 1989; Pascual Arribas et al., 2009; Torcida Fernández-Baldor et al., 2015; Xing et al., 2016c).

Most rounded sauropod pedal tracks are not well preserved. The original topotype trackways of *Elephantopoides barkhausensis* (Kaefer and Lapparent, 1974; Diedrich, 2011) and *Sauropodichnus giganteus* (Calvo, 1991), although showing nearly circular pedal track outlines, are poorly preserved and devoid of fine details of the internal track surface. These latter ichnotaxa are nomina dubia (Lockley et al., 1994a; also see comparative discussion on *Oobardjidama*). Some once-purported sauropod trackways with circular pedal impression outlines (e.g., the topotype of *Neosauropus lagosteiensis*,

Antunes, 1976) have been reinterpreted to be transmitted undertracks of bipedal dinosaurs (e.g., Santos et al., 1992; also note various reinterpretations of very large circular ‘manus-only’ Haenam trackway [Hwang et al., 2008, and references therein]). The absence to date of circular pedal impressions in the global record, with good preservation (including details of the digit I attendant bulge), emphasizes the uniqueness of Broome sauropod morphotype E. The foreshortened pedal track outline in morphotype E is a genuine aspect of this track type, and not due to poor preservation or deep transmission, which tends to be associated with rounded pedal track profiles (Pittman and Gillette, 1989:fig. 34.17K; e.g., Calvo, 1991; Thulborn, 2012; Mesa and Perea, 2015; Xing et al., 2015e). In summary, both impressions of morphotype E show finely preserved morphological details within the deep-walled rims, corroborating the relatively wide outline as actually reflecting the trackmaker’s behavior or its morphology, or both.

Finally, the separate specimen referrals to Broome sauropod morphotype E occur in close proximity to tracks of *Oobardjidama* and morphotype D, and it is plausible that these rather morphologically disparate impressions were produced by the same trackmaker. The main points of similarity between morphotype E and other tracks in the entire study area occur especially between these three morphotypes, e.g., the similar form of the medially flanking pad bulge to the impression of digit I occurring both in morphotype E and in *Oobardjidama*. Concurrently, DP14-9 of Broome sauropod morphotype E shares with impressions referred to morphotype D deeply divaricated impressions of digits I–III, with impressions of digits I and II being elongate. Hence, it seems intuitive that future discoveries might blur the present distinctions among the sauropod morphotypes in the study area. However, pending new finds, assumptions that the geometric variation among these pedal impressions is produced from a single trackmaker needs to address these differences adequately and rule out potential differences in in vivo anatomy as a basis for some of the variation in the tracks. Despite the well-preserved nature of the impressions DP30-1 and DP14-9, which seem to represent high fidelity plantar molds of sauropod autopodia, we avoid the creation of an ichnotaxon for this track type given their respective isolated occurrences. Globally concurrent ichnosystematic comparisons of sauropod tracks are best operated with a combination of trackway parameter and ipsilateral couplet information, which are regrettably lacking in these pedal impressions.

Medial pad bulges and plantar callosities. Several sauropod pedal impressions from the Yanijarri–Lurujarri study area show a distinct sub-impression situated adjacent to the impression of digit I within the medial track wall. These are especially prominent in Broome sauropod morphotype E and in the holotypic pedal impression of *Oobardjidama foulkesi* (DP45-8[rp2]), although the sub-impressions differ significantly between these. Often, the sub-impressions are demarcated from the impression of digit I, as in the above two morphotypes, but in other cases they are a simple rounded medial swelling of the impression of digit I (e.g., Broome sauropod morphotype C [Fig. 32] or the typical condition in *Brontopodus birdi* [Farlow et al., 1989]; Pittman, 1989; Farlow et al., 2012).

As implied in the preceding systematic descriptions, we consider the particularly defined sub-impressions to indicate a combination of pliability in the medioplantar pad of the in vivo autopodium of the trackmaker (creating a medial-ward bulge) and a discrete localized thickening of the plantar soft tissue (i.e., a prominent callus/callosity). However, the slight craniomedial bulge preserved in most pedal impressions simply reflects the osteological shape of the beveled and laterally flexed interphalangeal joint of the hallux, which bears a large ungual (Nair and Salisbury, 2012:378; Romano and Whyte, 2012). Regarding the sharply defined condition, during a protracted step phase of the pes impressing into firm or increasingly firmer substrate, the plantar soft tissue around the hallucal region contorts medially. This implies that the

preservation of these (and other similar features) within track outlines ought to be partially contingent on the properties of the original tracking substrate.

In descriptions of natural molds of sauropod pedes elsewhere, the relatively shallower hallucal medial bulge is seldom noted. Perhaps this is because many impressions do not preserve clear details of the plantar surface of the pedal. Nonetheless, the morphology has been illustrated frequently enough in previous research on well-preserved sauropod pedal tracks. For example, a kink in the medial track wall of pedal tracks of *B. birdi*, in cases where it is preserved (e.g., Bird, 1939:259; Farlow et al., 1989:fig. 7; Farlow, 1992:fig. 10), indicates that a bulge in the soft padding of digit I had comparable broadness to those of Broome sauropod morphotype E but was more limited to the cranial portion (30–40%) of the track. Castanera et al. noted the medial-ward swelling for the impression of digit I in a mold and cast track set of a left pes from the Lower Cretaceous Las Cerradicas tracksite (Castanera et al., 2011:230).

Pittman (1989:fig. 15.12) depicted a well-preserved MP couplet of *Brontopodus birdi* (among many referred trackways from Davenport Ranch, Texas) and specified that an indentation along the medial track wall indicated the “location of the metatarsal-astragalar articulation (at the arrow in Fig. 15.12)” (Pittman, 1989:150). The same interpretation was offered for other *B. birdi* tracks from the Briar Plant site (Pittman and Gillette, 1989:325–326). This position may not necessarily reflect the location of the tarsometatarsal juncture because the proximal articular end of the eusauropod metatarsus does not contact or approach the substrate. Being posed at an inclined angle (Upchurch et al., 2004; Bonnan, 2005), it is unlikely to leave a consistent direct trace at the interface between substrate and autopodial plantar surface.

In a decelerating pedal step, weight is initially transmitted via the metatarsus (Bonnan, 2005), so most sauropod pedal impressions tend to be relatively more deeply impressed cranially than caudally (Bates et al., 2008:1006), corresponding to the digitometatarsal and heel pad (sensu plantar pad of Bonnan, 2005) regions of impression, respectively (e.g., Farlow et al., 1989, or as shown in Broome sauropod morphotype A). Therefore, some sideward squeezing of the initially impressing and weight-bearing digitometatarsal pad, where it is pliable enough, is expected, as often shown in the cranial half of sauropod pedal impressions. Unusually, tracks of Broome sauropod morphotype E have a relatively deeper lateral (craniolateral) sub-impression than other regions, whereas those of *Brontopodus* and other ichnotaxa are deeper medially (craniomedially). Perhaps, this indicates that metatarsals III and IV may have communicated a greater proportion of the weight during a pedal in-step in the specific trackmaker of morphotype E.

The second feature of the bulged sub-impression attending the impression of digit I in Broome sauropod morphotype E (and *Oobardjidama*) is the presence of an internal demarcation, via an axially aligned ridge within the tracks. This margin defines a surficial callosity zone at the craniomedial plantar surface, separated by a crease from the remaining surface of the digitometatarsal padding in the sauropod autopodium. To support such an inferred morphology, Wright (2005:fig. 9.6) illustrated two well-preserved track casts from the Upper Jurassic of western U.S.A. with internal furrows occurring parallel to the medial margins of the casts. The furrows mirror the approximate position of the shallow axially aligned ridges within the impression of digit I that occur in exemplars of Broome sauropod morphotype E. Xing et al. (2010:fig. 4) described a sauropod pedal cast with evidence of a “blunt pad or callosity on the plantar surface of digit I” from the Lower Cretaceous of Jiangsu (Xing et al., 2010:452). The natural cast of a left pedal track from the Las Cerradicas tracksite (see above) presents a ridge that separates the medial swelling

from the remaining track surface area (Castanera et al., 2011: fig. 6). Recently, Xing et al. (2016b) illustrated various excellently preserved sauropod natural molds with corresponding casts from the Late Jurassic Shimiaogou tracksite, Sichuan, that exhibit high levels of detail of the pedal plantar surface (Xing et al., 2016b:184). At least one natural mold plus cast set, 'LP3' of the trackway 'SMG-S3,' shows a trace of a medial callosity-defining ridge (Xing et al., 2016b:fig. 10 [unlabeled]). This confined area of the cast of LP3 corroborates in size and shape the form of the plantar callosity schematized previously by Xing et al. (2010) and Castanera et al. (2011), and those we infer for *Oobardjidama* and Broome sauropod morphotype E.

#### OTHER SAUROPOD TRACKS (Figs. 35, 36, 60H, I; Table 10)

Additional to the track morphologies described above, numerous other tracks and traces formed by sauropods occur within the study area in the Broome Sandstone. These additional specimens are too incomplete with regard to certain aspects of their morphology, precluding any form of secure referral to an existing ichnotaxon or track morphotype. Although none is presently linked to *Oobardjidama foulkesi* or the proposed Broome sauropod morphotypes, it is expected that future surveys of the

Broome Sandstone will transform the systematic ichnology presented herein in two ways. Firstly, we expect some rearrangement of our assignments of specimens and revised assessments of diagnoses concerning the proposed morphotypes. Secondly, many currently non-assignable specimens may be fitted more precisely into future ichnosystematic schemes. The following sauropod impressions, although indeterminate, are briefly described because they add further information on the range of sauropod track morphologies or inform on sauropod trackmaker paleobiology during the deposition of the Broome Sandstone.

**Referred Material**—UQL-DP8-16, a pedal track and associated additional sauropod tracks occurring within close proximity; UQL-DP29-1, a sauropod manual track overprinting a sauropod pedal track; UQL-DP9-2, an isolated manual track, all preserved as natural moulds. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Location, Horizon, and Age**—The tracks are preserved in situ at DP8, DP9, and DP29, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derive from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**DP9-2**—This specimen (Fig. 35A–C) is an isolated reniform manual impression (47 cm wide and 23 cm long) with subparallel

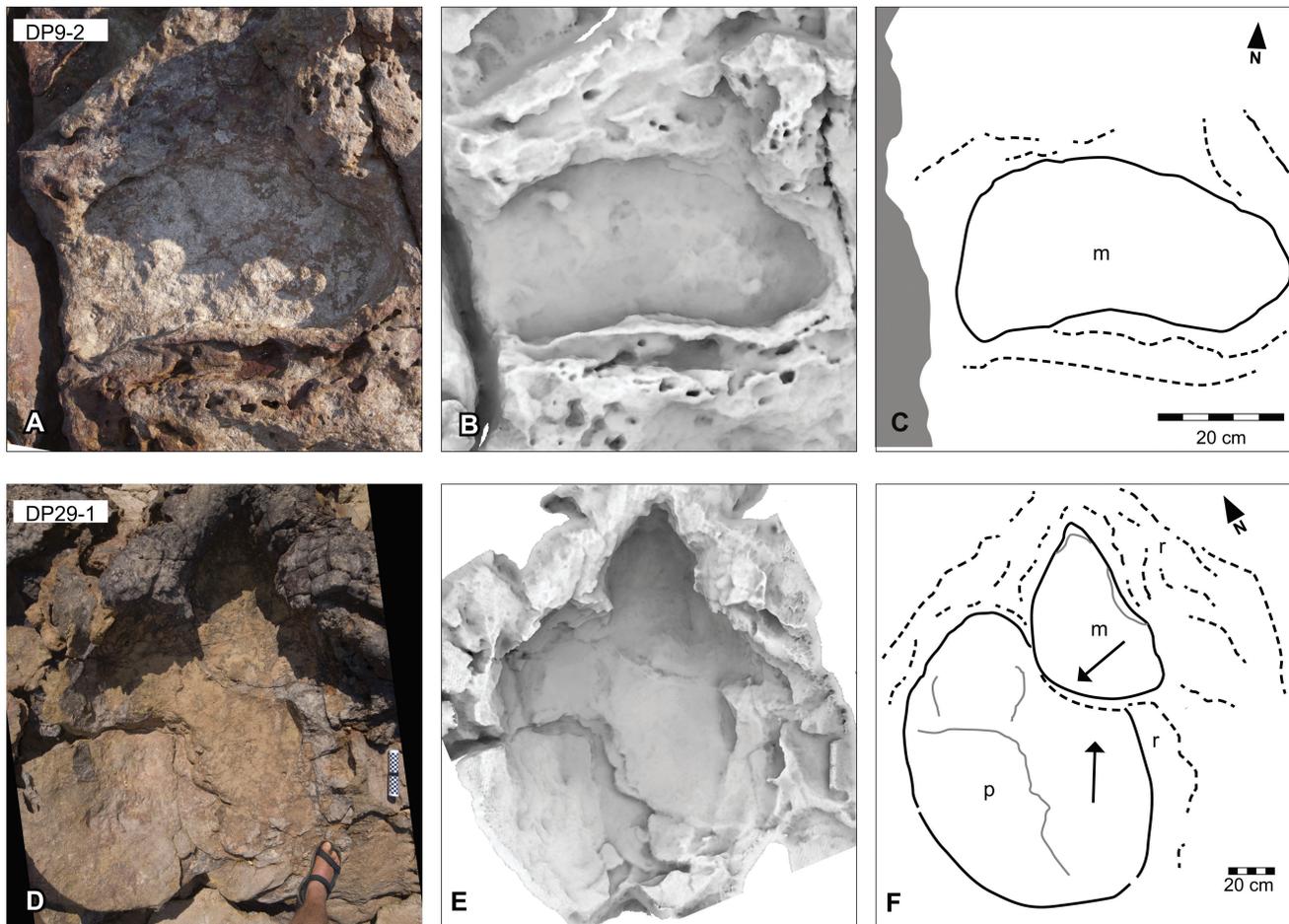


FIGURE 35. Unassigned sauropod tracks, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Manual impression, UQL-DP9-2, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Superimposed manual and pedal impressions, UQL-DP29-1, preserved in situ as **D**, photograph; **E**, ambient occlusion image; and **F**, schematic interpretation (arrows indicating the tracking direction of individual tracks). **Abbreviations:** **m**, manual impression; **p**, pedal impression; **r**, expulsion rim. See Figure 19 for legend.

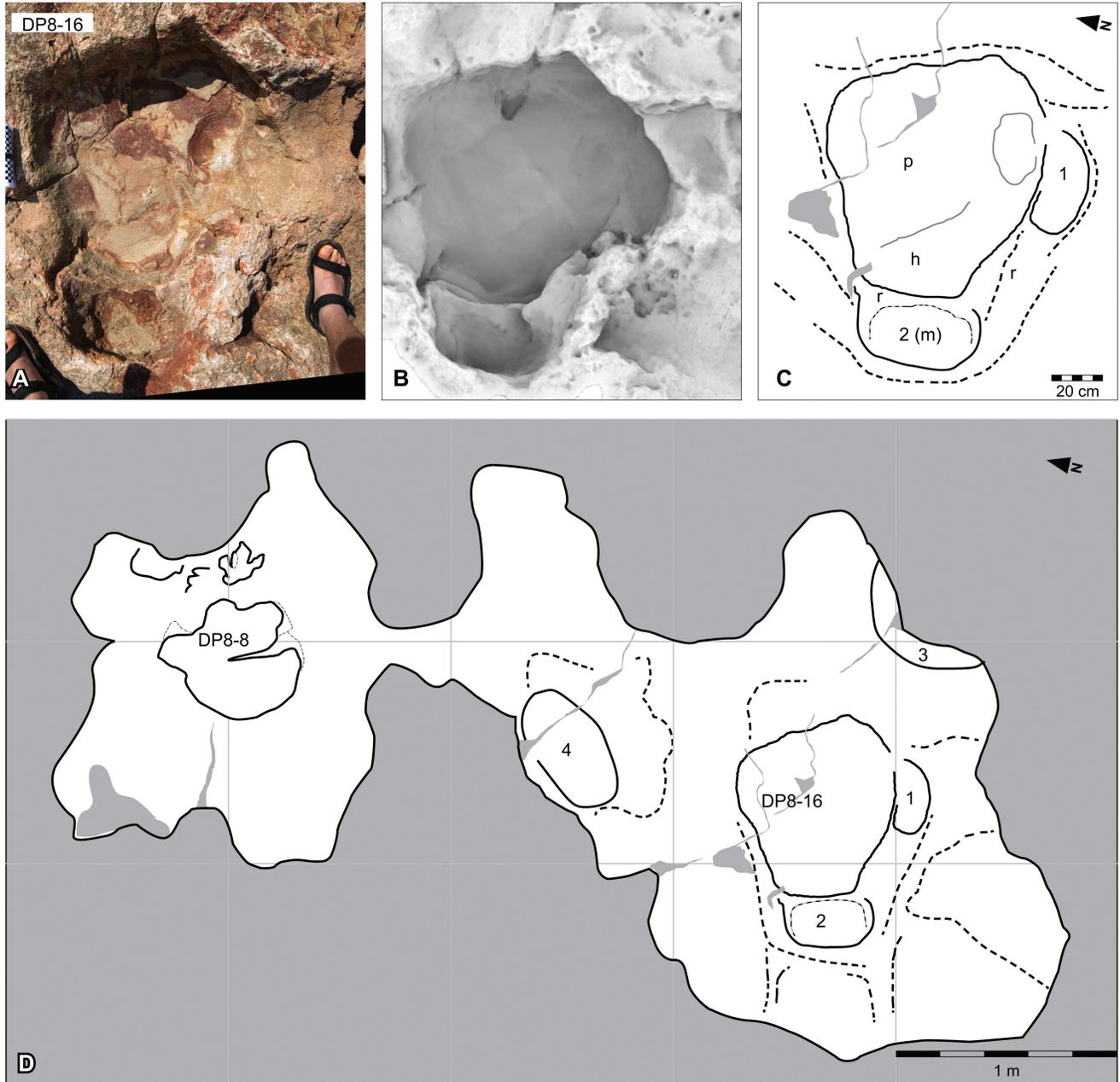


FIGURE 36. Unassigned sauropod tracks, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Pedal impression, UQL-DP8-16 preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, schematic map of localized platform containing associated sauropod (UQL-DP8-16 + associated numbered tracks) and *Garbina roeorum* (UQL-DP8-8) tracks. **Abbreviations:** 1–4, additional sauropod track impressions; h, heel; m, manual impression; p, pedal impression; r, expulsion rim. See Figure 19 for legend.

cranial and caudal margins. The track is approximately 5 cm deep and is delineated by a thin rim caudally. The craniocaudally broader eastern portion and slightly tapering opposite half only weakly imply that the impression was made by a right manus. The track occurs in proximity to tracks referred to Broome sauropod morphotype A (DP9-1 and DP9-11) but can be distinguished from the manual track of morphotype A by its relative broadness (Table 10) and near-symmetrical shape. Although it seems probable that a single trackmaker formed very closely situated sauropod tracks (e.g., DP9-2 and nearby sauropod

impressions), the absence of pedal track information for DP9-2 precludes a more specific referral.

Of biomechanical interest, DP9-2 indicates that the manus of its trackmaker was distally splayed, rather than forming a tight colonnade. This is noteworthy given that this impression is among the clearest-preserved manual tracks surveyed from the region. As a result, the shape of DP9-2 loosely resembles the manual impressions assigned to *Titanopodus mendozensis* (González Riga and Calvo, 2009). The better-preserved manual impressions assigned to *Brontopodus* spp. (Farlow et al., 1989;

TABLE 10. Measurements of isolated sauropod tracks and track couplets from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP), assignment	Couplet length (cm)	P length (cm)	Max. P width (cm)	Min. P width at HC (cm)	P L/max. W	P EI	M length (cm)	M width (cm)	M L/W	Max. ID (cm)	Min. ID (cm)	Couplet IR (%)	HR (%)
8-30, BSM A	178	105	71	57	1.47	1.64	54	50	1.08	30	19	13.7	32.4
22-4, BSM A	220	130	89	80	1.49	1.54	68	80	0.85	40	25	14.8	36.7
9-1, BSM A	225	135–140	125	92	1.08	1.24	67	92	0.73	(37)	(17)	(12.0)	33.5
9-11, BSM ?A	>240	175	140	100	1.25	1.46	>45	~80	—	42	12	~10	~23–33
8-1, BSM ?A	300	170–175	125	70	1.36	1.74	60	80	0.75	(75)	(75)	(25.0)	27.5–30.0
14-20, BSM ?A	210	140–145	110	—	1.27	~1.4	41	61	0.67	(15)	(5)	(5.0)	~16
45-14, BSM ?A	—	97	85	61	1.14	1.32	—	—	—	—	—	—	—
1-1, BSM B	112	85	80	72	1.06	~1.1	36	52	0.69	0	0	0	17.6
14-17, BSM C	128	87	66	51	1.32	1.49	33	~52	0.63	19	6	9.8	26.6
14-10, BSM D	—	76	58	42	1.31	1.52	—	—	—	—	—	—	—
11-4, BSM D	—	90	64	42	1.53	1.85	—	—	—	—	—	—	—
14-9, BSM E	—	67	79	54	0.85	1.01	—	—	—	—	—	—	—
30-1, BSM E	—	82	83	58	0.98	1.16	—	—	—	—	—	—	—
9-2, Indet.	—	—	—	—	—	—	23	47	0.49	—	—	—	—
29-1(m), Indet.	—	—	—	—	—	—	45	81	0.53	—	—	—	—
29-1(p), Indet.	—	135–140	115	95	1.17	1.28	—	—	—	—	—	—	—
8-16(p), Indet.	—	78	71	46	1.1	1.33	—	—	—	—	—	—	—
8-16(*4'), Indet.	—	—	—	—	—	—	40	80	0.50	—	—	—	—

BSM = Broome sauropod morphotype; EI = elongation index [formula:  $2 \times \text{pedal track length} / (\text{max. P width} + \text{min P width})$ ]; HC = heel constriction—width measurement taken either at the cranial margin of the heel pad demarcation, and if not preserved, minimum width at the mid-track; HR = heteropody ratio; ID = interautopodial distance (by default as MP couplets, with corresponding PM couplets listed in parentheses); IR = interautopodial index ratio, a proportional measure of non-impressed length of the couplet [formula:  $0.5 \times (\text{max. ID} + \text{min ID}) / \text{couplet length}$ ]; by default as MP couplets, with corresponding PM couplets listed in parentheses; M = manual track; P = pedal track.

Pittman, 1989; Kim and Lockley, 2012), *Polyonyx gomesi* (Santos et al., 2009), and Broome sauropod morphotype A (Table 10) have length to width ratios in the range of 0.65–1.00, whereas DP9-2 (at 0.53) exceeds even the relatively slender proportions of *Titanopodus* (average = 0.61; González Riga and Calvo, 2009).

**DP29-1, Large Manual and Pedal Tracks Preserved in Close Association, and Associated Trampled Area**—Site UQL-DP29 comprises numerous sauropod-only tracks on a stretch of platform approximately 15 m long by 6 m wide. The recognizable impressions vary in their preservation, size, and inferred orientations, and there is presently no clear support for the presence of any definitive trackways. This tracksite is best considered a sauropod ‘trampled area’ (akin to those described in Thulborn, 2012), which are typically small zones with dense sauropod tracks and traces. At the southern end of the spectrum, two MP couplets are present, but these are heavily weathered and partially eroded. At least one of these demonstrates rounded manual and pedal shapes; they likely represent transmitted (deeper) aspects of the couplet to an extent due to partial erosion of the original tracking stratum.

Two of the better-preserved tracks at this site with clear morphological details that are certainly not transmitted are an associated pedal and manual track (DP29-1; Fig. 35D–F). Based on the interpretation below, we do not recognize these as a normal sequential couplet. The pedal impression is very large (at least 135 cm long and 115 cm wide), oval-shaped, and up to 30 cm deep. A thick rim occurs around the margins of the north-facing half of the impression, but it becomes weak around the southern half (Fig. 35). The internal surface of the heel region is incomplete. The expulsion rim around this section only weakly outlines the track, adding to the uncertainty surrounding the absolute scope of this track. Feasibly, a length of 135 cm underestimates the length of the impression. The cranial half is more deeply impressed than the heel region, as occurs for other sauropod pedal impressions in the study area (see remarks for Broome sauropod morphotypes A and E). Potential phalangeal marks are present along the inner walls of the north-aligned half of the impression.

The enormous and deep manual impression (45 cm long, 81 cm wide, ~30 cm deep) overprints the pedal track, as

evidenced by the outlining rim of the manual track traversing the pedal track outline (Fig. 35). The manual impression is reniform, with a southwest facing convex margin and a northwest facing concave margin (slightly obscured by overhanging rim sediment in Fig. 35). The northern end of the impression is narrow and deeply set within a thick expulsion rim, whereas the southern end—also acute in form but relatively shallower—could extend in a shallower trace over the disrupted pedal track rim. Even incorporating this latter uncertain trace, we cannot resolve if the track is a left or right manual impression because the outline is still nearly symmetrical. The shallower area could equally represent the pollex impression or a caudolateral ‘tail’ that is similar to the form documented in Broome sauropod morphotype A. The trackmaker of the manual impression was moving westwards, based on the orientation of the convex-concave outline.

Although the manual and pedal impressions of DP29-1 are associated in the field, they collectively do not form a natural sequential couplet. The manual track overprints the pedal track, and the inferred tracking orientations do not complement each other. The manual impression is aligned in a nearly westerly direction, whereas the pedal impression indicates either a north-east (probable) or southwest (unlikely) tracking direction. Because a pedal step spatially follows a manual step, any noticeable overprinting within a couplet should result from the pedal stride forward interrupting the caudal margin of the manual track rim, and not vice versa.

Both impressions of DP29-1 are notable due to their enormous size, thus building on the record of very large sauropod tracks from the study area (see remarks on Broome sauropod morphotype A). The pedal impression is comparable in size to the referred exemplars of Broome sauropod morphotype A, and some of these tracks also appear to share a non-piriform ovate outline. Despite the similarities, we are unable to refer the pedal impression of DP29-1 to that morphotype because it lacks a characteristic heel demarcation and measurements of the trackway (e.g., heteropody, interautopodial distance) are absent. Although the massive size of the manual impression of DP29-1 is on a par with those of morphotype A, it is more similar to the lenticular manual track shape of morphotype B

(DP1-1) and the horseshoe-like manual track outlines made by probable semi-submerged sauropods (Ishigaki, 1989; Castanera et al., 2010).

**DP8-16, and Associated Superimposed Tracks**—An exposure of regularly sand-blanketed rocky platform (UQL-DP8) contains a number of sauropod (Fig. 36) and thyreophoran (Fig. 48) track impressions. The sauropod tracks are concentrated on the southern end of the platform (Fig. 36D) and include at least five impressions, three of which are superimposed (Fig. 36A–C). The impressions are slightly to moderately eroded due to long-term intertidal action, although their margins are well delineated via the retention of expulsion rims. The superimposed impressions were previously illustrated and cursorily identified by Thulborn et al. (1994:92 and fig. 4A) as a natural ?MP couplet with an overall length of 155 cm (1994:fig. 4, caption).

Regarding our labeling, all the sauropod impressions on the small contiguous rock platform are currently DP8-16, with the ‘main track’—the larger pedal track outline in the middle of the set of overprinted impressions—designated DP8-16(p). The remaining sauropod impressions are sequentially suffixed ‘1–4,’ with DP8-16(2) being the ‘manus’ track in Thulborn et al.’s arrangement. The image in Thulborn et al. (1994:fig. 4A) shows DP8-16 obliquely at a low angle and can be somewhat equated with our depiction (Figs. 36A–C) if their image is rotated 180° clockwise. The impressions on the platform DP8 are associated with abundant molds of plant debris (also noted in Thulborn, 2012:20).

The superimposed subset of impressions comprises three discernible entities (recognizable by the presence of partial rims at various depths): a medium-sized pedal impression (DP8-16(p)), a possible manual impression (DP8-16[2]), and an indeterminate trace that has several plausible interpretations (DP8-16 [1]). Thulborn et al. (1994) considered DP8-16(p) to be a novel type of sauropod track, rather than being referable to *Brontopodus* as per most sauropod impressions in the study area, although they did not adequately outline why this was the case (the authors mentioned that the diversity of sauropod tracks would be determined in future work). Thulborn et al. (1994:92) identified DP8-16(p) as an “unusually long and subrectangular pes with well-defined digit I,” whereas DP8-16 (2) was captioned as being a part of a “sauropod manus-pes couple comprising” a “smaller, shallower and step-like impression of the manus” (relative to the pedal track) (Thulborn et al., 1994:91).

More recently, Thulborn (2012:fig. 30) depicted DP8-16, showing it obliquely from a northwestern aspect, with sand filling in the impression of DP8-16(2), obscuring it (however, the presence of this track was not mentioned). In the caption for the figure, the pedal impression was reidentified as cf. *Brontopodus*, with the tracking direction being eastwards based on the “conspicuous traces of unguals along the lateral edge of the print” (Thulborn, 2012:20). According to this information, one would resolve the main impression to be a right pedal track.

The previous interpretations of DP8-16 are problematic in several minor details. First, the length of the collective impressions DP8-16(p+2) have been significantly exaggerated at 155 cm long (Thulborn et al., 1994:92), when it is realistically about 100–110 cm long, depending on the orientation measured and the extent of rim included. The main pedal impression is conservatively 78 cm (medium to large size; Table 10). Second, we were unable to verify any traces of a well-defined digit I, or other unguals, as previously claimed (Thulborn et al., 1994:92; Thulborn, 2012:20). The image of DP8-16(p) as shown by Thulborn (2012:fig. 30) shows the track filled with water and demonstrates a routine trend for tracks found higher in the littoral column of the study area to have their track margins/rim walls color-stained (also see description of DP45-14 under Broome sauropod morphotype A).

Third, the main pedal impression is indeed orientated eastwards, based on the wider margin of a piriform outline representing the cranial section. Given this direction, the location of DP8-16(2), as the ‘manus’ impression, occurring at the western end of the heel region of DP8-16(p) would mean that the two impressions form a PM couplet (rather than a ‘conventional’ MP couplet; see Materials and Methods). Thulborn et al. (1994) did not specify the tracking direction for the manual track, so a PM couplet arrangement remains viable. However, the deeper impression for DP8-16(p) appears to cut across the floor of the shallower impression of DP8-16(2), as a secondary event (Fig. 36B). Although this has produced a thin elevated ridge between the two impressions at this intersection, part of a shallower impression is conserved within the bounds of the broad external rim that contains both tracks (at the southern section) but is outside of the resultant thin ridge (Fig. 36B, C). This shallow area—a remnant of the now severed impression DP8-16 (2)—therefore indicates that DP8-16(2) had been unspicifiably larger before being overprinted by DP8-16 (p) and thus may not necessarily have been a manually impressed shape.

Although DP8-16(2) and DP8-16(p) could represent a natural but partially superimposed couplet formed by a single sauropod trackmaker, we consider it prudent to treat each track individually, particularly because all the impressions, including DP8-16(3+4), are inconsistent in size. It is thus unclear if all/most of the impressions were formed by one sauropod sequentially, or irregularly, or if they made by multiple individuals. Based on the preserved intersecting rims, the first-impressed track (DP8-16[2]) could have been formed by either a manus (one larger than the present semicircular outline indicates in Fig. 36C) or a pes (probably oriented eastwards). Track DP8-16(p) was impressed after DP8-16(2), partially overprinting the earlier-made track and thus obliterating a segment of a preexisting outlining rim. Hence, this sequence of events leaves DP8-16(2) exposed as currently preserved, being either (1) the major part of an original manual impression area or (2) only the heel portion of an original pedal track.

The main pedal impression DP8-16(p) is deeper than DP8-16 (2). This is either because it was impressed into an already formed basin or because it was caused by a larger, weightier autopodium than the one making DP8-16(2). We cannot indisputably determine if DP8-16(p) is a left or right pedal impression. The cranial half of the pedal track outline is broadly triangular, resembling the cranial margin of DP8-30 (Broome sauropod morphotype A). The slightly deeper southern area within the cranial half of the impression has a shallow ovate sub-impression (Fig. 36A). The combination of these suggests, weakly, that DP8-16(p) is a left exemplar (i.e., deeper medially with a bulged callosity sub-impression at digit I; see remarks for Broome sauropod morphotype E). A slight ridge within the caudal half of the impression potentially demarks a heel pad.

Lastly, DP8-16(1), if it was formed by a separate step, might be an impression of a manus or it represents a truncated impression of a once-larger pedal track. In the latter scenario, it could have been formed prior to DP8-16(p) because it shares a continuous external rim with DP8-16(2). An alternative interpretation is that DP8-16(1) is actually a part of DP8-16(p), specifically being a large sub-impression of a bulged callous pad that extends medially from the impression of digit I (see remarks for Broome sauropod morphotype E).

The remaining two non-overprinted impressions, DP8-16(3, 4), are preserved as well-outlined, incomplete depressions. DP8-16(3) probably is a remnant of a pedal impression, whereas DP8-16(4) appears to be a large manual impression of comparable size to some of the other larger manual tracks already described (Table 10). Neither impression preserves morphological details that would elucidate further comparative remarks.

## BIPEDAL ORNITHISCHIAN TRACKS

*WINTONOPUS LATOMORUM* Thulborn and Wade, 1984  
(Figs. 37–40, 61A, 62A, B, S12; Table 11)

**Holotype**—QM F10319, the natural mold of a right pes.

**Type Locality, Horizon, and Age**—The holotype specimen is from interbedded sandstones and siltstones at Lark Quarry Conservation Park, near the town of Winton, central-western Queensland, Australia, and derives from the Upper Cretaceous portion (upper Cenomanian–lower Turonian; Tucker et al., 2013) of the Winton Formation.

**Referred Material**—QM F10330, the natural mold of a left pes, described by Thulborn and Wade (Thulborn and Wade, 1984) as the holotype of ‘*Skartopus australis*.’ Romilio et al. (2013) considered ‘*S. australis*’ as a preservational variant of *Win. latomorum* and consequently made it a junior synonym of

the latter. UQL-DP23-1, the natural mold of a left pes (Figs. 37A–D, 61A, 62A, S12), preserved in close association with several other *Win. latomorum* tracks and additionally represented by WAM 12.1.12, a rigid polyurethane resin replica; UQL-DP23-2, a 7.1-m-long continuous trackway, comprising at least seven pedal tracks (Figs. 37D, E, 38A, B), all preserved as natural molds (additionally represented by WAM 12.1.13, a rigid polyurethane resin replica of UQL-DP23-2[rp2]); UQL-DP5-1, a 4.3-m-long continuous trackway, comprising at least four pedal tracks (Fig. 39A–F), all preserved as natural molds (additionally represented by WAM 12.1.14, a rigid polyurethane resin replica of UQL-DP5-1[lp1]); UQL-DP-V-2, a 4.8-m-long continuous trackway, comprising at least five pedal tracks (Fig. 39E, G), all preserved as natural molds; UQL-DP5-3, a 5.5-m-long continuous trackway, comprising at least five pedal tracks (Figs. 39E, H, 40D, E), all preserved as natural molds; UQL-DP5-4(lp1) and UQL-DP5-4(rp1), the natural molds of a left and a right pes,

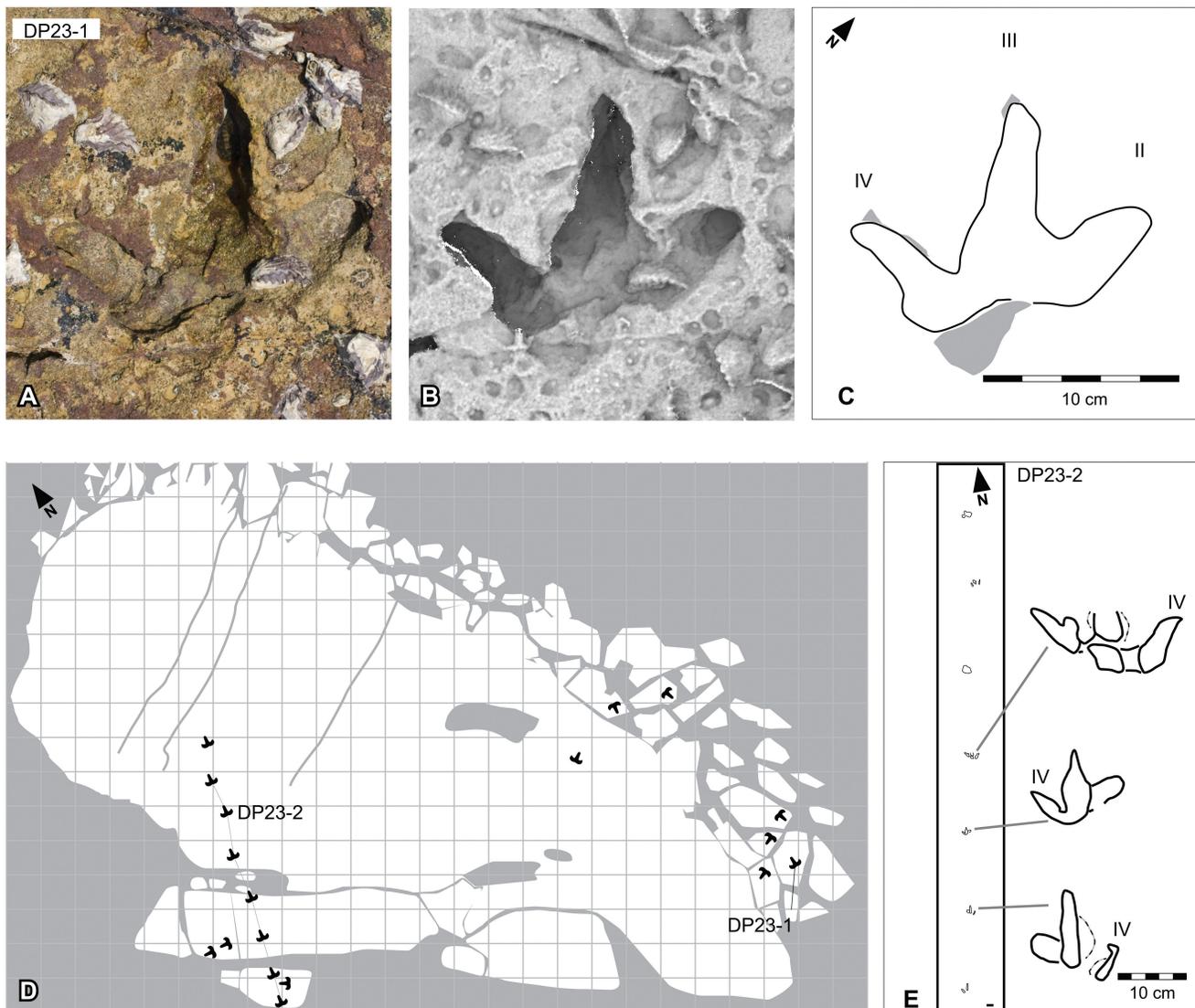


FIGURE 37. *Wintonopus latomorum* Thulborn and Wade, 1984, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Pedal impression, UQL-DP23-1, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, the schematic map of the UQL-DP23 platform containing multiple tracks. **E**, the UQL-DP23-2 trackway as a schematic map. See Figure 19 for legend.

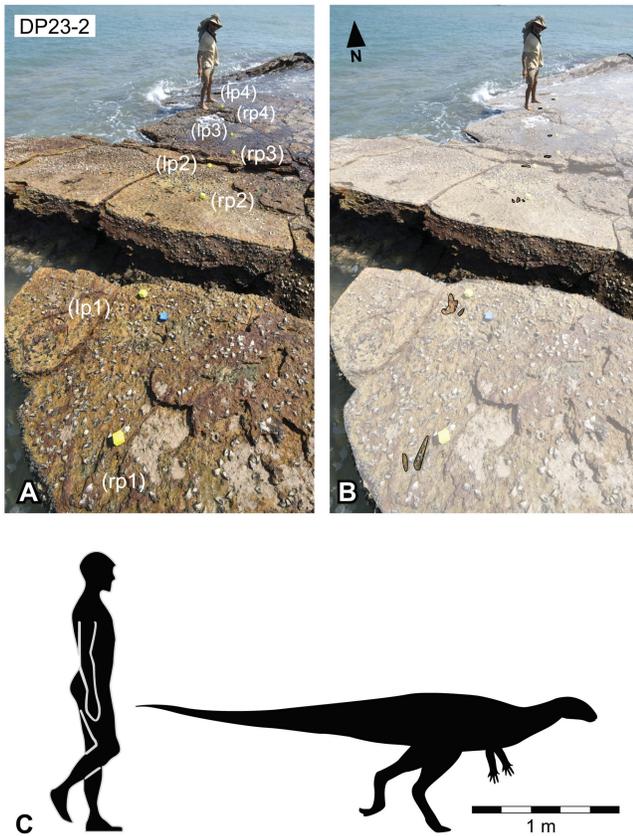


FIGURE 38. *Wintonopus latomorum* Thulborn and Wade, 1984, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Damian Hirsch alongside the UQL-DP23-2 trackway as **A**, photograph; and **B**, photograph with track overlay. **C**, silhouette of hypothetical *Wintonopus latomorum* trackmaker based on UQL-D23-1, compared with a human silhouette. See Figure 19 for legend.

respectively (Figs. 40A, B, 62B), that form a 0.9-m-long trackway; UQL-DP5-5, an isolated natural mold of a left pes (Fig. 40C). (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality, Horizon, and Age**—The referred specimens include those housed in QM, collected from Lark Quarry, near the town of Winton, central-western Queensland, Australia, and derive from the Upper Cretaceous portion (upper Cenomanian–lower Turonian; Tucker et al., 2013) of the Winton Formation, and those preserved in situ on rock platforms at DP23, DP5 in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia in the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone (Figs. 37–40).

**Emended Diagnosis**—Pedal tracks: very small to large size (proximodistal length 5–26 cm, mediolateral width 3.5–32 cm), tridactyl, mesaxonic, typically wider than long, with an average maximum proximodistal length to maximum mediolateral width ratio of 0.6–1.2; individual digital impressions proportionately moderately elongated and narrow (the maximum width of each digital impression is 13–41% of the total track length); the apex of individual digital impressions is typically rounded to bluntly acuminate; central digital impression (digit III) usually extends distally beyond the distal-most extent of the impressions of digit II and IV by between a fifth and a half of the total

track length (digit extension to track length ratio 0.21–0.52), and the impressions of digits II and IV extend distally to approximately the same level relative to the principal track axis; the most proximal portion of the track is formed from the proximal part of the impression of digit IV; total divarication angle between the axes of impressions of digits II and IV is variable (58–108°); divarication of axes of impressions of digits II and III (26–66°) and that of digits III and IV (24–53°) are also variable; a metatarsodigital pad impression is rarely present; the proximal track margin is typically bilobed and asymmetrical, formed from the proximal margins of the impressions of digit II and IV with the concavity positioned more proximolaterally than proximomedially; the proximal margin of digital impression II is more distally positioned than that of digital impressions III and IV; ungual impressions typically absent. Trackway: typical pace angulation between 140° and 170°; typical stride length 11–24 times the maximum pedal track length; typical pace 6–12 times the maximum pedal track length. Pedal tracks are inwardly rotated relative to the trackway midline.

**Description**—There are many tracks in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula that can be confidently assigned to *Wintonopus latomorum*. These occur as isolated tracks (Figs. 37A–D, 40C), tracks in close association with other tracks of the same ichnospecies, or as tracks that form part of consecutive trackways (Figs. 37D, E, 38A, B, 39C–H).

Track DP23-1 is a small-sized, tridactyl, mesaxonic, left pedal track (Figs. 37A–C, 61A, 62A, S12) that is preserved in close association with other *Win. latomorum* tracks, but that cannot confidently be assigned to a trackway (Fig. 37D). It was figured by Thulborn (2012:fig. 28) and assigned to cf. *Wintonopus* but not described. The track is wider than long, with a track length to track width ratio of 0.8 (13.4 cm long, 17.1 cm wide), which is higher than that of the holotype track from Lark Quarry, Queensland (0.6). The digit III impression digit extension to track length ratio is 0.49, such that the impression of digit III extends distally farther than the digit II impression, followed by the digit IV impression. The proximal margin of digit IV forms the proximal-most portion of the track. The divarication angle between digital impressions II and III (35°) is less than that for digital impressions III and IV (52°). The digital impressions are moderately elongated for III and IV and short for II, although each impression is proportionately narrow (digital impression width to track length ratio of 0.24–0.37), with a blunt to slightly pointed distal tip. The track lacks both digital and metatarsodigital pad impressions.

Track DP5-1(lp1) is a small left track that is the first pedal track of the trackway DP5-1, which comprises four pedal tracks (Figs. 39A–F). The track has been figured previously by Long, both as a schematic (Long, 1990:127, 1998:67) and as a photograph (Long, 1990:131). This track is slightly longer than wide (19 cm long, 18 cm wide), with a track length to width ratio of 1.1. The track is strongly mesaxonic with a digital impression extension to track length ratio of 0.44. The distal impressions of the digit tips are bluntly pointed with the proximal and distal margins of the impressions of digit II and IV being subequal. All the tracks that constitute trackway DP5-1 have the divarication angle between the impressions of digits II and III (44–66°) greater than that between the impressions of III and IV (24–35°). The first track of this trackway DP5-1(rp1) is longer than wide (20 cm long, 17 cm wide) and includes an impression of the metatarsodigital pad. It was possibly formed by a trackmaker with a hip height of between 0.8 and 1.0 m. The pace length varies between 1.3 and 1.4 m, which is between 9.1 and 12.4 times the track length, and a stride length of approximately 2.76 m. The trackways are very narrow, with a pace angulation of 165–170°. Using these values, we can estimate trackmaker

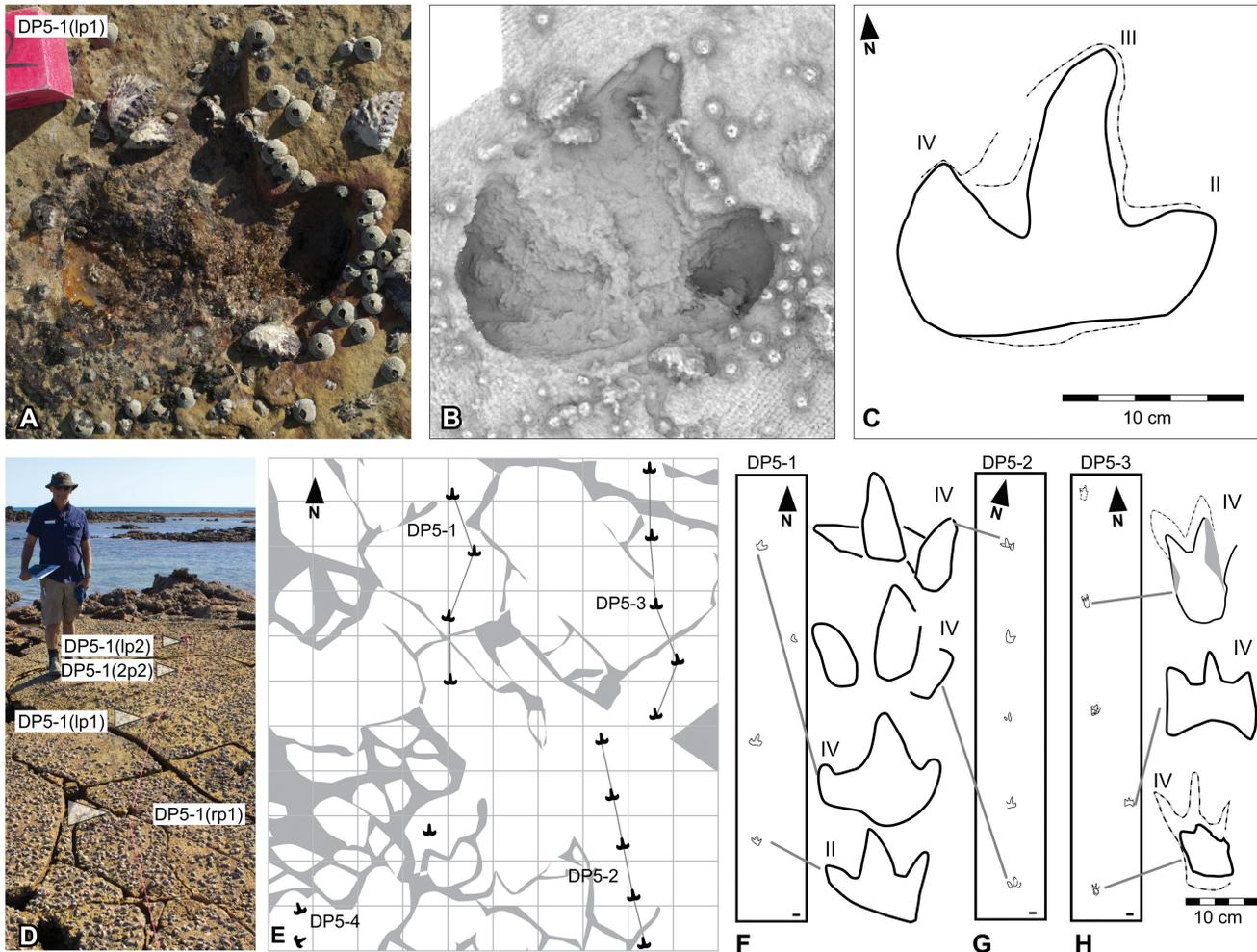


FIGURE 39. *Wintonopus latomorum* Thulborn and Wade, 1984, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Pedal impression, UQL-DP5-1(lp1), preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, photograph of trackway UQL-DP5-1 with Nigel Clarke for scale. **E**, the schematic map of the UQL-DP5 platform containing multiple tracks. The schematic maps of trackways **F**, UQL-DP5-1; **G**, UQL-DP5-2; and **H**, UQL-DP5-3. Scale bar equals 10 cm. Map grid spacing of 1 m. See Figure 19 for legend.

speed (Thulborn and Wade, 1984) to approximately 4.7 m/s (17.1 km/h).

Other *Win. latomorum* trackways (DP23-2, DP5-1, –2, and –3; Figs. 37D, E, 38A, B, 39D–H) are narrow-gauge (pace angulation 160–176°), with high pace lengths relative to track length (pace equivalent to an average of 7.1–8.4 times track length). The tracks within these trackways are small- to medium-sized and do not have an impression of a metatarsodigital pad. For the trackways DP23-2, DP5-1, –2, and –3, we estimate trackmaker speed as approximately 6.0, 4.7, 3.9, and 4.6 m/s (i.e., 21.4, 17.1, 14.2, and 16.4 km/h), respectively (see Materials and Methods for trackmaker hip height calculations and Table S1).

Many of the tracks within the DP5-3 trackway resemble the ichnotaxon '*Skartopus australis*' (Fig. 39H). These tracks are characterized by elongate and narrow digital impressions. They are longer than wide, with a track length to width ratio between 1.2 and 2.5 and lack the impression of the metatarsodigital pads. They are deep in the proximal and central portions of the track, with the track depth continuously decreasing distally, suggesting that the distal portions of these tracks are pedal drag marks (Romilio et al., 2013). These drag marks are also observed in

other '*Skartopus*'-like tracks, such as DP5-4(lp1) and DP5-4(rp1) from the same platform (Fig. 40A, B).

Track DP5-5 (Fig. 40C) is another possible example of *Win. latomorum*. The track is the natural mold of a left pes with elongated, distally blunt digital impressions. The morphology is similar to that of DP23-1 with the exception of the proximal track margin, which is eroded and caudally extends the track, giving the illusion of the presence of a metatarsodigital pad impression.

**Remarks**—The holotype and paratype materials of *Win. latomorum*, along with replica specimens, are housed in the QM, with the in situ specimens located at Lark Quarry. Thulborn and Wade (1984) used these specimens to describe the ichnotaxon. These authors explained that this ichnotaxon is highly variable in track morphology, and that the movement of the trackmaker's pes whilst in contact with the substrate could explain such variation. The variability of track morphology was reason for these authors to base the diagnosis of *Win. latomorum* primarily on tracks with minimal disturbance. Other morphotypes were used to illustrate the degree to which tracks could vary.

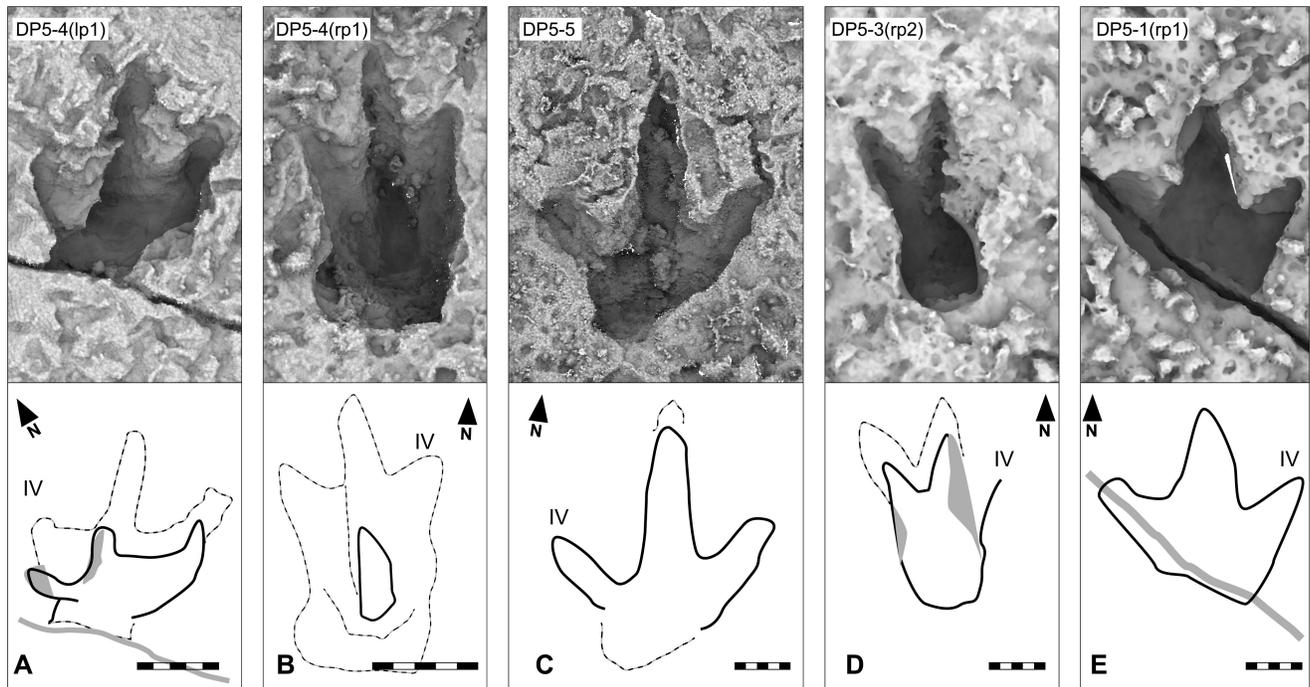


FIGURE 40. *Wintonopus latomorum* Thulborn and Wade, 1984, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. 3D images with ambient occlusion and schematics of in situ tracks: A, UQL-DP5-4(lp1); B, UQL-DP5-4(rp1); C, UQL-DP5-5; D, UQL-DP5-3(rp2); and E, UQL-DP5-1(rp1). Scale bar equals 5 cm. See Figure 19 for legend.

Tracks that resemble *Wintonopus* have previously been recognized at Walmadany (Long, 1992a, 1993, 1998), but little in the way of detailed morphological description has been provided, including a lack of ichnospecies assignment. Recently, McCrea et al. (2012) proposed that the assignment of some of the Broome tracks to *Wintonopus* by previous authors was dubious; they stated without elaboration that the ‘robust morphology’ and ‘trackway parameters’ indicated that these were theropod tracks, specifically cf. *Irenichnites*. Given that *Wintonopus* is characterized by the absence of a metatarsodigital pad impression, McCrea et al. (2012:fig. 19B) utilized ‘heeled’ tracks (including DP5-4[lp1] and DP5-5; Fig. 40A, C) as evidence of the uncertainty of this ichnotaxon’s presence in the Broome Sandstone. We identify the proximal margins of these tracks as being eroded surfaces that do not reflect the true morphology of pristine tracks. During our study, in addition to the tracks found previously (Long, 1990, 1992a, 1998; McCrea et al., 2012; Thulborn, 2012), we found multiple examples of tracks that could be assigned to *Wintonopus*, many in close association or forming part of distinct, well-defined trackways.

The tracks from the Broome Sandstone assigned here to *Win. latomorum* compare favorably with the holotype and topotype tracks from Lark Quarry in terms of overall track morphology, including being typically wider than long, with moderately elongated digital impressions. Other congruent characteristics include the divarication angle between the impressions of digit II and III being greater than that between those of digit III and IV, the lack of a metatarsodigital pad impression, and the proximal track margin being the proximal portion of the impression of digit IV. The Broome trackways are similar to those at Lark Quarry (see Romilio et al., 2013) in terms of their high pace angulation, inward track rotation, and large pace and stride lengths relative to track length. Our assignment of the Broome

tracks to *Win. latomorum* represents the first confirmed occurrence of the ichnospecies outside of the Winton Formation; it not only expands the geographic range of this ichnotaxon from eastern (central-western Queensland) to western (Dampier Peninsula, WA) Australia but also its temporal range (Valanginian–lower Turonian).

Another ichnotaxon from Lark Quarry that was recognized by Thulborn and Wade (1984) is ‘*Skartopus australis*.’ This ichnotaxon was characterized as having small, symmetrical tracks with elongate and narrow digital impressions. Similar to Lark Quarry, we also found such tracks in the Broome Sandstone in close association with tracks assignable to *Win. latomorum*. However, most of the Broome tracks were considerably larger than ‘*S. australis*’ from Lark Quarry (some as much as 4 times longer than the maximum length considered diagnostic of ‘*S. australis*’ by Thulborn and Wade (1984). Many of the Broome tracks also occurred in close proximity to tracks previously assigned to *Wintonopus* (see Long, 1992a, 1993, 1998), or even form parts of distinct trackways that contain other tracks that can confidently be assigned to *Win. latomorum*. It is unclear why the other associated tracks were not mentioned in these earlier reports, but we suspect that this may have been due to the fear of theft or vandalism (see Long, 1990, 1992a). Recent investigations of ‘*S. australis*’ from Lark Quarry have found that this ichnospecies should be considered a junior synonym of *Win. latomorum* due to the co-occurrence of these tracks within *Wintonopus* trackways, and the recognition of the supposedly elongated digital impressions being drag marks (Romilio et al., 2013). Depth profiles of the Broome tracks are almost identical to those of many of the *Win. latomorum* and ‘*S. australis*’ tracks from Lark Quarry (Figs. 39H, 40A, B). In light of this reinterpretation, it is not surprising that ‘*S. australis*’ tracks have been found in the Broome Sandstone in association with its senior synonym *Win. latomorum*.

TABLE 11. Measurements of tracks assigned to *Wintonopus latomorum* Thulborn and Wade, 1984, from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	II^III	III^IV	Total^	bdl II (II/L)	bdl III (III/L)	bdl IV (IV/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)	Pace (cm)	Stride (cm)
23-1(lp)	13.4	17.1	0.8	6.5 (0.49)	35	52	87	7.4 (0.55)	9.2 (0.69)	8.5 (0.63)	4.4 (0.33)	4.9 (0.37)	3.2 (0.24)	—	—
23-2(lp1)	14	—	—	—	—	43	—	10.2 (0.73)	6.8 (0.49)	—	—	2.0 (0.14)	2.5 (0.80)	—	—
23-2(rp1)	13	13	1.0	6.8 (0.52)	66	28	94	—	11.2 (0.86)	5.2 (0.4)	3.2 (0.25)	2.4 (0.18)	1.0 (0.1)	118	—
23-2(lp2)	11	14	0.8	4.5 (0.41)	55	53	108	6.1 (0.55)	10.5 (0.95)	6.8 (0.62)	2 (0.18)	4.0 (0.36)	2.5 (0.23)	117	235
23-2(rp2)	—	22	—	—	45	24	69	8.8	—	9.1	2	—	3.0	111	227
23-2(lp3)	—	—	—	—	—	—	—	—	—	—	—	—	—	127	237
23-2(rp3)	10.5	13.5	0.8	3.0 (0.29)	—	31	—	5.2 (0.5)	—	7.2 (0.69)	1.5 (0.14)	—	1.5 (0.14)	130	255
23-2(lp4)	10.5	15	0.7	—	—	30	—	—	7.2 (0.69)	4.9 (0.47)	—	2.5 (0.24)	3.0 (0.29)	101	229
5-1(rp0)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5-1(rp1)	20	17	1.2	4.2 (0.21)	44	24	68	7.8 (0.46)	6.7 (0.34)	3.6 (0.18)	2.7 (0.14)	4.2 (0.21)	2.2 (0.11)	—	—
5-1(lp1)	19	18	1.1	8.3 (0.44)	45	35	80	7.1 (0.37)	10.8 (0.57)	8.2 (0.43)	4.5 (0.24)	4.5 (0.24)	3.5 (0.18)	128	—
5-1(rp2)	16	14	1.1	6.0 (0.38)	—	—	—	—	—	—	—	4.2 (0.26)	3.3 (0.21)	138	265
5-1(lp2)	16	18	0.9	—	66	35	101	7.4 (0.46)	7.1 (0.92)	8.8 (0.55)	4.5 (0.28)	4.5 (0.28)	—	140	276
5-2(rp1)	14	22	0.6	7.0 (0.5)	26	32	58	9.7 (0.69)	12.9 (0.92)	7.1 (0.51)	4.1 (0.29)	5.7 (0.41)	—	—	—
5-2(lp1)	15	16	0.9	7.5 (0.5)	30	—	—	6.9 (0.46)	9.9 (0.66)	—	3 (0.2)	3.4 (0.23)	—	120	—
5-2(rp2)	17	20	0.9	—	—	—	—	5.0 (0.29)	11.7 (0.69)	—	2.2 (0.13)	3.3 (0.19)	—	120	240
5-2(lp2)	20	16	1.3	—	—	—	—	5.2 (0.26)	11.1 (0.56)	—	4 (0.2)	5.2 (0.26)	—	112	227
5-2(rp3)	19	20	1.0	6.7 (0.35)	64	27	91	7.3 (0.38)	7.4 (0.39)	10.4 (0.55)	3.3 (0.17)	4.8 (0.25)	4.7 (0.25)	132	238
2-3	10.5	13	0.8	4.0 (0.38)	62	45	107	3.6 (0.34)	5.3 (0.5)	7.0 (0.67)	3.0 (0.29)	2.5 (0.24)	2.0 (0.19)	—	—
5-3(lp1)*	20	8	2.5	—	—	—	—	—	—	—	—	—	—	—	—
5-3(rp1)*	13	10	1.3	—	—	—	—	—	—	—	—	—	—	130	—
5-3(lp2)*	18	12	1.5	—	—	—	—	—	—	—	3.0 (0.17)	2.3 (0.13)	2.0 (0.11)	121	247
5-3(rp2)*	17	10	1.7	—	—	—	—	—	—	—	—	—	—	148	267
5-3(lp3)*	24	13	1.8	—	—	—	—	—	—	—	1.9 (0.08)	3.7 (0.15)	2.1 (0.09)	153	298
5-II-4.1	16	13	1.2	—	—	—	—	—	—	—	—	—	—	—	—
5-4.2*	19	11	1.7	4.6	21	20	40	3.0	6.0	3.0	3.0	3.0	4.0	—	—
5-5	15	16	0.9	5.7 (0.31)	49	43	94	5.3 (0.35)	8.3 (0.55)	4.9 (0.33)	2.2 (0.15)	5.0 (0.33)	3.0 (0.2)	—	—
11-3	44.6	44.9	1.0	15.2 (0.34)	46	34	80	14.1 (0.32)	17.4 (0.39)	12.0 (0.27)	16.0 (0.36)	21.0 (0.47)	13.0 (0.29)	—	—

bdl = basal digital impression length; bdw = basal impression width; De = digital impression extension; II = impression of digit II; III = impression of digit III; IV = impression of digit IV; L = track length; W = track width. ^ denotes angle between respective digital impressions. \* denotes 'drag trace.'

Of all the Broome Sandstone ornithopod tracks, *Win. latomorum* are the smallest. The ichnospecies most closely resembles *Win. middletonae*, ichnosp. nov., with regard to features considered diagnostic of the ichnogenus (e.g., lack of a metatarsodigital pad impression). However, *Win. latomorum* can be distinguished from *Win. middletonae* on account of its more elongate, relatively narrow, and distally acuminate digital impressions, and the overall asymmetrical track outline. The most obvious feature that distinguishes *Win. latomorum* from other non-*Wintonopus* ornithopod tracks in the Broome Sandstone is the lack of a metatarsodigital pad impression, suggestive of a trackmaker that adopted a subunguligrade posture rather than the digitigrade often associated with basal ornithopods (Romilio et al., 2014).

Other similarities between *Win. latomorum* from the Broome Sandstone and those from Lark Quarry include the high pace and stride lengths relative to track length and the broadly congruent orientation of trackways. Both of these characteristics are suggestive of group running behavior (Thulborn and Wade, 1984). However, the various tracksites involved differ in terms of the number of trackmakers that can be identified. At DP5, only three *Win. latomorum* trackmakers are discernible from the trackways. At Lark Quarry, many dozens were originally asserted as formed by running trackmakers (Thulborn and Wade, 1984) although only one trackway (equivalent to a trackmaker moving at a mammalian equivalent of a trot) was shown by these authors in what was originally interpreted as a dinosaur 'stampede' (Thulborn and Wade, 1984). Romilio et al. (2013) figured several Lark Quarry trackways, purportedly formed by small-bodied ornithopods that included walking, running, and swimming trackmakers. Interestingly, these dinosaur swim traces differed in size and indicated their formation by different-sized, partially buoyed trackmakers contacting the river bottom when the river flowed at different water levels. The Broome Sandstone *Win. latomorum* do not resemble dinosaur swim traces (also see

McAllister, 1989; Whyte and Romano, 2001a; Gierlinski et al., 2004; Lockley and Foster, 2006; Milner et al., 2006; Ezquerria et al., 2007), nor those *Wintonopus* swim traces found at Lark Quarry. The Broome Sandstone tracks DP5-1, -2, and -3 more likely represent the traces of running individuals. Of the three trackways found at DP5, we estimate that trackmaker speed varied between individual trackmakers (4.7, 3.9, and 4.6 m/s based on trackways DP-V-1, -2, and -3, respectively). Whether the DP5 Broome Sandstone *Win. latomorum* represent a small group of dinosaurian trackmakers running together is highly speculative and difficult to ascertain with certainty. This issue notwithstanding, it is clear that the pedal tracks indicate a potentially cursorially adapted subunguligrade trackmaker, with the trackway data suggesting that individuals ran in the same direction, at the same location, and very likely at close to the same time.

Thus far we are not aware of tracks assignable to *Win. latomorum* in the Broome Sandstone at tracksites outside of the study area. Although locally common at some tracksites, these tracks are generally quite rare compared with those of larger bipedal ornithopods, thyreophorans, and the ubiquitous sauropods. This may be an indication that the trackmakers were rare animals, or that they had a preference for particular areas or paleoenvironments. In addition, similar to the other small tracks (e.g., Broome theropod morphotype A), the small size of most *Win. latomorum* tracks might make them harder to find or more prone to erosion.

*WINTONOPUS MIDDLETONAE*, ichnosp. nov.  
(Figs. 41, 61B, 62C, S13; Table 12)

**Etymology**—The species name honors Louise Middleton for her lifelong passion for the discovery, documentation, and conservation of Broome Sandstone dinosaurian ichnites.

**Holotype**—WAM 12.1.15, a rigid polyurethane resin replica of UQL-DP14-7, the natural mold of a left? pes.

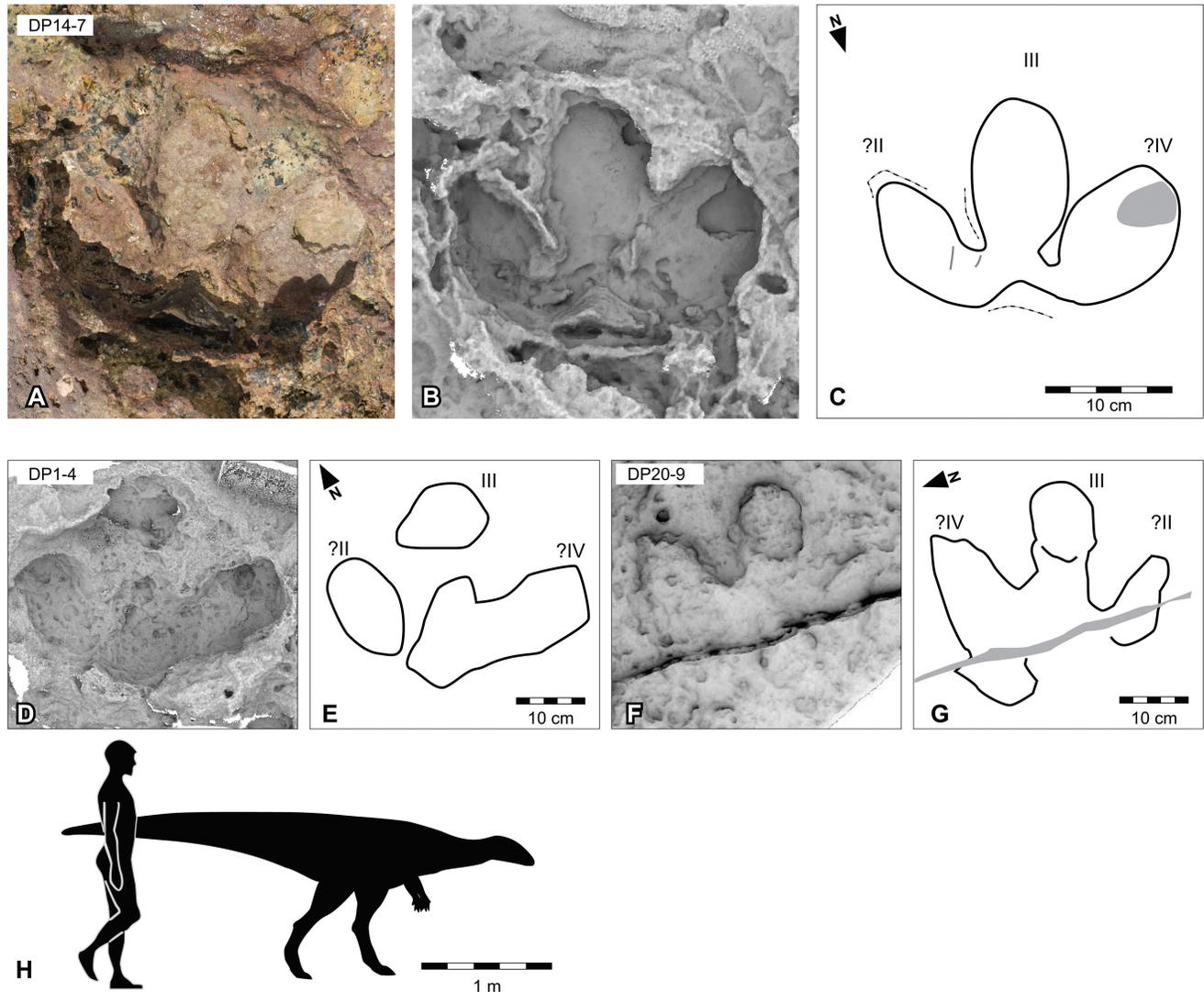


FIGURE 41. *Wintonopus middletonae*, ichnosp. nov., from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Pedal impression, topotype UQL-DP14-7, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Pedal impression, UQL-DP1-4, preserved in situ as **D**, ambient occlusion image and **E**, schematic interpretation. Pedal impression, UQL-DP9-9, preserved in situ as **F**, ambient occlusion image and **G**, schematic interpretation. **H**, silhouette of hypothetical *Wintonopus middletonae* trackmaker based on UQL-DP14-7, compared with a human silhouette. See Figure 19 for legend.

**Topotype**—DP14-7, the natural mold of a left? pes preserved in situ (Figs. 41A–C, 61B, 62C, S13).

**Type Locality, Horizon, and Age**—The holotype specimen is preserved in situ at UQL-DP14, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Referred Material**—Other tracks that can be assigned to *Wintonopus middletonae* include UQL-DP1-4, the natural mold of a right? pes, preserved in situ at UQL-DP1 (Fig. 41D, E); UQL-DP9-9, the natural mold of a ?left pes (Fig. 41F, G), preserved in situ at UQL-DP9. All these tracks occur in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, in the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone. (From this point onwards, except in

figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Diagnosis**—Pedal tracks: small- to medium-sized (proximodistal length 19–25 cm, mediolateral width 28–36.6 cm), tridactyl, mesaxonic (digital impression extension to track length ratio 0.3–37), wider than long, with an average maximum length to maximum width ratio approximately 0.7–0.8; individual digital impressions moderately elongated, broad, and generally oval in shape (the maximum width of each digital impression is 36–45% of the total track length, the latter measured along the principal track axis). The apex of the digital impression is typically rounded. The central digital impression (digit III) usually extends distally beyond the impressions of digits II and IV (relative to the principal track axis) by about a third of the track length; the impression of digit IV extends slightly farther proximally than that of digital impression II; axes of the impressions of digits II and III typically intersect distal to the intersection of

TABLE 12. Measurements of tracks assigned to *Wintonopus middletonae*, ichnosp. nov., from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	II^III	III^IV	Total^	bdl II (II/L)	bdl III (III/L)	bdl IV (IV/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)
14-7	19	28	0.7	7 (0.37)	27	55	82	12.8 (0.67)	12.8 (0.67)	12.1 (0.64)	8.5 (0.45)	8.5 (0.45)	7.0 (0.36)
1-4	24.9	36.6	0.7	7.5 (0.30)	36	55	91	14.1 (0.57)	12.4 (0.5)	11.7 (0.47)	9.7 (0.39)	11.1 (0.45)	10.0 (0.4)
9-9	24.4	32	0.8	8.5 (0.35)	45	47	92	9.5 (0.4)	13.3 (0.55)	12.1 (0.5)	7.2 (0.30)	9.4 (0.39)	7.6 (0.31)

bdl = basal digital impression length; bdw = basal impression digit width; De = digital impression extension; II = impression of digit II; III = impression of digit III; IV = impression of digit IV; L = track length; W = track width. ^ denotes angle between respective digital impressions.

the axes of the impressions of digits III and IV in large tracks, and at roughly the same position for smaller tracks; total divarication of the axes of impressions of digits II and IV is narrow (82–92°), as is the divarication of axes of impressions of digits II and III (27–47°) and digits III and IV (47–55°); single digital pad impressions of each digital impression may be present, with the formula of 1/II, 1/III, 1/IV; a metatarsodigital pad impression is absent, such that the proximal track margin is typically bilobed, with each lobe representing the proximal margins of the digital impressions of II and IV.

**Description**—Three isolated tracks were observed in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula that can be confidently assigned to *Wintonopus middletonae* (Fig. 41).

Track DP14-7 is the best-preserved track that can be assigned to *Win. middletonae* (Fig. 41A–C) and for this reason was chosen as the type specimen. It is a left? pedal track of medium size, wider than long (track length 19 cm long, 28 cm wide), a track length to track width ratio of 0.7, with the distal tip of the impression of digit III extending beyond the impressions of digits II and IV by approximately one third of the total track length (the digital impression extension to track length ratio is 0.37). The divarication of the axes of impressions of digits II and III (27°) is smaller than that of digits III and IV (55°). The well-preserved, oval-shaped digital impressions lack digital pad impressions. The track lacks a metatarsodigital pad impression and instead has a bilobed proximal track margin formed from the proximal portions of the impressions of digits II and IV.

Track DP1-4 (Fig. 41D, E) is a well-preserved track showing features characteristic of *Win. middletonae*. It is a right? track of medium size, wider than long (track length 24.9 cm long, 36.6 cm wide), with a track length to track width ratio of 0.7. The distal tip of the impression of digit III extends beyond the impressions of digits II and IV by approximately one third the total track length (the digital impression extension to track length ratio is 0.3). The digital impressions are proportionately broad and distally rounded. The track has a rounded, proximal enlargement that is aligned with the axis of the impression of digit IV and may represent an impression of the metatarsodigital pad or possibly an erosional feature.

A photograph and schematic of DP20-9 (Fig. 41F, G) appeared in McCrea et al. (2012:figs. 28D, 30) without any accompanying description. Based on comparisons with other tracks assigned herein to *Win. middletonae*, in particular DP1-4, the track appears to pertain to a left pes. Although the shallow impressions of three digits are apparent, the rear portion of the track is disrupted by a mediolaterally aligned crack, such that the proximal outline is hard to interpret with certainty. Tracing a depth contour just inside the external margin of the digital impressions indicates that the proximal margin of the impressions of digits II and IV probably did not extend far beyond the crack, and thus that the impression of a metatarsodigital pad was probably lacking. Assuming that this outline is correct, the track is wider than it is long (track length to track width ratio of 0.8), with digital

impression width and digital impression length to track length ratios of 0.30–0.39 and 0.39–0.55, respectively. The impression of digit III extends beyond the distal extent of the impressions of digit II and IV, making the track mesaxonic (the digital impression extension to track length ratio is 0.35). The impression of digit IV extends slightly farther distally than that of digit II, and its long axis intersects the principal track axis just proximal to that of the impression of digit II. The impressions of digits III and IV are proportionately broad and distally rounded, although the impression of digit II appears more acuminate. There is a suggestion of a single digital pad impression in the impression digit III, but the track is too eroded to be certain of this. The total divarication angle between the axes of the impressions of digits II and IV is 92°. The divarication angle between the axes of the impressions of digits II and III is roughly equivalent to that between the axes of the impressions of digits III and IV (45° and 47°, respectively).

**Remarks**—*Wintonopus middletonae* is the second ichnospecies of *Wintonopus* to be recognized in Australia. In common with *Win. latomorum*, *Win. middletonae* has a proximal track margin that is often concave (equivalent to the “posterior margin of [the] foot[-print] convex forward” of Thulborn and Wade [1984:421]) and lacks a metatarsodigital pad impression. Although we were unable to assign a clear trackway to *Win. middletonae*, the left or right assignment of tracks was possible following comparisons with *Win. latomorum*, which typically has the proximal margin of the impression of digit IV as the most proximal portion of the track margin. It is hoped that future discoveries or further analysis of currently described tracks will verify this. *Wintonopus middletonae* can be distinguished from *Win. latomorum* on account of the broader digital impressions that tend to be rounded distally, as well as the bilobed proximal track margin typically being more symmetrical.

McCrea et al. (2012:figs. 28C, D, 30) illustrated several Broome Sandstone ornithopod tracks, including DP1-4 and DP9-9 (see below section describing *Amblydactylus* cf. *A. kortmeyeri*). These authors regarded all the ornithopod tracks that they encountered in their survey of the Broome Sandstone to be tentatively referable to *Amblydactylus*, stating that they “mostly differ in subtle details,” without elaborating as to what these details were (McCrea et al., 2012:45). *Amblydactylus* is diagnosed as being a tridactyl pedal track with pointed digital impressions (Sternberg, 1932; Currie and Sarjeant, 1979), although in *A. kortmeyeri* the impression of digit IV is more rounded distally. The impression of digit II also extends farther distally than that of digit IV (Currie, 1983, 1995). Although DP1-4 is a tridactyl pedal track, all of its digital impressions have distinctly rounded tips, with the impression of digit IV extending distally slightly farther than that of digit II relative to the principal track axis. The published data on described ichnospecies of *Amblydactylus* also indicates a track outline that is concave proximomedially and convex proximolaterally (Sternberg, 1932; Currie and Sarjeant, 1979), a feature that is not consistent with the linear to bilobate proximal margin seen on DP1-4 (or the more gently

concave outline seen on DP9-9; see *Amblydactylus* cf. *A. kortmeyeri* below) due to the absence of any clear metatarsodigital pad impression. We therefore regard DP1-4 and other tracks here assigned to *Win. middletonae* to be distinct from *Amblydactylus* on account of the shape and orientation of the digital impressions, the overall track outline, and absence of the metatarsodigital pad impression.

*Wintonopus middletonae* shares a number of features with *Walmadanyichnus hunteri*, ichnogen. et ichnosp. nov. (see below), another Broome ornithopod ichnotaxon. In the type specimens of each ichnotaxon (DP14-7 and DP11-5, respectively), similarities occur with regard to the rounded digital impressions and the distomedial drag mark associated with the impression digit II (Figs. 41A–C and 42A–C, respectively). The occurrence of these features on both tracks may be due to similarities in the pedal kinematics of each trackmaker, an indication of these tracks pertaining to two closely related trackmakers, or both. We do not believe that *Win. middletonae* and *Wal. hunteri* tracks represent ontogenetic variants associated with a single trackmaker, considering that small and large *Wal. hunteri* leave prominent metatarsodigital pad impressions, whereas this was not the case with *Win. middletonae*. Interestingly, the proximal extension of the impression of digit IV in *Win. middletonae* may be comparable to the unification of the proximal portion of the impression of digit IV and metatarsodigital pad impression on *Wal. hunteri*, a trait that is best exemplified by DP11-5 (Fig. 42A–C). Despite these differences, it seems likely that both ichnospecies pertain to trackmakers with a subunguligrade stance (sensu Moreno et al., 2007), *Win. middletonae* trackmakers lacking a metatarsodigital pad, and *Wal. hunteri* trackmakers having one.

*Wintonopus middletonae* tracks have a low track length to track width ratio, ranging from 0.28 to 0.37. The small to large tracks of the ichnotaxon *Ornithopodichnus* are also noted for having “usually wide tracks” (Lockley et al., 2012:93), with track length to track width mean ratio ranges of 0.84–0.94 (calculated from Lockley et al., 2012) and 0.56–1.26 (Kim et al., 2009). Although *Win. middletonae* has proportionately wider tracks than *Ornithopodichnus*, the lower average ratio in the former is a combination of wide digital impressions and the lack of the metatarsodigital pad impression, which would otherwise contribute to a longer track length.

The ornithopod ichnotaxa *Caririchnium* (Leonardi, 1984; Lockley, 1987; Lee, 1997; Huh et al., 2003; Lockley et al., 2003; Matsukawa et al., 2005; Xing et al., 2007, 2012) and *Hadrosauropodus* (Gierlinski, 2008; Xing et al., 2009b; Fanti et al., 2013) display some similarities to *Win. middletonae*, most notably with regard to the shape of the broad, oval digital impressions, and the often bilobed proximal track margin. However, the latter similarity is only superficial, because the bilobed margin in *Caririchnium* and *Hadrosauropodus* is formed from the distal portion of the metatarsodigital pad impression, whereas in *Win. middletonae* it is formed by the proximal margins of the digit II and IV impressions.

Track DP9-7 (Fig. 41A–C) resembles the tridactyl tracks of the ‘Bi’ morphotype from the Upper Jurassic (Aeleanian–Bajocian) Ravenscar Group of the Cleveland Basin, Yorkshire, U.K., as described and figured by Romano and Whyte (2003:figs. 20, 25), particularly with respect to the three large oval digital impressions. However, the digital impressions of the ‘Bi’ morphotype do not converge proximally, with some tracks showing evidence of a metatarsodigital pad impression, a feature not observed in *Win. middletonae*. We estimate (based on Romano and Whyte, 2003:fig. 20) that the ‘Bi’ morphotype has a digital impression extension to track length ratio of approximately 0.41, and total divarication angle of 56°, both of which fall outside the range we estimate for *Win. middletonae*.

On DP1-4 (Fig. 41D, E), the possession of a straight lateral margin on the impression of digit IV that is continuous with the

proximal extension of the track is similar to the condition seen in *Jiayinosauropus johnsoni* specimen J F1 from the Upper Cretaceous Zhutian Formation in the Nanxiong Basin, Guangdong, China (Xing et al., 2009b). However, in *Jiayinosauropus*, this part of the track appears to represent a metatarsodigital pad impression, a feature that is absent from *Win. middletonae*. Further comparisons with J F1 are limited because the proximal portion of the track is incomplete (Xing et al., 2009b). Additional shared features between DP1-4 and *Jiayinosauropus* include similar divarication angles and track length to track width ratios. *Jiayinosauropus* differs from DP1-4 and other *Win. middletonae* tracks in having more slender digital impressions. Given these differences and the poor preservation of the J F1 track, we feel that it is wise to regard *Wintonopus*, and in particular *Win. middletonae*, as distinct from *Jiayinosauropus*.

Among identifiable ornithopod tracks that could be located in the study area, those assignable to *Win. middletonae* occur across two of the three main track-bearing areas (Walmadany and Yanijarri). Although the low abundance of these tracks indicates that the trackmaker responsible for them was not a common element of the area’s dinosaurian fauna, it was nonetheless widespread and does not appear to have had a preference for a specific area or paleoenvironment. As yet, we are not aware of *Win. middletonae* occurring at other tracksites outside of the study area.

*WALMADANYICHNUS*, ichnogen. nov.

*WALMADANYICHNUS HUNTERI*, ichnosp. nov.

(Figs. 14D, 42, 43, 61C, 62D, S14; Table 13)

**Etymology**—The ichnogenus name is a reference to Walmadany [walmadaɲ], the Nyulnyulan word for James Price Point. Walmadany was a powerful Ngumbarl warrior and Jabirjibirri Maja (Law Boss) who once lived at the camp that now bears his name (see Fig. 1). Paddy Roe buried his remains in the sand dunes above the camp when the former was middle-aged. The ‘ny’ in Walmadany is pronounced as a ‘n’ sound (i.e., palatal, not alveolar), with the tongue on the lower teeth. The ichnospecies name honors Richard Hunter, Goolarabooloo Maja and Traditional Custodian for the Northern Tradition of the Song Cycle, who has an intimate knowledge of dinosaurian tracks and tracksites along the Dampier Peninsula coastline.

**Holotype**—WAM 12.1.16, a rigid polyurethane resin replica of UQL-DP11-5, the natural mold of a right pes.

**Topotype**—UQL-DP11-5, the natural mold of a right pes preserved in situ in association with several other tracks that can be assigned to *Wal. hunteri* (Figs. 42A–C, 61C, 62D, S14).

**Type Locality, Horizon, and Age**—The topotype specimen is preserved in situ at UQL-DP11, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Referred Material**—Other tracks preserved in situ on rock platforms of the Broome Sandstone in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, that can be assigned to *Walmadanyichnus hunteri* include UQL-DP11-18, at least two pedal impressions (sequential left and right) laying in situ as natural molds (Fig. 43A, B), preserved in situ at UQL-DP11; UQL-DP45-19, an isolated in situ natural mold of a right? pes (Fig. 43C, D), preserved in situ at UQL-DP45; UQL-DP44-4, an isolated in situ natural mold of a right? pes (Fig. 43E, F), preserved in situ at UQL-DP44; UQL-DP11-8, an isolated in situ natural mold of a right? pes (Fig. 43G, H), preserved in situ at UQL-DP11. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

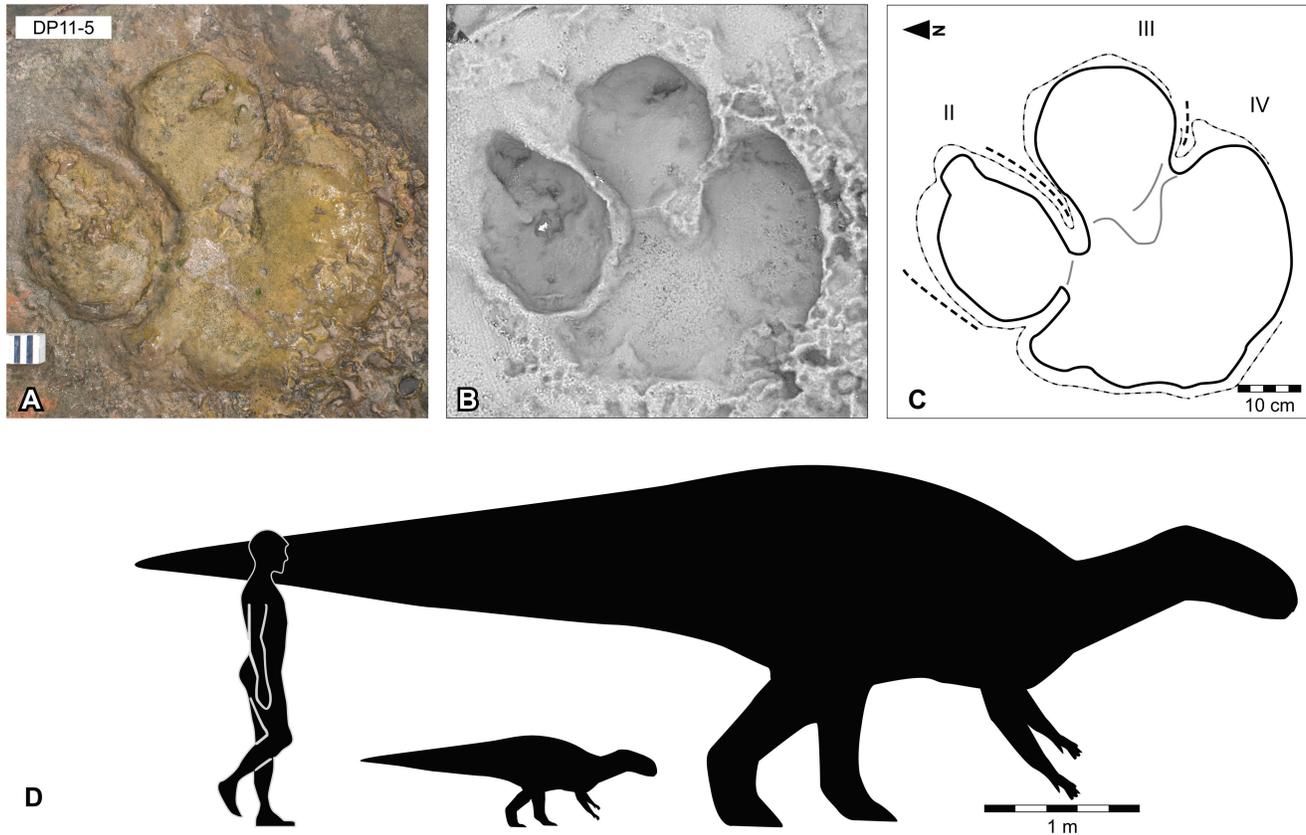


FIGURE 42. *Walmadanyichnus hunteri*, ichnogen. et ichnosp. nov., from the Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia. Left pedal impression, topotype UQL-DP11-5, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, silhouettes of hypothetical *Walmadanyichnus* trackmakers based on UQL-DP11-5 and UQL-DP11-8 (Fig. 43G, H), compared with a human silhouette. See Figure 19 for legend.

**Diagnosis**—Pedal tracks: small- to large-sized (proximodistal length 12.9–80 cm, mediolateral width 12.1–81 cm), tridactyl, mesaxonic (digital impression extension to track length ratio 0.20–0.28), as wide as long, with an average maximum track length to maximum track width ratio of approximately 1.0–1.1; circular track shape; individual digital impressions rounded to circular, with the impression of digit III typically being the broadest impression (maximum digital impression width to track length ratio of 0.32–0.49) being widest at the mid-length of the digital impression; the widest part of impression of digit II (0.22–0.37) is also at the mid-length of the digital impression, whereas for the impression digit IV (0.25–0.41) it is typically more proximal; central digital impression (digit III) longer than the impressions of digits II and IV, which extend distally to approximately the same level relative to the principal track axis; axes of the impressions of digits III and VI typically intersect distal to the intersection of the axes of the impressions of digits II and III; total divarication angle between the axes of impressions of digits II and IV 55–77°; divarication of axes of the impressions of digits II and III (17–56°) and that for digits III and IV (21–46°) are variable; the impression of digit II is typically distally the most acuminate of the digital impressions; digital impressions have a single pad impression, with the formula of 1/II, 1/III, 1/IV; on well-preserved tracks, the impression of digits II and III form distinct and separate impressions, whereas the proximal end of

the impression of digit IV is continuous with the single, large metatarsodigital pad impression; the proximal margin of the metatarsodigital pad impression is generally rounded, although it may be bilobed on the proximolateral margin; hallucal impression absent on all tracks.

**Description**—Track DP11-5 (Figs. 43A–C, 61C, 62D, S14) is well preserved and reveals clear detail of the morphology of the plantar surface of the trackmaker's pes. It occurs in association with multiple (at least four) partial tracks, potentially of the same ichnotaxon. It is a tridactyl, right? pedal track, of large size, wider than long (61.3 cm proximodistal length, 63 cm mediolateral width), with a track length to track width ratio of 1.0. The track is mesaxonic, with the impression of digit III extending the farthest distally (digital impression extension to track length ratio of 0.24). The digital impressions are proportionately large and oval, being subequal (approximately 53%, 47%, and 40% of the maximum track length for the impressions of digits II, III, and IV, respectively). The impression of digit III is roughly circular and is proximally in contact with the distal portion of the metatarsodigital pad impression. The impression of digit II is tear-shaped, with the apex positioned distally, and is separate from the metatarsodigital pad impression. The metatarsodigital pad impression has an irregular outline, with a proximolateral indentation.

Trackway DP11-18 (Fig. 43D, E) is the largest set of tracks that we can confidently assign to *Wal. hunteri*, comprising at least

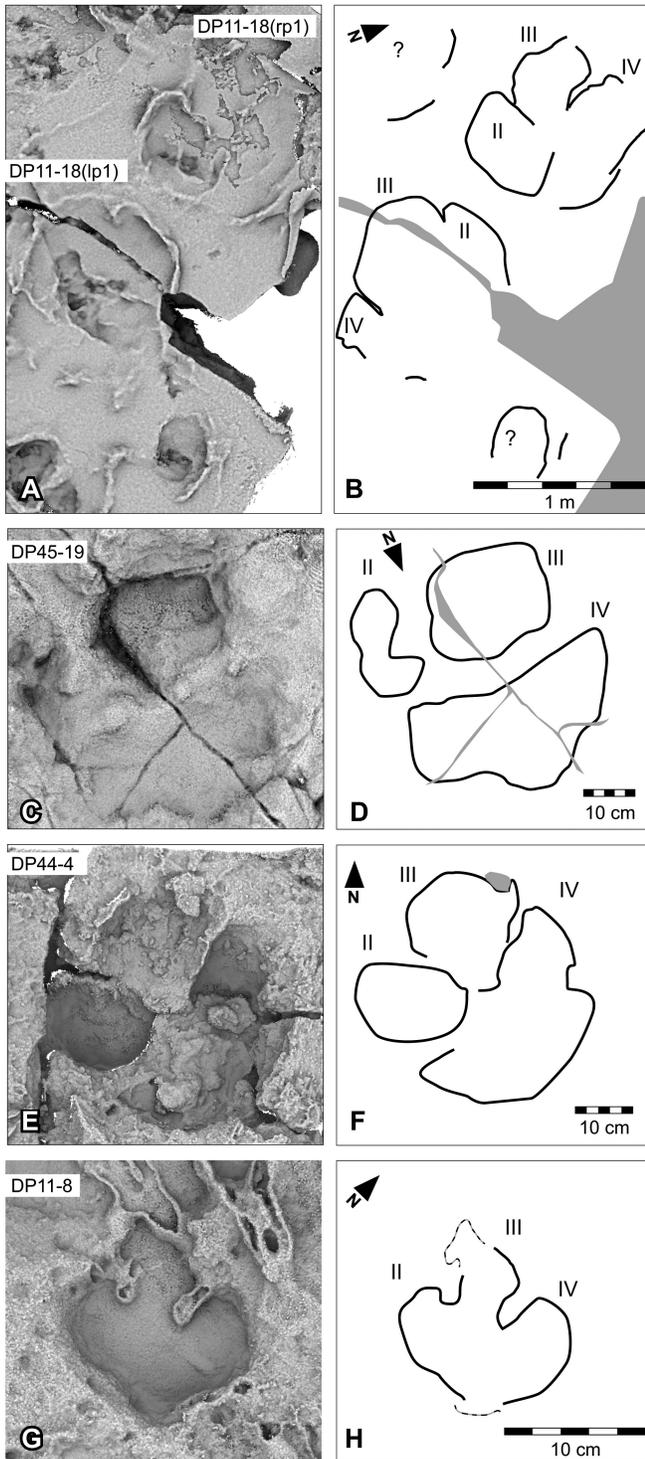


FIGURE 43. *Walmadanyichnus hunteri*, ichnogen. et ichnosp. nov., from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Trackway of pedal impressions, UQL-DP11-18, preserved in situ as **A**, ambient occlusion image and **B**, schematic interpretation. Pedal impression, UQL-DP45-19, preserved in situ as **C**, ambient occlusion image and **D**, schematic interpretation. Pedal impression, UQL-DP45-4, preserved in situ as **E**, ambient occlusion image and **F**, schematic interpretation. Pedal impression, UQL-DP11-8, preserved in situ as **G**, ambient occlusion image and **H**, schematic interpretation.

one left and one right pedal impression, and potentially a third imprint. These occur in association with other tracks, some of which may pertain to the same ichnotaxon, whereas others differ morphologically. The first track in the sequence, DP11-18(lp1), is circular, has the side and distal margins moderately well preserved, and measures 81 cm in mediolateral width. The following track, DP11-18(rp1), is well preserved and shares the circular overall track outline. The impression of digit III is rounded, with the proximal margin continuous with the metatarsodigital pad impression and part of the impression of digit II, whereas the impression of digit IV is continuous with the metatarsodigital pad impression. The track has a proximodistal length of 80 cm and a mediolateral width of 75 cm (the track length to track width ratio is 1.1); it is mesaxonic, with the impression of digit III extending beyond the other digital impressions (digital impression extension to total track length ratio 0.20). The broad digital impressions have a mediolateral width that ranges from 32% to 37% of the maximum track length. The pace length between these two tracks is 101 cm, and another potential *Wal. hunteri* impression occurs craniomedial to DP11-18(rp1), suggesting a pace and stride measurements of 80 and 152 cm, respectively. The principal axis of these tracks seems to be directed cranially, without significant inwards or outwards rotation relative to the trackway. The DP11-18 tracks represent the largest specimens of *Walmadanyichnus* and the largest ornithopod tracks in Australia thus far described.

Tracks DP11-19 and DP44-4 (Fig. 43C, D and G, H, respectively) are both isolated right pedal tracks of large size, with DP11-19 having a proximodistal length of 48.5 cm and a mediolateral width of 50.5 cm, and with DP44-4 at 69.9 and 60.8 cm for the same measurements. Similar to the holotype track DP11-5, these tracks have large, rounded impressions of digit III, bluntly pointed impressions of digit II, and an impression of digit IV that is unified with the metatarsodigital pad impression. Track DP11-19 is mesaxonic and is slightly wider than long (track length to track width ratio of 1.0), whereas DP44-4 is longer than wide (track length to track width ratio of 1.1). The impression of digit III is the longest on both tracks, with the impressions of digit II extending more distally than the impression of digit IV on DP11-19, whereas the opposite occurs on DP44-4. The digital impression extension to track length ratio is roughly equivalent for both tracks (0.28 for DP11-19 and 0.26 for DP44-4). These tracks have a broad central impression of digit III (width of 49% and 39% of the maximum track length for DP11-19 and DP44-4, respectively), with the width of the digit II and IV impressions being roughly one-quarter of the maximum track length (although the width of the impression of digit IV of DP44-4 is difficult to determine).

Track DP11-8 (Fig. 43G, H) is an isolated small track that represents the smallest example so far discovered that can be assigned to *Walmadanyichnus*. The track is a right pedal impression, longer than wide (12.9 cm proximodistal length, 12.1 cm mediolateral width) with a track length to track width ratio of 1.1. The digital impressions are rounded, with the impression of digit III being roughly circular in shape. The medial portions of the impressions of digit II and IV are continuous with the rounded metatarsodigital pad impression (the impression of digit II to a lesser degree). An indentation occurs proximal to the impression of digit II. The digital impressions are broad, with impressions of digits II, III, and IV having widths that are approximately 25%, 40%, and 28% of the maximum track length, respectively, and a digital impression extension to track length ratio of 0.27. The divarication of the axes of the impressions of digits II and III ( $45^\circ$ ) is greater than the divarication of axes of the impressions of digits III and IV ( $35^\circ$ ). Features of this track are consistent with an assignment to *Wal. hunteri*. The preservation of this track may be credited to the track surface being

more resilient to erosion. However, the areas surrounding this track show partial erosion through the resilient layer and may account, in part, for the track being found in isolation.

**Remarks**—Tracks assigned to *Walmadanyichnus hunteri* are some of the most distinctive dinosaur ichnites encountered in the Yanijarri–Lurujarri section of the Dampier Peninsula. Many of the tracks are particularly noteworthy because of their large size. Some of the largest (e.g., DP11-18; Fig. 43A, B) exceed the size of many of the area's sauropod tracks, with a maximum proximodistal length of 80 cm and a mediolateral width of 81 cm. Indeed, the largest tracks that can be confidently assigned to *Wal. hunteri* have a greater proximodistal length than any other non-sauropod dinosaurian tracks in the Broome Sandstone, with the exception of DP9-12 (cf. *G. roeorum*; Fig. 48C, D). *Walmadanyichnus* could also potentially include some of the area's smallest pedal tracks, with DP11-8 (Fig. 43G, H; maximum proximodistal length 12.9 cm) belonging to what is very likely a juvenile individual of the *Wal. hunteri* trackmaker.

The trackway DP11-18, which comprises two, and potentially three, *Wal. hunteri* tracks, provides measurements suggestive of a walking trackmaker. Based on speed calculations from track length measurements (Alexander, 1976), the DP11-18 trackmaker was very large (approximately 3.2 m tall at the hip) and was traveling at approximately 1.45 km/h.

Of the other ornithopod tracks from the Broome Sandstone, *Wal. hunteri* is most similar to *Wintonopus middletonae*. Both track types have distally rounded digital impressions, a singular digital pad impression for each digital impression (observed in well-preserved tracks), and a large maximum digital impression width to track length ratio (up to 49% and 45% in *Wal. hunteri* and *Win. middletonae*, respectively). *Walmadanyichnus* can be distinguished from both ichnospecies of *Wintonopus* on account of the circular overall morphology, the presence of a metatarsodigital pad impression, and generally larger absolute size, and from *Win. middletonae* on account of the more circular, rather than oval, digital pad impressions.

*Walmadanyichnus hunteri* shares several morphological features with other large tridactyl ornithopod ichnogenera, in particular *Caririchnium* (Leonardi, 1984; Lockley, 1987; Lee, 1997; Huh et al., 2003; Lockley et al., 2003; Matsukawa et al., 2005; Xing et al., 2007, 2012), *Hadrosauropodus* (Gierlinski, 2008; Xing et al., 2009b; Fanti et al., 2013), and *Iguanodontipus* (Sarjeant et al., 1998; Meyer and Thüring, 2003b; Diedrich, 2004). These ichnotaxa have pedal pad impressions that are arranged in a quadripartite manner (i.e., one metatarsodigital pad and three digital pad impressions). Overall, the digital pad impressions of *Iguanodontipus*, *Caririchnium*, and *Hadrosauropodus* are similar to those of *Wal. hunteri* in being relatively short and broad, with a typically round to oval outline (Lockley, 1987; Lockley et al., 2003), although some tracks may show proportionately elongate digital impressions that are sometimes pointed (see Lee, 1997; Sarjeant et al., 1998). *Caririchnium* also typically has a bilobed proximal track margin (but not always, see Leonardi, 1984;

Bakker, 1996; Gierlinski and Sabath, 2008), whereas in *Iguanodontipus* (Sarjeant et al., 1998; Meyer and Thüring, 2003b; Diedrich, 2004), *Hadrosauropodus* (Lockley et al., 2003), and *Walmadanyichnus* this feature is more variable. Well-preserved *Iguanodontipus*, *Caririchnium*, and *Hadrosauropodus* trackways also often include manual impressions (Leonardi, 1984; Currie et al., 1991; Lockley et al., 2003; Xing et al., 2007), but this is not always the case (Heckert and Lucas, 1998; Zhang et al., 2006). No clear manual tracks have been found in association with any of the pedal tracks that we have assigned to *Wal. hunteri*. Where *Iguanodontipus*, *Caririchnium*, and *Hadrosauropodus* have all the digital impressions separated from the metatarsodigital pad impression, *Walmadanyichnus* differs on account of the impression digit IV being unified with the metatarsodigital pad impressions. Multiple Broome Sandstone specimens share this trait, making us consider it likely to be an accurate reflection of the pedal anatomy of the trackmaker rather than having arisen as consequence of preservation. Consequently, this feature means that *Wal. hunteri* can be distinguished from *Caririchnium* and *Hadrosauropodus*.

*Walmadanyichnus hunteri* shares several features with the *Hadrosauropodus nanxiongensis* specimen NDM.F2, a track assigned to and thought to come from the Upper Cretaceous Zhutian Formation of Shaoguan, Guangdong Province, China (Xing et al., 2009b; fig. 4B, pl. I). These similarities relate to their overall circular track morphology, the degree of mesaxony, and the proportionately broad and rounded digital impressions. The impression of digit IV also appears unified with the metatarsodigital pad impression. However, *H. nanxiongensis* is highly morphologically variable, and other specimens (including the holotype) bear no close resemblance to *Wal. hunteri*, suggesting that some of the features seen on NDM.F2 may be the result of preservational differences rather than being reflective of a morphology that is similar to the latter ichnotaxon. On the basis of these observations, we therefore regard *Wal. hunteri* to be distinct from *H. nanxiongensis*.

Some aspects of *Wal. hunteri* are reminiscent of tracks assigned to *Ornithopodichnus* from the Lower Cretaceous of the South Korean Peninsula (Kim et al., 2009; Lockley et al., 2012). The overall rounded track morphology with circular digital impressions of tracks assigned to *Ornithopodichnus* is similar to *Wal. hunteri*, as is the total track length to track width ratio of 0.94 (Kim et al., 2009) or less (Lockley et al., 2012). However, diagnostic features of *Ornithopodichnus* include digital impressions that are shallowly separated only in the distal part, a condition distinct from the digital impression separation (particularly for the impressions of digit III and IV) observed in *Wal. hunteri*.

The general outline of some blunt-toed tracks from Cal Orcko, Bolivia, as figured by Lockley et al. (2002a; fig. 6A) also resembles *Wal. hunteri* tracks. However, these illustrations lack sufficient detail, and the tracks lack adequate description, making meaningful comparisons difficult.

TABLE 13. Measurements of tracks assigned to *Walmadanyichnus hunteri*, ichnogen. et ichnosp. nov., from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	II <sup>^</sup> III	III <sup>^</sup> IV	Total <sup>^</sup>	bdl II (II/L)	bdl III (III/L)	bdl IV (IV/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)	Pace (cm)	Stride (cm)
11-5	61.3	63	1.0	14.7 (0.24)	23	46	69	32.4 (0.53)	29.1 (0.47)	32.4 (0.40)	20.4 (0.33)	22.0 (0.34)	18.4 (0.3)	—	—
11-18(lp1)	—	81	—	—	—	—	—	—	—	—	—	—	—	101	152
11-18(rp1)	80	75	1.1	15.6 (0.20)	26	38	64	48.6 (0.61)	27.1 (0.34)	48.6 (0.61)	29.7 (0.37)	33 (0.32)	27.3 (0.34)	80	—
11-18(lp2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
45-19	48.5	50.5	1.0	13.5 (0.28)	17	38	55	21.9 (0.45)	23.3 (0.48)	21.9 (0.45)	10.5 (0.22)	24 (0.49)	12.5 (0.26)	—	—
45-4	69.6	60.8	1.1	18.1 (0.26)	56	21	77	18.3 (0.26)	34.3 (0.49)	18.3 (0.39)	18.3 (0.26)	26.9 (0.39)	17.3 (0.25)	—	—
11-8	12.9	12.1	1.1	3.5 (0.27)	45	35	80	4.4 (0.34)	5.1 (0.40)	4.4 (0.35)	3.2 (0.25)	5.1 (0.40)	3.6 (0.28)	—	—

bdl = basal digital impression length; bdw = basal digital impression width; De = digital impression extension; II = impression of digital II; III = impression of digit III; IV = impression of digit IV; L = track length; W = track width. <sup>^</sup> denotes angle between respective digit impressions.

TABLE 14. Measurements of tracks assigned to *Amblydactylus* cf. *A. kortmeyeri*, from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	II <sup>^</sup> III	III <sup>^</sup> IV	Total <sup>^</sup>	bdl II (II/L)	bdl III (III/L)	bdl IV (IV/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)
9-3	44.6	44.9	1	15.2 (0.34)	46	34	80	14.1 (0.32)	17.4 (0.39)	12 (0.27)	16 (0.36)	21 (0.47)	13 (0.29)

bdl = basal digital impression length; bdw = basal digital impression width; De = digital impression extension; II = impression of digit II; III = impression of digit III; IV = impression of digit IV; L = track length; W = track width. <sup>^</sup> denotes angle between respective digital impressions.

The unification of the impression of digit IV with the metatarsodigital pad impression is a striking diagnostic feature of *Wal. hunteri*. This may in part be functionally analogous to the more proximally positioned proximal track margin of the impression of digit IV of *Win. latomorum*, with the presumption of some degree of morphological similarity in the pedal skeleton and associated soft tissue of their respective trackmakers, and may have locomotor and evolutionary significance (Romilio et al., 2014).

Tracks that can be unambiguously assigned to *Wal. hunteri* are common in the study area, occurring at multiple localities. At present, we are not aware of this type of track occurring in other parts of the Dampier Peninsula. At least within the paleoenvironment associated with the Yanijarri–Lurujarri section of the Dampier Peninsula (see Paleoenvironmental Interpretation), this suggests that the *Wal. hunteri* trackmaker was a common component of the Broome Sandstone’s dinosaurian fauna. Additionally, the large size of these tracks may make them easier to find relative to other dinosaur ichnites, more likely to be preserved and less likely to be lost to erosion.

#### AMBLYDACTYLUS CF. *A. KORTMEYERI* (Figs. 44, 61D, 62E, S15; Table 14)

**Referred Material**—UQL-DP9-3, the natural mold of a possible right pes (Figs. 44, 61D, 62E, S16). (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality and Horizon**—The referred specimen is preserved in situ at DP9, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—Track DP9-3 is a large right pedal impression (length 44.6 cm, width 44.9 cm; Fig. 44A–C). It is tridactyl and mesaxonic (digital impression extension to track length ratio 0.34) and as long as wide, with a maximum length to maximum width ratio of 1.0. The impression for digit III is triangular in outline, whereas digital impressions II and IV are rounded, with the widest position for each at the hypex (the approximate maximum digital impression width to track length ratio of 0.36, 0.47, and 0.29 for digital impressions II, III, and IV, respectively). The central digital impression (III) is the longest, with a basal digital impression length 39% of the total track length. The distal tip of the impression of digit IV is positioned farther distally than that of II. The axes of the impressions of digits III and IV intersect distal to the intersection of the axes of the impressions of digits II and III, and the total divarication angle between the axes of the impressions of digits II and IV is 80°, with the divarication of axes of the impressions of digits III and IV (34°) greater than the divarication of axes of impressions of digits II and III (46°). The track outline is very gently concave proximomedially and convex proximolaterally. The proximal margin of the track is convex. The digital pad impressions are proximally unified, and there is no clear distinction of the metatarsodigital impression. Ungual and hallucal impressions are absent.

**Remarks**—Among other dinosaurian tracks in the study area, DP9-3 is most similar to those assigned to *Wintonopus latomorum*, particularly those of the trackway DP5-1. *Wintonopus latomorum* tracks show considerable morphological variation, likely due to trackmaker movement, sediment rheology, and subsequent erosion. Tracks DP5-1 (l1 and r2) show a broad concavity of the proximal track margin that resembles that of DP9-3, albeit much smaller. In the absence of other tracks and trackway data, we are unable to assert the extent of erosive loss to this track margin. In light of this, some aspects of the morphology of DP9-3 are also reminiscent of *M. broomensis* (e.g., DP11-1; Fig. 20D, E), although DP9-3 has proportionately shorter digit impressions.

McCrea et al. (2012) referred all Broome Sandstone ornithopod tracks to cf. *Amblydactylus*. These authors provided a stylized outline of DP9-3 without comment (McCrea et al., 2012:fig. 28C, ‘P001’) other than referring to the track in the caption as pertaining to an ornithopod. We are in agreement, and DP9-3 does share a number of features with *A. kortmeyeri* (Currie and Sarjeant, 1979:figs. 3, 5a, b). The track outline is slightly wider than it is long (maximum track length to width ratio 0.99), which is consistent with *A. kortmeyeri* (Currie and Sarjeant, 1979) but different from that for the type tracks of *A. gethingi*, all of which are slightly longer than they are wide (see Sternberg, 1932:fig. 8, topotype track; Currie, 1983:fig. 1, holotype track PMA P78.11). The total divarication angle on DP9-3 (80°) is also within the range of *A. kortmeyeri* (70–80°; Currie and Sarjeant, 1979), but higher than that of *A. gethingi* (56°; Sternberg, 1932). Similar to most tracks assigned to *A. kortmeyeri*, the impression of digit IV on DP9-3 is broader and more rounded than the impressions of digits II and III, whereas in *A. gethingi* all the digit impressions taper to a point (Sternberg, 1932; Currie and Sarjeant, 1979). However, the absence of digital pad impressions on DP9-3 is more reminiscent of the condition associated with tracks assigned to *A. gethingi* than *A. kortmeyeri*, which typically have distinct digital pad impressions, particularly for digit II (e.g., PMA P76.11.11; Currie and Sarjeant, 1979:fig. 2b). We note that Currie (1983:fig. 1) illustrates digital pad outlines on PMA P78.11. Track DP9-3 can be distinguished from both *A. gethingi* and *A. kortmeyeri* on account of its more gently concave proximomedial outline. In light of these observations, DP9-3 is probably best placed in *Amblydactylus* cf. *A. kortmeyeri*. If correct (and following the reassignment of the Winton Formation large Lark Quarry tracks from *Amblydactylus* [Romilio and Salisbury, 2011] to cf. *Iguanodontipus* [Romilio et al., 2014]), then this may be the only track in Australia that is assignable to *Amblydactylus*.

Track DP9-3 can be distinguished from *Caririchnium* (Leonardi, 1984; Lockley, 1987; Lee, 1997; Huh et al., 2003; Lockley et al., 2003; Matsukawa et al., 2005; Xing et al., 2007, 2012; Díaz-Martínez et al., 2015) and *Hadrosauropodus* (Gierlinski, 2008; Xing et al., 2009b; Fanti et al., 2013; Díaz-Martínez et al., 2015) by virtue of it lacking separate pad impressions (i.e., one metatarsodigital pad and three digital impressions), having more distally tapered digital impressions, and lacking any associated manual tracks. Although we acknowledge that the lack of pad impressions in DP9-3 may relate to either the way the track was formed (i.e., a reflection of the substrate) or to subsequent erosion of the internal track surface, we consider differences in the

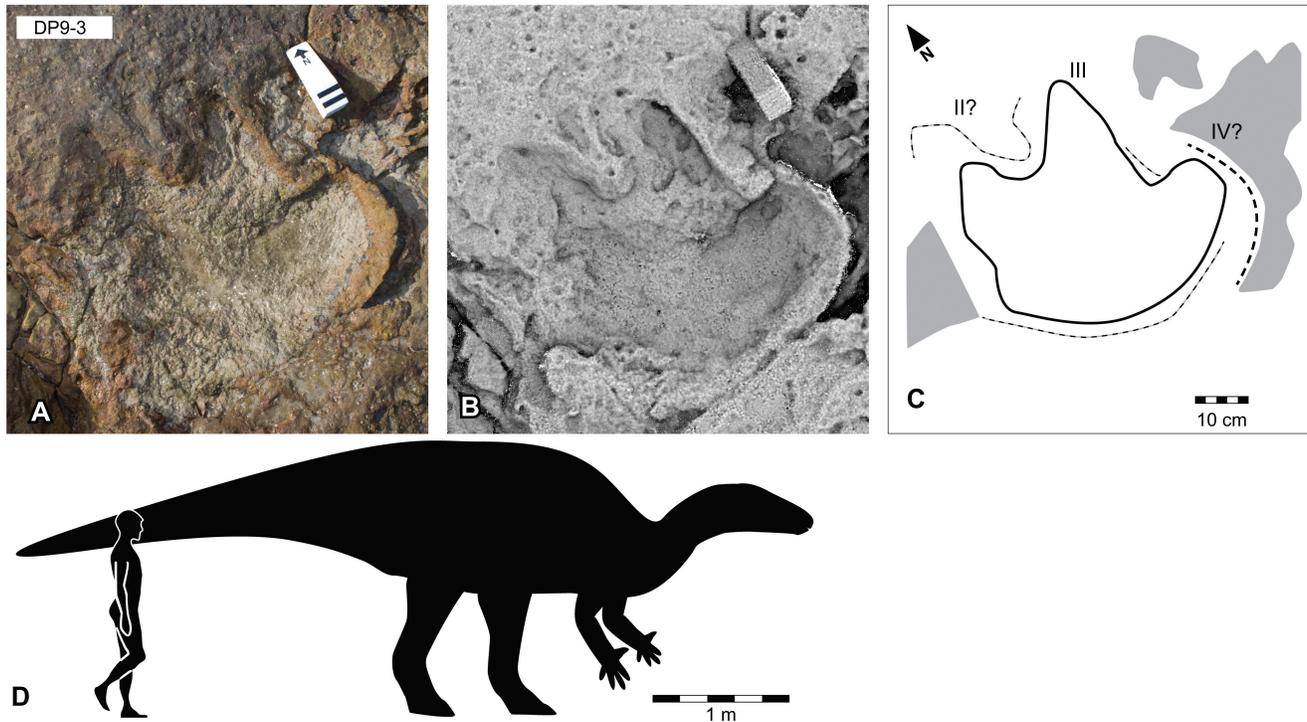


FIGURE 44. *Amblydactylus* cf. *A. kortmeyeri* from the Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia. Pedal impression, UQL-DP9-3, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, silhouettes of hypothetical *Amblydactylus* cf. *A. kortmeyeri* trackmaker based on UQL-DP9-3, compared with a human silhouette. See Figure 19 for legend.

overall track outline sufficient grounds on which to distinguish it from *Caririchnium* and *Hadrosauropodus*.

Track DP9-3 does bear some resemblance to *Iguanodontipus burreyi* (Sarjeant et al. 1998) with its triangular digital impressions. Photographs of tracks assigned to *I. burreyi* reveal a more consistent proximal track margin than those observed in DP9-3, and schematics provided by Sarjeant et al. (1998) appear too generalized for detailed comparison. *Iguanodontipus billsarjeanti* (Meyer and Thüring, 2003b; reassigned to *Caririchnium* by Díaz-Martínez et al., 2015) has more clearly defined digital and metatarsodigital pad impressions (one metatarsodigital pad and three digit impressions) and associated manual tracks, making them distinct from DP9-3.

With these observations in mind, we consider it best to assign DP9-3 to *Amblydactylus* cf. *A. kortmeyeri*. DP9-3 is currently the only track in the study area that can be assigned to *Amblydactylus* cf. *A. kortmeyeri*, and we are not aware of this type of track occurring elsewhere along the Dampier Peninsula coastline within the Broome Sandstone. This may indicate that this track's trackmaker had a preference for a particular habitat type, or, more likely, that it was a rare component of the area's dinosaurian fauna. Further documentation of ornithopod tracks within the Broome Sandstone is required to test these ideas.

#### QUADRUPEDAL ORNITHISCHIAN TRACKS

*GARBINA*, ichnogen. nov.

*GARBINA ROEORUM*, ichnosp. nov.

(Figs. 45–49, 63A, 64A, B, S16, S17; Table 15)

**Etymology**—*Garbina* [garbina] is a Nyulnyulan word for shield (see Fig. 3A) and is used in reference to the likely

thyreophoran ('shield bearer') nature of the trackmaker. The species name honors the Roe family, members of whom are the current Traditional Custodians of the Northern Tradition of the Song Cycle and its associated traditional law and culture, as well as the country in which the type locality occurs.

**Holotype**—WAM 12.1.19 and WAM 12.1.20, rigid polyurethane resin replicas of the natural mold of a left pedal track (UQL-DP14-1[1m1]) and a left manual track (UQL-DP14-1 [1m1]).

**Topotype material**—UQL-DP14-1, a single continuous trackway (at least 5 m long) comprising at least 17 consecutive tracks, all preserved in situ as natural molds (Figs. 46A–F, 63A, 64A, B, S16, S17).

**Type Locality, Horizon, and Age**—The topotype trackway is preserved in situ at UQL-DP14, in the intertidal zone of the Yanijjarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Referred Material**—Other tracks that can be assigned to *Garbina roeorum* include UQL-DP14-22 (Fig. 47A, B), the natural mold of a left manus, preserved in situ at UQL-DP14; UQL-DP14-23 (Fig. 47C, D), the natural mold of a left manus, preserved in situ at UQL-DP14; UQL-DP32-1 (Fig. 47E), the natural mold of a left manus, preserved in situ at UQL-DP32; UQL-DP1-6 (Fig. 47G), the natural mold of a left manus, preserved in situ at UQL-DP1; UQL-DP8-8 (Fig. 48A, B), the natural mold of a right MP couplet, preserved in situ at UQL-DP8; UQL-DP9-12 (Fig. 48C, D), the natural mold of a left pes, preserved in situ at UQL-DP9, preserved in close association with several other tracks of unknown ichnotaxonomic affinity; UQL-DP44-1 (Fig. 48G), the natural mold of a left pes, preserved in situ at

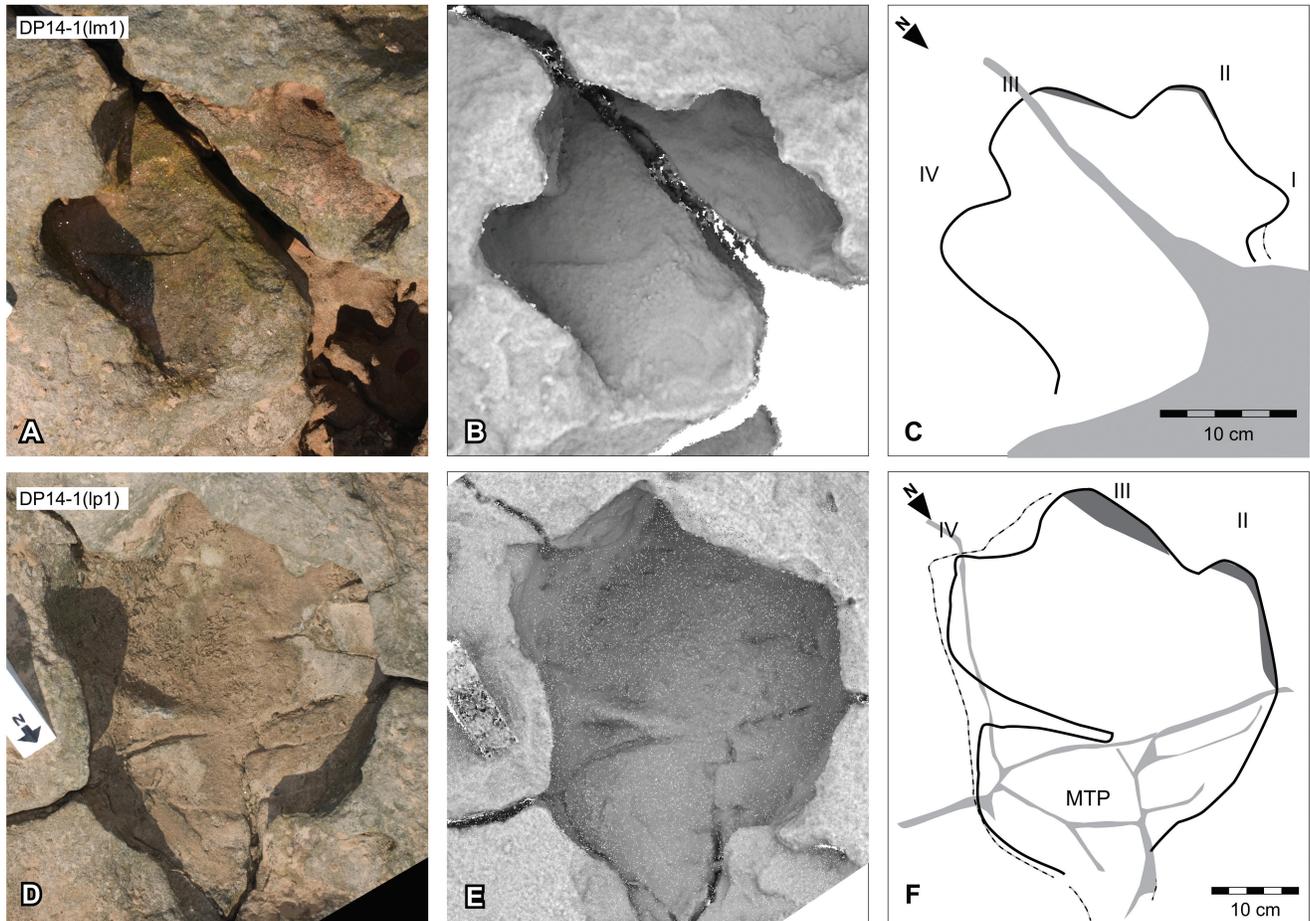


FIGURE 45. *Garbina roeorum*, ichnogen. et ichnosp. nov., from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Left manual impression, UQL-DP14-1(lm1), preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. Left pedal impression, UQL-DP14-1(lp1), preserved in situ as **D**, photograph; **E**, ambient occlusion image; and **F**, schematic interpretation. **Abbreviations:** MTP, metatarsal pad impression. See Figure 19 for legend.

UQL-DP44; UQL-DP14-34 (Fig. 49A, B), the natural mold of a ?right pes, preserved in situ at UQL-DP14; the pedal only trackway UQL-DP14-24 (Fig. 49A, B), consisting of two sequential natural molds of a right and a left pes, preserved in situ at UQL-DP14; the pedal only trackway UQL-DP14-18 (Figs. 33A–C, 50E, F, 51C, D), consisting of two, likely non-immediate, sequential natural molds of a right and a left pes, preserved in situ at UQL-DP14; UQL-DP14-15 (Fig. 49E, F), the natural mold of a ?left pes, preserved in situ at UQL-DP14, additionally represented by WAM 12.1.21, a rigid polyurethane resin replica. UQL-DP45-20 (Fig. 49G, H), the natural mold of a ?right pes, preserved in situ at UQL-DP45. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Diagnosis**—Manual tracks: medium- to large-sized (proximodistal length 11.9–21.4 cm, mediolateral width 17.2–25.4 cm), tetradactyl, paraxonic, typically wider than long, with an maximum proximodistal length to maximum mediolateral width ratio of 0.6–1.1; individual manual digital impressions proportionately short and broad (the maximum width of each digital impression 16–50% of the total track length); apex of each digital impression blunt to slightly tapered; impressions of digits II and III extend subequally (i.e., paraxonic) distally beyond the

impression of digits I and IV by about one-third the maximum track length; impression of digit I often positioned more distal relative to the impression of digit IV; impressions of digits II, III, and IV subequal in size, with the impression of digit I typically narrower; total divarication angle between the axes of the impressions of digits I and IV 137–170°; divarication of axes between digital impressions variable (12–60°, 39–78°, and 26–54° for I^II, II^III, and III^IV, respectively); proximal track margin variable in shape; metacarpodigital pad impression may or may not be present; impressions of digital pads and unguals impressions absent; manual impressions occur craniolateral to pedal tracks, but placement can vary; manual impressions may be absent, only faintly impressed, or as deeply impressed as associated pedal impressions. Pedal tracks: medium- to very large-sized (length of unified digital-metatarsodigital portion of track 25.8–44 cm; total length of tracks that include a metatarsal pad impression 42–80 cm; width 32.5–70 cm), tridactyl, mesaxonic (toe extension to track length ratio 0.14–0.21), typically wider than long for the unified digital-metatarsodigital portion of the track, with a maximum proximodistal length to maximum mediolateral width ratio of 0.54–0.9, or longer than wide when the metatarsal pad is impressed with a maximum length to maximum width ratio of 1.1–1.7; individual digital impressions

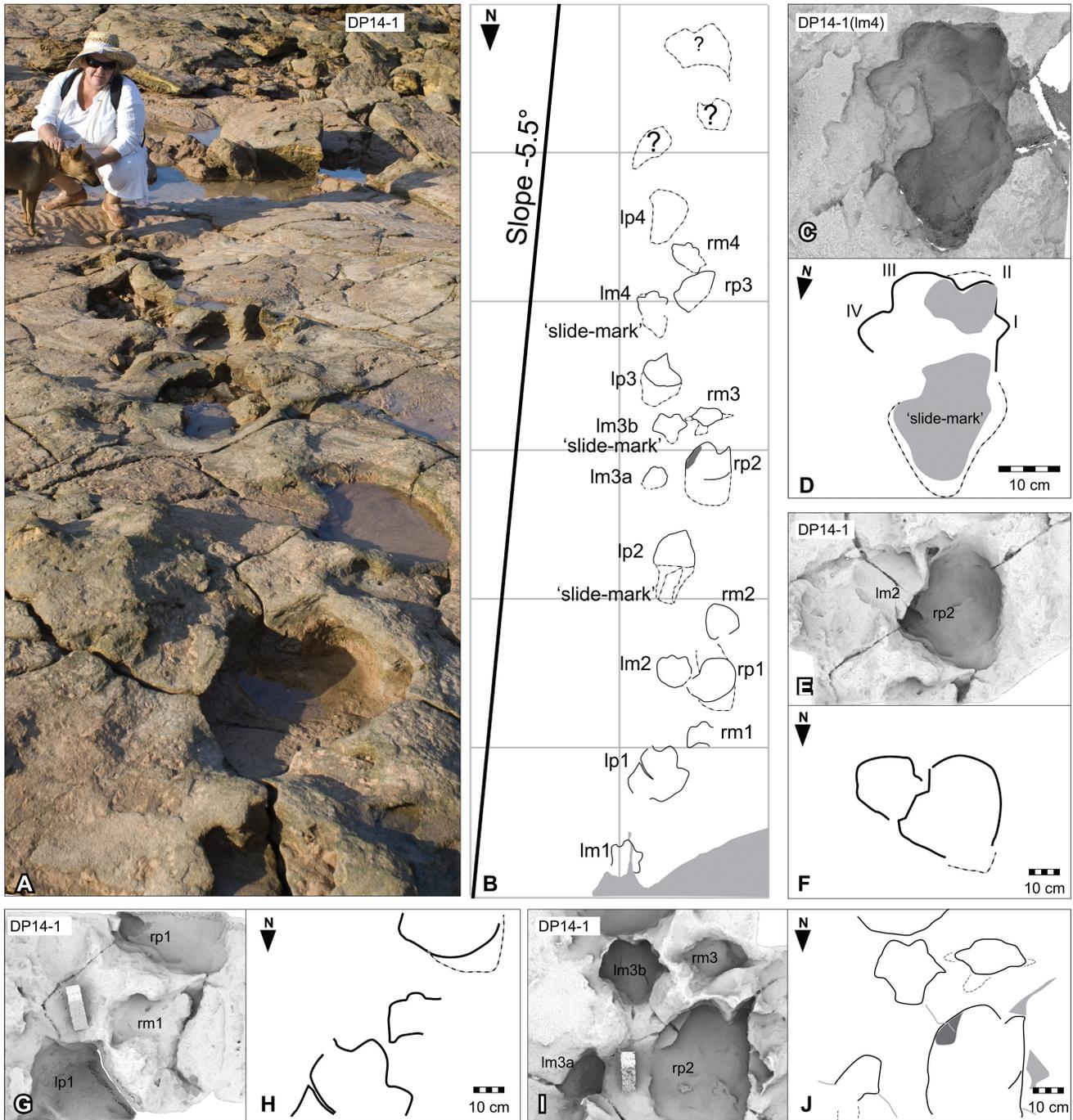


FIGURE 46. *Garbina roeorum*, ichnogen. et ichnosp. nov., from the Yanijarri-Lurujarri section of the Dampier Peninsula, Western Australia. Topotype trackway, UQL-DP14-1, preserved in situ as **A**, photograph (with Louise Middleton and her dog Missy) and **B**, schematic map. Left manual impression, UQL-DP14-1(lm4), preserved in situ as **C**, ambient occlusion image; and **D**, schematic interpretation. Coupled left manual and pedal impressions, UQL-DP14-1(lm2/rp2), preserved in situ as **E**, ambient occlusion image; and **F**, schematic interpretation. Track series UQL-DP14-1(lp1/rm1/rp1), preserved in situ as **G**, ambient occlusion image; and **H**, schematic interpretation. Track series UQL-DP14-1(lm3a,b/rp2/rm3/lp3), preserved in situ as **I**, ambient occlusion image; and **J**, schematic interpretation. See Figure 19 for legend.

proportionately short (the maximum length of each digital impression 17–51% of the total track length excluding the metatarsal pad impression) and broad (the maximum width of each digital impression 17–40% of the total track length excluding the metatarsal pad impression), and rounded distally;

impression of digit III extends distally beyond the impressions of digits II and IV by 14–21% of the total track length excluding the metatarsal pad impression; hypex of the impressions of digits III and IV usually broader than that of digits II and III, and more pronounced in bipedal pedal

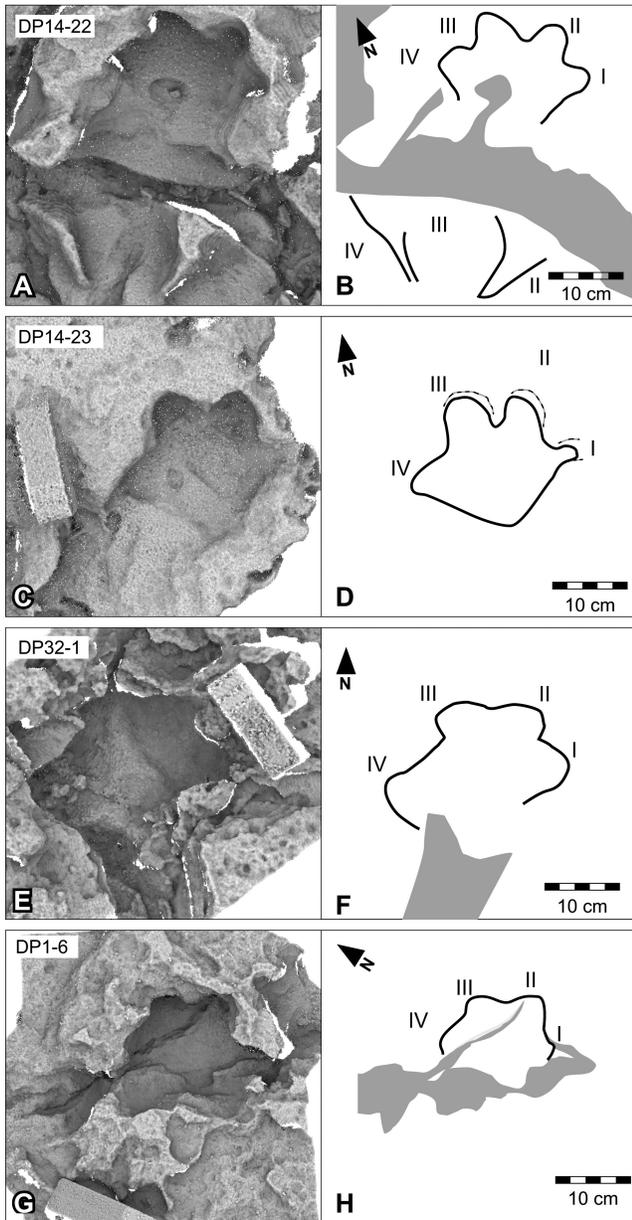


FIGURE 47. Other manual impressions of *Garbina roeorum*, ichnogen. et ichnosp. nov., from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Coupled left manual and pedal impressions, UQL-DP14-22, preserved in situ as **A**, ambient occlusion image; and **B**, schematic interpretation. Left manual track, UQL-DP14-23, preserved in situ as **C**, ambient occlusion image; and **D**, schematic interpretation. Left manual impressions, UQL-DP32-1, preserved in situ as **E**, ambient occlusion image; and **F**, schematic interpretation. Manus track UQL-DP1-6, preserved in situ as **G**, ambient occlusion image; and **H**, schematic interpretation. See Figure 19 for legend.

track; total divarication angle between the axes of impressions of digits II and IV  $57\text{--}93^\circ$ ; divarication of axes between impressions of digits II and III ( $27\text{--}46^\circ$ ) and III and IV ( $30\text{--}50^\circ$ ) similar; when present, the metatarsal pad impression is wide and irregularly shaped; when absent, the metatarsal pad impression is gently convex distally, and continuous with the proximal margin of the impression of the unified digital-

metatarsodigital pad; impressions of digital pads and unguals absent. Trackway (quadrupedal): manual track pace length approximately 2–6 times maximum manual track length; manual track stride length approximately 3–5 times maximum manual track length; manual tracks inwardly rotated, or directed cranially relative to the trackway orientation; metatarsal pad impression present in ‘quadrupedal’ tracks; pace angulation of pedal track is approximately  $133^\circ$  ( $129\text{--}142^\circ$ ); pedal pace length (excluding metatarsal pad) approximately 3 times pedal track length; pedal track stride length approximately 3–5 times the maximum pedal track length (excluding metatarsal pad). Trackway (bipedal): the metatarsal pad impression absent; pedal track pace length approximately two times the maximum pedal track length; pedal tracks inwardly rotated relative to trackway orientation; trackway is ‘narrow’-gauge, with the medial margin of the pedal tracks crossing the trackway midline.

**Description**—Trackway DP14-1 is at least 5 m long, with a maximum gauge width of less than 0.6 m (measured across the lateral track margins of lm3a and rp2), and occurs on a track surface that declines with a dip of  $5.5^\circ$  (Fig. 46A, B). The trackway is oriented south and is perpendicular to the declined surface. Possible tracks occur immediately before (north) and after (south) the trackway that may also form a part of it. Three possible tracks that precede the main section of trackway (within a distance of 1 m) are oriented to the southwest and occur on the same tracking surface. Approximately 50 m south of the trackway, a shallow north–south-trending depression that includes a MP couplet track (DP14-22; Fig. 47A, B) and several other poorly preserved manual and pedal tracks of similar size and morphology to the tracks preserved on DP14-1. Although it is possible that this set of tracks may represent a continuation of DP14-1, the lack of continuity between them makes this difficult to confirm.

Within the main DP14-1 trackway, the manual tracks are separate from the pedal tracks such that no overprinting occurs. The manual tracks vary in terms of their state of preservation and placement. Some manual tracks show a clear tetradactyl outline, whereas others have poor digital impression preservation. In addition, some manual tracks include elongated metacarpodigital pad impressions, a probable slide mark leading into the track, or both (Fig. 46B). The track sequence is typically a progression of a single manual track followed by a single pedal track, except for two consecutive left manual tracks (lm3A, B), where the trackmaker seems to have momentarily touched down with the manus as it turned into the slope (the shallowly impressed lm3a), before touching down again (the similarly shallowly impressed lm3b) as it slipped during the placement of the ipsilateral pes (lp2). The second of these two tracks, lm3b, has an elongated proximal track margin, whereas the subsequent left manual impression lm4 (Fig. 46I, J) has a more elongated proximal margin that may represent a slip trace, a metacarpal pad impression, or both. The pedal tracks also vary in preservation, ranging from well-preserved tridactyl impressions with a unified digital-metatarsodigital pad impression, to irregularly shaped, indistinct depressions. The more distinct pedal tracks show elongations to the proximal track margin, most likely representing part of a metatarsal pad impression, sliding or slipping traces, or both.

One of the best-preserved manual tracks in the DP14-1 topotype trackway is the first left one (lm1; Figs. 45A–C, 63A, 64A). This track is tetradactyl and paraxonic, with short, rounded, and broad digital impressions. The internal track surface is distinctly flat, lacking digital pad impressions, suggesting a continuous digital-metacarpodigital pad. A crack extends from the lateral margin of the impression of digit II. Coupled left manual and pedal impressions, through to the lateral margin of the impression of digit IV, and sections of the proximal track margin are absent due to erosion. The preserved external track outline (not

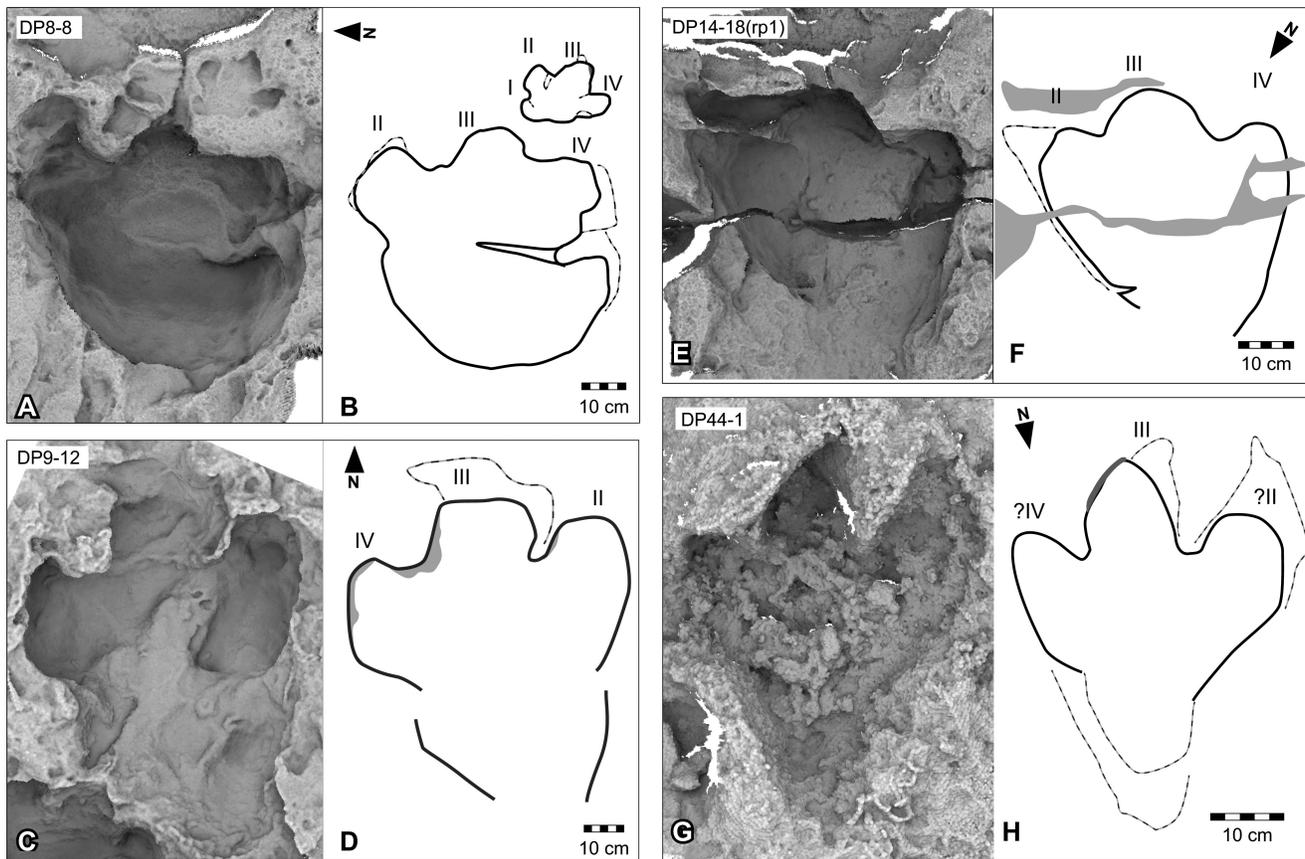


FIGURE 48. Other tracks of *Garbina roeorum*, ichnogen. et ichnosp. nov., and tracks referable to cf. *Garbina*, from the Yanijjarri–Lurujjarri section of the Dampier Peninsula, Western Australia. Coupled right manual and pedal impressions, UQL-DP8-8, preserved in situ as **A**, ambient occlusion image; and **B**, schematic interpretation. Possible left pedal impression, UQL-DP9-12 (cf. *Garbina*), preserved in situ as **C**, ambient occlusion image; and **D**, schematic interpretation. Right pedal impression, UQL-DP14-18(rp1), preserved in situ as **E**, ambient occlusion image; and **F**, schematic interpretation. Possible left pedal impression, UQL-DP44-1, preserved in situ as **G**, ambient occlusion image; and **H**, schematic interpretation. See Figure 19 for legend.

accounting for the missing proximal outline) is 21.4 cm wide and 18.5 cm long (track length to maximum width ratio approximately 0.86). The fourth left manual track (lm4) has well-preserved distal margins of the digital impressions II–IV (Fig. 46A–D), but the impression of digit I is eroded. The proximal margin of this track is elongated and may represent a slide trace, but the true track surface is lost and is eroded deep in this region and that of the impression of digit IV.

The best-preserved and most informative pedal track in the type trackway is the first left one (lp1; Figs. 45D–F, 63A, 64B). This track is tridactyl and mesaxonic, with a reduced impression of digit IV. Digital pad impressions are absent, with the internal track surface forming a single, unified digital-metatarsodigital pad impression that is partially separated from an irregularly shaped and proximally open metatarsal pad impression by a ridge that extends from the lateral side of the track to approximately half way across its width. The proximal margin of the metatarsal pad impression is asymmetric, being more deeply impressed caudolaterally. The track has a width of 35 cm and lengths of 51 and 35 cm (with and without the metatarsal pad impression, respectively).

The MP couplet DP8 (DP8-8; Fig. 48A, B) displays features that are consistent with the tracks of the DP14-1 trackway and also provides additional morphological information. The manual impression is similar in terms of its size and proportions (length 14.9 cm, width 21 cm) to the tetradactyl manual tracks in DP14-1 and is paraxonic, with the impressions of digits II and III being

the most cranially positioned digital impressions, and the impression of digit I being considerably smaller than the others (its total length being approximately 20% of track length). The internal surface of the DP8-8 manual and pedal tracks are essentially flat, with no indication of separate digital pad impressions. The pedal impression is large (proximodistal length 50.9 cm, mediolateral width 55.3 cm), tridactyl, with short (digital impression length approximately 15–19% of track length) and broad digital impressions (digital impression width approximately 28–33% of track length) that are cranially rounded. The pedal track has a low ridge that separates the proximal portion of the digital-metatarsodigital pad impression from the distal metatarsal pad impression. The proximal margin of the track is gently convex. The cranial portion of the track resembles bipedal *Garbina* tracks (Fig. 49), with the lateral digital impression (of digit IV) having a broad hypex and a craniolaterally directed digital axis; the digital impressions are broad and distally rounded, and the impression of the metatarsodigital pad is short and broad. The depth of this pedal track (approximately 22 cm) relative to the manual track (approximately 4 cm deep) may account for such similarities, indicating that the trackmaker was placing considerably more weight on the hind legs than the front.

Trackway DP14-22 is a MP couplet that may form part of the topotype trackway of *G. roeorum* (Fig. 47A, B). The manual track is a left with well-preserved short, rounded, and broad digital impressions. Although much of the proximal track margin

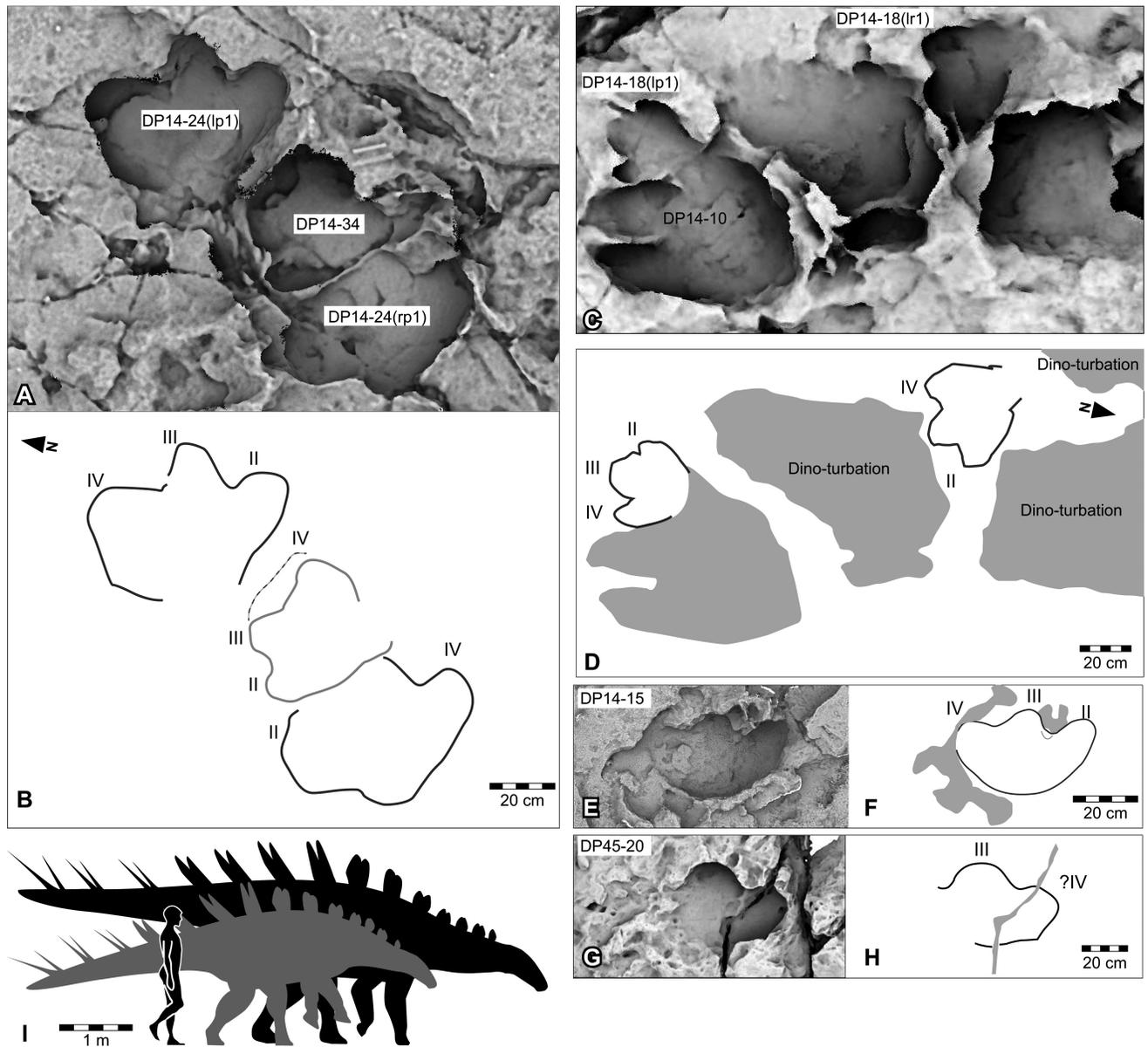


FIGURE 49. Tracks referable to *Garbina roeorum*, ichnogen. et ichnosp. nov., from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. The pedal impressions only trackways UQL-DP14-24 (black outlines) and UQL-DP14-34 (gray outlines), preserved in situ as **A**, ambient occlusion image (underside) and **B**, schematic interpretation. The pedal impression only trackway UQL-DP14-18 (black outlines), preserved in situ as **C**, ambient occlusion image; and **D**, schematic interpretation. Pedal impression, UQL-DP14-15, preserved in situ as **E**, ambient occlusion image; and **F**, schematic interpretation. Possible right pedal impression, UQL-DP45-20, preserved in situ as **G**, ambient occlusion image; and **H**, schematic interpretation. **I**, silhouettes of hypothetical *Garbina* trackmaker based on UQL-DP14-1 (as a quadruped) and UQL-DP14-15 (as a biped), compared with a human silhouette. See Figure 19 for legend.

has eroded, we estimate the track to be approximately 17 cm long and 20 cm wide. The caudally associated pedal impression is poorly preserved, with only some cranial portions of the broad and rounded digital impressions discernible. The hypices of the pedal digital impressions appear narrower relative to other *G. roeorum* tracks. This may be due to erosion, or if it does represent a true track feature, it may indicate that the toes of the trackmaker were flexed when the track was made. Alternatively, the pedal track may have been overprinted by a different trackmaker.

Manual impression DP14-23 (Fig. 47C, D) has short (proximodistal length 18 cm, mediolateral width 21.9 cm), blunt digital

impressions and lacks evidence of internal track features. The impressions of digits II and III on this track are subequal and of paraxonic symmetry, whereas those of digits I and IV are directed medially and laterally, respectively, with the impression of digit I being smaller than those of the other digits. The mid-portion of the proximal margin is bluntly pointed (DP14-23). Another manual track that can be assigned to *G. roeorum* is DP32-1 (Fig. 47E, F). Although all of the digital impressions are subequal in size, we tentatively interpret this as a left manual track based on the impression of digit I being positioned more cranially than the impression of digit IV. This track has been

TABLE 15. Measurements of tracks assigned to *Garbina roeorum*, ichnogen. et ichnosp. nov., and cf. *Garbina*, from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	L (excl. MTP)	W (cm)	L/W (excl. MTP)	De (De/L)	I^II	II^III	III^IV	Total ^	Pace (cm)	Stride (cm)
14-1(lm1)	18.5	21.4	0.86	—	60	58	26	137	—	—
14-1(rm1)	14.6	17.4	0.84	—	83	55	—	—	91	—
14-1(lm2)	24	22.5	1.07	—	—	—	—	—	47	—
14-1(rm2)	23	23	1.00	—	—	—	—	—	47	126
14-1(lm3a)	22	24	0.92	—	—	—	—	—	106	76
14-1(lm3b)	21.4	23.9	0.90	—	70	57	49	150	35	125
14-1(rm3)	12.5	21	0.60	—	—	—	—	—	26	135
14-1(lm4)	16	26	0.60	—	83	43	44	127	72	82
14-1(rm4)	20	25	0.80	—	—	—	—	—	39	108
14-1(lp1)	51 (31.5)	35	1.5 (0.9)	7.5 (0.15, 0.24)	—	34	42	76	—	—
14-1(rp1)	44	37	1.2	—	—	—	—	—	73	—
14-1(lp2)	60 (32)	35	1.7 (0.9)	—	—	—	—	—	86	143
14-1(rp2)	42 (25.4)	32.5	1.3 (0.8)	—	—	—	35	—	60	137
14-1(lp3)	41	34	1.30	—	—	34	44	90	64	109
14-1(rp3)	30	35	0.90	—	—	—	—	—	58	110
14-1(lp4)	—	—	—	—	—	—	—	—	50	101
14-22(m)	17	22	0.77	—	50	78	54	150	—	—
14-22(p)	—	39	—	—	—	36	45	81	—	—
14-23(m)	18	21.9	0.82	—	60	56	50	170	—	—
1-6(m)	11.9	17.2	0.69	—	52	55	52	155	—	—
32-1(m)	16.3	25.4	0.64	—	64	84	54	166	—	—
8-8(rm)	14.9	20.9	0.71	—	12	39	44	88	—	—
8-8(rp)	50.9 (25.8)	55.3	0.9 (0.47)	7.1 (0.13)	—	50	43	93	—	—
14-18(rp1)	38.7	45.0	0.86	7.5 (0.19)	—	30	27	57	—	—
14-18(lp1)	35.5	40.3	0.9	9.7 (0.27)	—	32	40	72	—	—
44-1	36.8	35.6	1.0	6.7 (0.18)	—	31	40	67	—	—
45-20	35.3	—	—	—	—	—	40	—	—	—
9-12(lp)	80 (43)	70	1.14 (0.54)	6 (0.14)	—	33	33	66	—	—
14-15(lp)	25.8	41.7	0.6	3.6 (0.14)	—	43	38	81	—	—
14-34(rp)	41.9	41.9	1.0	8.9 (0.21)	—	24	55	79	—	—
14-24(rp)	41.1	49.4	0.83	—	—	—	—	—	85	—
14-24(lp)	44.6	61.5	0.73	9.8 (0.21)	—	46	46	92	—	—

Track (UQL-DP)	bdl I (I/L)	bdl II (II/L)	bdl III (III/L)	bdl IV (IV/L)	bdw I (I/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)
14-1(lm1)	3.4 (0.18)	6.2 (0.34)	8.7 (0.47)	6.8 (0.37)	2.9 (0.16)	3.1 (0.17)	5.1 (0.28)	3.9 (0.21)
14-1(rm1)	3.3	3.2	4.3	—	4.4	5.4	7.2	—
14-1(lm2)	—	—	—	—	—	—	—	—
14-1(rm2)	—	—	—	—	—	—	—	—
14-1(lm3a)	—	—	—	—	—	—	—	—
14-1(lm3b)	3.8 (0.18)	4.6 (0.21)	3.6 (0.17)	2.1 (0.1)	4.1 (0.19)	8.2 (0.38)	10.3 (0.48)	7.8 (0.36)
14-1(rm3)	—	—	—	—	—	—	—	—
14-1(lm4)	4.0 (0.25)	2.1 (0.13)	4.0 (0.25)	4.0 (0.25)	2.9 (0.18)	5.6 (0.35)	11.1 (0.63)	7.1 (0.44)
14-1(rm4)	—	—	—	—	—	—	—	—
14-1(lp1)	5.2 (0.1, 0.17)	13.5 (0.26, 0.43)	16 (0.31, 0.51)	—	—	5.5 (0.11, 0.17)	13 (0.25, 0.41)	9.5 (0.19, 0.3)
14-1(rp1)	—	—	—	—	—	—	—	—
14-1(lp2)	—	—	—	—	—	—	—	—
14-1(rp2)	—	—	5.5 (0.13, 0.22)	—	—	—	8.8 (0.21, 0.35)	5.7 (0.14, 0.22)
14-1(lp3)	—	—	—	—	—	—	—	—
14-1(rp3)	—	—	—	—	—	—	—	—
14-1(lp4)	—	—	—	—	—	—	—	—
14-22(m)	3.6 (0.21)	4 (0.24)	5.9 (0.35)	4.4 (0.26)	6.7 (0.39)	8 (0.47)	6.5 (0.38)	4.4 (0.26)
14-22(p)	—	—	—	—	—	16.6	10.3	25
14-23(m)	3.7 (0.21)	4.5 (0.25)	4.9 (0.27)	4.6 (0.26)	3.2 (0.18)	5 (0.28)	6.1 (0.34)	6 (0.33)
1-6(m)	2.4 (0.2)	1.4 (0.12)	2.3 (0.19)	3.2 (0.27)	4.5 (0.38)	5.1 (0.43)	5.6 (0.47)	5.2 (0.44)
32-1(m)	3.5 (0.21)	5 (0.31)	3.1 (0.19)	3.8 (0.23)	5.4 (0.33)	7.1 (0.44)	7.3 (0.45)	5.8 (0.36)
8-8(rm)	2.8 (0.19)	6 (0.40)	10.1 (0.68)	7 (0.47)	3.6 (0.24)	4.9 (0.33)	6.8 (0.46)	3.8 (0.26)
8-8(rp)	—	9.6 (0.19)	7.7 (0.15)	7.9 (0.16)	—	16.7 (0.33)	15.2 (0.30)	14.4 (0.28)
14-18(lrp1)	—	9.3 (0.24)	9.6 (0.25)	7.8 (0.20)	—	17.1 (0.44)	17.4 (0.45)	16.50 (0.43)
14-18(rp1)	—	7.4 (0.21)	15 (0.42)	12 (0.34)	—	10.3 (0.29)	16.5 (0.46)	12.2 (0.34)
44-1	—	6.2 (0.17)	11.8 (0.32)	9.9 (0.27)	—	8.6 (0.23)	11.1 (0.30)	12.8 (0.35)
45-20	—	—	9.2 (0.26)	10.5 (0.29)	—	—	29 (0.82)	19.5 (0.55)
9-12(lp)	—	8.2 (0.1, 0.19)	14.9 (0.19, 0.35)	20.2 (0.25, 0.47)	—	11.8 (0.15, 0.27)	21.9 (0.27, 0.51)	24.7 (0.31, 0.57)
14-15(lp)	—	10.30 (0.4)	6.90 (0.27)	5.90 (0.23)	—	11.90 (0.46)	10.6 (0.41)	10.8 (0.42)
14-34(rp)	—	8.9 (0.21)	8.9 (0.21)	8.4 (0.20)	—	11.0 (0.26)	12.3 (0.29)	15.0 (0.38)
14-24(rp)	—	—	—	13.1 (0.32)	—	—	—	17.9 (0.44)
14-24(lp)	—	14.4 (0.32)	11.90 (0.27)	13.25 (0.30)	—	17.85 (0.40)	14.4 (0.32)	20.7 (0.46)

bdl = basal digital impression length; bdw = digital impression digit width; De = digital impression extension; I = impression of digit I; II = impression of digit II; III = impression of digit III; IV = impression of digit IV; L = track length; MTP = metatarsal pad impression; W = track width. ^ denotes angle between respective digital impressions.

modified through erosion, lacking its proximal portion. The manual impression is proportionately wider than any of the *G. roeorum* tracks at DP14 (length 18 cm and width 21.9 cm).

Track DP9-12 (Fig. 48C, D) is a very large, natural mold of a left pes that is longer than wide (80 cm proximodistal length and 70 cm mediolateral width; track length to track width ratio of 1.1). The track preserves proportionately large digital-metatarsodigital and metatarsal pad impressions, which form 54% and 46%, respectively, of the total track length, with medial and lateral concavities located approximately halfway along the proximodistal length of the track, similar to the demarcation seen on the type pedal track (DP14-1[lp1]). The digital impressions are short and rounded and are separated by squared-off, open hypices, similar to DP8-8 (Fig. 48A, B). Compared with the latter track, the digital impressions on DP9-12 are more elongated. The overall distal track outline is weakly mesaxonic (the digital impression extension to track length for the digital-metatarsodigital pad portion of the track is 0.14; when the metatarsal pad impression is included, this ratio is 0.08). The impressions of digits II, III, and IV are proportionately broad, equating to approximately 27%, 51%, and 57%, respectively, of the length of the digital-metatarsodigital portion of the track. The total divarication angle is 66°, with the divarication of the axes of impressions of digits II and III (33°) the same as that for III and IV (33°), both of which fall within the range displayed by the pedal tracks in DP14-1. The lateral hypex is broader than the lateral surface. The proximal margin of the metatarsal pad impression is slightly asymmetrical, with a greater extension proximolaterally, and is consistent with other *G. roeorum* pedal tracks. However, given its large size relative to other *G. roeorum* pedal tracks, we provisionally place it in cf. *Garbina*.

Tracks DP14-18 (Figs. 33A–C, 49E, F, 50C, D) are tridactyl, natural molds of two pedal impressions, preserved in close association with a number of large sauropod and ornithopod tracks. Track DP14-18(rp1) is deep, wider than long (38.7 cm proximodistal length and 45.0 cm mediolateral width; track length to track width ratio of 0.86), and with weakly mesaxonic digital impressions (toe extension to track length ratio of 0.19). The gently tapered digital impressions are proportionately short and broad (maximum digital impression width to track length ratios of 0.47, 0.49, and 0.48, respectively, for the impressions of digits II, III, and IV). The total divarication angle between the axes of impressions of digits II and IV is 57°, with the divarication of the axes of impressions of digits II and III and digits III and IV being 27° and 30°, respectively. The digital and metatarsodigital pad impressions are unified. The proximal margin of the track grades gently into the surrounding track surface, and there is a low ridge extending into the internal track surface halfway along the left margin. The latter ridge is interpreted to represent a groove between the distal unified digital-metatarsodigital pad and a weakly impressed proximal metatarsal pad impression, concordant with the condition seen on the topotype pedal track DP14-1(lp1) (Fig. 45D–F). Track DP14-18(lp1) is a left pedal track that overprints the distolateral portion of the sauropod track DP14-10 (Figs. 33D–F, 49C, D). The track is medium-sized (track length 35.5 cm long, 40.3 cm wide), with a track length to track width ratio of 0.9, with broad digital impressions that acuminate distally. The distal tip of the impression of digit III extends beyond the impressions of digits II and IV by approximately one-quarter the total track length (the digit extension to track length ratio is 0.27), with a total divarication angle of 72°. The proximal margin of the track is open, a feature shared with DP14-18(rp1). The track rotations of DP14-18(rp1) and (lp1) are inwardly turned relative to the trackway midline, similar to that observed in the topotype trackway (Fig. 46B); however, the distance separating these ichnites (approximately 126 cm) greatly exceeds the pace measurements (and often stride lengths) of other tracks we assign to *G. roeorum* (see Table 16). This, and the track-bearing horizon being heavily dinoturbated (Fig. 49C), suggests that any intermediately laid tracks may have been lost due to overprinting by other trackmakers.

At least six other tracks at DP14 (-15, -35, -24[r], and -24[l]), DP44-1 and DP45-20 show features that are congruent with the digital-metatarsodigital portion of the pedal tracks in DP14-1 and DP8-8, but lack any clear indication of a metatarsal pad impression, nor are they associated with any obvious manual tracks. These tracks thus appear to show that the *G. roeorum* trackmaker could employ a bipedal stance and gait.

Track DP44-1 (Fig. 48G, H) is tridactyl, with short, broad digital impressions with widths between 23% and 35% of the maximum track length. The track is of large size (36.8 cm long, 35.6 cm wide) and slightly longer than wide. The digital impressions are rounded at the apex, although the distal margins of these have drag marks that are pointed. The metatarsal pad impression is elongated yet narrow, constituting approximately a third of the track width.

Trackway DP14-24 (Fig. 49A, B) comprises a right and a left pedal impression. Both are large, tridactyl natural molds, wider than long (respectively 41.1 and 44.6 cm proximodistal length and 49.5 and 61.5 cm mediolateral width), with respective track length to track width ratios of 0.8 and 0.7. The cranial portion of the right track is deformed by the medial margin of DP14-34. The left track is mesaxonic (digit extension to track length ratio 0.21), with well-rounded individual digital impressions that are proportionately short and broad (maximum digit impression width to track length ratios of 0.28, 0.34, and 0.44, for the impressions of digits II, III, and IV, respectively). The divarication between the axes of the impressions of digits II and III and that of digits III and IV are equal (46°), yet the hypex is much broader between III and IV than between II and III, similar to DP14-1(lp1) (Figs. 45D, F, 48A, B, G–H) and DP14-18 (Fig. 48E, F). Individual digital and metatarsodigital pad impressions are absent, and the proximal track margin is convex, with no clear indication of a separate metatarsal pad impression. Manual impressions are absent, suggesting that the trackmaker was bipedal.

Track DP14-34 (Fig. 49A, B) is associated with the trackway DP14-24. The relatively smaller width (maximum mediolateral width 41.9 cm) and the deformation this track causes to DP14-24 (r1) precludes it from being part of that trackway. Track DP14-34 resembles the digital-metatarsodigital portion of DP14-18 (lp1) (Fig. 48E, F) and DP14-15 (see below) in overall morphology (tridactyl, weakly mesaxonic, broad rounded digital impressions, broad hypex between the impressions of digits III and IV) and is nearly identical in width to the latter (the maximum mediolateral width difference is 0.2 cm). The proximal track margin of DP14-35 differs from DP14-15 in having what is likely an impression of the distal portion of the metatarsal pad that caudally elongates the track, resulting in an overall greater track length, as occurs in DP14-18 (Fig. 48E, F). Given the similar width and proximity of tracks DP14-35 and DP14-15, it is possible that they were made by the same trackmaker, but this cannot be confirmed.

Track DP14-15 (Fig. 49E, F) is a tridactyl and weakly mesaxonic (digital impression extension to track length ratio 0.14) natural mold of a possible left pes that lies approximately 5 m from DP14-24 and DP14-34 (Fig. 49A, B). The track is medium-sized in length (the maximum proximodistal length is 25.8 cm) but large-sized in width (the maximum mediolateral width is 41.7 cm), with a maximum length to maximum width ratio of 0.6. The individual digital impressions are rounded and are proportionately short and broad, with the impression of digit II being slightly wider than the impressions of digits III and IV (maximum digital impression width to track length ratios of 0.46, 0.41, and 0.42, respectively). The impression of digit IV is slightly longer than the others but extends cranially to approximately the same level as the impression of digit II relative to the principal track axis. The total divarication angle between the axes of the impressions of digits II and IV is 81°. The divarication of the

axes of the impressions of digits II and III ( $43^\circ$ ) is slightly smaller than that for digits III and IV ( $38^\circ$ ). Individual digital and metatarsodigital pad impressions are absent. The proximal track margin is convex, and there is no indication of a metatarsal pad impression.

Track DP45-20 (Fig. 49G, H) is a partial, possible right pedal track that preserves the impressions of digits III and IV and their proximolateral margin. The track is large (the maximum proximodistal length is 35.3 cm) and bears a strong resemblance to DP14-15 (Fig. 49E, F) as well as at the distal portion of DP8-8 (Fig. 48A, B). The individual digital impressions are rounded and are proportionately short and very broad in relation to the incompletely preserved proximal track margin (maximum width to track length ratios for the impressions of digits III and IV of 0.82 and 0.55, respectively). The total divarication angle between the axes of the impressions of digits III and IV is  $40^\circ$ , and, similar to track DP14-15, the preserved proximolateral track margin is curved, with no indication of a metatarsal pad impression.

**Remarks**—*Garbina roeorum* represents the first named quadrupedal ornithischian ichnotaxon from Australia. The combination of a tetradactyl manual track with a tridactyl pedal track seen in *G. roeorum* is consistent with tracks that are typically assigned to thyreophorans and, more specifically, stegosaurians (Whyte and Romano, 1994; Lockley and Hunt, 1998; Milàn and Chiappe, 2009; Belvedere and Mietto, 2010; Cobos et al., 2010; Mateus et al., 2011). Tracks considered to be representative of thyreophorans have been reported previously from the Broome Sandstone (Long, 1990, 1992a, 1998, 2002; Molnar, 1991; Thulborn et al., 1994, 1998; Rich and Vickers-Rich, 2003a; Scanlon, 2006; Rich, 2007; McCrea et al., 2012), but none has received detailed description. A single manual track, also thought to pertain to a thyreophoran, has been described from the Middle Jurassic (Bajocian–Bathonian) Walloon Coal Measures at Balgowan, Darling Downs, Queensland (Hill et al., 1966:30–31, replica QM F5701). Comparisons with these tracks and other potential thyreophoran tracks from the Broome Sandstone recorded during this study are discussed below, as are differences from and similarities to other purported thyreophoran tracks from around the world.

Among other dinosaurian tracks from the Broome Sandstone, *G. roeorum* manual tracks compare best with those assigned herein to Broome thyreophoran morphotype B (DP14-15; Fig. 54A–C). Both track types are similar in terms of their overall outline, being wider than they are long, with proportionately short, broad digital impressions. An obvious difference relates to the number of digital impressions associated with each track type: Broome thyreophoran morphotype B is pentadactyl, whereas *G. roeorum* is tetradactyl. It is conceivable that the *Garbina* trackmaker may have been pentadactyl but often only impressed four of these digits into the manual tracks. Unless thyreophoran morphotype B manual tracks are considered aberrant examples of *G. roeorum*, however, there is no other evidence to support this idea, and we consider the two track types to be distinct.

The manual tracks of *G. roeorum* are very similar to the possible stegosaurian track from the Middle Jurassic Walloon Coal Measures of Balgowan, initially described by Hill et al. (1966:30–31, pl. XV, fig. 5; also see Molnar, 1991:fig. 37E, replica QM F5701). Thulborn (1990) was in agreement with Hill et al.'s (1966) trackmaker identification of this track, whereas others have suggested more inclusive affinities, such as a thyreophoran (Scanlon, 2006) or potentially “any other contemporaneous quadrupedal dinosaur (ankylosaur, sauropod, scelidosaur)” (Molnar, 1991:660). This single manual track is tetradactyl with short, broad digital impressions. Similar to the manual tracks of *G. roeorum*, the digital impressions are arranged in a loose arc, with the impression of what is likely digit I being the smallest, whereas all the other digit impressions are roughly equivalent in

size. The track is proportionately slightly wider (a maximum proximodistal length of 21.5 cm long and a maximum mediolateral width of 26.6 cm) than manual tracks assigned to *G. roeorum*, but this is the only major difference. The main difference is that the impression of digit IV is more cranially positioned when compared with the impression of digit I (relative to the paraxonic axis of the track) rather than the impression of digit I lying more cranially to the digit IV, as is observed in *G. roeorum*. Our own 3D evaluation (unpublished data) of the Walloon Coal Measures track indicates that the proximal margin is continuous (albeit faintly) with the impressions of digits I and IV, forming a caudally directed triangular apex ( $\sim 90^\circ$ ) in line with the impression of digit II, making it similar to DP14-23 (Fig. 47C, D). An independent and faint digit-like impression lies caudal to the impression of digit IV. Although it appears to be separate from the main track, in the absence of further specimens, it hard to determine if the latter impression represents part of the same or a different track, an erosional feature, or an artifact of the casting process. For the time being, we do not consider this impression to be extraneous to the tetradactyl manual track. As such, we regard the Walloon Coal Measures track to be assignable to cf. *G. roeorum*. This assignment may strengthen the likelihood that the Walloon Coal Measures track was made by a stegosaurian (see below for further discussion on the stegosaurian affinities of *Garbina*).

*Garbina roeorum* is distinct from thyreophoran tracks identified as having been made by ankylosaurs, including those of *Metatrapous valdensis* (Haubold, 1971; Thulborn, 1990; Lockley and Meyer, 2000). In common with *G. roeorum*, the latter has tetradactyl manual tracks and trackways that display a stride length of 140 cm and narrow gauge width. However, as with other likely ankylosaurian ichnotaxa, *Met. valdensis* differs from *G. roeorum* on account of its tetradactyl pedal tracks and the more elongated and triangular digital impressions associated with both the manual and the pedal tracks both of which additionally have conical unguis impressions (Haubold, 1971; Hornung and Reich, 2014). Interestingly, the much larger tetradactyl pedal impression shown by Hornung and Reich (2014:fig. 5) shares morphological similarities with *G. roeorum* tetradactyl manual tracks. These include the subequal size of the impressions of digits II–IV, the impression of digit I being smaller, and the overall more compact nature of the track. Additionally, unguis impressions and the mesaxonic arrangement of digital impressions of *Met. valdensis* manual tracks are features not observed in *Garbina*.

*Tetrapodosaurus borealis* (Sternberg, 1932; McCrea et al., 2001), another likely ankylosaurian ichnotaxon, has a different number of digital impressions on both the manus and the pedal tracks (pentadactyl and tetradactyl, respectively) from *G. roeorum*, along with considerably more elongated digital impressions and a wide-gauge trackway. Tracks DP14-1 and DP8-8 additionally show that the manus tracks of *G. roeorum* are smaller in proportion to the pedal tracks (approximately one-third to one-half the pedal track size), unlike the condition displayed by *Tetrapodosaurus*, where the manual and pedal tracks are of similar size relative to each other (McCrea et al., 2001). Recently, McCrea et al. (2012) reported on the presence of *T. borealis* within the Broome Sandstone, after being shown two tracks that are here assigned to *G. roeorum*: DP8-8 (Fig. 48A, B) and DP1-6 (Fig. 47G, H) by one of us (S.W.S.). Confusingly, in their text they refer to these tracks as pentadactyl (consistent with *Tetrapodosaurus* manus tracks), but the outlines they show are either tetradactyl (DP8-8) or seemingly hexadactyl (DP1-6) (see McCrea et al., 2012:fig. 28A [QD 1], B [P 018]). In the case of DP1-6, McCrea et al. (2012) appear to have mistakenly interpreted the elongated metacarpodigital pad impression or erosional feature at the proximal track margin of an additional digital impression. We observed a similar feature on other *G. roeorum* manus

tracks, including some that occur within the DP14-1 trackway (Fig. 46A, B). A number of manus tracks in the latter trackway have a well-preserved proximal track margin that is sublinear, lacking any elongation or erosion, and clearly demonstrate that the manus was tetradactyl. Based on these observations, we consider the referral of DP8-8 (Fig. 48A, B) and DP1-6 (Fig. 47G, H) to cf. *T. borealis* by McCrea et al. (2012) to be in error.

*Qijiangpus sinensis*, another potential ankylosaurian ichnotaxon (Xing et al., 2007), shows some similarities to *G. roeorum*. As occurs with some manus tracks attributed to *G. roeorum* (e.g., DP14-1; Fig. 45A–C), the manus tracks of *Qijiangpus sinensis* are pentagonal. But in the case of *G. roeorum* tracks, the pentagonal outline is typically the result of either slippage or erosion of the proximal track margin. Significantly, *Qijiangpus sinensis* can be distinguished from *G. roeorum* on account of the manus tracks being pentadactyl and mesaxonic, with the impressions of digits I and IV extending to the proximal track margin, whereas the pedal tracks are tetradactyl and less massive than the manus track.

Interestingly, *Garbina* manus tracks resemble likely ankylosaurian pedal tracks from the Cenomanian Duvegan Formation, Canada (McCrea et al., 2001:fig. 20.23), and the ?Maastrichtian El Molino Formation, Bolivia (McCrea et al., 2001:fig. 20.27, trackway T/3/5/2) in terms of their overall paraxonic track outline, the number of digital impressions associated with each track, and the proportionately short, blunt digital impressions. Although it is possible that the Duvegan Formation specimen may not be a pedal track, because it appears to be an isolated specimen, those from the El Molino Formation trackway are likely to be pedal tracks that display a high degree of morphological variability (see McCrea et al., 2001:fig. 20.27, trackway T/3/5/2).

Similarities exist between the manus impressions of *G. roeorum* and the quadrupedal ornithischian ichnotaxon *Shenmuichnus youngteihardorum* from the Lower Jurassic Fuxian Formation, in Shenmu County, Shaanxi Province, China (Li et al., 2012). The digital impressions of *S. youngteihardorum* are very rounded, short, and broad, but they seem to vary from tetradactyl to pentadactyl impressions within a single trackway (Li et al., 2012:fig. 6). The elongated, rather ornithopod-like digital impressions of the *Shenmuichnus* pedal tracks are also quite distinct from the short, blunt digital impressions seen on the pedal tracks of *G. roeorum*.

*Garbina* shares a number of features with tracks assigned to *Deltapodus*, purportedly made by stegosaurians (Whyte and Romano, 1994, 2001b; Lires et al., 2002; Gierlinski and Sabath, 2008; Milàn and Chiappe, 2009; Belvedere and Mietto, 2010; Cobos et al., 2010; Zhang et al., 2012; Xing et al., 2013a). *Garbina* is similar to *Deltapodus* in having mesaxonic and tridactyl pedal tracks with blunt digital impressions, with a long metatarsal pad impression (but see below for comments on likely *Garbina* tracks where the metatarsal pad impression is reduced or absent). The two ichnotaxa can be distinguished from each other on account of *Deltapodus* having triangular pedal track morphology with a slight concavity on the lateral margin, and trackway data indicating a wider gauge (see Whyte and Romano, 1994:fig. 7). *Deltapodus curriei* (Xing et al., 2013a) additionally has a more rounded proximal track margin than other *Deltapodus* ichnospecies. Of note is the fact that *Deltapodus* pedal tracks lack distinct pad impressions, whereas *G. roeorum* has a distinct separation between the distal digital-metatarsodigital pad impression and that of the proximal metatarsal pad impression. The manus tracks of *Deltapodus* also differ from those assigned to *G. roeorum* in being crescent-shaped, entaxonic, and with very short distal digital outlines.

The isolated, natural mold of a 25.5 cm long tridactyl pedal track from Gujarat, India (Mohabey, 1986), shares features with *Garbina* pedal tracks with regard to the short, gently rounded

digital impressions, weak mesaxony, and its elongated ?metatarsal pad impression. The Gujarat track is morphologically similar to *Deltapodus* pedal tracks (particularly *D. brodricki*; see Whyte and Romano, 1994) in having a triangular proximal track outline. Distinct from *Deltapodus*, but similar to *G. roeorum*, the plaster cast of this track figured in Mohabey (1986) appears to show a faint, mediolaterally aligned ridge midway along its length, separating the unified digital-metatarsodigital pad impression from the metatarsal pad impression. The mesaxony of the Gujarat track is weaker (toe extension to track length ratio estimated by us as approximately 0.09) than that of *Garbina*. Interestingly, this ichnite was originally identified as a sauropod manus track (Mohabey, 1986), being in very close proximity (~1 m) to assumed sauropod eggs (see Wilson et al., 2010).

The other potential stegosaurian ichnotaxon that *Garbina* is similar to is *Stegopodus*. The type ichnospecies of *Stegopodus*, *S. czerkasi*, is known from the Upper Jurassic (Kimmeridgian–Tithonian) Morrison Formation of Utah (Lockley and Hunt, 1998; Gierlinski and Sabath, 2008:figs. 2, 3; Mossbrucker et al., 2009:fig. 1b) and Wyoming (Bakker, 1996:fig. 2a) and has a digital impression formula that is consistent with that of stegosaurians for which complete manual and pedal skeletons are known (i.e., a functionally tetradactyl manus and a tridactyl pes; Gilmore, 1914; Thulborn, 1990; Galton and Upchurch, 2004; Senter, 2010). The holotype manual and pedal tracks upon which *Stegopodus czerkasi* is based are isolated natural casts, thought to have weathered from the same horizons and transported down-slope (Lockley and Hunt, 1998). Gierlinski and Sabath (2008) have questioned the assignment of these two casts to a single ichnotaxon, noting that if they originated from the same trackway, they did not form a natural (ipsilateral) couplet because the manual cast is from a right limb imprint and the pedal cast is from a left one. Between 1998 and 2008, the only other ichnites that emerged from the Morrison Formation (or elsewhere in the Upper Jurassic) that could be assigned to *Stegopodus* were pedal tracks (Gierlinski and Sabath, 2008; see below). But Mossbrucker et al. (2009) briefly described and figured a MP couplet (MNHM-1010/CU 189.11) on a loose boulder of Morrison Formation sandstone from the ‘Lake’s Yale Quarry 5’ in Colorado, the site of the discovery of the holotype of *Stegosaurus armatus* (Marsh, 1877). The manus track is similar to the natural cast that Lockley and Hunt (1998) assigned to *S. czerkasi*, having four blunt digital impressions, with that of digit I being the most pronounced and that of digit IV being only weakly expressed. The pedal track is longer than wide (length to width ratio of 1.3 based on the dimensions provided by Mossbrucker et al. (2009) and has three blunt digital impressions, with that of digit II being the largest and most triangular; the impressions of digits III and IV have a more rectangular outline, with near-parallel sides and squared-off ends. Digital pad impressions are absent on both tracks, indicating that the digital and metatarsodigital/metacarpodigital pads of the respective manus and pes were continuous. The pedal track is noteworthy in that it is elongated proximally by what appears to be a metatarsal pad impression, shown as a white area in the schematic interpretation of Mossbrucker et al. (2009:fig. 2). Although not commented on by Mossbrucker et al. (2009), the latter impression appears to be separated from the unified digital-metatarsodigital pad impression by a transverse ridge. The shape of the pedal track, with its more pronounced digital impressions, and in particular the apparent metatarsal pad impression, differentiates it from pedal tracks previously assigned to *S. czerkasi*, with some of the differences leading Mossbrucker et al. (2009) to propose that there may be two stegosaurian trackmakers in the Morrison Formation. Although not directly comparable to *G. roeorum*, these tracks and others assigned to *Stegopodus* provide important clues as to the ichnotaxonomic affinities of *G. roeorum*, as well as the likely locomotor behavior of its trackmaker(s).

The manual tracks assigned *S. czerkasi* by Lockley and Hunt (1998) have the digital impressions more distally directed relative to the principal track axis, with a total divarication angle between the impressions of digits I and IV of approximately 68° based on the manus track shown by Gierlinski and Sabath (2008: fig. 2a). A similar or slightly higher value can be calculated for the Lake's Yale Quarry 5 manus tracks (70–90°). This degree of digital impression divarication is in sharp contrast to the condition in *G. roeorum* where the total divarication angle is much larger (137–191°). In terms of the shape and size of the digital impressions, the manual tracks of *G. roeorum* are very similar to those of *Stegopodus* (I ≥ II = III > IV), although the small impression of digit I and large impression of digit IV of *Garbina* is the reverse of that observed in *Stegopodus* (see Lockley and Hunt, 1998).

The pedal tracks of *G. roeorum* differ from those of *S. czerkasi* with respect to the former's presence of a well-defined metatarsal pad impression; the one exception is the Lake's Yale Quarry 5 track, but we note that this track may not pertain to *S. czerkasi* sensu Gierlinski and Sabath (2008). Other aspects of *G. roeorum* and *Stegopodus czerkasi* pedal tracks are very similar. Gierlinski and Sabath (2008:34–35) provided measurements for four *S. czerkasi* specimens that reveal a track length to width ratio between 0.75 and 0.92, which is very similar to the same measurements for the unified digital-metatarsodigital pad impressions of *G. roeorum* (0.77–0.9). The same portion of the Lake's Yale Quarry 5 track is proportionately longer (1.3). Both *G. roeorum* and *S. czerkasi* also have proportionately short, rounded digital impressions that are weakly mesaxonic. But in the tracks assigned to *Stegopodus*, the divarication between the impressions of digits II and III is greater than that of digits III and IV, and the width of the impression of digit II is greater than that of digits III and IV. The abaxial divarication angles for *G. roeorum* pedal tracks, on the other hand, are roughly equal, and the width of the impression of digit II is variable. *Garbina roeorum* tracks can further be distinguished from pedal tracks assigned to *Stegopodus* on account of the latter's proximally elongated impression of digit IV, which results in an asymmetrical proximal track outline. On *G. roeorum*, the margin of the unified digital-metatarsodigital pad impression is proximally convex relative to the principal track axis. The Lake's Yale Quarry 5 pedal track has more elongated digital impressions than *G. roeorum*, with those of digits III and IV being almost parallel to each other. The proximal margin of this track is more uniformly convex than any of the *Stegopodus czerkasi* tracks, and this track in this respect approaches *G. roeorum* tracks.

The proximal extent of the metatarsal pad impression in *Stegopodus* (Gierlinski and Sabath, 2008) and *Stegopodus*-like tracks (Mossbrucker et al., 2009:fig. 2) is variable and may be related to whether the trackmaker was quadrupedal or bipedal at the time of track formation. This is also the case for pedal tracks we have assigned to *G. roeorum*. In the type pedal track (DP14-1[lp1]; Fig. 45D–F), a low, laterally positioned ridge separates the distal (digital-metatarsodigital pad impression) and proximal (metatarsal pad impression) parts of the track. The presence of this ridge is distinct in the other pedal tracks that have associated manus impressions (e.g., DP8-8; Fig. 48A, B). In the pedal only track DP14-18 (Fig. 48E, F), the ridge is much smaller (<5 cm) and the metatarsal pad impression is also reduced, forming little more than an open proximal margin. The same open margin is repeated in DP14-24 and DP14-34 (Fig. 49A, B), yet these tracks lack the ridge. On others, such as DP14-15 (Fig. 49C, D), a metatarsal pad impression and associated ridge are absent. Although the shape and proportions of these tracks are concordant with the unified digital-metatarsodigital pad impression of the type and referred tracks, the absence of a metatarsal pad impression and reduction/lack of a lateral ridge are major points of difference. A second point of difference is that DP14-15, -18, -24,

and -34 lack associated manus tracks, suggesting a bipedal trackmaker. Interestingly, several manual-pedal track associations of *Garbina* (e.g., DP8-8), including several within the type trackway, have a manual impression that is much shallower than that of the pes (see DP14-1[rm1]; Fig. 46 G, H). This strongly suggests formation by a trackmaker that at the time of track formation carried considerably more body weight at the hind limbs, which would be a likely prerequisite for bipedalism. As outlined earlier, Gierlinski and Sabath (2008) have proposed that numerous isolated, similarly shaped tridactyl pedal tracks from the Morrison Formation in the Cleveland-Lloyd Dinosaur Quarry, near Price, Utah (Mossbrucker et al., 2009:fig. 1b), and those from Wyoming (Bakker, 1996:fig. 2a) pertain to *S. czerkasi*. The same track morphology is also seen in tracks and trackways now assigned to *Stegopodus* sp. from the Upper Jurassic Tereñes Formation of Asturias, Spain (Gierlinski and Sabath, 2008:fig. 6b), originally considered to pertain to an ornithopod (Piñuela et al., 2002). Significantly, the Tereñes Formation trackways lack manus tracks. Based on this, and the rarity of *Stegopodus*-type manus tracks in the Morrison Formation, Gierlinski and Sabath (2008) have proposed that these tracks, as well as those assigned to *Stegopodus* sp. from the Tereñes Formation, were made by a bipedal stegosaurian.

Tracks such as DP14-15, DP14-34, and DP14-24 and the majority of pedal tracks assigned to *Stegopodus* that lack a metatarsal pad impression could only have been produced by a trackmaker with a functionally digitigrade stance, akin to the one that is typically associated with basal ornithopods (see Leonardi, 1984; Bakker, 1996; Gierlinski and Sabath, 2008). Although it is clear that the Tereñes Formation *Stegopodus* sp. trackway (Gierlinski and Sabath, 2008:fig. 6b) was made by a bipedal trackmaker, the same can only be inferred for other isolated *Stegopodus* tracks (Gierlinski and Sabath, 2008), as well as *G. roeorum* (DP14-15, DP14-34, and DP14-24) based on the absence of closely associated manus tracks. On the other hand, pedal tracks such those that occur in the DP14-1 trackway (e.g., DP14-1[lp1]) and the Lake's Yale Quarry 5 *Stegopodus* specimen of Mossbrucker et al. (2009), both of which incorporate a metatarsal pad impression, could only have been made by a trackmaker that adopted the more plantigrade posture that is more typically associated with stegosaurians (Thulborn, 1990), as is inferred for *Deltapodus* (Whyte and Romano, 1994, 2001b; Gierlinski and Sabath, 2008). The association of manus tracks with these assumed plantigrade tracks confirms that their respective trackmakers were quadrupedal, and this is clearly the case for the type trackway of *G. roeorum*, although the variable depth of the manus impressions relative to the pedal impressions is suggestive of a trackmaker adopting hind limb-dominated locomotion.

The variable expression of a metatarsal pad impression in *G. roeorum* pedal tracks, even within a continuous trackway, indicates that both functionally plantigrade and digitigrade postures were possible for its trackmaker, and it suggests that the degree of flexion and extension in the metatarsodigital joint and the tarsal joint was also variable. Assuming that the *G. roeorum* trackmaker was a stegosaurian, the shorter length of the forelimbs relative to the hind limbs might have required the animal to assume a more plantigrade pedal posture in order for the manus to touch the ground. As a consequence, the stride length of the hind limbs would have approached that of the shorter forelimbs, permitting a symmetrical quadrupedal gait. Lifting the forelimbs off the ground would have freed the hind limbs to stride more freely, with extension of the metatarsodigital joint and the tarsal joint elevating the metatarsus, resulting in a functionally digitigrade posture. In this context, we hypothesize that the *G. roeorum* trackmaker was a facultative biped, analogous to the two extant terrestrial pangolins (the ground pangolin,

*Smutsia temminckii*, and the giant pangolin, *S. gigantea*; Kingdon, 1974; Sweeney, 1974).

Lockley et al. (2008a:62) expressed apprehension at the assignment of *Stegopodus* (sensu Gierlinski and Sabath, 2008, and tracks like it) to a stegosaurian trackmaker, considering it “intriguing” that such animals would alternate between digitigrade pedal tracks when bipedal and plantigrade pedal tracks when quadrupedal. Apesteguía and Gallina (2011:271) regarded discussions of bipedal and quadrupedal stances in stegosaurs as “irrelevant in animals that were anatomically capable to use both stances.” The variability of pedal track morphology of *Garbina* strongly suggests that both digitigrade and plantigrade stances were possible for assumed stegosaurian trackmakers and supports earlier suppositions that these animals were likely to have been facultative bipeds (Marsh, 1880; Bakker, 1996; Gierlinski and Sabath, 2008).

The ‘Tunasniyoj’ thyreophoran ichnotaxa A and B of the Upper Jurassic–Lower Cretaceous La Puerta Formation, in Bolivia (Apesteguía and Gallina, 2011), represent distinct morphotypes that differ in the number of digital impressions and overall morphology when compared with *G. roeorum* pedal tracks. However, shared between these pedal impressions is a clear separation between the distal and proximal portions of the track that has not been described in other tracks attributed to stegosaurian trackmakers. In the ‘Tunasniyoj’ thyreophoran ichnotaxon A, a medial ridge partially divides these regions, whereas the ‘Tunasniyoj’ thyreophoran ichnotaxon B has the “heel mark” isolated by several centimeters (Apesteguía and Gallina, 2011:269). If the heel impression represents the metatarsal pad impression (not explicitly stated by the authors) separated from the more cranial plantar surface, then these may characterize the pedal morphology of a southern hemisphere lineage of stegosaurs currently unknown in the northern hemisphere. This possibility aside, the tetradactyl nature of the pedal tracks assigned to ‘Tunasniyoj’ thyreophoran ichnotaxa A and B suggests to us that these tracks cannot confidently be assigned to a stegosaurian trackmaker.

Another interesting aspect of tracks that can be assigned to *G. roeorum* is variability in the orientation of the digital impressions on the manus. Although some of the differences between various manus tracks are likely due to erosion or inconsistent track preservation (as a consequence of differing degrees of substrate interaction with the manus of the trackmaker), some of the variation in digital impression orientation suggests that the trackmaker had some capacity to extend or flex the manual digits, perhaps in response to variable track surface conditions, as is evident in the type track DP14-1. A capacity for manual flexibility in the *G. roeorum* trackmaker may be another factor supporting the idea of facultative bipedalism in some stegosaurians.

To conclude, in light of the well-preserved track and, in some instances, associated trackway data, along with the distinctiveness of the track morphology compared with other described quadrupedal ornithischian tracks, we feel confident in our recognition of *Garbina roeorum* as a new ichnotaxon. The morphology of the tracks suggests that the trackmaker was a stegosaurian thyreophoran with hind limb–dominated locomotion capable of both quadrupedal and bipedal stances.

Tracks assignable to *G. roeorum* occur throughout the study area. At some sites, such as DP14, they are one of the most common track types, outnumbered only by the ubiquitous sauripod tracks. Although this suggests that at least in the Yanijarri–Lurujarri section of the Dampier Peninsula, the dinosaurs responsible for these tracks were probably a well-represented component of the area’s dinosaurian fauna, we are not aware of any other tracks that can be assigned to *G. roeorum* in other exposures of the Broome Sandstone, such as at Minyirr and Reddell Beach. As to whether this is a consequence of the two areas preserving evidence for different dinosaurian faunas or an indication that

the *G. roeorum* trackmaker had habitat preferences that restricted them from areas now represented by sites in the Minyirr and Reddell Beach region is unclear and requires further field work and documentation.

*LULUICHNUS*, ichnogen. nov.

*LULUICHNUS MUECKEI*, ichnosp. nov.  
(Figs. 50, 51, 63B, 64C, S18; Table 16)

**Etymology**—The ichnogenus name honors the late Paddy Roe OAM, who also went by the name Lulu. Roe was a Nyikina and Goolarabooloo Elder, and former Traditional Custodian and Maja (Law Boss) for Jabirrabirri, Ngumbarl, and Djugun countries, the Northern and the Southern tradition of the Song Cycle, and the dinosaurian tracks of the Broome Sandstone. The ichnospecies name honors Prof. Stephen Muecke, an ethnographer who spent many years with Roe documenting and writing about his stories (see Roe, 1983; Benterrak et al., 1996).

**Holotype**—WAM 15.12.701, a rigid polyurethane resin replica of the natural mold of a left MP couplet (UQL-DP45-6[lp1, lm1]), with the pedal track additionally represented by NMV P230370-B, a plaster replica (concave/negative epirelief).

**Topotype Material**—UQL-DP45-6, a discontinuous trackway (2.6 m long) comprising five tracks (lp1, lm1, lp2, ?rp2, ?lp3), all preserved in situ as natural molds (Figs. 50, 63B, 634C, S18).

**Locality, Horizon, and Age**—All the specimens were originally preserved at UQL-DP45 in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derive from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Referred Material**—Other tracks that can be assigned to *Luluichnus mueckei* include UQL-DP45-5A, the natural mold of a left MP couplet, preserved on two isolated boulders at UQL-DP45, additionally represented by WAM 15.12.702A and B, a rigid polyurethane resin replica in two parts; UQL-DP45-5A(p) is also represented by WAM 15.12.703, a silicon rubber cast, taken from the track by J. Long in 1991 before the platform broke up; UQL-DP45-5B, the natural mold of a possible manual-pedal-manual track triplet, preserved on an isolated boulder at UQL-D45, preserved in close association with UQL-DP45-5A, additionally represented by WAM 15.12.702B, a rigid polyurethane resin replica (Fig. 51); UQL-DP45-16, the natural mold of a ?left pes, preserved in situ at UQL-DP45, additionally represented by WAM 15.12.704, a rigid polyurethane resin replica, and NMV P230370-A, a latex cast and plaster replica, is assigned to cf. *Luluichnus* (Fig. 52). (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Diagnosis**—Manus tracks: medium- to large-sized (proximodistal length 11–14 cm, mediolateral width 19.5–22 cm), typically wider than long, with a proximodistal length to maximum mediolateral width ratio of approximately 0.6; overall track morphology oval with indistinct/absent digital impressions; digital pad impressions absent. Pedal tracks: small- to medium-sized (proximodistal length 15–22.5 cm, mediolateral width 16–20.7 cm), tri-dactyl, mesaxonitic, longer than wide (maximum proximodistal length to maximum mediolateral width ratio of 1.0–1.3); individual digital impressions proportionately short (maximum length of each digit impression to maximum proximodistal track length ratio of 0.13–0.35); individual digit impressions fairly broad (maximum width of each digit impression to maximum proximodistal track length ratio of 0.2–0.37); digit II and IV impressions extend subequally relative to the principal track axis; total divarication angle between the axes of the impressions of digits II and IV 30–55°; divarication of axes between impressions of digits II and III (21–35°) and digits III and IV (15–39°) approximately the same. Trackway (quadrupedal): pace angulation of pedal

track approximately  $133^\circ$  ( $129\text{--}142^\circ$ ); pedal track stride length approximately 5.8 times the maximum pes length; pedal track pace length approximately 3.3 times the pedal track length. Pedal tracks can be laterally or medially rotated relative to the trackway orientation; manual tracks laterally rotated, and directed cranio-lateral relative to the trackway orientation.

**Description**—As best as we can determine, DP45-6 appears to represent a discontinuous trackway that comprises at least two left pedal tracks, one of which (DP45-6[lp1]) might be associated with a faint manual track (DP45-6[lm1]; Figs. 50, 63B, 64C, S18). An outline of DP45-6(lp1) was published by Long (1990:67, 1998:127). The trackway is approximately 2.6 m long and 50 cm across the width of the pedal tracks; it includes stride lengths of 110 and 122 cm, with pace lengths of 65 and 66 cm. The potential manual track (DP45-6[lm1]) is a faint, roughly oval-shaped depression of small size (approximate proximodistal length 11 cm, mediolateral width 19.5 cm), and wider than long, with a maximum length to maximum width ratio of 0.56. No digital impressions are discernible. This manual track is positioned approximately 10 cm cranio-lateral to the pedal track DP45-6(lp1). The latter is the natural mold of left pes DP45-6(lp1) (plaster replica NMV P230370-B), which is tridactyl and mesaxonic (digital impression extension to track length ratio 0.11), of small size, and longer than it is wide (approximate proximodistal length 19.2 cm, mediolateral width 16.4 cm), with a maximum length to maximum width ratio of 1.2. The digital impressions

are triangular, moderately elongated, acuminate distally, and broadest across the hypices. The impressions of digits II and IV extend distally to approximately the same level. The total divarication between the axes of the impressions of digits II and IV is  $55^\circ$ , with the divarication of the axes of the impressions of digits II and III ( $28^\circ$ ) approximately equal to the divarication of the axes of the impressions of digits III and IV ( $27^\circ$ ). Individual digital and metatarsodigital pad impressions are absent. The track tapers slightly proximally, curving into a nearly straight proximal margin.

The second pedal track within the trackway (DP45-6[lp2]; Fig. 51D) is at least 20.3 cm long (the distal portion of the track is eroded and extends into a crack) and 20.7 cm wide and has a rounded proximal track margin. The internal proximal surface of the track is distinctly concave rather than sublinear as in preceding pedal track, most likely due to erosion. The total divarication between the axes of the impressions of digits II and IV is  $55^\circ$ , with the divarication of the axes of the impressions of digits II and III ( $35^\circ$ ) larger than the divarication of the axes of the impressions of digits III and IV ( $22^\circ$ ). Track DP45-6(lp2) is similar to DP45-6(lp1) with regard to the digital impressions being triangular, moderately elongate, and the impressions of digits II and IV being broadest across the hypices, with the distal position of the impressions of digits II and III being subequal. The tracks vary in the total divarication between the axes of the impressions of digits II and IV ( $55^\circ$  in DP45-6[lp2] and  $30^\circ$  in DP45-6[lp1]),

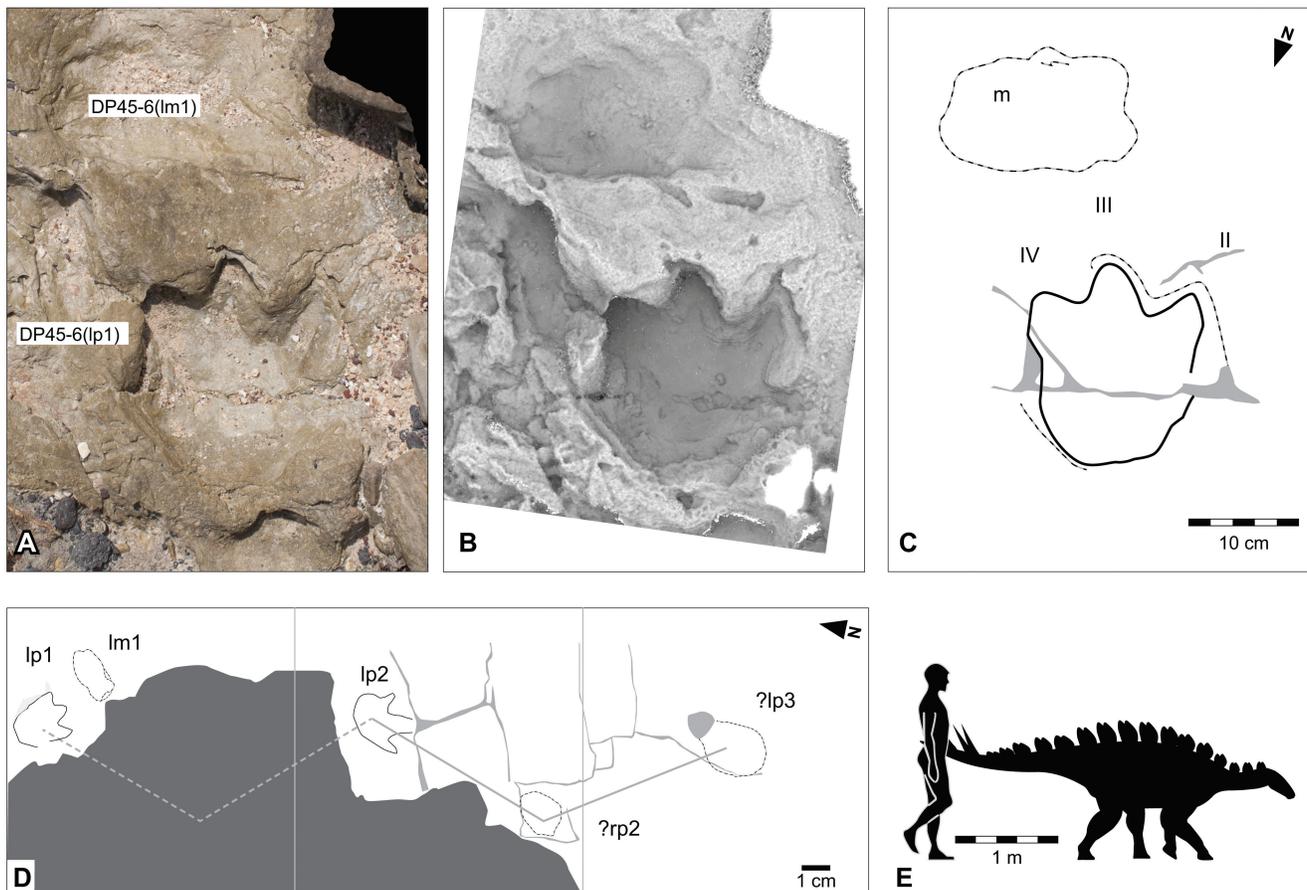


FIGURE 50. *Luluichnus muckei*, ichnogen. et ichnosp. nov., from the Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia. Coupled left manual and pedal impressions, UQL-DP45-6(lp1)+(lm1), preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, topotype trackway UQL-DP45-6. **E**, silhouette of hypothetical *Luluichnus* trackmaker based on UQL-DP45-6, compared with a human silhouette. See Figure 19 for legend.

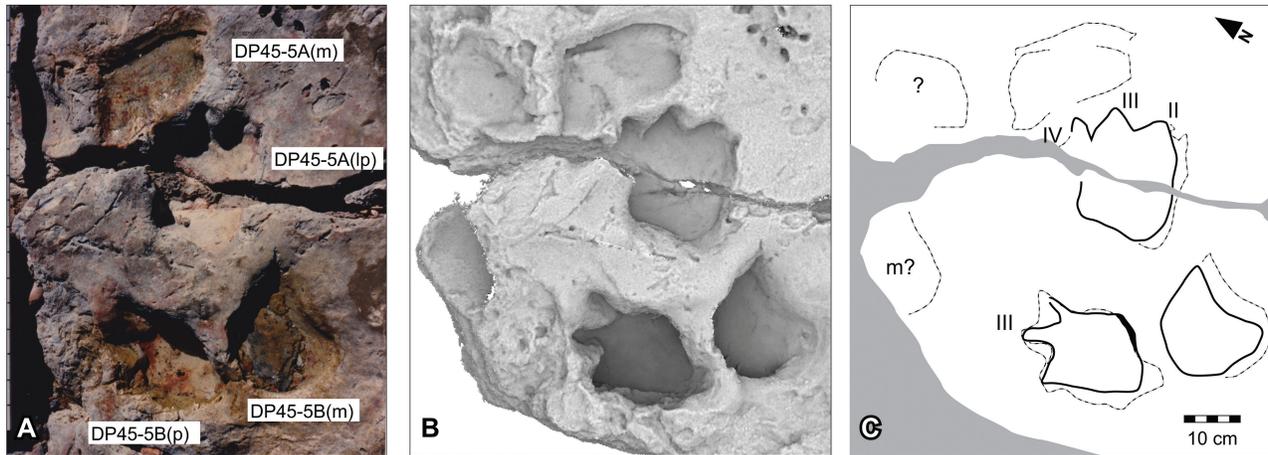


FIGURE 51. *Luluichnus mueckeii*, ichnogen. et ichnosp. nov., from the Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia. Coupled left manual and pedal impressions, UQL-DP45-5A (upper) and possible sequential manual, pedal and manual impressions, UQL-DP45-5B (lower). **A**, photograph of the tracks in situ (ca. 1990; Paul Foulkes Collection, courtesy K. Foulkes); **B**, ambient occlusion image of digitally reconstructed ex situ specimens; **C**, schematic interpretation. See Figure 19 for legend.

but they share a greater divarication between the axes of the impressions of digits II and III ( $35^\circ$  in DP45-6[lp2] as opposed to  $15^\circ$  in DP45-6[lp1]) than that of digits III and IV ( $22^\circ$  in DP45-6[lp2] as opposed to  $15^\circ$  in DP45-6[lp1]). The overall shape also differs slightly, with the proximal margin of DP45-6(lp2) being convex as opposed to that of DP45-6(lp1), which is nearly straight. As to whether these differences are a consequence of variable preservation, erosion, or a combination of both is unclear. The longer impression of digit III on DP45-6(lp2) is due to the presence of a prominent crack in the track surface. Despite these differences, the size and proportions of DP45-6(lp2) and its position relative to DP45-6(lp1) in the absence of any other tracks lead us to conclude these tracks very likely form part of a trackway sequence.

The next two possible pedal tracks within this trackway (DP45-6[rp1] and DP45-6[lp3]) are both shallow, oval-shaped depressions of small to medium size (15 cm long proximodistally and 16 cm wide mediolaterally for DP45-6[rp1]; 25 cm long and 19 cm wide for DP45-6[lp3]). Whereas the size and position of these tracks are consistent with being made by the same trackmaker that made DP45-6(lp1) and DP45-6(lp2), differences in the external track outlines and degree of preservation are striking and unusual.

Trackway DP45-5A, a potential MP couplet (Fig. 51), can also be assigned to *Luluichnus mueckeii*. Track DP45-5A(m) is a sub-oval manual impression positioned cranially and to one side of DP45-5A(p), a tridactyl pedal track. The pedal impression has been split craniocaudally as a result of the portion of platform that it was originally preserved in having broken up (see Appendix 2 for further details on various events associated with this). Prior to the platform breaking up, the track was cast by Long (WAM 15.12.703) and photographed by both Long (2002:10–13, pl. 1) and Paul Foulkes (Fig. 51A). Long (1990:67, 1998:127) also provided schematic outlines of the pedal track. The photographs and the cast show that the cranial and caudal portions of the track were separated by a crack. Based on the position of an associated manus trace, we interpret DP45-5A(p) to be the impression of a left pes. Once joined back together, the two halves of DP45-5A(p) show that the shape of the track conform with that shown in the photos and captured by the cast: it is longer than wide and medium-sized (approximate proximodistal

length 21 cm, mediolateral width 16 cm), with a maximum length to maximum width ratio of 1.3. The proximal margin is gently concave, with the lateral (left) margin extending farther proximally than the medial (right) margin. The proximolateral margin is gently concave. The digital impressions are proportionately short (digital impression extension to total track length ratio is 0.18) and triangular, with that of digit III extending slightly farther distally than those of digits IV and II. The total divarication between the axes of the impressions of digits II and IV is  $72^\circ$ , with the divarication of the axes of the impressions of digits II and III ( $35^\circ$ ) approximately equal to the divarication of the axes of the impressions of digits III and IV ( $37^\circ$ ). Individual digital and metatarsodigital pad impressions are absent. The manual impression DP45-5A(p) is wider than long (approximate proximodistal length 14.5 cm, mediolateral width 17 cm) and lacks evidence of digital impressions.

Trackway DP45-5B is a potential manual-pedal-manual triplet (Fig. 51) that occurs on the same portion of platform (albeit now split) as DP45-5A. Despite their close proximity, the relationship between DP45-5B and DP45-5A is unclear. The perpendicular orientation of the principal axis of each pedal track and the difference in size (DP45-5B[p] being smaller than DP45-5A[p]) likely preclude these sets of tracks from being consecutive impressions within the same trackway. As such, we regard them as pertaining to different individual trackmakers.

Track DP45-5B(p) is a tridactyl, mesaxonic pedal track of small size and is longer than wide (approximate proximodistal length 19 cm, mediolateral width 15 cm), with a maximum length to maximum width ratio of 1.3. Similar to DP45-5A, the proximal margin of the track is obliquely oriented, with the longer margin presumably being the medial one, making it a right track. If correct, then the possible manual tracks cranial and caudal to it are laterally positioned within the trackway, and the left side of the trackway has been lost to erosion. The divarication angles between the impressions of digits II and III and digits III and IV of DP45-5B(p) are subequal ( $35^\circ$  and  $37^\circ$ , respectively), resembling the condition in DP45-6(rp1) and DP45-16 (see below). Individual digital and metatarsodigital pad impressions are absent. In DP45-5B(p), the impressions of digits III and IV are proportionately long (43% and 39% of the track length, respectively) when compared with the digit II impression (12% of the

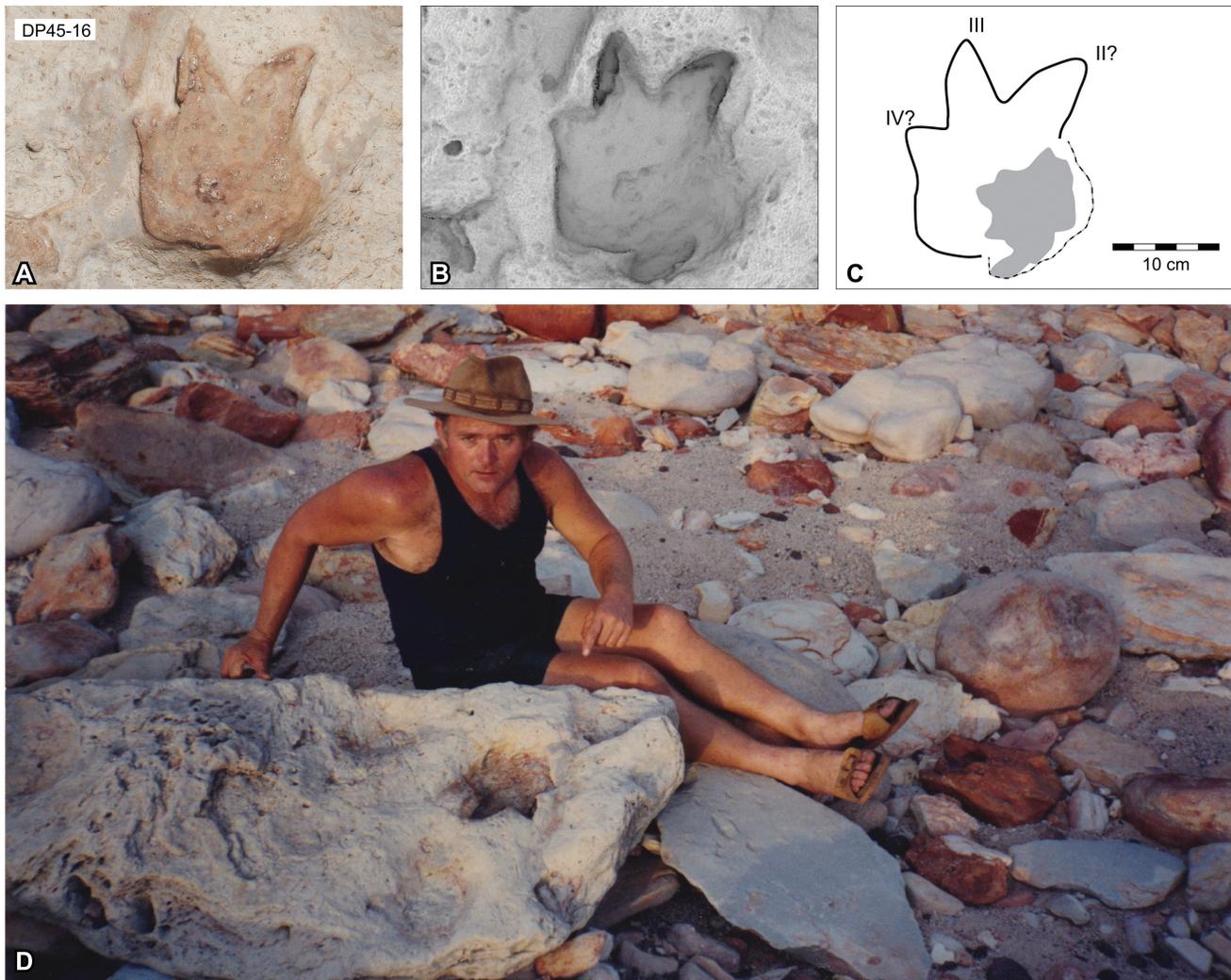


FIGURE 52. cf. *Luluichnus*, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Possible pedal impression, UQL-DP45-16, preserved ex situ as **A**, photograph; **B**, 3D image with ambient occlusion; and **C**, schematic interpretation. **D**, Paul Foulkes alongside UQL-DP45-16 ca. 1990 (Paul Foulkes Collection, courtesy K. Foulkes). See Figure 19 for legend.

track length) and those of the other pedal tracks assigned to *L. mueckekei* (DP45-6[lp1] and DP45-5B; ~17% and 18% of track length, respectively). Given its depth, the apparent elongation of the digital impressions is likely the result of the trackmaker's pes being dragged through the sediment as the foot exited the track.

The manus impression DP45-5B(rm1) is positioned caudolateral to DP45-5B(p) and, based on the assumed orientation of the track sequence, appears to be strongly inwardly rotated (i.e., ~60°). Given this position, we tentatively regard this as a right manus track. It is of small to medium size (approximate proximodistal length 14.5 cm, mediolateral width 17 cm), wider than long, with a maximum length to maximum width ratio of 0.8. The track lacks digital impressions, making it reminiscent of the cranial margin of the manus impressions DP45-6(rm1) and DP45-5A. The depth and crescent-shaped outline contrast with other manus tracks assigned to *L. mueckekei*. Another potential manus impression is located craniolateral to DP45-6(rp1). If it is a track, only the caudal-most portion is preserved. Taking all this into account, it seems likely that DP45-5B represents a morphological variant of *L. mueckekei*. However, given that there are

differences between it and other tracks assigned to the ichnotaxon, we tentatively place it in cf. *Luluichnus*.

Track DP45-16 (Fig. 52) is problematic. It is of small size (approximate proximodistal length 22.1 cm, mediolateral width 18.4 cm), with a maximum length to maximum width ratio of 1.2. It resembles *Luluichnus* pedal impressions in being tridactyl with triangular digital impressions and a squarish outline distally. However, it differs from DP45-6(lp1) and DP45-5A(p) in that two of the digital impressions are similarly sized, being approximately 35% of the track length and over twice the length of the remaining one (13% of the track length). The total divarication between the axes of the digital impressions is 86°. Individual digital and metatarsodigital pad impressions are absent, and the proximal track margin is convex. Additionally, the deeper right side of the track bulges to form a concave margin that also extends caudally. We interpret this area as having been modified by erosion. Based on its peculiar morphology, we are not certain whether it is a left or a right track and tentatively assign it to cf. *Luluichnus*.

TABLE 16. Measurements of tracks assigned to *Luluichnus mueckeii*, ichnogen. et ichnosp. nov., and cf. *Luluichnus*, from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UOL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	II <sup>^</sup> III	III <sup>^</sup> IV	Total <sup>^</sup>	bdl II (II/L)	bdl III (III/L)	bdl IV (IV/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)	Pace (cm)	Stride (cm)
45-6(lm1)	11	19.5	0.6	—	—	—	—	—	—	—	—	—	—	—	—
45-6(lp1)	19.2	16.4	1.2	2.1 (0.11)	21	26	47	3.3 (0.17)	3.7 (0.19)	2.9 (0.15)	5.7 (0.3)	5.2 (0.27)	3.4 (0.18)	65	110
45-6(lp2)	20.3	20.7	1.0	5.5 (0.27)	24	39	63	4.8 (0.24)	7.3 (0.36)	3.6 (0.18)	4.8 (0.24)	7.3 (0.36)	3.6 (0.18)	—	—
45-6(lp3)	15	16	0.9	—	—	—	—	—	—	—	—	—	—	66	—
45-6(lp4)	25	19	1.3	—	—	—	—	—	—	—	—	—	—	—	122
45-5A(p1)	21	16	1.3	2.3 (0.11)	24	23	47	4 (0.19)	3 (0.14)	4.5 (0.21)	5.5 (0.26)	7.4 (0.35)	4.7 (0.22)	—	—
45-5A(m1)	14	22	0.6	—	—	—	—	—	—	—	—	—	—	—	—
45-5B(p1)	19	15	1.3	3.5 (0.18)	35	37	72	3.5 (0.18)	3.5 (0.18)	3.5 (0.18)	5.0 (0.26)	7.0 (0.37)	6.0 (0.32)	—	—
45-5B(m1)	14.5	17	0.8	—	—	—	—	—	—	—	—	—	—	—	—
45-16	22.1	18.4	1.2	5.3 (0.23)	42	45	86	7.7 (0.35)	7.1 (0.32)	2.8 (0.13)	6.0 (0.27)	5.7 (0.26)	4.4 (0.2)	—	—

bdl = basal digital impression length; bdw = basal digital impression width; De = digital impression extension; II = impression of digit II; III = impression of digit III; IV = impression of digit IV; L = track length; W = track width. <sup>^</sup> denotes angle between respective digital impressions.

**Remarks**—Tracks DP45-5A(p) and DP45-6(lp1) appear to represent tridactyl pedal tracks of stegosaurian origin, as has been suggested previously (Long, 1990, 1998; Scanlon, 2006; Milàn and Chiappe, 2009; Kear and Hamilton-Bruce, 2011). As far as we have been able to ascertain, DP45-5A and DP45-5B (Fig. 51) are the purported ‘stegosaurian trackway’ referred to by Long (1990, 1992a, 1993, 1998, 2002), as well as the infamous ‘stolen stegosaur track’ (see Appendix 2 for details). Confusingly, however, in his figures, Long (1990, 1993, 1998) links DP45-5A(p) with the right manus impression of DP45-15 (Figs. 56, 65E, 66E, S21). The two sets of tracks are not related—and, as will be discussed below, the manus impression of DP45-15 is distinct from the manus tracks assigned to *L. mueckeii* (DP45-6[lm1], DP45-5A[m], and DP45-5B[m])—and is best placed in its own morphotype (Broome thyreophoran morphotype B).

The overall shape of the pedal tracks assigned to *L. mueckeii* is similar to some of the pedal tracks of *Garbina roorum* (Figs. 47D–F, 50A–D, 51A–D) and, outside of the Broome Sandstone, pedal tracks assigned to *Deltapodus brodericki* from the Upper Jurassic (Aeleanian–Bajocian) Ravenscar Group of the Cleveland Basin, Yorkshire, U.K. (Whyte and Romano, 1994, 2001b), and the Brushy Basin Member of the Upper Jurassic (Kimmeridgian–Tithonian) Morrison Formation, Utah (Milàn and Chiappe, 2009), and *Deltapodus* sp. from the Upper Jurassic Tereñes Formation of Asturias, Spain (Lires et al., 2002; Garcia-Ramos et al., 2006; Gierlinski and Sabath, 2008:fig. 9B). Similar to both *Garbina* and *Deltapodus* pedal tracks, DP45-6(lp1), DP45-5A(p), and DP45-5B(p) are weakly mesaxonic, with proportionately short digital impressions. The latter tracks also differ from pedal tracks assigned to *Garbina* in that there is no separate metatarsodigital pad impression. If the metatarsodigital pad impression on the type pedal track of *Garbina* (DP14-1[lp1]) is excluded, then the outline of the digital part of the track is proportionately much shorter than that for DP45-6(lp1) (an average maximum proximodistal length to maximum mediolateral width ratio of 0.8–0.9 vs. 1.2 for DP45-6[lp1]). The latter ratio for DP45-6(lp1) is still lower than that for *Deltapodus* tracks, which are typically twice as long as they are wide (Whyte and Romano, 2001b). The digital impressions of DP45-6(lp1) and DP45-5A(p), although proportionately short and broad at their base, are much more pointed than the well-rounded digital impressions on the pedal tracks assigned to *Garbina* and in particular *Deltapodus*. The bluntly rounded digital impressions on *Deltapodus* pedal tracks are sometimes barely discernible, extending distally only a small distance from the hypex. The more linear proximal margin and overall broader and more squarish track outline of DP45-6(lp1) and DP45-5A(p) also contrast with the more tapered proximal margin and more triangular track outline of *Deltapodus* pedal tracks (see Milàn and Chiappe, 2009). Based on these

observations, we consider DP45-6(lp1) to be distinct from both *Garbina* and *Deltapodus* pedal tracks.

Apestequía and Gallina (2011) regarded the pedal track DP45-5A(lp1) as tetradactyl, contrasting with our tridactyl interpretation. Their interpretation is based on a comparison with pedal tracks assigned to La Puerta Formation ichnotaxon A of Bolivia (Apestequía and Gallina, 2011:fig. 2A–D), which appear to have been formed by a trackmaker with syndactylous digits I and II. The apparent ‘extra’ digital impression on DP45-5A(p) occurs midway along the midlateral track margin. This comparison was based on the simplified track drawing from Long (1990:67), which was subsequently reproduced by others (e.g., Scanlon, 2006). Unfortunately, Long (1990) did not include in his drawing the location of cracks and missing track regions. Our examination of the ex situ track shows that this ‘extra digital impression’ is an erosional feature associated with the main crack that passes through the track. At the time of Long’s investigation, the crack was already wide (~5 cm) (Fig. 51A). This crack has subsequently widened, splitting the boulder and DP45-5A(p) into two (see Fig. 51B, C and Appendix 2). However, the lateral internal track outline is linear and provides no evidence for an extra digit. We therefore do not consider DP45-5A(p) to be tetradactyl and, as such, regard it as distinct from pedal tracks assigned to ichnotaxon A from the La Puerta Formation by (Apestequía and Gallina, 2011).

The stegosaurian ichnotaxa *Deltapodus brodericki* (Whyte and Romano, 1994, 2001b), *Deltapodus* sp. from the Upper Jurassic Tereñes Formation of Asturias, Spain (Lires et al., 2002; Garcia-Ramos et al., 2006; Gierlinski and Sabath, 2008:fig. 9B), cf. *Apulosauripus* sp. from the Lower Cretaceous (Albian) Dakota Group of Colorado (Kurtz et al., 2001; Gierlinski and Sabath, 2008:fig. 9C), and some unnamed tracks from the Lower Jurassic (Pliensbachian) Aganane Formation of Morocco (Jenny and Jossen, 1982) share characteristics with *L. mueckeii*. The manual impressions assigned to the former track types are proportionately wide relative to the pedal track, with outlines ranging from ovoid to crescentic, lack digital impressions, or the digital impressions are poorly defined or very short and rounded. Also similar to *L. mueckeii*, the pedal tracks are elongated, with short, tridactyl digital impressions. Nevertheless, a number of important differences are apparent. Assuming that DP45-5A, DP45-5B, and DP45-6 each represent different sets of natural manual-pedal track associations of the same track type, the degree of heteropody between the two tracks is also much lower (i.e., the manus tracks are proportionately much smaller relative to pedal tracks in the various *Deltapodus* type tracks listed above, whereas DP45-5A, DP45-5B, and DP45-6 have pedal and manual impressions of comparable size). Additionally, some of the well-preserved *Deltapodus* manus tracks show indications of a medially directed pollex impression and the pedal tracks have

distally rounded digital impressions, both features that differentiate them from the tracks assigned to *L. mueckeii*.

Track DP45-6(lm1), the likely manus track associated with DP45-6(lp1), is dissimilar to any of the other confirmed dinosaurian manus tracks in the study area or other sites within the Broome Sandstone. Lacking any clearly discernible digital impressions, its mediolaterally oval shape is most similar to the manus tracks of sauropods (e.g., Broome sauropod morphotype B, DP1-1, Fig. 31; uncertain Broome sauropod morphotype DP9-2, Fig. 35A–C), but differs with respect to its convex caudolateral margin and arcuate medial and lateral margins. The aforementioned sauropod manus tracks all have a broadly reniform outline, with convex medial and lateral margins, and, where their outline has not been affected by the cranial pressure bulge associated with the succeeding pedal track, have a concave caudal margin (e.g., uncertain Broome sauropod morphotype DP9-2; Fig. 35A–C). Some of the better-preserved manus tracks assigned to other sauropod ichnotaxa such as *Brontopodus birdi* (see 1989) also have the concave medial and lateral margins seen on DP45-6(lm1), but they are proportionately more elongated craniocaudally relative to the principal track axis, which gives them a more horseshoe-shaped outline. This does resemble the deep cf. *Luluichnus* manus impression DP45-5B(rm1), which has a crescentic outline and lacks discernible digit impressions. In those Broome Sandstone sauropod pedal tracks that are tridactyl (e.g., Fig. 33A), the digital impressions are elongate, broad along their entire length, distally blunt, with little spacing between hypices, which strongly contrasts with the short, acuminate digital impressions of the *Luluichnus* pedal tracks.

Although occurring within the same trackway, the differences between the pedal impressions DP45-6(lp1) and DP45-6(lp2) (Fig. 50D) are hard to reconcile. After being shown this track by one of us (S.W.S.), McCrea et al. (2012:fig. 19d) subsequently identified it as a tridactyl theropod track, but they in their illustration do not account for the exaggerated extension of the central (III) digital impression. This feature, and the very scalloped nature of the internal track surface, is, to our mind, a consequence of erosion. Given its overall size and shape, tridactyl nature, and position relative to DP45-6(lp1) and DP45-6(lm1), we tentatively consider DP45-6(lp2) to form part of a related trackway sequence. Perplexingly, no manual tracks occur near DP45-6(lp2), or, for that matter, any of the other succeeding pedal tracks in this possible trackway sequence (Fig. 50D). This would imply that one of the following: (1) the other manual tracks associated with each of these pedal tracks were only weakly impressed and are no longer discernible due to erosion; (2) the DP45-6 trackmaker transitioned from a quadrupedal gait (as evidence by DP45-6[lp1 and lm1]) to a bipedal gait (as evidenced by DP45-6 [lp2, rp2, and lp3]); (3) DP45-6(lm1) is not a manual track, or if it is, it is not associated with DP45-6(lp1) and the trackway comprises pedal tracks only; or (4) DP45-6(lp1) and DP45-6(lm1) were not made by the same trackmaker that made the other three pedal tracks (DP45-6 [lp2, rp2, and lp3]). In the absence of any other similar-sized tracks in the immediate vicinity, although possible, option 4 seems unlikely. Evidence in favor of any one of the remaining three options is ambiguous at best.

Trackway DP45-16 first appeared as a photograph in Rich and Vickers-Rich (2003a:89), being reproduced in Rich (2007:24) and labeled as the impression of a “stegosaur’s hindfoot.” It resembles other pedal tracks we attribute to *Luluichnus* in being longer craniocaudally than it is wide and having distally acuminate digital impressions, but it differs on account of two of the digital impressions being much larger than the third and the possible medial bulging of the metatarsodigital part of the track (but this is likely the result of erosion). Elongation of two of the digital impressions is also seen in DP45-5B(p). Both tracks occur at the same tracksite (DP45), and we are confident that DP45-5B can be assigned to *L. mueckeii*. Although all of these tracks now

occur on loose boulders, it is tantalizing to speculate that they were made by the same trackmaker, with DP45-5B(p) and DP45-16 possibly being morphological variants of *L. mueckeii*. Nevertheless, pending the discovery of additional tracks and trackway data permitting more convincing comparisons of DP45-16 with DP45-5A, DP45-5B, and DP45-6, we provisionally place this track in cf. *Luluichnus*.

To conclude, the pedal tracks that form part of DP45-5A, DP45-5B, and DP45-6 appear to represent a track type that is distinct from any other tridactyl dinosaur trace, either from the Broome Sandstone or elsewhere, and most likely pertain to a thyreophoran trackmaker. In accordance with other thyreophoran tracks, and typically those linked to stegosaurians, the pedal impressions are tridactyl, with acuminate digital impressions, and occur in association with proportionately large, oval-shaped manus tracks, lacking clear digital impressions. We therefore consider such tracks as distinct in their own right and assign them to the new ichnotaxon *Luluichnus mueckeii*. At present, tracks that can be assigned to *Luluichnus mueckeii* are restricted to a single tracksite, indicating that the trackmaker was a rare component of the dinosaurian fauna of the Broome Sandstone, possibly with a preference for a particular paleoenvironment.

#### BROOME THYREOPHORAN MORPHOTYPE A

(Figs. 53, 63D, 64D, S19; Table 17)

**Referred Material**—UQL-DP8-17, the natural mold of a ?right manus, additionally represented as WAM 15.12.705, a rigid polyurethane resin replica. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality, Horizon, and Age**—The referred specimen is preserved in situ at DP8, in the intertidal zone of the Yanijjarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—Track DP8-17 (Figs. 53, 63D, 64D, S19) is a tetradactyl, paraxonic (basal digital impression length to track length ratio 0.33–0.68) natural mold of a ?right manus. The track is medium-sized and is wider than it is long (maximum proximodistal length 9 cm, maximum mediolateral width 29 cm), with a maximum length to maximum width ratio of 0.31. The individual digital impressions are proportionately short and broad, extending to approximately the same extent distally; the impressions of digits II, III, and IV are subequal in length and slightly more distally positioned relative to those of the digits I and V. The total divarication between the axes of the impressions of digits I and V is 162°. Individual digital and metatarsodigital pad impressions are absent. The proximal track margin is gently convex medially, becoming straight laterally.

**Remarks**—Track DP8-17 was figured by McCrea et al. (2012: fig. 28a) after this and other in situ thyreophoran tracks in the study area were shown to them by one of us (S.W.S.). McCrea et al. (2012:34) refer to DP8-17 as a pentadactyl track. It is unclear whether this was an oversight on the part of McCrea et al., the result of a preconceived notion of the track morphology, or discrepancies associated with using acetate tracings of the track surface outlines as a primary data source (McCrea et al., 2012:7). Our analysis of this track indicates that it is tetradactyl.

Among dinosaurian tracks from the Broome Sandstone, DP8-17 most closely resembles manus tracks assigned to *G. roeorum*, being tetradactyl and paraxonic, with short, broad digital impressions. However, it is distinct from *G. roeorum* in having the digital impressions aligned in an almost straight line rather than a loose arc. This characteristic also distinguishes this track from the manus track from the Middle Jurassic Walloon Coal Measures at Balgowan, Darling Downs, Queensland (Hill et al., 1966), assigned herein to cf. *G. roeorum*.

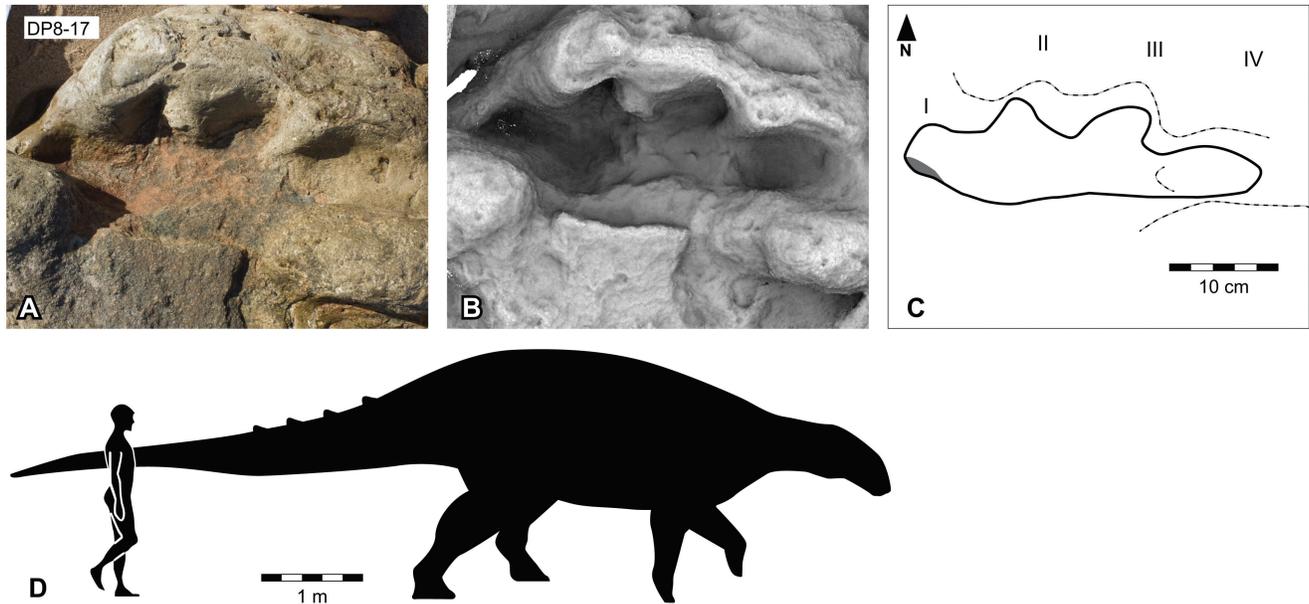


FIGURE 53. Broome thyreophoran morphotype A, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Possible right manual impression, UQL-DP8-17, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, silhouette of hypothetical Broome thyreophoran morphotype A trackmaker based on UQL-DP8-17, compared with a human silhouette. See Figure 19 for legend.

Track DP8-17 differs from all other dinosaur manus impressions from the Broome Sandstone, or any other Australian thyreophoran tracks, chiefly by virtue of its low proximodistal length to mediolateral width ratio. It is, however, very similar to the manus tracks from the Upper Jurassic–Lower Cretaceous La Puerta Formation of Bolivia described as ichnotaxon B by Apesteguía and Gallina (2011:fig. 2f). In common with DP8-17, these tracks have a low proximodistal length to mediolateral width track ratio (approximately 0.33 compared with 0.31 in DP8-17) and are tetradactyl and paraxonic. The digital impressions are short, broad, and subequal, and the proximal track margin is nearly straight and parallel to the long (mediolateral) axis of the track. Also similar to DP8-17, these tracks display large divarication between the lateral and medial digital impressions:  $131^\circ$  for the La Puerta ichnotaxon B manus tracks (based on Apesteguía and Gallina, 2011:fig. 3f) and  $164^\circ$  for DP8-17. The divarication angles of the digital impressions of the two tracks are also similar, with the angles between the impressions of digits II and III being nearly identical, and in both tracks, the angle between the impressions of digits I and II is more than double that between III and IV:  $69^\circ$  ( $I^\wedge II$ ),  $37^\circ$  ( $II^\wedge III$ ), and  $25^\circ$  ( $III^\wedge IV$ ) for La Puerta ichnotaxon B manus tracks (based on Apesteguía and Gallina, 2011:fig. 3f), and  $85^\circ$  ( $I^\wedge II$ ),  $38^\circ$  ( $II^\wedge III$ ), and  $41^\circ$  ( $III^\wedge IV$ ) for DP8-17.

In the absence of DP8-17 being associated with a pedal impression or a trackway, we consider this track to possibly represent a right manual impression based on the similarities with ichnotaxon B from the La Puerta Formation of Bolivia. Apesteguía and Gallina (2011) suggest that La Puerta Formation ichnotaxon B tracks could have been made by a stegosaurian, although in light of their tetradactyl pedal impressions, we suspect that an ankylosaurian affinity for the trackmaker is more likely.

Also similar to DP8-17 are some pedal tracks from trackways in the Upper Jurassic–Lower Cretaceous El Molino Formation, also in Bolivia, described by McCrea et al. (2001:fig. 20.27, trackway T/4/5/1). Because these tracks lack a metatarsal pad impression, it is possible that the trackmaker walked on the more distal

phalanges with a subunguligrade stance, or possibly, as suggested by McCrea et al. (2001:442), the trackmaker's pedes penetrated more deeply into the sediment, and it is this deeper layer that is now exposed. As a consequence, any similarity between this set of pedal tracks and DP8-17 is superficial and is most likely the result of variable preservation rather than similar morphology of the trackmaker's pes.

Although DP8-17 represents a track morphotype that is distinct from any other tracks preserved in Broome Sandstone, in the absence of any associated pedal tracks or trackway data, we feel that it not appropriate to name it. Given the likely thyreophoran nature of this track, we hereby refer it to Broome thyreophoran morphotype A. At present, DP8-17 is the only example of this particular track morphotype within the Broome Sandstone, suggesting that the trackmaker was a rare component of the area's Early Cretaceous dinosaurian fauna.

#### BROOME THYREOPHORAN MORPHOTYPE B (Figs. 54, 643E, 64E, S20; Table 17)

**Referred Material**—UQL-DP45-15(m), the natural mold of a right manus, additionally represented by WAM 15.12.706, a rigid polyurethane resin replica, WAM 94.6.9a, a gray latex cast (convex/positive hyporelief), WAM 94.6.9b, a white silicon cast (convex/positive hyporelief), and SAM P35757, a rigid epoxy resin and fiberglass replica (concave/negative epirelief). (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Locality, Horizon, and Age**—The specimen comes from DP45, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone. Track DP45-15 was taken to the Western Australian Museum in 1991 but was returned to Broome in 1994.

**Description**—Track DP45-15(m) is the natural mold of a single, pentadactyl, mesaxonic (basal digital impression length to track length ratio 0.33–0.68), right manus (Figs. 54, 643E, 64E, S20). The track is of medium size, wider than long (approximate proximodistal length 14.6 cm, mediolateral width 21.5 cm), with a maximum proximodistal length to maximum mediolateral width ratio of 0.68. Individual digital and metatarsodigital pad impressions are absent, indicating that entire palmar surface of the manus was covered in a continuous pad. The digital impressions are proportionately short and broad (maximum digital impression width to track length ratio 0.24–0.36). The impression of digit III extends farthest relative to the principal track axis, followed by the impressions of digits II and IV, and then the impressions of digits I and V, which are more proximally positioned. The total divarication angle between the axes of the impressions of digits I and V is  $104^\circ$ . The digital impressions are variable in length, ranging from 3.2 to 6.1 cm, with the impression of digit V being the shortest and that of digit I being the longest. The hypex between the impressions of digits IV and V is much more broadly concave than the narrow, more acutely angled hypices between the impressions of digits II and III and digits III and IV. The proximal track margin is slightly concave.

Closely associated with DP45-15(m) is a partial pedal track, DP45-15(p) (Fig. 54). Only the distal portion of this track is preserved. It is tridactyl, medium-sized (mediolateral width 20 cm; preserved proximodistal length of 16.6 cm), and mesaxonic. Whether this is a left or right track is unclear, making the determination of the numbering of the impressions of digits II and IV ambiguous. But given its close association with DP45-15(m), we tentatively interpret it as a right pedal track. The impressions of digits ?II and III are distally rounded and separated from the shallower, bluntly pointed impression of digit ?IV by a proximodistal ridge. The total

divarication between the axes of the impressions of digits ?II and ?IV is  $87^\circ$ . The digital impressions are roughly equal in width, ranging from 3.5 to 5 cm, with the impression of digit ?II being the narrowest and that of digit III being the widest. The hypex between the impressions of digits ?II and III is indistinct, likely due to erosion.

If DP45-15(m) and DP45-15(?p) represent a natural MP couplet, then the manual track lies craniomedial to the pedal track and the manus was strongly pronated. Alternatively, the trackmaker may have been in a sharp left turn when the manus was placed in the substrate.

**Remarks**—A photograph of DP45-15(m) first appeared in Long (1990:67). Another photograph of the entire DP45-15 boulder with both the manual and pedal track visible subsequently appeared in Dayton (1991), but with both tracks overlain with outlines. Long (1990:67) also published an outline interpretation of the DP45-15 manual track, but he linked it with the pedal track of DP45-5A (herein referred to *Luluichnus mueckeii*). In his brief accounts of these tracks and through the inclusion of outlines of DP45-15 and DP45-5A together as possible stegosaurian manual and pedal tracks in his figures, Long (1990:67, 1992a, 1993, 1998:127, 2002) implied either that these tracks were naturally associated or that they formed part of a trackway sequence. Alternatively, Long's (1990:67, 1992a, 1993, 1998:127, 2002) reference to a 'trackway' may relate to the manual and pedal tracks on the DP45-15 boulder. The outline of the DP45-15 pedal impression that was published by Dayton (1991) does appear to resemble Thulborn's (1990:fig. 6.39) conjectural stegosaurian pedal track, which both Long (1990, 1992a, 1993, 1998, 2002) and others (Thulborn et al., 1994; Thulborn, 1998; Henderson et al., 2000; Rich and Vickers-Rich, 2003a; Willis and Thomas, 2005) have stated helped with the initial determination of the tracks (DP45-15[m] and DP45-5A[lp]) as having been

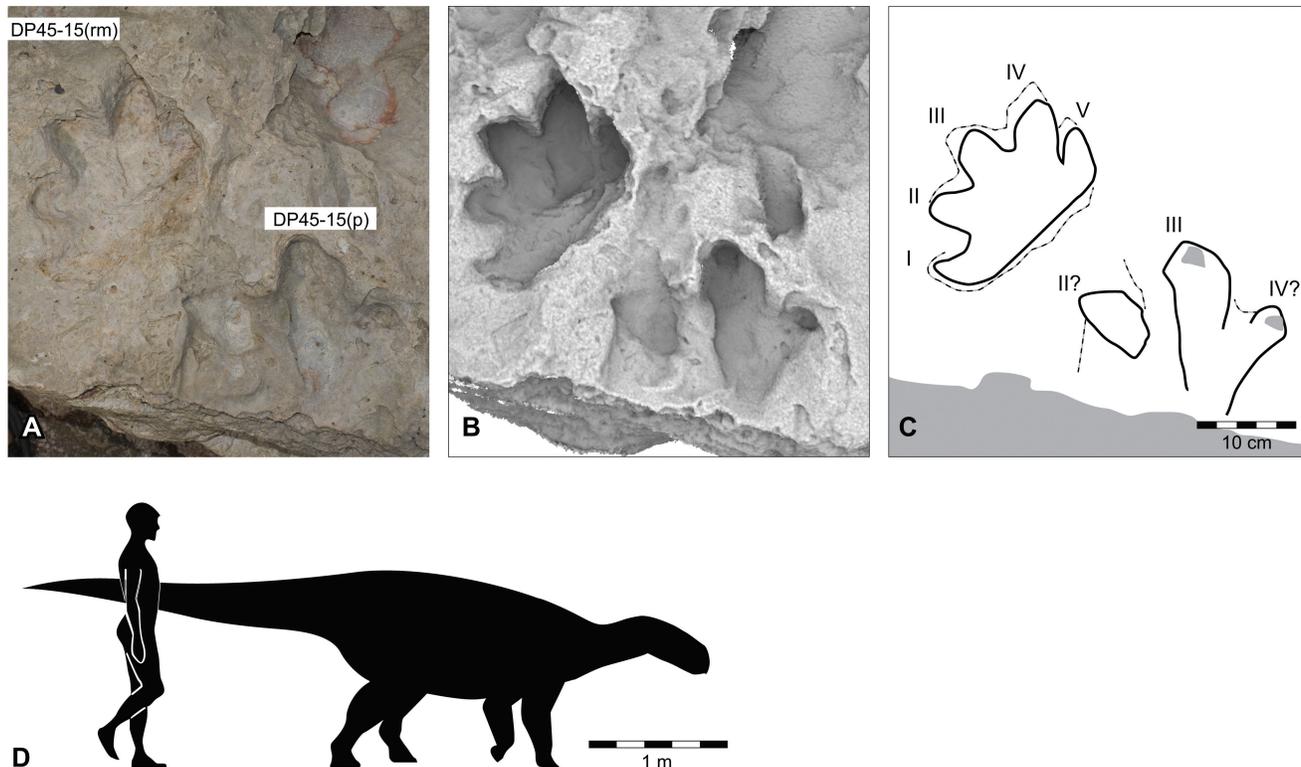


FIGURE 54. Broome thyreophoran morphotype B, from the Yanijjarri–Lurujarri section of the Dampier Peninsula, Western Australia. Right manual impression and associated ?right pedal impression, UQL-DP45-15, preserved in situ as **A**, photograph; **B**, ambient occlusion image; and **C**, schematic interpretation. **D**, silhouette of hypothetical Broome thyreophoran morphotype B trackmaker based on UQL-DP45-15(m), compared with a human silhouette. See Figure 19 for legend.

TABLE 17. Measurements of tracks assigned to Broome thyreophoran morphotypes A and B, from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UOL-DP)	Length (cm)	Width (cm)	L/W	De (De/L)	I <sup>^</sup> II	II <sup>^</sup> III	III <sup>^</sup> IV	IV <sup>^</sup> V	Total	bdI (I/L)	bdII (II/L)	bdIII (III/L)	bdIV (IV/L)	bdV (V/L)	bdw I (I/L)	bdw II (II/L)	bdw III (III/L)	bdw IV (IV/L)	bdw V (V/L)
8-17	9	29	0.3	—	85	38	41	—	162	4.1 (0.46)	3 (0.33)	3.8 (0.42)	6.1 (0.68)	—	2.3 (0.26)	3.7 (0.41)	5 (0.56)	4.9 (0.54)	—
45-15(m)	13.5	19.7	0.7	—	14	28	62	3	104	6.1 (0.45)	4.2 (0.31)	4.50 (0.33)	5.40 (0.4)	3.20 (0.24)	4.0 (0.3)	3.30 (0.24)	4.40 (0.33)	4.90 (0.36)	3.80 (0.28)
45-15(p)	3.1	5.5	—	—	—	—	—	—	47	3.1	5.5	—	—	—	4.3	6.8	—	—	—

bdI = basal digital impression length; bdw = basal digital impression width; De = digital impression extension; II = impression of digit II; III = impression of digit III; IV = impression of digit IV; V = track length; W = track width. ^ denotes angle between respective digital impressions.

made by a stegosaurian. Regardless of exactly which tracks he was referring to, Long (1990, 1992a, 1993, 1998, 2002) considered the association of pentadactyl manual tracks with tridactyl pedal tracks to be indicative of a stegosaurian trackmaker. Thulborn subsequently appears to confirm this identification, although specific statements ranged from “quadrupedal ornithischians” (Thulborn et al., 1994:87) to “quadrupedal ornithischians provisionally identified as thyreophorans (armoured dinosaurs, perhaps stegosaurs)” (Thulborn et al., 1994:1) and “thyreophoran[s] provisionally identified as stegosaurs” (Thulborn, 2002:85, 92), and it is not entirely clear which tracks are being referred to. Regardless of the ambiguity surrounding these various accounts, illustrations by Long (1990:67, 1998:127, 130) of a pentadactyl manual track (DP45-15[m]) and a tridactyl pedal track (DP45-5A[lp]) as possible stegosaurian ichnites have been misinterpreted by others as these two tracks representing a natural association (e.g., Scanlon, 2006; Milàn and Chiappe, 2009; Senter, 2010; Apesteguía and Gallina, 2011).

We have been able to ascertain that prior to its removal in 1991, the boulder on which the DP45-15 manual and pedal tracks are preserved was several meters from the platform that the DP45-5 tracks occurred on, and that neither set of tracks was directly associated with the (still) in situ DP45-6 trackway (assigned herein to *Luluichnus*). Although all these tracks appear to be preserved in the same track horizon at DP45, any clear connection between the now ex situ boulders (DP45-15 and DP45-5A+B) and the larger in situ rock platform has long been lost as a result of erosion. This, combined with our current knowledge of *Luluichnus* manual tracks lacking digital impressions and thus being distinct from the pentadactyl manual track on DP45-15, suggests that DP45-6 and DP45-15 are not associated nor are they part of a trackway. In the absence of other track or trackway data, it is therefore not possible to confidently ascertain if these different tracks pertain to the same trackmaker or ichnotaxon. Moreover, despite the fact that the manual and pedal tracks on DP45-15 are closely associated, we do not think it possible to confidently assign them to a single trackmaker, nor a single ichnotaxon. These manual and pedal tracks differ in terms of their principal axes of alignment, with the long axis of the manual track at 35° to that of the pedal track; Fig. 54A–C). The pronation of the manus is much greater than is observed in any other quadrupedal ornithischian trackway that we are aware of. Alternatively, if the manual and pedal tracks are from the left side of the trackmaker’s body, the numbering of the digital impressions on both tracks would need to be reversed to how we have interpreted them, and the resulting supination of the manus would also be more extreme than that seen in other described thyreophoran trackways. In light of these observations, and in the absence of additional tracks to suggest otherwise, we do not consider DP45-15(m) and DP45-15(p) to represent a natural couplet.

Although they may not pertain to the same trackmaker, in terms of their overall size and general characteristics, DP45-15 (m) and DP45-15(p) are reminiscent of *Luluichnus mueckeii*. The absolute size of the manual track and at least the preserved part of the pedal track is comparable to the respective tracks assigned to *L. mueckeii*, as is the apparent degree of heteropody. The tridactyl nature of DP45-15(p) and the shape and size of its digital impressions is also similar to those pedal tracks assigned to *L. mueckeii*. But further comparisons are limited by the incomplete nature of the track. With regard to DP45-15(m), although its overall oval outline is similar to that of manual tracks assigned to *L. mueckeii* (e.g., DP45-6[lm1]; Figs. 50, 51), an obvious point of difference is the lack of digital impressions on the latter. Although DP45-6(lm1) is a shallow track, and the lack of digital impressions could either be a consequence of the manus having been only faintly impressed or the track being partly eroded, the lack of digital impressions on deeper *L. mueckeii* tracks (DP45-5A, B; Fig. 51) suggests that this is a morphological characteristic

of the trackmaker and hence the ichnotaxon. On this basis, and based on the tracks that we have been able to describe, we feel confident in distinguishing DP45-15(m) and DP45-15(p) from *L. mueckei*, but we recognize that further discoveries may show them to be assignable to the same ichnotaxon. For the time being, however, there is insufficient evidence to support this idea.

Among the other dinosaurian tracks of the Broome Sandstone, DP45-15(m) is most similar to manual tracks assigned to *Garbina roeorum*. Both track types are wider than they are long, with proportionately short, broad digital impressions arranged in a gentle arch. However, an obvious difference between the two tracks relates to the number of digital impressions: DP45-15(m) is pentadactyl and the manual tracks of *G. roeorum* are tetradactyl. Other purported pentadactyl manual tracks have been reported from the Broome Sandstone by McCrea et al. (2012: fig. 28a, b), but these appear to be erroneous. The ‘pentadactyl’ tracks that are illustrated by McCrea et al. (2012:fig. 28a) are actually tetradactyl. One of these tracks (DP8-17) we report as pertaining to Broome thyreophoran morphotype A (see Figs. 53, 63D, 64D, S19), whereas the other (DP8-8; see fig. 48A, B) is assignable to cf. *G. roeorum*. One of the other ‘pentadactyl’ tracks figured by McCrea et al. (2012:fig. 28a) appears to be hexadactyl. This track (DP1-6; see Fig. 47G, H) has at least three, possibly four, digital impressions, but we see no evidence for a fifth or sixth, and we have assigned it to *G. roeorum*, noting that the caudal margin of the track has been lost to erosion (see the remarks on *G. roeorum* for further details).

Outside of the Broome Sandstone, pentadactyl manual tracks similar to DP45-15(m) have been assigned to several ichnotaxa, most of which are typically regarded as pertaining to quadrupedal (or facultatively bipedal) ornithischians. These include *Tetrapodosaurus borealis* from the Lower Cretaceous (Aptian–Albian) Gething Formation and possibly the Lower Cretaceous (lower Albian) Gates Formation, both in Alberta (Sternberg, 1932; McCrea et al., 2012:fig. 28), *Hypsiloichnus marylandicus* from the Lower Cretaceous (Aptian) Patuxent Formation of Maryland and Virginia (Stanford et al., 2004:figs. 3.1, 3.2, 4–6), *Moyenisauropus* spp. from the Lower Jurassic (Hettangian) Holy Cross Mountains of Poland (Gierlinski and Potemka, 1987:figs. 7, 8b; Gierlinski, 1991:fig. 5, 1999:pl. II, Fig. 6), *Ceratopsipes goldenensis* from the Upper Cretaceous (Maastrichtian) Laramie Formation of Colorado (Lockley and Hunt, 1995), and two unnamed ichnotaxa (ichnotaxa C and D) from the Upper Jurassic–Lower Cretaceous La Puerta Formation of Bolivia (Apesteguía and Gallina, 2011). Manual tracks assigned to *Deltapodus brodericki* from the Upper Jurassic (Aeleanian–Bajocian) Ravenscar Group of the Cleveland Basin, Yorkshire, U.K. (Whyte and Romano, 1994, 2001b), and the Brushy Basin Member of the Upper Jurassic (Kimmeridgian–Tithonian) Morrison Formation, Utah (Milán and Chiappe, 2009), *Deltapodus* sp. from the Upper Jurassic Tereñes Formation of Asturias, Spain (Lires et al., 2002; Garcia-Ramos et al., 2006; Gierlinski and Sabath, 2008:fig. 9B), cf. *Apuilosauropus* sp. from the Lower Cretaceous (Albian) Dakota Group of Colorado (Kurtz et al., 2001; Gierlinski and Sabath, 2008:fig. 9C), and some unnamed tracks from the Lower Jurassic (Pliensbachian) Aganane Formation of Morocco (Jenny and Josen, 1982) are also of a similar shape to DP45-15(m) and are potentially pentadactyl, but the digital impressions (with the exception of likely medially directed pollex impressions) are proportionately very short and difficult to discern with certainty.

The manual impression DP45-15(m) is similar to manual tracks assigned to *Tetrapodosaurus borealis* in that both have well-defined, proportionately short, blunt digital impressions that are arranged in a loose arc. However, DP45-15(m) can be distinguished from *T. borealis* on account of its proportions (*T. borealis* manual tracks being longer proximodistally relative to their mediolateral width). Tracks assigned to *T. borealis* also have a much larger, typically caudally directed impression of

digit V (relative to the principal track axis) and a concave rather than linear proximal track margin (see Sternberg, 1932:75; McCrea et al., 2001:figs. 20.4, 20.12, and 20.13). The impression of digit I is also often caudally directed relative to the principal track axis in *T. borealis*, whereas in DP45-15(m) it is directed cranially (relative to the principal track axis).

In addition to the ‘pentadactyl’ tracks discussed previously, McCrea et al. (2012) also considered DP45-15(m) to be potentially assignable to *Tetrapodosaurus*, based on the morphology of the manual track (pentadactyl) and its purported association with a tetradactyl pedal track. Although DP45-15(m) is pentadactyl, it differs from the manual tracks of *Tetrapodosaurus* in a number of respects (discussed above) and is linked to a tridactyl not tetradactyl pedal track. For these reasons, we do not think it can be assigned to *Tetrapodosaurus*. McCrea et al. (2012:fig. 29) also figured what they considered to be a tetradactyl pedal track from outside the study area as cf. *Tetrapodosaurus borealis*. Although we have not been able to locate this track, based on the photos presented McCrea et al. (2012:fig. 29), we are not convinced that its morphology is comparable to that of the pedal tracks of *T. borealis*, or if it even represents a track. To conclude, we consider DP45-15(m) to be distinct from manual tracks assigned to *T. borealis*, and we find no additional evidence for any other tracks from the Broome Sandstone that can be referred to cf. *T. borealis*.

Track DP45-15(m) can be distinguished from manual tracks assigned to *Hypsiloichnus marylandicus* on account of the latter’s proportionately longer digital impressions, in particular that of digit V, which, similar to *T. borealis*, is caudally directed relative to the principal track axis. *Hypsiloichnus marylandicus* manual tracks also consistently lack a well-defined proximal margin (see Stanford et al., 2004:figs. 3.1, 3.2, 4–6), which may be indicative of the fact that they are typically regarded as having been made by a trackmaker that was not an obligate quadruped. This characteristic contrasts with the well-defined proximal track margin of DP45-15(m).

Similar to *Tetrapodosaurus*, *Ceratopsipes goldenensis* manus tracks share with DP45-15(m) proportionately short, triangular digital impressions that are arranged in a loose arc. However, the digital impressions of *C. goldenensis* tracks are shorter and more rounded than those of DP45-15(m), and the impressions of digits I and V are typically caudally directed relative to the principal track axis. The proximal track outline is also distinctly concave (Lockley and Hunt, 1995:fig. 10).

Manual tracks assigned to *Moyenisauropus* (Gierlinski and Potemka, 1987) are of similar proportions to DP45-15(m), with a maximum proximodistal length to mediolateral width ratio of approximately 0.6 (compared with 0.7 in DP45-15[m]). The triangular impressions of digits I–IV are also reminiscent of those on DP45-15(m), but what is interpreted as the impression of digit I is noticeably narrower, probably indicative of the fact that this impression may have been made by a medially directed pollex ungual. Compared with DP45-15(m), the impressions of digits I and V on *Moyenisauropus* spp. manual tracks are medially and laterally directed relative to the principal track axis, and the overall arcuate arrangement of the digital impressions is more uniform.

Of the two pentadactyl manual track morphotypes from the La Puerta Formation of Bolivia, DP45-15(m) most closely resembles ichnotaxon C (Apesteguía and Gallina, 2011:fig. 4). Although also pentadactyl, DP45-15(m) differs from ichnotaxon D (Apesteguía and Gallina, 2011:fig. 5) in that the latter manual tracks are proportionately much shorter proximodistally (maximum proximodistal length to mediolateral width of approximately 0.35 compared with 0.7 in DP45-15[m]), the digital impressions are uniformly shorter, and the proximal track margin is gently convex relative to the principal track axis. On the other hand, the overall proportions of La Puerta ichnotaxon C manual tracks are very similar to those of DP45-15(m) (the maximum proximodistal length to mediolateral width ratio for both tracks is approximately 0.6). The digital impressions associated with

both tracks are also similarly shaped and proportionately of approximately equivalent sizes relative to the overall track outline; both tracks are mesaxonic, with the impression of digit I offset from that of digit II, with the impression of digit III extending distally the farthest, and the impressions of digits II and IV extending distally to approximately the same level. The impressions of digits I and V are subequally more proximally positioned on both tracks. Also of note is the fact that the impression of digit V on both tracks is considerably smaller than the other digital impressions. Unlike DP45-15(m), the impressions of digits I–IV on the La Puerta ichnotaxon C manual tracks are tipped by small unguis impressions. The hypex between the impressions of digits I and II on the La Puerta ichnotaxon C manual tracks is only gently concave, and much less incised than the ‘U’-shaped hypex of DP45-15(m). The divarication angles between the various digital impressions are also slightly different: 55° (I^II), 31° (II^III), 15° (III^IV), and 3° (IV^V) for La Puerta ichnotaxon C manual tracks (based on (based on Apesteguía and Gallina, 2011: fig. 4), and 14° (I^II), 28° (II^III), 62° (III^IV), and 0° (IV^V) for DP45-15(m).

Apesteguía and Gallina (2011) suggested that the small size of the impression of digit V on La Puerta ichnotaxon C manual tracks and the narrow hypex between the impressions of digits V and IV indicated that, on the trackmaker, these digits were syndactylous. Although this supposition is hard to confirm based solely on the tracks, the position and size of the impression of digit V on both the La Puerta ichnotaxon C manual tracks and DP45-15(m) are consistent with conjectural stegosaurian manual tracks illustrated by Thulborn (1990:fig. 6.39), which was based on the reconstructed manual skeleton of USNM 4937 (after Gilmore, 1914), a Morrison Formation stegosaurian of indeterminate genus and species, originally described as *Stegosaurus sulcatus* (Maidment et al., 2008). The manus of this dinosaur is functionally tetradactyl, with a phalangeal formula of 2-1-1-1-0 (Gilmore, 1914; Thulborn, 1990; Senter, 2010: fig. 2). It is unclear whether any phalanges were present on digit V, but the distal end of metacarpal V suggests that at least one may have been present (Galton and Upchurch, 2004). Both DP45-15(m) and the La Puerta ichnotaxon C manual tracks are a very good match for this type of manual skeleton; on this basis, it seems plausible to assume that both were made by some type of stegosaurian trackmaker. However, the mediolaterally broad, pentadactyl pedal tracks associated with La Puerta ichnotaxon C are not consistent with the tridactyl pedal skeleton of stegosaurians (e.g., *Kentrosaurus* and *Stegosaurus*; Galton and Upchurch, 2004), and Apesteguía and Gallina (2011) consequently favored a basal thyreophoran trackmaker.

Despite the close similarity between DP45-15(m) and the La Puerta ichnotaxon C manual tracks, there are some minor morphological differences relating to the morphology and orientation of the digital impressions that allow these two track types to be distinguished from each other. Although the manual tracks can be considered representative of two very similar morphotypes, in the absence of any trackway data or the definitive association of DP45-15(m) with any pedal tracks (most notably DP45-15[p]), we do not think it possible to formally link this track with La Puerta ichnotaxon C, which, as yet, has not been named. In recognition of its distinctive morphology and pending the discovery and documentation of additional track data, we therefore place DP45-15(m) in Broome thyreophoran morphotype B.

Tracks of Broome thyreophoran morphotype B are rare in the study area, being restricted to a single track at one locality, and we are not aware of similar tracks occurring in other parts of the Dampier Peninsula. On this basis, until further discoveries or analysis of existing data show otherwise, it seems reasonable to assume that the trackmakers responsible for such tracks were rare within the Broome Sandstone’s dinosaurian fauna and may have displayed a preference for a specific habitat.

## INDETERMINATE DINOSAURIAN TRACKS

### BROOME INDETERMINATE DINOSAURIAN MORPHOTYPE A

(Figs. 55, 56, 60, S21; Table 18)

**Referred Material**—UQL-DP1-2, a trackway comprising at least nine pedal tracks, preserved as natural molds. (From this point onwards, except in figures and tables, the UQL portion of the specimen number will be excluded from references to these specimens.)

**Location, Horizon, and Age**—The referred trackway is preserved in situ at UQL-DP1, in the intertidal zone of the Yanijarri–Lurujarri section of the Dampier Peninsula, in the west Kimberley region of Western Australia, and derives from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone.

**Description**—Trackway DP1-2 is at least 16.2 m long and consistently less than 1.5 m wide and comprises nine approximately equal-sized (in area) tracks striking northwards (Fig. 55). Each impression is small (40–55 cm in length), whereas track depth (approximately 2–8 cm with respect to identified margins) varies considerably. The individual track outlines are variable, and in combination with the irregular topography of the rocky surface within the span of the trackway, we are not certain of an overarching common track shape. Several smaller complete and partial impressions occur near track 7 of the sequence (Fig. 55C, D), and although these may feasibly relate to the nine larger impressions of DP1-2, the disparity among them, and among tracks at DP1 in general, prompts us to cautiously treat these as extraneous for the time being. Additional poorly preserved isolated tracks occur congregated 10 m to the east of track 6 of DP1-2 (most are approximately 45–60 cm in length). These extraneous isolated tracks might also relate to the trackmaker of DP1-2, although we do not consider them further, given the spatial gap.

The best-preserved tracks in DP1-2 are the sixth and first impressions in that order, which are piriform and keyhole-shaped, respectively. Other tracks are poorly defined in outline, and a few are difficult to demark entirely, with their dimensions being uncertain. Each track is generally longer than wide (Fig. 55; Table 18). Some are associated with displacement rims (tracks 2, 3, 6–8). All nine tracks are considered pedal impressions on account of their similar size and the similar shapes of the best-preserved tracks of the sequence. The sixth track is piriform, with clear margins demarking the internal area of the track (Fig. 55E–G). A well-formed rim is parallel with the caudal and western margins of the track, and a narrow rim is present cranially. A small indentation on the right of the track may represent a digital impression; otherwise indications of phalanges are not obvious. The internal area of the cranial half of this impression is filled with sediment that constitutes partially removed infilling. The surface texture of this sediment is irregular, unlike the floor of the rear of the track, which is smooth, and which therefore corresponds to a mold of the foot of the trackmaker. The first track is deeply impressed caudally and has a narrow heel region with walls that are declined inwardly toward the center of the track. The fifth track, which is only partially preserved, appears to show a (?laterally) curved digital trace. Clear manual impressions were not recognized aside from nondescript faint traces associated with tracks 5 and 6, although these probably do not represent traces of significance.

It is difficult to establish which impressions are the left and right steps, respectively, because of the extreme narrowness of the trackway and the often non-alternating placements of several pairs of sequential steps within the trackway. A map of DP1-2 (Fig. 55C) demonstrates that tracks 1–2, 4–5, and 7–9 are almost aligned with each other with respect to the long axis of the trackway, whereas the relatively eastward-displaced positions of

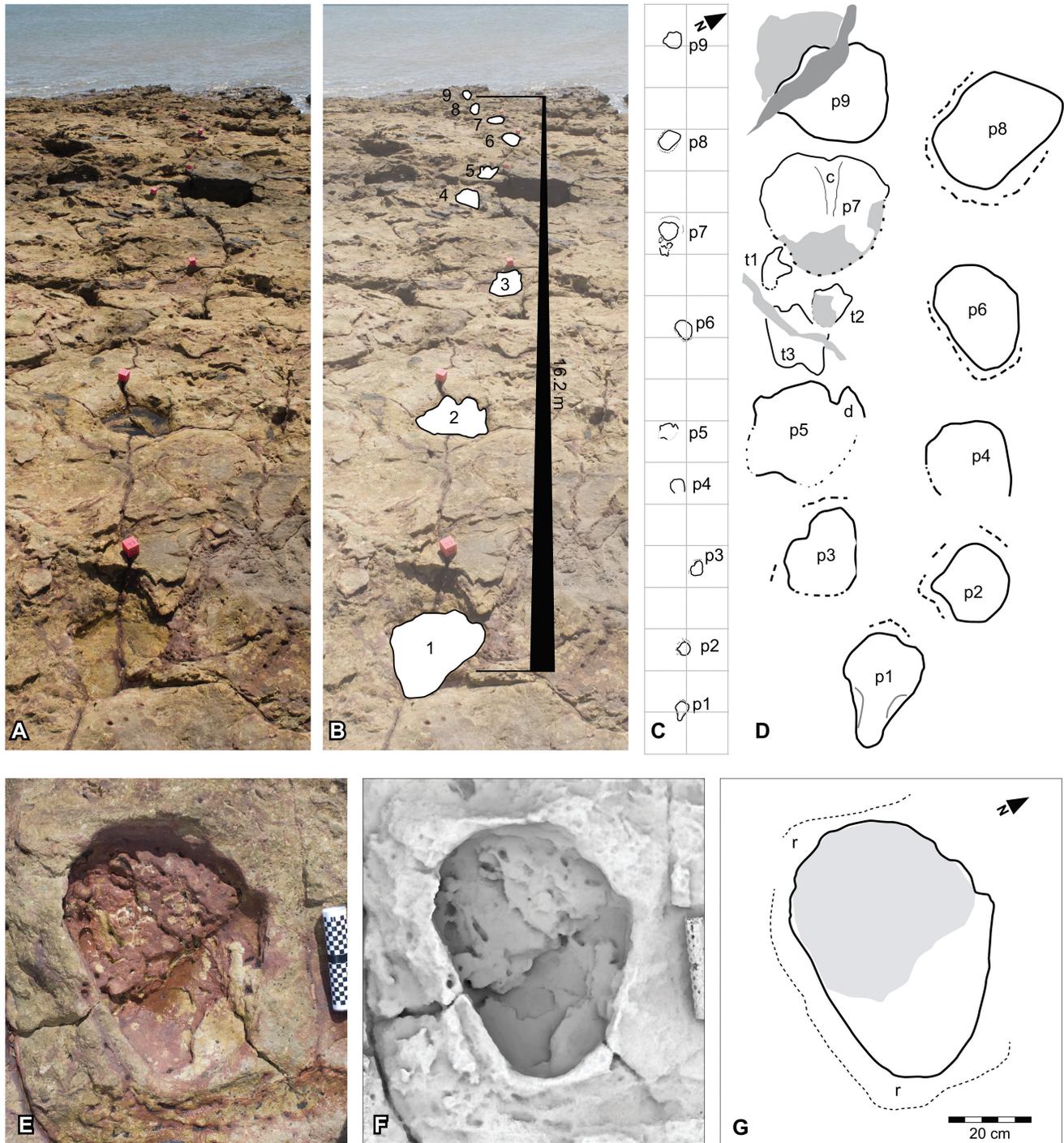


FIGURE 55. Broome indeterminate dinosaurian morphotype A, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Field photographs of trackway UQL-DP1-2, viewed from the south: **A**, photograph (painted cubes in A are placed at the cranial end of each track); and **B**, photograph overlain with positional traces of sequential tracks (not to scale). **C**, map of trackway UQL-DP1-2 on a 1 m grid. **D**, enlarged schematic outlines of individual pedal impressions, UQL-DP1-2(?lp3[p6]), preserved in situ as **E**, photograph; **F**, ambient occlusion image; and **G**, schematic interpretation. **Abbreviations:** c, internal crease/ridge; d, possible digital impression; h, heel region; r, rim; sf, sediment infill; t1–2, extraneous tracks, discussed in the text. See Figure 19 for legend.

tracks 3 and 6 are suggestive of being dextral impressions. However, the crossing-over of the trackway midline in sections precludes any extrapolation from the positions of seemingly displaced tracks, particularly because the best-preserved one,

track 6, appears outwardly rotated to the west with respect to the long axis of the trackway, thus hinting that it may instead be a left impression. Despite the inconsistent morphological preservation, DP1-2 presents some unusual trackway parameter

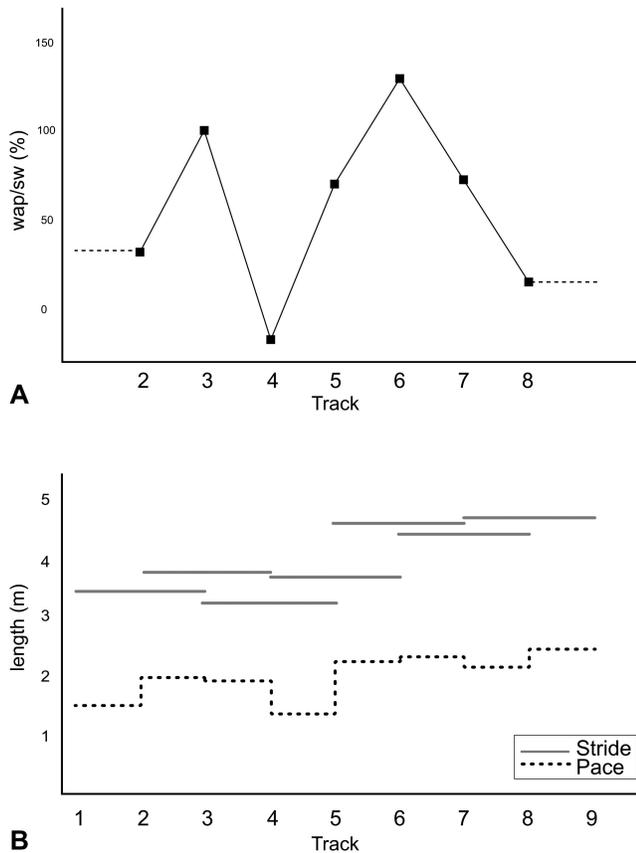


FIGURE 56. Broome indeterminate dinosaurian morphotype A, from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. Plots showing fluctuations in selected parameters along trackway UQL-DP1-2. **A**, a proxy for ‘trackway ratio’ (Romano et al., 2007), adapted for bipedal trackmakers: ratio =  $[\text{wap}/\text{sw}] \times 100$ , where **sw** is stride width (equal to pedal track width in bipeds), and **wap** is width of the pace angulation. Larger values indicate a wider gauge, and negative values indicate the footfalls have significantly crossed the trackway midline; **B**, pace and stride lengths (pace as dashed lines; stride lengths as solid gray lines).

information. The average pedal trackway ratio is 64.7% (Fig. 56A). Acknowledging the small sample size of tracks, the stride lengths appear to strongly increase toward the northern

end of the spectrum, whereas the pace lengths vary between 1.5 and 2.5 m, but they do not demonstrate as striking a trend (Fig. 56B).

**Remarks**—The candidates for the trackmaker of DP1-2 were either a large biped or a quadruped whose manual impressions were not preserved, degraded, or entirely obliterated. Due to the variable and in general poor preservation at the site, we consider both alternatives possible and thus review each option briefly. Track 6 in DP1-2, the most complete impression, resembles in size and shape many other small- to medium-sized sauropod tracks known from Europe or East Asia (e.g., Gierlinski and Sawicki, 1998; Gierlinski, 2009; Xing et al., 2015d, 2016c), initially leading us to consider that DP1-2 was produced by a sauropod trackmaker. In contrast, the keyhole outline of track 1 is suggestive of other small sauropod tracks from the Early Cretaceous of China (Xing et al., 2010:fig. 6), whereas the caudally narrow portion of this track is evocative of the form of the corresponding section in stegosaurian pedal tracks (such as figured in Whyte and Romano, 1994; Lockley and Hunt, 1998; Belvedere and Mietto, 2010). A similar caudal shape also occurs in some instances of the Broome stegosaurian ichnospecies *Garbina roeorum*, ichnogen. et ichnosp. nov. (Fig. 48), described herein, although these tracks tend to be comparatively shallower in that section.

Despite the morphology of tracks 1 and 6, the high pedal trackway ratio of 64.7% of DP1-2 substantially exceeds any previously calculated ratios of known narrow-gauge sauropod trackways (Romano et al., 2007:table 1), which disfavors both sauropodan and stegosaurian affinities. Even disregarding the first and last tracks in the sequence, for which the ‘overall width’ used to calculate the trackway ratio (Romano et al., 2007:259) is partly extrapolated from adjoining preserved tracks (the third and seventh tracks), a recalculated average pedal trackway ratio is still high at 60%. This latter scaled-down ratio still corresponds to a gauge far narrower than the narrowest-gauge sauropod trackway—those listed as *Parabrontopodus*-like (Romano et al., 2007:table 1). Similarly, stegosaur trackways exhibit a range of trackway gauge ratios much less than DP1-2, ranging between wide (Romano et al., 2007; Xing et al., 2013a) to marginally narrow (Cobos et al., 2010). It appears, based on the trackway parameter data, that DP1-2 is unlikely to be a sauropod or stegosaur trackway.

The high pace angulation between the tracks of DP1-2 (Table 18) is consistent with trackways of large bipeds rather than quadrupeds, as exemplified by Upper Jurassic and Cretaceous trackways from Langenberg and Lark quarries and Lotus Fortress (Romilio and Salisbury, 2011; Lallensack et al., 2015; Xing et al., 2015). Although none of the individual tracks bear morphologies expected of a bipedal dinosaur such as an iguanodontian or large theropod, it seems most prudent to rely on the

TABLE 18. Track and trackway measurements for Broome indeterminate dinosaurian morphotype A, from the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Track (UQL-DP)	Length (cm)	Width (cm)	L/W	Track rotation	Pace (cm)	Stride (?right autopodium) (cm)	Stride (?left autopodium) (cm)	Pace angulation
1-2(p1)	55	40	1.37	10°	—	—	na	na
1-2(p2)	40	38	1.05	~0°	152	na	—	171°
1-2(p3)	~42	38	~1.10	~0°	200	350	na	157°
1-2(p4)	>40	43	—	—	192	na	385	176°
1-2(p5)	60	55	1.09	~25°	141	336	na	158°
1-2(p6)	52	42	1.24	21°	234	na	375	158°
1-2(p7)	~43	45	~0.96	~0°	240	464	na	165°
1-2(p8)	~50	36	~1.39	~46°	225	na	460	178°
1-2(p9)	40	42	0.95	0°	250	475	na	na

Pace distances are between the track in the same data row and the preceding track; stride distances are between the track listed in the same data row and the preceding track of the same autopodium (two data rows before it); pace angulation at a given data row is the angle between the track of the same row, and of the tracks listed in preceding and succeeding data rows. na, not applicable.

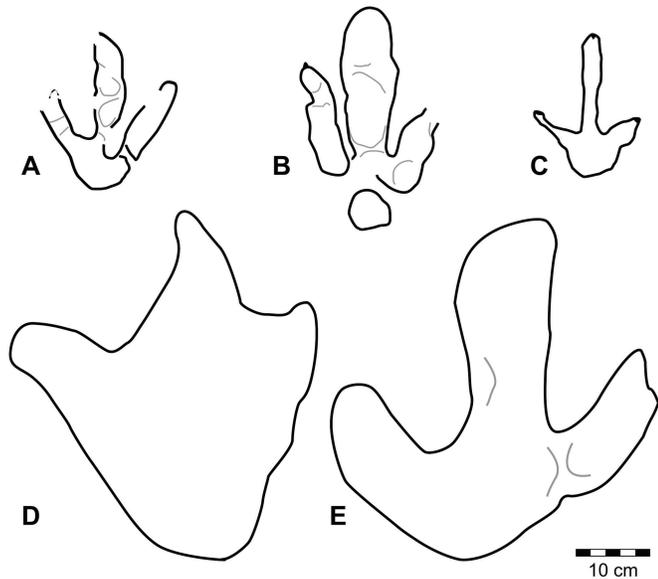


FIGURE 57. Schematic outlines of representative theropod tracks from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. **A**, *Megalosauropus broomensis*, left pedal impression, UQL-DP35-1; **B**, *Yangtzeopus clarkei*, ichnosp. nov., right pedal impression, UQL-DP57-1; **C**, Broome theropod morphotype A, possible left pedal impression, UQL-DP25-1; **D**, Broome theropod morphotype B, possible left pedal impression, UQL-DP52-1; and **E**, Broome theropod morphotype C, left pedal impression, UQL-DP6-3. All schematic outlines are to the same scale.

trackway pattern data as providing the best indicator of the trackmaker. Similar cases of bipedal trackways with individual impressions of poorly defined morphology due to degradation (Romilio and Salisbury, 2014), or to absence of preservation in whole (Lallensack et al., 2015) or parts of the trackway (Xing et al., 2015a; Smith et al., 2016), are known, which is in keeping with such an assignment for DP1-2.

## DISCUSSION

### Composition and Diversity of the Ichnofauna

For over two decades, the Broome Sandstone has been touted as having one of the most diverse dinosaurian ichnofaunas in the world. Following the initial work on *M. broomensis* (Glauert, 1952; Colbert and Merrilees, 1967), brief reports in the early 1990s suggested the occurrence of at least another nine types of tracks, referable to theropod, sauropod, ornithopod, and thyreophoran trackmakers, at scattered tracksites spread over more than 80 km of coastline north of Broome (Long, 1990: eight types of tracks; Long, 1992a: seven types of tracks; Long, 1993: six types of tracks; Thulborn et al., 1994: 10 types of tracks; Kenneally et al., 1996: eight types of tracks; Rich and Vickers-Rich, 2003a: 10 types of tracks). More recently, it has been proposed that the number of track types could be as high as 16 (Commonwealth of Australia, 2011: 15 types of tracks; Thulborn, 2012: 16 types of tracks), and that the sites are spread over more than 200 km of coastline (Commonwealth of Australia, 2011; Thulborn, 2012). Conversely, a recent government report by McCrea et al. (2012) suggests that the number of track types may have been inflated, and that there are only six to eight. Significantly, however, the only substantial research that has been published on any of the dinosaurian tracks from the Broome Sandstone is the original description of *M. broomensis* (Colbert and

Merrilees, 1967), a preliminary study of the sauropod tracks, and an account of the ways in which the heavy passage of sauropod trackmakers may have shaped the Dampier Peninsula's Early Cretaceous landscape (Thulborn et al., 1994; Thulborn, 2012). Descriptive accounts of the other types of dinosaurian tracks have been very limited in terms of detail and comprise only brief comments, sometimes accompanied by photographs or (often erroneous) schematics (e.g., Long, 1990, 1998; Thulborn et al., 1994; Thulborn, 2002, 2012; see Systematic Paleozoology for further details). In many instances, only the number of potential track types is stated, with no further clarification as to what these may pertain to beyond broad (ichno)taxonomic groups; namely, theropod, sauropod, ornithopod, and quadrupedal ornithischian trackmakers (e.g., Long, 1992a; Thulborn et al., 1994; Rich and Vickers-Rich, 2003a). Thus, with the majority of dinosaurian track types in the Broome Sandstone not having been adequately described and, for various reasons, the full extent and nature of the Dampier Peninsula's dinosaurian tracksites never having been addressed in detail, the overall scientific significance of the ichnofauna has remained enigmatic.

The results of this study indicate that intertidal exposures of Broome Sandstone within the Yanijarri–Lurujarri section of the Dampier Peninsula contain at least 11 and possibly as many as 21 different types of dinosaurian tracks (Table 19; Figs. 57, 59, 61, 63). Eleven of these track types can formally be assigned or compared to existing or new ichnotaxa, whereas the remaining 10 represent morphotypes that, although distinct, are currently too poorly represented to confidently assign to existing or new ichnotaxa. There are also a number of presently indeterminate tracks that may be assignable to new or existing track types and may further add to this list if and when data pertaining to new, presently undocumented tracks in the study area come to light. Among the ichnotaxa that we have recognized, only two (*Megalosauropus broomensis* and *Wintonopus latomorum*) belong to existing ichnotaxa, and two compare to new ichnotaxa but display a suite of morphological features suggesting that they may be distinct in their own right and are therefore placed in open nomenclature (one as cf. *Luluichnus* and one as cf. *Garbina*). Six of the ichnotaxa that we have identified are new: *Yangtzeopus clarkei*, *Oobardjidama foulkesi*, *Wintonopus middletonae*, *Walmadanyichnus hunteri*, *Garbina roeorum*, and *Luluichnus mueckeii*. In total, we have identified 21 different track types: five different types of theropod tracks (Figs. 57, 58), at least six types of sauropod tracks (Figs. 59, 60), four types of ornithopod tracks (Figs. 61, 62), and six types of thyreophoran tracks (Figs. 63, 64) (Table 19). We readily acknowledge that future research may demonstrate that some of the morphotypes and provisional assignments that we have proposed may be shown to pertain to new or existing ichnotaxa, either singularly or in combination, such that the total number of track types may change, but until such time when this can be demonstrated unequivocally, we feel that it is in the interests of taxonomic stability to treat all the morphotypes and comparative assignments (e.g., cf. *Garbina* and cf. *Luluichnus*) that we have recognized as distinct track types.

In accordance with the wishes of Goolarabooloo Traditional Custodians and in order to protect the tracksites in the absence of any existing management strategy, we are not at liberty to discuss the exact location of various tracks or tracksites within the study area. Nevertheless, a number of important points can be made with regard to the stratigraphic distribution and abundance of various track types within the main parts of the study area (e.g., the Yanijarri, Walmadany, and Kardilakan–Jajal Buru areas; Figs. 1, 65). Although each of these areas was found to contain multiple horizons pertaining to Lithofacies Association 2, in most instances the majority of tracksites in any one area appear to occur in a single horizon (see Figs. 9–11). Although the extent of each of the main track-bearing horizons is

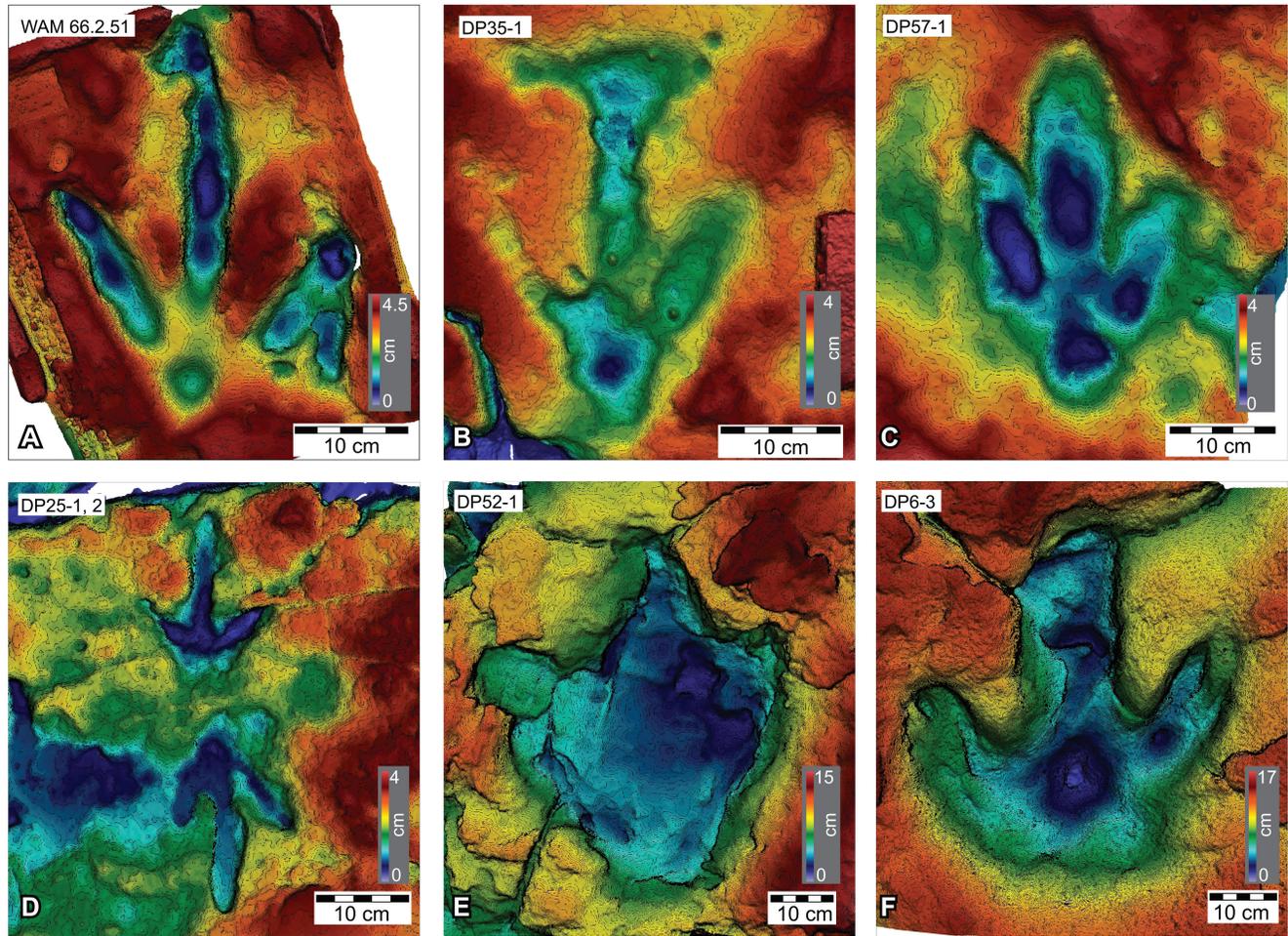


FIGURE 58. Color ramp images of selected theropod track DEMs. **A**, left pedal impression, *Megalosauropus broomensis*, left pedal impression, holotype WAM 66.2.51; **B**, *M. broomensis*, left pedal impression, UQL-DP35-1; **C**, *Yangtzeopus clarkei*, ichnosp. nov., right pedal impression, topotype UQL-DP57-1. **D**, Broome theropod morphotype A, left pedal impression, UQL-DP25-1 (top) and possible left pedal impression -2 (bottom); **E**, Broome theropod morphotype B, possible left pedal impression, UQL-DP52-1; **F**, Broome theropod morphotype C, possible left pedal impression, UQL-DP6-3. Elevation map (measured in mm) with contour lines (1mm vertically spaced).

punctuated in parts by either rubbly, heavily eroded areas or stretches of sand, it is possible to see that these horizons and the original track surfaces were quite extensive in terms of their geographic extent (approximately 2.5 km<sup>2</sup> in the case of the Walmadany area; see Fig. 5). Broadly speaking, in this context, each of these areas—Yanijarri, Walmadany, and Kardilakan–Jajal Buru—can be regarded as a single tracksite.

Significantly, we found that all of the main track types (theropod, sauropod, ornithopod, and thyreophoran) occurred in the Yanijarri, Walmadany, and Kardilakan–Jajal Buru areas, and that the relative level of diversity within each of these groupings was comparable between areas (Fig. 65). The area that contained the highest diversity of track types was Kardilakan–Jajal Buru, with 13 different types represented: four types of theropod tracks, at least three types of sauropod tracks, one type of ornithopod track, and five types of thyreophoran tracks. The Walmadany and Yanijarri areas contained 11 and eight different types of tracks, respectively. Walmadany has three types of theropod tracks, two types of sauropod tracks, four types of ornithopod tracks, two types of thyreophoran track, and one indeterminate track type, whereas Yanijarri has one type of theropod track,

four types of sauropod tracks, two types of ornithopod tracks, and one type of thyreophoran track.

The tracks of sauropods are far and away the most abundant dinosaur ichnites throughout the study area, suggesting not only a diverse (and potentially populous) sauropod fauna, but also a diverse set of behaviors for the trackmakers, confirming earlier reports (Thulborn et al., 1994; Thulborn, 2002, 2012). Despite their abundance, however, very few of these tracks can be confidently assigned to ichnotaxa and morphotypes on the basis of unequivocal diagnostic traits, or on combinations of morphological features that would unambiguously allow their referral. Several of the sauropod morphotypes that we have identified in the study are based on non-comparable parametric data (non-overlapping diagnostic information), which further undermines making cross-referrals or establishing novel ichnotaxa. Many of these problems stem from inconsistencies in preservation, erosion, degree of silicification, or a combination of all these factors. In addition, in many instances the sheer density of sauropod tracks (see Fig. 15A) has resulted in the ground becoming so heavily trampled that trackways, autopodial couplets, and even individual tracks are difficult to identify with certainty. Although the

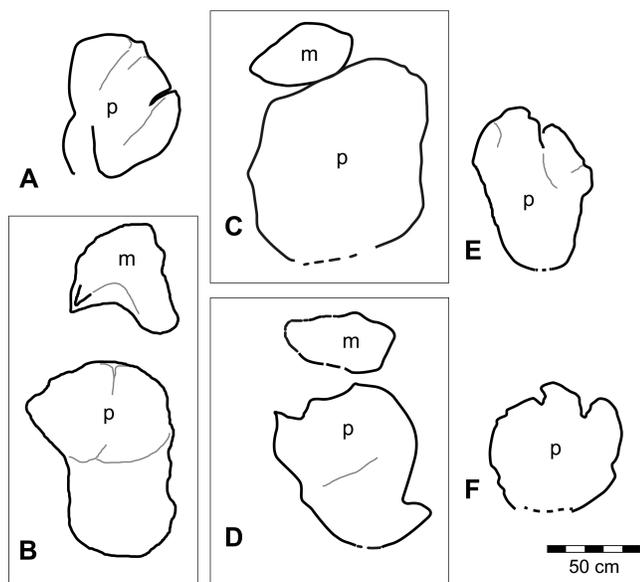


FIGURE 59. Schematic outlines of representative sauropod tracks from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. **A**, *Oobardjidama foulkesi*, ichnogen. et ichnosp. nov., right pedal impression, UQL-DP45-8(rp2); **B**, Broome sauropod morphotype A, coupled right manual and pedal impressions, UQL-DP8-30; **C**, Broome sauropod morphotype B, coupled manual and pedal impressions (ipsilateral side uncertain), UQL-DP1-1; **D**, Broome sauropod morphotype C, coupled right manual and pedal impressions, UQL-DP14-17; **E**, Broome sauropod morphotype D, right pedal impression, UQL-DP11-4; **F**, Broome sauropod morphotype E, left pedal impression, UQL-DP14-9.

majority of identifiable types of sauropod tracks are restricted to particular areas, it is noteworthy that in all the main track-bearing areas, there was at least two, sometimes as many as four, different types of sauropod tracks. It is very likely that with ongoing documentation and research, the number of diagnosable sauropod ichnotaxa within the Broome Sandstone will increase, and our understanding of the variation that exists within these ichnotaxa will improve.

After the ubiquitous sauropod tracks, *Walmadanyichnus hunteri* and *Garbina roerorum* are the next most abundant track types within the study area, being well represented in each of the main track-bearing areas. Indeed, in some areas, *Wal. hunteri* tracks outnumber the tracks of sauropods, suggesting that the large ornithopod trackmaker responsible for these tracks was an important part of the area's herbivorous dinosaurian fauna (see below for further discussion on the likely composition of the Broome Sandstone dinosaurian fauna). Tracks that can be confidently assigned to other ichnotaxa and morphotypes were less frequently encountered in each of the main areas, but in some instances they were locally abundant (e.g., *Wintonopus latomorum*; see Figs. 37–40). The tracks of theropods were numerically the least common of all the main track types in each of the main track-bearing areas.

Contrary to previous accounts of dinosaurian tracks in the Broome Sandstone (Thulborn et al., 1994; Thulborn, 2002, 2009; e.g., Commonwealth of Australia, 2011, 2012), we found no evidence for an association of particular track types with discrete paleoenvironmental settings, at least within the section of coastline that we focused on. The main track-bearing horizons in each of the main areas (Yanijarri, Walmadany, and Kardilakan–Jajal Buru) all pertain to the same lithofacies

association (LFA-2; thinly interbedded siltstones and sandstones, Fl, Sh, Sr, Bt, and Tr), many of which have been subsequently silicified to form laterally continuous sheet-like horizons (Fl, Sh; see Tables 2–5), being structurally and texturally similar, such that they likely derive from and were deposited in very similar paleoenvironmental settings. In each area, the sequences of the strata above and below the main track-bearing horizons are very similar (see Figs. 9–11). Given the lack of appreciable dip throughout the study area, and the fact that, where discernible, track-bearing horizons within each of the main areas are separated from each other laterally by a continuum of facies associations that are consistent with what would be expected for the distal fluvial to deltaic portions of a large braid plain, it is possible that these areas are broadly contemporaneous and represent different limbs of the prograding fluvial system. Alternatively, each of these areas may represent part of a repeated sequence of similar-, but different-aged lithofacies associations. More detailed stratigraphic work is needed to test these ideas. Nevertheless, the only noteworthy difference that we observed between the track-bearing horizons in each area is related to the amount of plant material that was present and minor differences in track preservation (mainly due to the degree of post-deposition silicification). Where it occurs, we do not consider the presence of plant material at certain tracksites to be indicative of an in situ swamp/forest paleoenvironment sensu Thulborn et al. (1994). As was first noted by McLoughlin (1996), although locally abundant in some areas, the vast majority of plant fossils in the Broome Sandstone are allochthonous. Although the completeness of some remains suggests that they have been transported only a short distance prior to burial (see Fig. 17E, F), their presence does not appear to be indicative of a particular habitat at any one tracksite. Rather, their occurrence within certain horizons and at particular tracksites is consistent with our interpretation of the broader depositional setting and most likely reflects minor differences in topography, fluctuations in fluvial discharge during flood events, or both. Some banks and channel systems may have been more prone to the accumulation of plant debris than others, with the most complete material possibly occurring closer to adjacent vegetated banks than less complete material, which may have traveled a greater distance. In all instances, however, the horizons in which plant remains were observed were similar (i.e., those assignable to LFA-2), and in many instances large parts of these same horizons (and hence individual tracksites) were seemingly devoid of plant fossils. We saw only rare evidence of autochthonous plant material (e.g., corns or root traces), as has been described in exposures of Broome Sandstone at Minyirr (McLoughlin, 1996). The occurrence of autochthonous ‘stumps,’ as reported previously by Thulborn (Commonwealth of Australia, 2011; Thulborn, 2012), could not be confirmed for tracksites in our study area. Although Thulborn does not provide any photos or detailed descriptions, we suspect that his ‘stumps’ are what we have interpreted as water escape structures (Fig. 14C, D). Rather than evoking an image of large dinosaurs weaving their way through some kind of ‘swamp forest,’ we envisage these raised, crater-like structures to have formed as a consequence of some of the heavier dinosaurian trackmakers (e.g., sauropods and large ornithopods) moving across the gently undulating sand lobes that had been blanketed with sheet-flood sediments. The weight transmitted through the feet of these dinosaurs appears to have compacted the water-laden sediment, forcing water upwards and thereby rupturing the track surface.

If, as we suspect, tracksites within each of the main areas are broadly coeval, it is not surprising that, preservational issues aside, not all the track types occur in each of the main track-bearing areas.

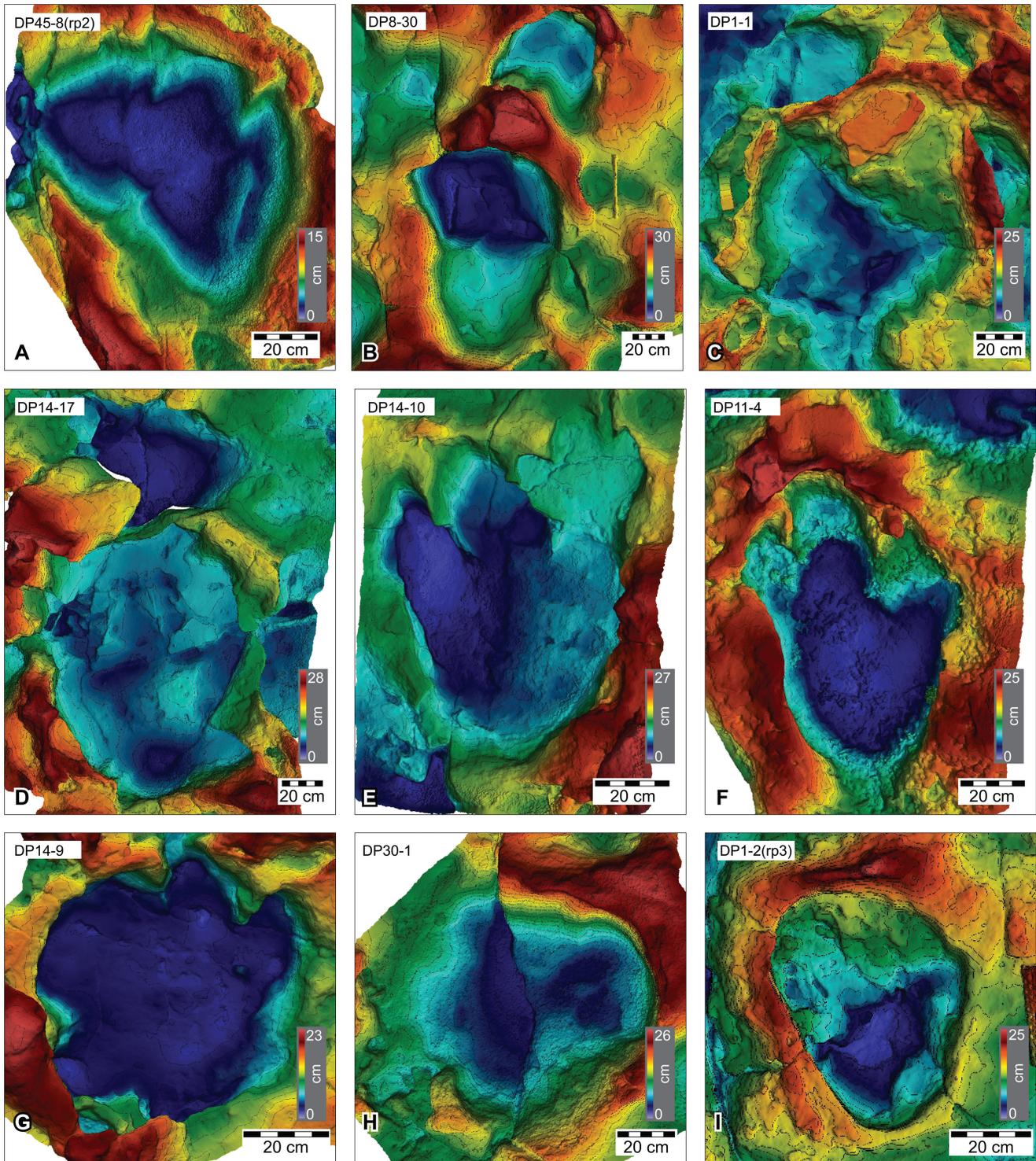


FIGURE 60. Color ramp images of selected sauropod and indeterminate track DEMs. **A**, *Oobardjidama foulkesi*, ichnogen. et ichnosp. nov., right pedal impression, UQL-DP45-8(rp2); **B**, Broome sauropod morphotype A, coupled right manual and pedal impressions, UQL-DP8-30; **C**, Broome sauropod morphotype B, coupled manual and pedal impressions (ipsilateral side uncertain), UQL-DP1-1; **D**, Broome sauropod morphotype C, coupled right manual and pedal impressions, UQL-DP14-17; **E**, Broome sauropod morphotype D, right pedal impression, UQL-DP14-10; **F**, Broome sauropod morphotype D, right pedal impression, UQL-DP11-4; **G**, Broome sauropod morphotype E, left pedal impression, UQL-DP14-9; **H**, Broome sauropod morphotype E, right pedal impression, UQL-DP30-1; **I**, Broome indeterminate dinosaurian morphotype A, right? pedal impression, UQL-DP1-2(p6). Elevation map (measured in cm) with contour lines (1 mm vertically spaced).

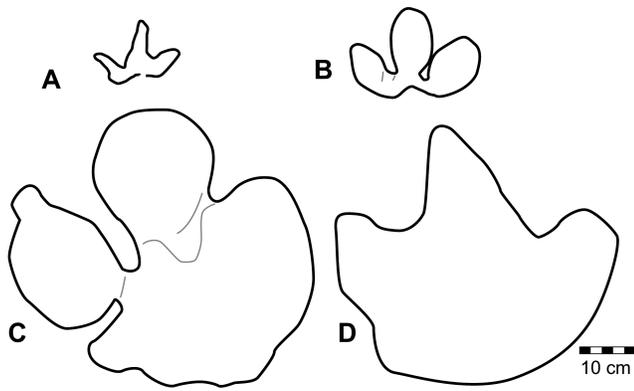


FIGURE 61. Schematic outlines of representative ornithomorph tracks from the Yanijarri–Lurujarri section of the Dampier Peninsula, Western Australia. **A**, *Wintonopus latomorum*, left pedal impression, UQL-DP23-1; **B**, *Wintonopus middletonae*, ichnosp. nov., possible right pedal impression, UQL-DP23-7; **C**, *Walmandyichnus hunteri*, ichnogen. et ichnosp. nov., right pedal impression, toptotype UQL-DP11-5; **D**, *Amblydactylus* cf. *A. kortmeyeri*, possible right pedal impression, UQL-DP9-3. All schematic outlines are to the same scale.

Although some track types (e.g., *M. broomensis*, Broome sauropod morphotype A, *Wal. hunteri*, and *G. roeorum*), do occur in all three areas, potentially suggesting the presence of the same type of track-makers over a broad geographic area (~20 km), another is restricted to two (e.g., *Win. middletonae*) and sometimes only one (e.g., *O. foulkesi* and Broome theropod morphotype C). Such variability in the apparent distribution and abundance of various track types across the study area likely relates to differences in the abundance of particular trackmakers, their behavior (e.g., whether they were gregarious, wide-ranging, or had small home ranges), the preservational potential of their tracks, and the degree to which their tracks can be differentiated from others.

In contrast to earlier reports, we saw no evidence for a repeated association of *Megalosauropus broomensis* with the tracks of sauropods (specifically tracks assignable to *Brontopodus*; see sauropod track section on the lack of evidence for *Brontopodus* in the Broome Sandstone) in our study area. Thulborn (2009) considered this association to be reminiscent of the occurrence of *Eubrontes? glenrosensis* (cf. *Megalosauropus* in Thulborn, 2009) and *Brontopodus* tracks in the Albian Glen Rose Formation, Texas, and an indication that an “ecological association of allosaurid theropods and brachiosaurid sauropods was widespread in lagoonal environments at middle to low latitudes

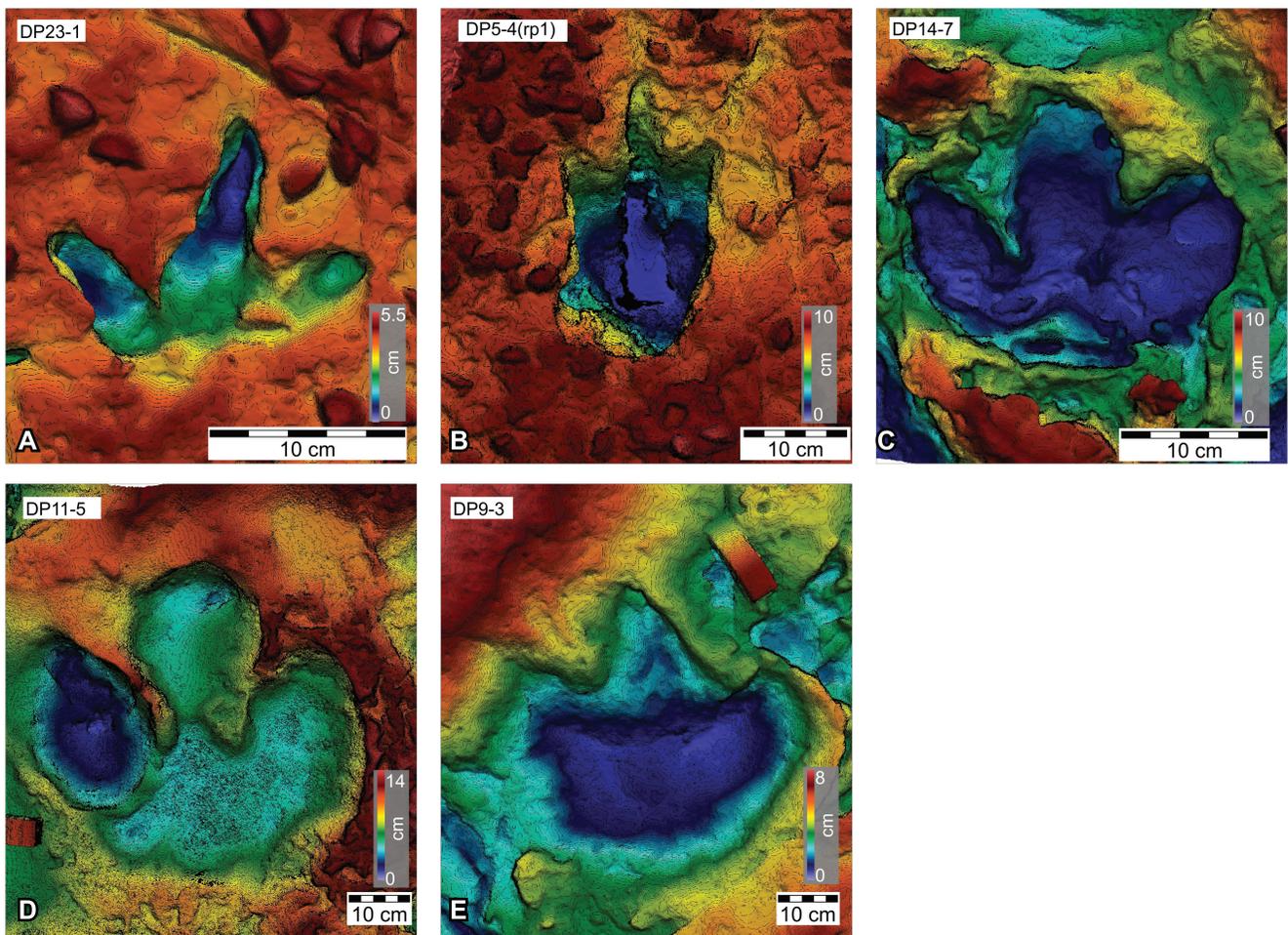


FIGURE 62. Color ramp images of selected ornithomorph track DEMs. **A**, *Wintonopus latomorum*, left pedal impression, UQL-DP23-1; **B**, *Win. latomorum*, right pedal impression, UQL-DP23-4(rp1); **C**, *Win. middletonae* ichnosp. nov., possible right pedal impression, toptotype UQL-DP14-7; **D**, *Walmandyichnus hunteri*, ichnogen. et ichnosp. nov., right pedal impression, toptotype UQL-DP11-5; **E**, *Amblydactylus* cf. *A. kortmeyeri*, possible right pedal impression, UQL-DP9-3. Elevation map (measured in mm) with contour lines (1 mm vertically spaced).

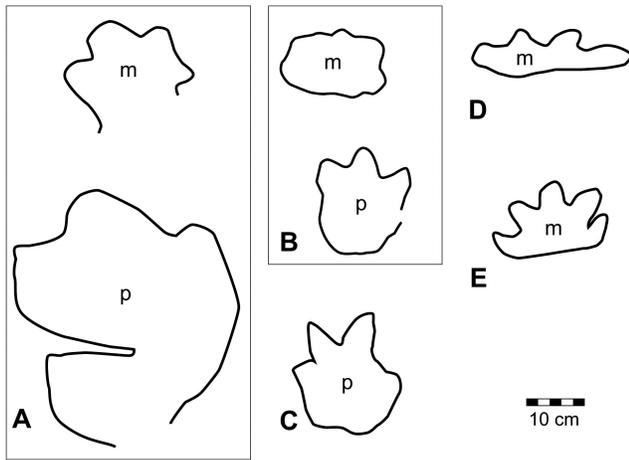


FIGURE 63. Schematic outlines of representative thyreophoran tracks from the Yanijjarri–Lurujjarri section of the Dampier Peninsula, Western Australia. **A**, *Garbina roeorum* ichnogen. et ichnosp. nov., left manual (top) and pedal (bottom) impressions, UQL-DP14-1 (preserved as a PM couplet in the toptype trackway); **B**, *Luluichnus mueckeii* ichnogen. et ichnosp. nov., coupled left manual and pedal impressions, UQL-DP45-6; **C**, cf. *Luluichnus* UQL-DP45-16; **D**, Broome thyreophoran morphotype A, possible right manual impression, UQL-DP8-17; **E**, Broome thyreophoran morphotype B, right manual impression, UQL-DP45-15. All schematic outlines are to the same scale.

during the Early Cretaceous.” Although it is never stated explicitly, Thulborn’s (2009:90) assertion is probably based on tracksites in the Minyirr and Reddell Beach area near Broome, where the tracks of *M. broomensis* are much more abundant (see Colbert and Merrilees, 1967) than in exposures of the Broome Sandstone in the Yanijjarri–Lurujjarri section of the Dampier Peninsula. As occurs throughout the Broome Sandstone, sauro-pod tracks are the most abundant track types in the Minyirr and Reddell Beach area. Our own preliminary surveys of this area indicate that, although they also occur, the tracks of bipedal ornithopods and quadrupedal ornithischians are much rarer, as is alluded to by Thulborn et al. (1994) and Thulborn (2002, 2012) (also see McCrea et al., 2012). This area is approximately 30 km south of Kardilakan–Jajal Buru, with tracks occurring in different lithofacies associations to those encountered in our study area. We concur with McCrea et al. (2012) that strata in this area indicate interbedded floodplain or delta plain and eolian depositional environments, with ephemeral shallow water bodies. This likely depositional setting is in contrast to the one associated with track-bearing horizons in the Yanijjarri–Lurujjarri area, which is indicative of an environmental transgression between the distal fluvial to deltaic portions of a large braid plain, with migrating sand bodies and periodic sheet floods. In this context, the depositional setting associated with tracksites in the Minyirr and Reddell Beach likely represents environments that were closer to the coast and potentially stratigraphically lower than

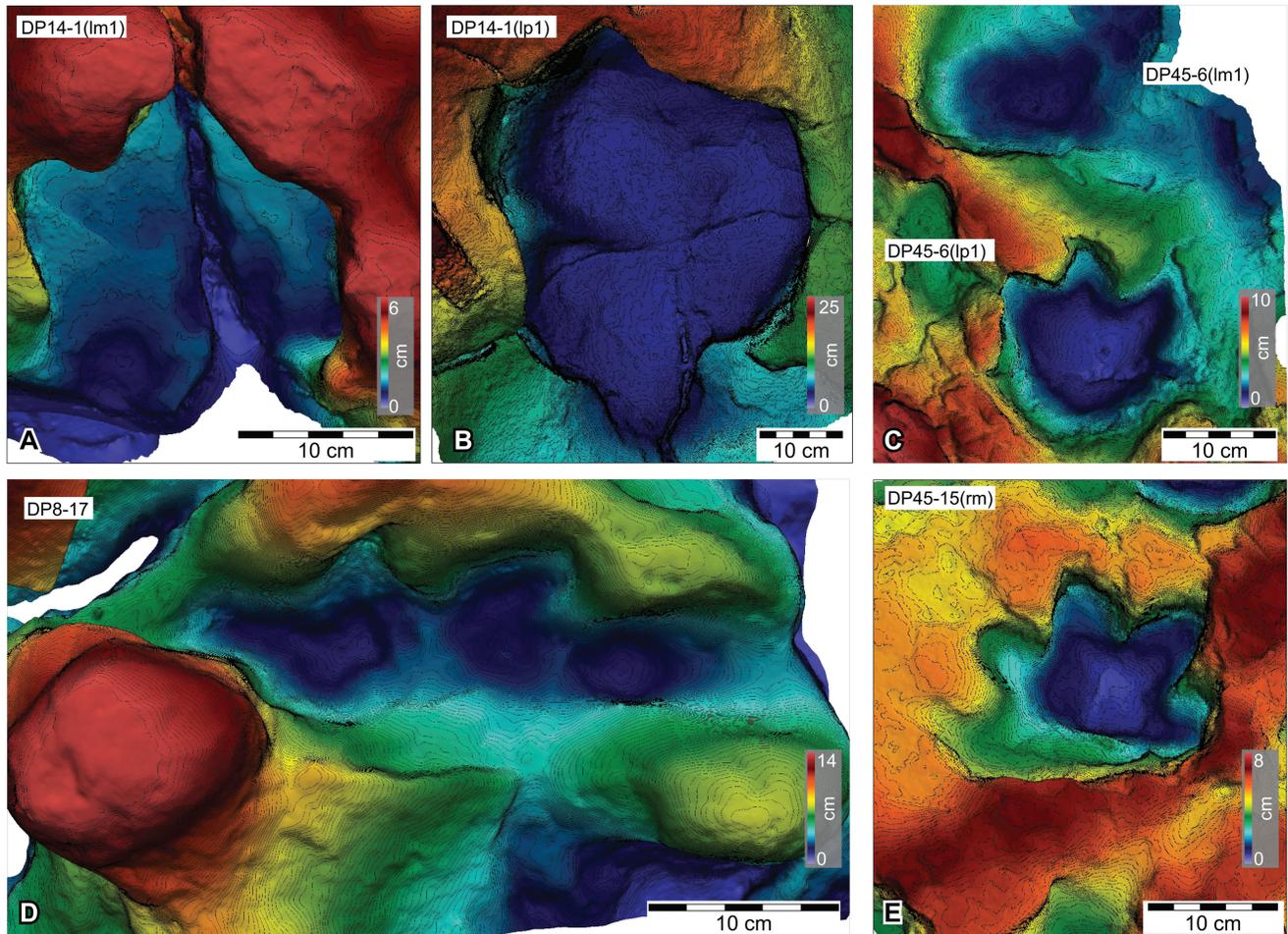


FIGURE 64. Color ramp images of selected thyreophoran track DEMs. **A**, **B**, *Garbina roeorum*, ichnogen. et ichnosp. nov., left manual and pedal impressions, UQL-DP14-1 (lm1) and (lp1), respectively (preserved as a PM couplet in the toptype trackway); **C**, *Luluichnus mueckeii*, ichnogen. et ichnosp. nov., coupled left manual and pedal impressions, UQL-DP45-6; **D**, Broome thyreophoran morphotype A, possible right manual impression, UQL-DP8-17; **E**, Broome thyreophoran morphotype B, right manual impression, UQL-DP45-15. Elevation map (measured in mm) with contour lines (1 mm vertically spaced).

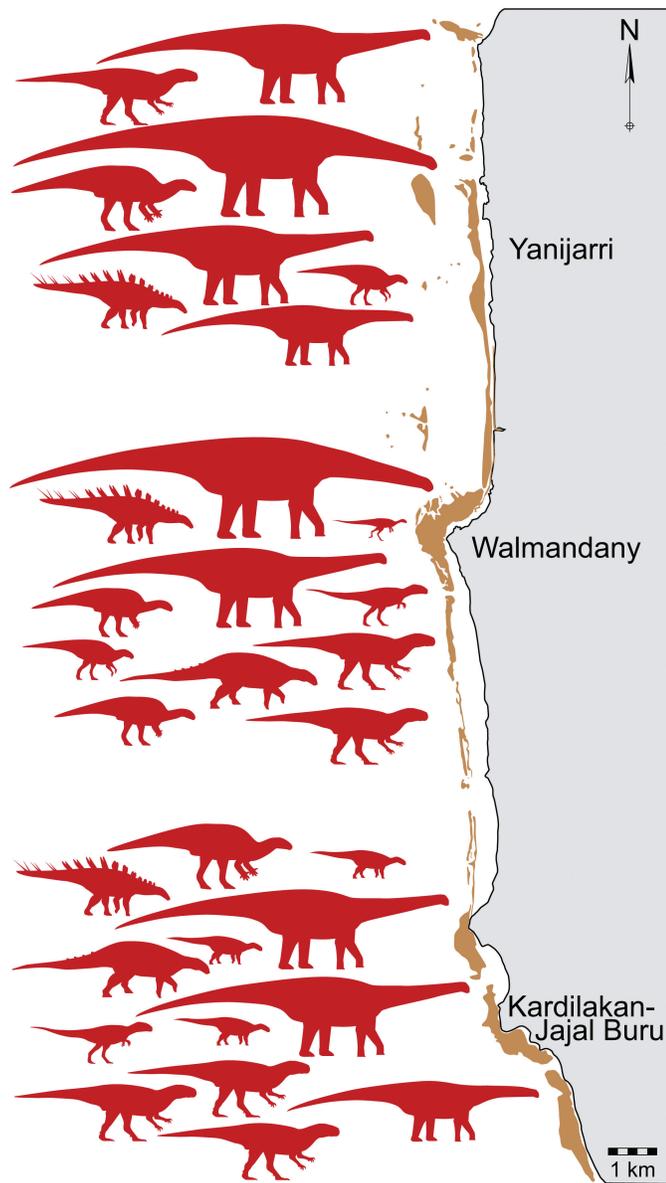


FIGURE 65. Diversity of dinosaurian ichnospecies/track morphotypes specific to the Kardilakan–Jajal Buru, Walmadany, and Yanijjarri sections of the Dampier Peninsula, Western Australia. Silhouettes denote inferred trackmaker ichnotaxa, of which there are 13 different types at Kardilakan–Jajal Buru, 11 at Walmadany, and eight at Yanijjarri. See legend in figure 66 for trackmaker size categories.

those in the Yanijjarri–Lurujjarri area. Thus, differences in the abundance of certain track types (e.g., *M. broomensis*) between these two areas may indeed relate to differences in the paleoenvironmental setting associated with track-bearing strata. On this point, we agree with Thulborn (2009) that the theropod responsible for the tracks assigned to *M. broomensis* may have had a preference for the more coastally situated habitats. Further work examining the distribution of particular track types is required to refine this supposition, particularly for tracksites outside of our main study area such as those at Minyirr and Reddell Beach.

Similarly, we also saw no evidence for the restriction of tracks assignable to smaller dinosaurs (e.g., *Win. latomorum*) to “elevated” areas at Walmadany, away from the “lower-lying”

areas that were trodden by sauropods (Thulborn, 2012:figs. 24, 25, 28). Based on this observation, Thulborn (2012:19) thought it “tempting to suppose that the smaller dinosaurian trackmakers preferred the higher ground, thereby avoiding the heavy traffic of sauropods.” Although there were some tracksites at Walmadany where *Win. latomorum* are the only tracks one encounters, and other areas that have been heavily trampled by sauropods, we recorded at least three sites where the tracks of *Win. latomorum* occurred alongside and interspersed among numerous sauropod tracks. Moreover, there were only three sites in the entire study area where the tracks of smaller dinosaurs did not occur alongside the tracks of sauropods. Whether the trackmakers responsible for the range of tracks at each tracksite traversed these surfaces at the same or different times is beyond the scope of the present study, but all these dinosaurs clearly moved over the same ground at some point during the preservation of the track surface. Although some of the ‘lower-lying’ areas at Walmadany that Thulborn refers to in his study (see Thulborn, 2012:figs. 24, 25, 28) do contain the remnants of many sauropod tracks, the original hummocky topography does not appear to that have been enhanced by the trampling of these trackmakers. Indeed, the only apparent exaggeration to the already gently undulating terrain that we could see is the effect created by undercutting of the more resilient track-bearing horizons of LFA-2 by erosion of the more friable underlying uppermost horizons of LFA-1. The result has been for the track-bearing platforms to fracture and slump around their edges, as is apparent in some of Thulborn’s photos (Thulborn, 2012:figs. 24, 25, 28). On the other hand, there are a number of instances where sauropods have traversed the undulating terrain and had no effect on the topography other than to leave their tracks (see Fig. 16). A more thorough assessment of the overall topography of the track-bearing surfaces at places such as Walmadany is likely required in order to properly resolve this issue.

#### Comparisons with Other Non-Avian Dinosaurian Ichnofaunas

The diversity of non-avian dinosaurian track types seen in the Broome Sandstone in the Yanijjarri–Lurujjarri section of the Dampier Peninsula, each of the main track-bearing areas (Kardilakan–Jajal Buru, Walmadany, and Yanijjarri) within this stretch of coastline, and many of the area’s individual tracksites is unparalleled in Australia, and even globally (see Appendix 1 and Fig. 66).

Within Australia, after the Broome Sandstone, the next most diverse dinosaurian ichnofaunas come from the Lower Jurassic Razorback Beds at Mt. Morgan, southwest of Rockhampton, in the Fitzroy region of Queensland, and the Middle Jurassic (Bajocian–Bathonian) Walloon Coal Measures at Balgowan, Darling Downs, Queensland. Both of these units are currently thought to contain seven to eight dinosaurian ichnotaxa/track morphotypes, some of which are shared with the Broome Sandstone. Other Australian tracksites have a much lower diversity of track types than the Broome Sandstone: the Upper Triassic (Carnian) Ipswich Coal Measures have two types of theropod tracks, assigned to *Eubrontes* (Staines and Woods, 1964; Haubold, 1971; Thulborn, 1986, 2003) and cf. *Grallator* (Thulborn, 1986, 2000); the Lower Cretaceous (late Aptian–early Albian) Eumeralla Formation of the Otway Group in southern Victoria has produced one possible ornithomimid track and two types of theropod tracks based primarily on shared similarities of divarication and track length (Flannery and Rich, 1981; Martin et al., 2012); and Lark Quarry, central-western Queensland, in the Upper Cretaceous (Cenomanian–Turonian) portion of the Winton Formation, has two types of ornithomimid tracks (Romilio and Salisbury, 2011, 2014; Romilio et al., 2013; see Thulborn and Wade [1984] and Thulborn [2013] for an alternative interpretation of some of the Lark Quarry tracks).

Recent work on the Mt. Morgan ichnofauna by Cook et al. (2010) identified at least seven track types, four of which pertain to theropod trackmakers and three to ornithopods. Identifiable theropod tracks have been assigned to cf. *Eubrontes*, *Grallator*, and *Skartopus*, and ornithopod tracks to *Anomoepus*, which is also known from the similarly aged Precipice Sandstone at Carnavon Gorge, Queensland (Thulborn, 1994). The remaining theropod track and two ornithopod tracks were regarded by Cook et al. (2010) as indeterminate based on their poor preservation. Additional theropod tracks were observed by Staines and Woods (1964) in a different part of the cavern system to the one that Cook et al. (2010) focused on, with schematic representations of these appearing in Molnar (1991:fig. 37h, i) and Scanlon (2006:fig. 5b). At present, it is not clear whether the tracks observed by Staines and Woods (1964) are different from those described by Cook et al. (2010), because comparisons were not presented in the latter study. Romilio et al. (2013) subsequently considered *Skartopus* a junior synonym of the ornithopod ichnotaxon *Wintonopus*, with the recommendation that the Mount Morgan *Skartopus* be regarded as an indeterminate theropod track. In light of these issues, the number of track types in the Mt. Morgan ichnofauna could potentially be as high as eight or as low as three if the indeterminate tracks are regarded as preservational variants of those that can be more confidently identified.

Similar issues surrounding our current understanding of the Mt. Morgan ichnofauna also plague the Middle Jurassic (Bajocian–Bathonian; Grant-Mackie et al., 2000) Walloon Coal Measures of the Clarence-Moreton Basin in the Darling Downs and Brisbane-Moreton areas of Queensland. As many as eight possible track types have been identified in numerous mines throughout the coalfields since the 1930s, including four types of theropod tracks, three types of ornithopod tracks, and one type of thyreophoran track. Unfortunately, with the exception of the work by Hill et al. (1966), none of these tracks is described, such that their precise ichnotaxonomic status remains unclear, as does the composition of the ichnofauna.

Theropod tracks from the Walloon Coal Measures have previously been assigned to ‘*Changpeipus bartholomaii*’ and *Eubrontes*. ‘*Changpeipus bartholomaii*’ was erected by Haubold (1971) based on an oblique photograph of two in situ tracks from a presumed trackway, originally published in Bartholomai (1966:149, unnumbered figure). Photographs of casts (QM F5702 and QM F5700) of the same tracks or schematics based on these have also appeared in Hill et al. (1966:pl. XV, 4), Molnar (1991:fig. 37c, g), Thulborn (2003), and Scanlon (2006:fig. 5c). The assignment of these tracks to *Changpeipus* by Haubold (1971) and the taxonomic validity of the ichnospecies are questionable given the nature of the material used to establish the ichnotaxon (oblique photos) and the lack of any detailed description or diagnosis. Thulborn (1999) was the first to suggest the occurrence of *Eubrontes*-like tracks in the Walloon Coal Measures, but as with Haubold (1971), the tracks in question are not described in any detail nor are any images provided. Turner et al. (2009:fig. 6d) included a figure of a theropod track from the Walloon Coal Measures that they also assigned to *Eubrontes* without justification, but it is unclear if this was one of tracks mentioned previously by Thulborn (1999). A smaller tridactyl track of likely theropod affinities has been figured (but not described) by Hill et al. (1966), Molnar (1991:fig. 37d), and Scanlon (2006:fig. 5c). Photographs of other theropod tracks from the Walloon Coal Measures hint at the presence of additional morphotypes (e.g., Grant-Mackie et al., 2000:table 2; Rich and Vickers-Rich, 2003a:68, top unnumbered figure; Turner et al., 2009:fig. 6c–e), but pending further work, the ichnotaxonomic affinities of these tracks (and thus their bearing on the composition of the ichnofauna) remain unclear. Similarly, little detail exists on the three possible types of ornithopod tracks from the Walloon Coal Measures: one track assigned to cf. *Anomoepus* and another (or

multiple tracks) to a quadrupedal cf. *Wintonopus* by Thulborn (1999) and Grant-Mackie et al. (2000:table 2). The same authors also mention but do not figure a large ornithopod track, which may pertain to another morphotype. A possible stegosaurian track from Balgowan, initially described by Hill et al. (1966:31, pl. XV, Fig. 5) is herein assigned to cf. *G. roeorum* (see above).

Many of the individual tracksites within the Yinijarri–Lurujarri section of the Dampier Peninsula contain a comparable diversity of track types to those currently recognized as pertaining to either the Mt. Morgan area or Walloon Coal Measures, and some, such as UQL-DP45 and UQL-DP14, considerably more. All of the main track-bearing areas (Yinijarri, Walmadany, and Kardilakan–Jajal Buru) have a higher diversity of track types than these ichnofaunas, and as a whole, the Broome Sandstone has around three times the number currently recognized from either area. Significantly, the Yinijarri–Lurujarri ichnofauna, and that of the Broome Sandstone more broadly, is the only dinosaurian ichnofauna in Australia to include the tracks of sauropods, and, with the exception of the single manual track assigned to cf. *G. roeorum* from the Walloon Coal Measures, the only one to include tracks of quadrupedal ornithischians. The diversity of tracks pertaining to bipedal ornithopods (at least four) and theropods (five) also currently exceeds that of any other dinosaurian ichnofauna in Australia. The sheer abundance of tracks and trackways, and the variation in preservation, both in terms of likely behaviors represented and modes of track formation (see Thulborn, 2012), is also without parallel.

Globally, there is also no other discrete dinosaurian ichnofauna pertaining to a single geological formation that contains as many track types as the Broome Sandstone in the Yinijarri–Lurujarri section of the Dampier Peninsula. Although there are many areas that contain an abundance of tracks and trackways, as best as we have been able to ascertain, none appears to be equal to the Broome Sandstone in terms of the overall diversity of track types that are represented. After the Broome Sandstone (21 non-avian dinosaurian track types), the next most diverse non-avian dinosaurian ichnofaunas likely come from the Middle Jurassic Saltwick and Scalby formations of the Cleveland Basin, U.K., and the Late Cretaceous (Campanian) Blackhawk Formation, Utah, U.S.A.

The Saltwick and Scalby formations of the Cleveland Basin, U.K., have a combined total of 17–18 types of dinosaurian tracks, only some of which have been named. These represent a minimum of three types of theropod tracks, two types of sauropod tracks, at least three types of ornithopod tracks, and one type of thyreophoran track (Romano and Whyte, 2003; Whyte et al., 2007) spread across approximately 10 million years of deposition. The Blackhawk Formation of Utah, U.S.A., is estimated to contain 14 different types of non-avian dinosaur track types, pertaining to theropods, ornithopods, and a thyreophoran (Parker and Rowley, 1989). At present, none of these tracks are described or named.

Most other well-known formations and/or track-bearing areas contain no more than 10 or so non-avian dinosaur track types. These include the Lower Cretaceous (Aptian) Gething Formation of the Western Canadian Sedimentary Basin, Canada (eight types of non-avian dinosaurian tracks); the Lower Cretaceous (Aptian–Albian), Jindong Formation of the Gyeongsang Basin, Korea (six types of non-avian dinosaurian tracks); the Upper Jurassic (Kimmeridgian) Morrison Formation of the San Juan Basin, U.S.A. (nine types of non-avian dinosaurian tracks); the Upper Jurassic (Kimmeridgian) Vega, Terenes, and Lastres formations of the Gijón–Villaviciosa Basin, Spain (nine types of non-avian dinosaurian tracks); the Upper Jurassic (Tithonian–Kimmeridgian) Lourinhã Formation of the Lusitanian Basin, Portugal (up to seven different types of non-avian dinosaurian tracks); the Lower Cretaceous (pre-Aptian) Sousa Formation of

the Rio do Peixe (Sousa) Basin, Brazil (six to eight types of non-avian dinosaurian tracks); and the Lower or Middle Jurassic Botucatu Formation of the Sao Bento Group, Brazil (eight or nine types of non-avian dinosaurian tracks).

The Lower Cretaceous (Aptian) Gething Formation of the Western Canadian Sedimentary Basin, Canada, contains eight named dinosaurian tracks, distributed across four or five different stratigraphic levels. These include four types of theropod tracks, three types of ornithopod tracks, and one type of thyreophoran track (Sternberg, 1932; Romano and Whyte, 2003).

Although well known, the numerous dinosaurian tracks in the Lower Cretaceous (Aptian–Albian) Jindong Formation of the Gyeongsang Basin, Korea, occur in multiple sites and stratigraphic levels (Lockley et al., 2008b). The composition of the track fauna is remarkably consistent across different sites. Thus far, up to six different types of non-avian dinosaur track types have been recognized, including one type of sauropod track (Lockley et al., 2008b), up to three types of theropod tracks (Lockley et al., 2006b:fig. 10; Matsukawa et al., 2006:fig. 8b), and three types of ornithopod tracks (Lockley et al., 2006b, 2008b; Matsukawa et al., 2006; Kim et al., 2009; Lim et al., 2012).

Over 50 sites, with up to nine dinosaur track types, are known to occur in the Upper Jurassic (Kimmeridgian) Morrison Formation of the San Juan Basin, U.S.A. (Foster and Lockley, 2006). These include two types of sauropod tracks (Bird, 1941; Farlow et al., 1989; Lockley et al., 1994a; Foster and Lockley, 2006), three types of theropod tracks, three types of ornithopod tracks, and one type of thyreophoran track (Foster and Lockley, 2006). The most abundant ‘tracksite’ in this formation is in the Purgatoire River area, which has up to 1300 tracks and trackways distributed across four stratigraphic levels and an area of 500,000 km<sup>2</sup> (Foster and Lockley, 1995, 2006; Lockley et al., 2008a; Farlow et al., 2012). Amongst the trackways are 41 that can be assigned to theropods, 40 to sauropods (*Brontopodus* ichnosp. and *Parabrontopodus mcintoshi*), and two to ornithopods. Most tracks occur in Bed 2 (Foster and Lockley, 2006).

The Upper Jurassic (Kimmeridgian) Vega, Terenes, and Lastres formations of the Gijón–Villaviciosa Basin, Spain, are collectively referred to as the ‘Asturias.’ Together, they contain up to nine non-avian dinosaur track types, assignable to two types of sauropods, three types of theropods, a large bird-like dinosaur, three types of ornithopod tracks, and one type of thyreophoran track (Lockley et al., 2008a). The diversity of each formation is lower. The similarly aged Upper Jurassic (Tithonian–Kimmeridgian) Lourinhã Formation of the Lusitanian Basin, Portugal, has at least 14 different tracksites, containing up to seven different types of non-avian dinosaurian tracks, including three types of sauropod tracks, three types of theropod tracks, and one type of thyreophoran track (Mateus and Milàn, 2010).

The Lower Cretaceous (pre-Aptian) Sousa Formation of the Rio do Peixe (Sousa) Basin, Brazil, has at least 17 track-bearing localities (tracksites) spanning numerous stratigraphic levels (Leonardi and Carvalho, 2007). Although the Sousa Formation is thought to contain a high diversity of dinosaurian track types, the majority of described exemplars have yet to be assessed in an ichnotaxonomic sense. Named tracks include three types of theropod tracks and three types of ornithopod tracks. Sauropod and thyreophoran tracks have also been recorded. A single locality in the Lower or Middle Jurassic Botucatu Formation of the Sao Bento Group, Brazil, is known to contain eight or nine types of dinosaurian tracks, including examples assignable to small and large theropods and large ornithopods (Leonardi, 1994).

Thus, barring any future revisions, we conclude that the Broome Sandstone in the Yanijarri–Lurujarri section of the Dampier Peninsula currently contains the highest diversity of dinosaurian ichnotaxa anywhere in the world. The high

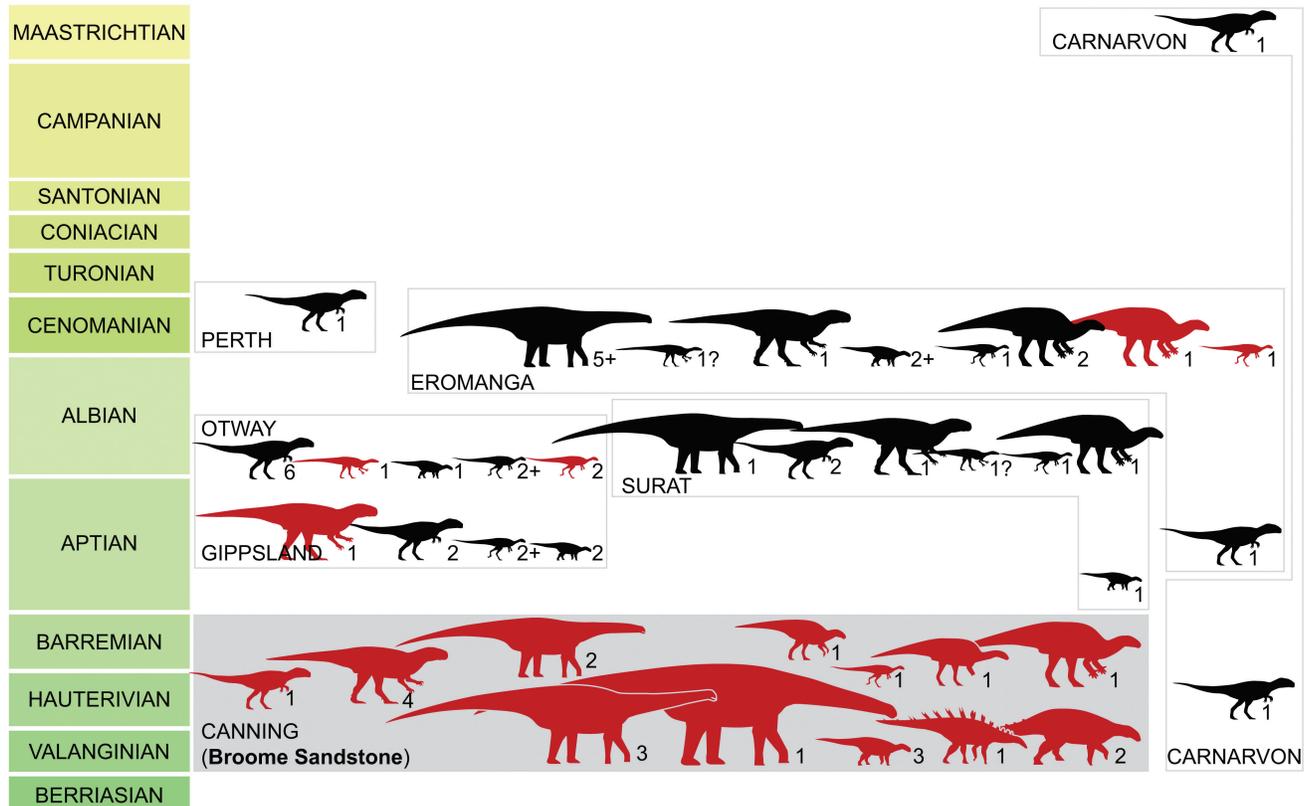
abundance of sauropod, large ornithopod (*Walmadanyichnus*), and thyreophoran (in particular *Garbina*) tracks at certain track-sites is also unique globally for the Lower Cretaceous and provides enormous potential for future paleoecological and behavioral studies.

### Implications for Understanding the Composition and Paleobiogeographic Relationships of Australia’s Early Cretaceous Dinosaurian Faunas

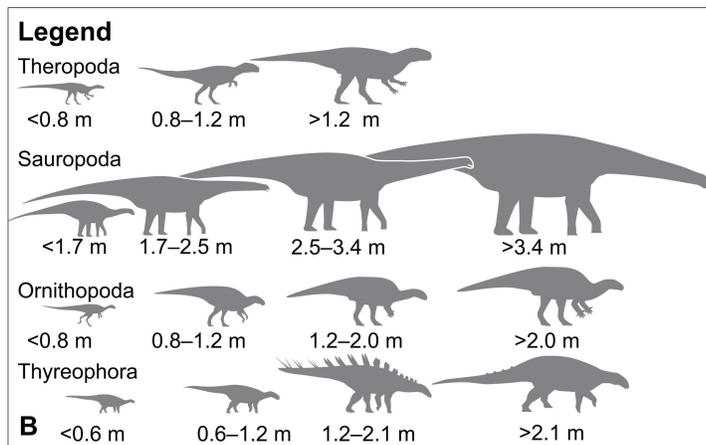
Rarely, if ever, is it possible to confidently link ichnological data to specific body fossil taxa. For non-avian dinosaurs, even when body fossils and ichnites occur in the same formation, unambiguous species- or genus-level assignments are difficult to establish (Farlow, 1992, 2001; Farlow and Lockley, 1993; Farlow et al., 2013). Absolute certainty can only be achieved when direct association can be made between a body fossil and its tracks (see Voigt et al., 2007). Nevertheless, where diagnostic characteristics of the pedal and manual skeleton of various body fossil taxa manifest themselves in tracks, assignments of various ichnotaxa and track morphotypes to higher taxonomic clades can be rationalized (Baird, 1957; Haubold, 1971; Leonardi, 1987; Thulborn, 1990; Lockley, 1991, 2000a; Farlow, 1992, 2001; Farlow and Lockley, 1993; Farlow and Chapman, 1997; Smith and Farlow, 2003; Farlow et al., 2013). Characters such as the number and the relative size of digital impressions, the configuration of autopodial and metapodial pad impressions, and digital impression divarication angles can all be used to link tracks to likely trackmakers (Smith and Farlow, 2003; Farlow et al., 2013). Once various trackmaker assignments have been established, tracks can be used in combination with body fossils to address behavioral, paleoecological, biostratigraphic, and paleobiogeographic issues.

No vertebrate body fossils are known from the Broome Sandstone. As a consequence, ichnites are the only record we have of the dinosaurian fauna that inhabited this part of Australia during the Valanginian–Barremian. In order to make meaningful statements about the likely composition of the dinosaurian fauna that existed at the time the various track-bearing horizons in the Broome Sandstone were deposited, and to facilitate comparisons with other dinosaurian faunas, we have assigned ichnotaxa and track morphotypes to various size categories within higher taxonomic groupings, using hip height estimates from the best-represented tracks for each track type based on various track size categories (Tables 1, 19; Fig. 66). As stated earlier, we acknowledge that future research may demonstrate that the number of track types may need to be revised, and as a consequence, so will the inferred composition of the area’s dinosaurian fauna. But until such time as this can be demonstrated unequivocally, we feel that it is important to retain transparency between the likely number of track types and the likely number of trackmakers.

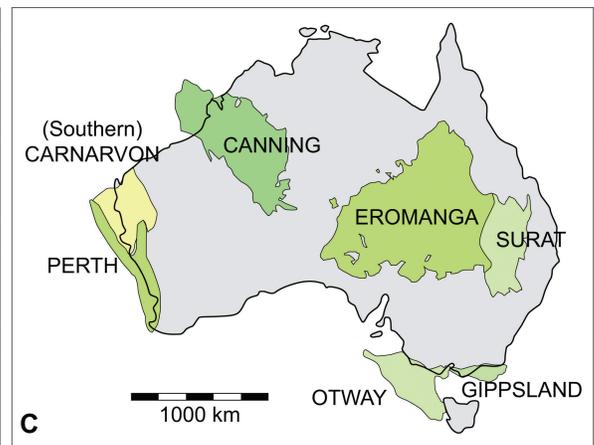
Based on the track types described herein, we can infer that at the time various track-bearing horizons of the Broome Sandstone were deposited, the Yinijarri–Lurujarri section of the Dampier Peninsula supported a highly diverse dinosaurian fauna (Appendix 1; Figs. 65, 66). The inferred theropod trackmaker fauna comprised four large-bodied forms and one medium-bodied form. The large-bodied theropod trackmakers are represented by tracks assignable to *M. broomensis*, Broome theropod morphotype B, Broome theropod morphotype C, and *Y. clarkei*. These theropod trackmakers had average estimated hip heights ranging from 132 cm for *Y. clarkei* to over 165 cm for *M. broomensis* (177–200 cm), 188 cm for Broome theropod morphotype B, and 168–187 cm for Broome theropod morphotype C. Hip height estimates of trackmakers based on tracks assigned to *M. broomensis* from the Minyirr and Reddell Beach area fall within a slightly smaller range (114–139 cm, average 124 cm) but would still be considered large. The single medium-bodied theropod



**A**



**B**



**C**

FIGURE 66. **A**, temporal distribution and taxonomic diversity of Australian Cretaceous dinosaurian faunas, grouped according to depositional basin. Black silhouettes denote taxa based on body fossils, red silhouettes denote ichnotaxa or track morphotypes. The height of each box denotes the age of the main formations in which the fossils occur rather than the entire age range of the depositional basin. **B**, size categories based on approximate hip height. **C**, relative positions of Cretaceous depositional basins across Australia, adapted from Turner et al. (2009:fig 1).

trackmaker is represented by tracks assignable to Broome theropod morphotype A, which we infer to have had hip height of around 81 cm.

The inferred sauropod fauna of the Yinijarri–Lurujarri section of the Dampier Peninsula comprised a minimum of six distinct trackmakers, with estimated trackmaker hip heights ranging from medium (>170 cm) to very large (up to ~540 cm). The single very large-bodied form is represented by Broome sauropod morphotype A, which had an estimated hip height ranging from 326 to 542 cm. Three large-bodied sauropod trackmakers include

Broome sauropod morphotypes B (264 cm), C (270 cm), and D (235–279 cm, average 257 cm). A fourth nearly large-bodied trackmaker, morphotype E, straddles our medium to large size range for hip height (207–255 cm, average 230 cm). In addition to these trackmakers, there is at least one genuinely medium-bodied form represented by *O. foulkesi* (220–242 cm, average 234 cm). Indeterminate sauropod tracks also point to the presence of what may be an additional number of very large- to medium-bodied trackmakers (represented by UQL-DP3-1 and UQL-DP8-16; 418–434 and 241 cm, respectively), but whether

these pertain to existing trackmaker groups is unclear given the ambiguous ichnotaxonomic status of the tracks.

At least four different bipedal ornithopod trackmakers can be inferred from tracks preserved in the Broome Sandstone of the Yinijarri–Lurujarri section of the Dampier Peninsula. These include one small-bodied form, represented by tracks assigned to *Win. latomorum* (estimated hip height of 55–100 cm); one medium-bodied form, represented by *Win. middletonae* (95 cm); one large-bodied form, represented by *Amblydactylus* cf. *A. kortmeyeri* (178 cm); and one very large-bodied form, represented by *Wal. hunteri* (52–320 cm, average 218 cm).

The inferred thyreophoran fauna of the Yinijarri–Lurujarri section of the Dampier Peninsula comprises at least six different

trackmakers: three medium-bodied forms, represented by and *L. mueckekei* (98 cm), cf. *Luluichnus* (111 cm), and Broome thyreophoran morphotype B (133 cm); one large-bodied form, represented by *G. roeorum* (222–250 cm); and two very large-bodied forms, represented by Broome thyreophoran morphotype A (261 cm) and cf. *G. roeorum* (UQL-DP9-12; 420 cm).

In addition to being the primary record of dinosaurs in the western half of the Australian continent, the dinosaurian ichnofauna of the Broome Sandstone, and its inferred aforementioned dinosaurian trackmaker fauna, provides our only detailed look at Australia's dinosaurian fauna during the first half of the Early Cretaceous. As such, it fills an important temporal gap in the Australian fossil record and potentially provides a blueprint for

TABLE 19. Ichnotaxon/track morphotype and size categorization for selected tracks in the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Yinijarri–Lurujarri section of the Dampier Peninsula, Western Australia.

Ichnotaxon/track morphotype	Track		Size		
	UQL-DP	WAM	Track Length (L) * (cm)	Size category	Estimated trackmaker hip height (cm)
<b>Theropod</b>					
<i>Megalosauropus broomensis</i> Colbert and Merillees, 1976	35-1(lp)	—	>25	Large	~100
	11-1(lp)	—	44.3	Large	177.2
<i>Yangtzeopus clarkei</i> , ichnosp. nov.	57-1(rp) (topotype)	12.1.1 (holotype)	32.9	Large	131.6
Broome theropod morphotype A	25-1(lp)	12.1.2	20.3	Medium	81.2
Broome theropod morphotype B	52-1(?lp)	12.1.3	47	Large	188
Broome theropod morphotype C	6-3(lp)	12.1.4	46.8	Large	187.2
	8-18(lp)	12.1.5	42	Large	168
<b>Sauropod</b>					
<i>Oobardjidama foulkesi</i> , ichnogen. et ichnosp. nov.	45-8(rp2) (topotype)	12.1.6 (holotype)	71	Medium	220.1
Broome sauropod morphotype A	8-30(rMP)	12.1.7	105	Large	325.5
	22-4	—	130	Very large	403
	9-1	—	135–140	Very large	418–434
	8-1	—	170–175	Very large	527–542.5
	9-11	—	175	Very large	542.5
Broome sauropod morphotype B	1-1(MP)	12.1.8	85	Large	263.5
Broome sauropod morphotype C	14-17(rMP)	—	87	Large	269.7
Broome sauropod morphotype D	14-10(rp)	12.1.9A	76	Large	235.6
	11-4(rp)	12.1.10	90	Large	279.0
Broome sauropod morphotype E	14-9(rp)	12.1.11	67	Large	207.7
	30-1(rp)	—	82	Medium/ large	254.5
<b>Ornithopod</b>					
<i>Wintonopus latomorum</i> Thulborn and Wade, 1984	23-1(lp)	12.1.12	13.4	Small	67
	23-2(lp2)	12.1.13	11	Small	55
	5-1(rp1)	12.1.14	20	Medium	100
<i>Wintonopus middletonae</i> , ichnosp. nov.	14-7(?lp) (topotype)	12.1.15 (holotype)	19	Medium	95
<i>Walmadanyichnus hunteri</i> , ichnogen. et ichnosp. nov.	11-5(rp) (topotype)	12.1.16 (holotype)	61.3	Very large	245.2
	11-18(rp)	—	80	Very large	320
	11-8(rp)	—	12.9	Small	51.6
<i>Amblydactylus</i> cf. <i>A. kortmeyeri</i>	9-3(rp)	12.1.18	44.6	Large	178.4
<b>Thyreophoran</b>					
<i>Garbina roeorum</i> , ichnogen. et ichnosp. nov.	14-1(lm1) (topotype)	12.1.19 (holotype)	21.4*	Large	—
	14-1(lp1) (topotype)	12.1.20 (holotype)	37*	Large	222
	14-15(lp)	12.1.21	41.7*	Large	250.2
cf. <i>Garbina</i>	9-12(lp)	—	70*	Very large	420
<i>Luluichnus meuckei</i> , ichnogen. et ichnosp. nov.	45-6(lp) (topotype)	15.12.701 (holotype)	16.4*	Medium	98.4
cf. <i>Luluichnus</i>	45-16(?lp)	15.12.704	18.4*	Medium	111
Thyreophoran morphotype A	8-17(rm)	15.12.705	29*	Very large	261
Thyreophoran morphotype B	45-15(rm)	15.12.706	19.7*	Medium	133

See Table 1 for the determination of size categories. \* denotes that track size measurement is track width (W) (cm)—for thyreophoran tracks only.

the composition of Australia's subsequent mid-Cretaceous dinosaurian faunas. In a broader sense, the dinosaurian ichnofauna of the Broome Sandstone also adds an important data point for furthering our understanding of the paleobiogeographic relationships of Gondwanan dinosaurs at the start of the Early Cretaceous.

Most of our knowledge on the composition of Australia's Cretaceous dinosaurian fauna comes from body fossils that derive from mid-Cretaceous (Aptian–Turonian; Wagstaff and McEwen Mason, 1989; Dettmann et al., 1992; Bryan et al., 1997; Wagstaff et al., 1997; Tucker et al., 2011; Bryan et al., 2012) strata in three main sedimentary basins on the eastern side of the continent (Fig. 66; Appendix 1): the Albian–lower Turonian Rolling Downs Group of the Eromanga Basin in western Queensland, northeastern South Australia and northwestern New South Wales (Longman, 1933; Molnar and Pledge, 1980; Bartholomai and Molnar, 1981; Coombs and Molnar, 1981; Molnar, 1991, 1996b, 1996a, 2001a, 2001b, 2010, 2011a; Molnar and Clifford, 2000, 2001; Molnar and Salisbury, 2005; Rauhut, 2005a; Salisbury et al., 2006; Hocknull and Cook, 2008; Leahey et al., 2008, 2010, 2015; Hocknull et al., 2009; Agnolín et al., 2010; Barrett et al., 2010a; White et al., 2012, 2013b, 2015a, 2015b; Leahey and Salisbury, 2013; Novas et al., 2013; Poropat et al., 2013, 2015a, 2015b); the lower-middle-Albian Grimman Creek Formation of the Surat Basin in northwestern New South Wales (Woodward, 1910; Huene, 1932; Molnar, 1984, 1990, 1991, 2011b; Molnar and Galton, 1986; Long, 1998; Smith, 1999; Molnar and Salisbury, 2005; Agnolín et al., 2010; Salisbury et al., 2011; Novas et al., 2013; White et al., 2013a; Bell et al., 2016); and the upper Aptian–early Albian Eumeralla Formation and upper Aptian Wonthaggi Formation of the Otway and Gippsland basins, respectively, both of which crop out along the southern coastline of Victoria (Woodward, 1906; Molnar et al., 1981, 1985; Welles, 1983; Rich and Vickers-Rich, 1988, 1989, 1994, 1999, 2003a; Rich et al., 1989; Currie et al., 1996; Chure, 1998; Smith et al., 2008; Herne, 2009; Herne and Salisbury, 2009; Agnolín et al., 2010; Barrett et al., 2010b, 2011; Benson et al., 2010a, 2010b, 2012; Herne et al., 2010; Salisbury et al., 2011; Fitzgerald et al., 2012; Novas et al., 2013). A similarly aged but poorly represented fauna is also known from the Cenomanian–lower Turonian Molecap Greensand of the Perth Basin in southwestern Western Australia (Long, 1995; Agnolín et al., 2010). Australia's only post-Turonian non-avian body fossils come from the Maastrichtian Miria Formation in the southern Carnarvon Basin in the Gascoyne region of Western Australia (Long, 1992b; Agnolín et al., 2010). The only pre-Aptian body fossils come from the lower Aptian Minmi Member of the Bungil Formation of the Surat Basin in southwestern Queensland (Molnar, 1980b; Molnar and Frey, 1987; Agnolín et al., 2010) and the Valanginian–Aptian Birdrong Sandstone of the southern Carnarvon Basin, Gascoyne, Western Australia (Long and Cruickshank, 1996; Agnolín et al., 2010). The body fossil record has been augmented to some extent by ichnological data from the Winton Formation of the Eromanga Basin (Thulborn and Wade, 1979, 1984; Romilio and Salisbury, 2011, 2013, 2014; Thulborn, 2013), the Grimman Creek Formation (Molnar, 1991) of the Surat Basin, the Eumeralla Formation of the Otway Basin (Flannery and Rich, 1981; Molnar, 1991; Rich and Vickers-Rich, 2000; Kool, 2006, 2007; Scanlon, 2006; Martin et al., 2007, 2012), and Wonthaggi Formation of the Gippsland Basin (Kool, 2006, 2007; Martin et al., 2007). For a detailed listing of all described non-avian Cretaceous dinosaurian taxa from these depositional basins, see Appendix 1.

Based on the described body fossils and tracks from the various aforementioned sedimentary basins, Australia's mid-Cretaceous dinosaurian fauna was, until relatively recently, considered to be a mix of taxa that were possible Jurassic or earliest Cretaceous relicts (e.g., *Allosaurus* sp. [Molnar, 1981, 1991, 1992; Molnar et al., 1981, 1985; Welles, 1983; Rich et al., 1992; Chure,

1998; Henderson et al., 2000; Rich and Vickers-Rich, 2000]; *Austrosaurus mckillopi* and *Austrosaurus* sp. [Longman, 1933; Molnar, 1980a, 1981, 1989, 1992; Coombs and Molnar, 1981; Henderson et al., 2000]), members of enigmatic and potentially endemic clades (e.g., *Kakuru kujani* [Molnar and Pledge, 1980; Molnar, 1991, 1992; Henderson et al., 2000]; *Muttaborrasaurus* spp. [Molnar, 1980a, 1981, 1991, 1992, 1996a; Bartholomai and Molnar, 1981]; *Minmi* spp. [Molnar, 1980b, 1991, 1992, 1996b, 2001b; Molnar and Frey, 1987; Henderson et al., 2000]), or members of clades that are otherwise best known from the Cretaceous of Laurasia (e.g., 'hypsiphodontid' ornithopods [Molnar, 1980a, 1984, 1992; Molnar and Galton, 1986; Rich and Vickers-Rich, 1988, 1999, 2000; Rich et al., 1989; Long, 1998; Smith, 1999; Henderson et al., 2000]; dromaeosaurid theropods [Currie et al., 1996; Vickers-Rich, 1996]; ornithomimosaurian theropods [Rich and Vickers-Rich, 1994, 2000; Rich, 1996; Rich and Young, 1996; Vickers-Rich, 1996; Rich et al., 1997; Vickers-Rich and Rich, 1997]; oviraptorosaurian theropods [Currie et al., 1996; Rich and Vickers-Rich, 2000]; neoceratopsian ornithischians [Rich and Vickers-Rich, 1989, 1994, 2000, 2003b; Vickers-Rich and Rich, 1993, 1997; Rich, 1996; Rich and Young, 1996; Vickers-Rich, 1996; Rich et al., 1997; Henderson et al., 2000]). Only *Rapator ornitholestoides*, tentatively regarded as a possible abelosaurid by Rauhut (2005b), was seen to potentially indicate paleobiogeographic links with South America.

But new discoveries of megaraptoran theropods (Smith, 1999; Hocknull et al., 2009; White et al., 2012, 2013, 2015a, 2015b; Bell et al., 2016) and titanosauriform sauropods (Molnar, 2001a, 2010, 2011; Molnar and Salisbury, 2005; Salisbury et al., 2006; Hocknull et al., 2009; Poropat et al., 2013; Poropat et al., 2015a, 2015b) and critical reassessments of previously described specimens (Molnar, 2001a; Molnar and Salisbury, 2005; Agnolín et al., 2010; Herne et al., 2010; Novas et al., 2013; Poropat et al., 2013) are increasingly demonstrating that the composition of Australia's Aptian–Turonian dinosaurian fauna is typical of other Gondwanan landmasses during that time. Although the identification and phylogenetic relationships of many taxa and specimens remain contentious (e.g., the Victorian 'pygmy *Allosaurus*' astragalus [Hocknull et al., 2009; Benson et al., 2012; Fitzgerald et al., 2012] vs. [Agnolín et al., 2010] vs. [Novas et al., 2013]; the Victorian 'tyrannosauroid' specimens [Benson et al., 2010a, 2010b, 2012] vs. [Herne et al., 2010; Novas et al., 2013]; '*Timimus hermani*' and other Victorian 'ornithomimosaurian' specimens [Rich and Vickers-Rich, 1994; Benson et al., 2012] vs. [Agnolín et al., 2010; Novas et al., 2013]; the Victorian 'oviraptorosaurian' specimens [Currie et al., 1996; Benson et al., 2012] vs. [Agnolín et al., 2010]; the Victorian 'ceratosaurian' astragalus [Fitzgerald et al., 2012] vs. [Novas et al., 2013]; the Victorian 'spinosaurid' vertebra [Barrett et al., 2011; Benson et al., 2012] vs. [Novas et al., 2013]; other indeterminate Victorian theropod specimens [Benson et al., 2012] vs. [Novas et al., 2013]; various megaraptoran specimens [Rich and Vickers-Rich, 2003b; Benson et al., 2012] vs. [Smith et al., 2008; Agnolín et al., 2010; Salisbury et al., 2011; Bell et al., 2016]; '*Serendipaceratops arthurclarkei*' and other Victorian 'neoceratopsian' specimens [Rich and Vickers-Rich, 1994, 2003b; Rich et al., 2014] vs. [Agnolín et al., 2010]; *Kakuru kujani* [Molnar and Pledge, 1980] vs. [Rauhut, 2005a; Agnolín et al., 2010] vs. [Barrett et al., 2010a]), we follow Smith et al. (2008), Agnolín et al. (2010), and Novas et al. (2013) and regard the majority of specimens and taxa as being assignable to clades that would be expected in eastern Gondwana under varying models of faunal interchange with South America via Antarctica. Other than the presence of clades that were already cosmopolitan by the Late Jurassic (e.g., titanosauriform sauropods and possibly megaraptoran theropods), we are of the opinion that paleobiogeographic links between Australia's mid-Cretaceous dinosaurian faunas and those that are typical of the mid-Late Cretaceous of Laurasia remain unsubstantiated.

Similar to South America (e.g., see Bonaparte, 1986, 1999; Bonaparte and Kielan-Jaworowska, 1987; Novas, 2009), Africa (e.g., Fraas, 1908; Taquet, 1976; Kennedy et al., 1987; Sereno et al., 1994; Rauhut and Werner, 1997; Sereno et al., 1999; O'Leary et al., 2004; McPhee et al., 2016), and India-Madagascar during the Late Cretaceous (e.g., Jain and Bandyopadhyay, 1997; Dodson et al., 1998; Curry Rogers and Forster, 2001, 2004), the most abundant and diverse herbivorous dinosaurs in the Australian mid-Cretaceous are titanosauriform sauropods. In the Eromanga Basin, medium-sized basal somphospondyl and possible lithostrotian titanosauriforms not only appear to be more diverse than other types of dinosaurs, but their remains are also numerically more abundant (Coombs and Molnar, 1981; Molnar, 2001a, 2010, 2011; Molnar and Salisbury, 2005; Salisbury et al., 2006; Hocknull et al., 2009; Poropat et al., 2013, 2015a, 2015b). Small-bodied, non-hadrosauriform ornithopods are also an important component of Australia's mid-Cretaceous herbivorous dinosaurian fauna, occurring in the Eromanga (Hocknull and Cook, 2008), Surat (Molnar, 1984; Molnar and Galton, 1986; Long, 1998; Smith, 1999; Agnolín et al., 2010), and Gippsland and Otway (Rich and Vickers-Rich, 1988, 1989, 1999; Herne, 2009; Herne and Salisbury, 2009; Agnolín et al., 2010) basins, but it is only in the latter two southern basins that they appear to have been abundant and diverse (but see Thulborn and Wade, 1979, 1984, and Romilio et al., 2013 for ichnological evidence of likely higher abundances of these dinosaurs in the Eromanga Basin). Recent discoveries in South America (Martínez, 1998; Coria, 1999; Coria and Calvo, 2002; Novas et al., 2004; Calvo et al., 2007a; Coria et al., 2007; Novas, 2009; Ibiricu et al., 2010; Ibiricu et al., 2014) and the Antarctic Peninsula (Hooker et al., 1991; Coria et al., 2013; Barrett et al., 2014; Rozadilla et al., 2016) now indicate that, similar to Australia, both of these landmasses had a high diversity of non-hadrosauriform ornithopods during the Cretaceous. Similarly, small-bodied basal ornithopods (Lydekker, 1889; Haughton, 1915; Janensch, 1955, 1961b; Galton, 1981a, 1983; Heinrich, 1999; Hübner, 2007, 2011; Hübner and Rauhut, 2010) and larger-bodied styracosternan ornithopods (Taquet, 1976; Taquet and Russell, 1999) are also known from the Upper Jurassic and Cretaceous of Africa. Whether some of these basal ornithopods formed part of an endemic pan-Gondwanan radiation remains to be tested (Novas et al., 2004; Herne, 2013; Rozadilla et al., 2016). Excluding material for which identifications are contentious (see above), the overall abundance of theropods in the Australian mid-Cretaceous remains low relative to all other Gondwanan landmasses except for Antarctica (Novas et al., 2013). Nevertheless, our understanding of their diversity is improving, with a noticeable apparent diversification of medium-sized megaraptorans during the Aptian–Cenomanian across four eastern Australian basins (the Eromanga, Surat, and Gippsland, and Otway basins) (Salisbury et al., 2011; White et al., 2015a; Bell et al., 2016).

Some notable differences between the Cretaceous dinosaurian faunas of Australia and other Gondwanan landmasses still remain. Rebbachisaurid and dicraeosaurid sauropods, a common element of the Cretaceous dinosaurian faunas of South America (Calvo and Salgado, 1995; Salgado et al., 2004; Gasparini et al., 2007; Novas, 2007, 2009; Carballido et al., 2010; Ibiricu et al., 2012, 2015) and Africa (Janensch, 1929b, 1935–1936, 1961a; Taquet, 1976; Sereno et al., 1994; Buffetaut and Cuny, 1995; Sereno et al., 1999; Gheerbrant and Rage, 2006; Remes, 2009; McPhee et al., 2016), are currently not known from Australia. Other conspicuous absences include confirmed abelisaurid, noasaurid, and alvarezsaurian theropods (Agnolín et al., 2010; Novas et al., 2013). With the exception of alvarezsaurians, all these theropod clades are otherwise well represented in South America (Bonaparte, 1991, 1996; Novas, 2007, 2009; Agnolín et al., 2012; Novas et al., 2013), Africa (Sereno et al., 2004), and India-Madagascar (Sampson et al., 1998, 2001; Carrano et al.,

2002; Wilson et al., 2003; O'Connor, 2007; Novas et al., 2010), suggesting faunal continuity (most likely through Antarctica–Australia) at various times during the Late Jurassic and Early Cretaceous. Evidence for unenlagiine, carcharodontosaurian, spinosauroid, and tyrannosauroid theropods in Australia also remains contentious (Agnolín et al., 2010; Benson et al., 2010a, 2010b, 2012; Herne et al., 2010; Barrett et al., 2011; Fitzgerald et al., 2012; Novas et al., 2013; Bell et al., 2016). Unlike South America, Antarctica, Africa, and India-Madagascar (Gasparini et al., 1987, 1996; Olivero et al., 1991; Coria and Salgado, 2001; Nath et al., 2002; Salgado and Gasparini, 2004, 2006; Ridgwell and Sereno, 2010; Arbour and Currie, 2016), small-bodied ankylosaurian thyreophorans appear to have been widespread and potentially diverse during the mid-Cretaceous in Australia, with occurrences across the Eromanga (Molnar, 1996b, 2001b; Molnar and Clifford, 2000, 2001; Leahey et al., 2008, 2010, 2015; Agnolín et al., 2010; Leahey and Salisbury, 2013), Surat (Molnar, 1980b; Molnar and Frey, 1987; Agnolín et al., 2010), and Gippsland and Otway (Barrett et al., 2010b) basins. Specimens assignable to Ankylosauria have also been recovered from the Upper Cretaceous of New Zealand (Molnar and Wiffen, 1994). However, the overall abundance of these ornithischians seems to have been low relative to other herbivorous dinosaurs. Only one genus of large-bodied non-hadrosauriform ornithopod, *Muttaborrasaurus* (Bartholomai and Molnar, 1981; Molnar, 1996a; Agnolín et al., 2010), is known from the Eromanga Basin, with fragmentary remains pointing to the occurrence of a similar animal in the Surat Basin (Molnar, 1991; Long, 1998; Smith, 1999). Absent from the Australian mid-Cretaceous thus far are hadrosauriform ornithopods, which, although represented only by fragmentary remains, do occur in the Upper Cretaceous of South America (Brett-Surman, 1979; Bonaparte et al., 1984; Prieto-Márquez and Salinas, 2010) and Antarctica (Rich et al., 1999; Case et al., 2000).

The ichnofauna of the Broome Sandstone of the Yinijarri–Lurujarri section of the Dampier Peninsula indicates that many aspects of the composition of Australia's mid-Cretaceous dinosaurian fauna were already in place during the Valanginian–Barremian. Both sauropods and bipedal ornithopods were diverse and abundant, and thyreophorans were the only type of quadrupedal ornithischian. Notable differences include the higher diversity of large-bodied theropods (represented in the Broome Sandstone ichnofauna by *Megalosauropus broomensis* and Broome theropod morphotypes B and C), the immense size of some of the sauropods (in particular Broome sauropod morphotype A), the higher diversity of bipedal ornithopods (as many as seven trackmakers), including the presence of large-bodied forms (*Walmadanyichnus hunteri*) that show similarities with Late Cretaceous hadrosauroids, and the high diversity and abundance of thyreophorans (as many as six trackmakers), among which were likely stegosaurians (*Garbina roeorum* and *Luluichnus mueckeii*).

Theropod tracks in the Broome Sandstone point to the presence of a varied suite of carnivorous dinosaurs in the Valanginian–Barremian of Australia. The range of sizes and pedal morphologies that are present strongly suggests that the five different track types represent disparate theropod taxa. This is in contrast to the situation in the mid-Cretaceous, where medium- to large-bodied megaraptorans seem to predominate. The narrow, elongated digital impressions of *Megalosauropus broomensis* are a good match for the gracile pedal skeleton of megaraptorids such as *Australovenator wintonensis* (see White et al., 2013) and suggest that the theropod responsible for these tracks may be an early representative of this or a closely related clade (see Bell et al., 2016, for a discussion of the likely Early Cretaceous emergence of megaraptorids). However, tracks similar to *Megalosauropus broomensis* are known from a range of Upper Jurassic and mid-Cretaceous sites across North America,

Europe, and Asia (see Lockley et al., 1996a, 2000), and slender, elongate digits are not restricted to megaraptorans among theropods (Farlow et al., 2013). The morphologies displayed by Broome theropod morphotypes B and C are very different, however, and point to the presence of other clades of theropods in the Lower Cretaceous of Australia beyond those represented in the mid-Cretaceous body fossil record. In contrast to the situation in Europe and Asia, the Lower Cretaceous theropod record for the Gondwanan landmasses is extremely poor, providing little in the way of clues as to the types of taxa that may have inhabited this part of the world during that time interval. In South America, indeterminate tetanuran remains are known from the Valanginian Bajada Colorada Formation (Apesteguía and Bonaparte, 2004; Gianechini and Apesteguía, 2011), whereas the upper Barremian–lower Aptian La Amarga Formation has produced the basal abelisauroid *Ligabueino andesi* and some indeterminate theropod teeth (Bonaparte, 1986). The only other Lower Cretaceous Gondwanan theropod body fossils are the probable ornithomimosaurian coelurosaur *Nqwebasaurus thwazi* (de Klerk et al., 2000; Choiniere et al., 2012) and an indeterminate tetanuran (Forster et al., 2009), both from the Berriasian–Hauterivian Kirkwood Formation of South Africa. It is not until the Albian–Cenomanian that the diversity of Gondwanan theropods expands to include the more familiar carcharodontosaurids, spinosaurids, and more derived coelurosaurians (Novas, 2007; Novas et al., 2013). Abelisauroids, although likely having arisen during the Late Jurassic, do not become numerically abundant and taxonomically diverse in South America, Africa, and Europe until the Late Cretaceous (Carrano and Sampson, 2008; Novas, 2009; Smith et al., 2010; Osi and Buffetaut, 2011). Given that many of the theropod clades that come to characterize Gondwanan dinosaurian faunas during the latter half of the Cretaceous, particularly in South America, India–Madagascar, and Africa, belong to groups that had their origins in the Middle to Late Jurassic (Makovicky et al., 2005; Zhang et al., 2008; Hu et al., 2009; Novas et al., 2013), it is conceivable that any or all of these taxa may have been present in the Lower Cretaceous of Australia. During the Middle to Late Jurassic, there was geographic and faunal continuity between all the Gondwanan landmasses, and between the African part of Gondwana and North America and Europe (Holtz et al., 2004). By the Berriasian–Hauterivian, however, biogeographic links between Africa and North America had diminished, such that only southern Europe was connected with Gondwana. This arrangement appears to have allowed what were previously regarded as typical Gondwanan theropod lineages (abelisauroids, spinosaurids, carcharodontosaurians, and alvarezsaurids) to move into southern Europe, but prevented Laurasian theropod taxa from moving into Gondwana: the recently proposed ‘Eurogondwanan’ model of Ezcurra and Agnolin (2012). Whether abelisauroids, spinosaurids, carcharodontosaurians, and alvarezsaurids also dispersed into Australia during the Early Cretaceous (potentially accounting for some of the diversity of theropod tracks in the Broome Sandstone) is difficult to establish in the absence of definitive body fossil evidence. Unambiguous evidence for any of the aforementioned clades is still conspicuously absent from the mid-Cretaceous theropod record of Australia. Regardless of the types of theropod trackmakers that were present in Australia during the Valanginian–Barremian, the overall taxic diversity during this time appears to have been greater than during the mid-Cretaceous. The drop in diversity by the mid-Cretaceous suggests that some of Australia’s Lower Cretaceous theropod taxa went extinct in the interval between the Barremian and Aptian, with the resultant mid-Cretaceous theropod fauna acquiring a typical Gondwanan flavor, similar to that of broadly coeval faunas in southern Patagonia, dominated by megaraptorans but lacking abelisauroids.

Although it is difficult to ascertain exactly what types of sauropods are represented in the Broome Sandstone ichnofauna, with the exception of *Oobardjidama foulkesi*, it is apparent that nothing as large as the trackmaker responsible for the some of the tracks assigned to Broome sauropod morphotype A (estimated hip heights up to ~5.4 m) has yet been described from the Australian Cretaceous. Although there are unsubstantiated reports of undescribed material representative of very large titanosauriform sauropods from the southern part of the Eromanga Basin, described titanosauriforms from the Winton Formation, such as *Wintonotitan watsi* and *Diamantinasaurus matildae*, all fall within the medium size range, with estimated hip heights of 3–3.15 and 2.8 m, respectively (based on data from Hocknull et al., 2009; Holliday et al., 2010; Poropat et al., 2015a, 2015b; with allowances for inter-osteological soft-tissue gaps set at 10% [Holliday et al., 2010]). Some of the tracks assigned to Broome sauropod morphotype A are indicative of trackmakers comparable in size to the largest known sauropod taxa, such as ‘*Antarctosaurus*’ *giganteus* (upper Campanian, Plottier Formation, Argentina; Huene, 1929; Mannion et al., 2013), *Argentinosaurus huinculensis* (upper Cenomanian, Huincul Formation, Argentina; Bonaparte and Coria, 1993), *Dreadnoughtus schrani* (Campanian–Maastrichtian, Cerro Fortaleza Formation, Argentina; Lacovara et al., 2014), *Elaltitan lilloi* (middle Cenomanian–Turonian, Bajo Barreal Formation, Argentina; Mannion and Otero, 2012), *Turiasaurus riodevensis* (Jurassic–Cretaceous boundary, Villar del Arzobispo Formation, Spain; Royo-Torres et al., 2006), *Futalognkosaurus dukei* (upper Turonian–lower Coniacian, Portezuelo Formation, Argentina; Calvo et al., 2007b), ‘*Huanghetitan*’ *ruyangensis* (Cenomanian–Santonian, Hekou Group, China; Lü et al., 2007; Mannion et al., 2013), *Paralititan stromeri* (Cenomanian, Bahariya Formation, Africa; Smith et al., 2001), *Puertasaurus reuili* (Cenomanian–lower Maastrichtian, Pari Aike Formation, Argentina; Novas et al., 2005), and *Notocolossus gonzalezparejasi* (upper Cenomanian–lower Santonian, Plottier Formation, Argentina; González Riga et al., 2016). Most of these taxa are titanosaurian titanosauriforms, with the majority deriving from the Upper Cretaceous (Cenomanian–Maastrichtian) of Argentina. Prior to the Turonian, diplodocoids, particularly rebbachisaurids, appear to be the dominant sauropods in Argentinian dinosaurian communities (Lamanna et al., 2001; Carvalho et al., 2003; Salgado et al., 2006; Novas, 2007). Rebbachisaurids are also the dominant sauropod taxa in the mid-Cretaceous ‘Continental Intercalaire’ and earlier strata of northern Africa (e.g., *Nigersaurus*, *Rebbachisaurus*), with their geographic range extending into broadly coeval parts of southern Europe (Fanti et al., 2015). The occurrence of very large-bodied sauropods in the Valanginian–Barremian of Australia is not surprising, but whether these were gigantic titanosaurians or non-titanosaurian sauropods is difficult to establish based purely on tracks. During the Late Jurassic, large-bodied brachiosaurid titanosauriforms are known from both the Northern and Southern Hemispheres, including North America (e.g., *Brachiosaurus altithorax* Riggs, 1903), Africa (*Giraffatitan brancai* [Janensch, 1914]), and possibly Europe and South America (Rauhut, 2006a; D’Emic, 2012; Mannion et al., 2013; Rauhut et al., 2015). Following the Jurassic–Cretaceous boundary, confirmed occurrences of brachiosaurids are restricted to the Lower Cretaceous (Aptian–Albian) of North America (e.g., *Cedarosaurus*, Tidwell et al., 1999; D’Emic, 2013; *Venenosaurus*, Tidwell et al., 2001; *Abydosaurus*, Chure et al., 2010). The recent recognition of a likely brachiosaurid in the Lower Cretaceous (Barremian–Aptian) Paja Formation of Colombia (*Padillasaurus leivaensis*, Carballido et al., 2015) and a possible brachiosaurid vertebra from the Berriasian–Hauterivian Kirkwood Formation of South Africa (McPhee et al., 2016) indicates that the clade may have persisted through to the Lower Cretaceous in the

northern parts of Gondwana (Carballido et al., 2015). The occurrence of large-bodied brachiosaurids in the Valanginian–Barremian of Australia is conceivable, and they would suggest that these titanosauriforms were more widespread across Gondwanan landmass than the current body fossil record indicates. Regardless of the taxonomic affinities of the largest Broome Sandstone sauropod trackmakers, the high diversity and abundance of these dinosaurs in the ichnofauna is reminiscent of that seen in Late Jurassic dinosaurian faunas from North America and Asia. The Lower Cretaceous dinosaurian fossil record is poor relative to other time slices, particularly so in the Gondwanan landmasses. Nevertheless, the high diversity of the sauropod ichnofauna in the Broome Sandstone indicates that the high sauropod diversity seen during the Late Jurassic may have persisted in some parts of Gondwana after the Jurassic/Cretaceous extinction event that appears to have impacted on the clade elsewhere (Raup and Sepkoski, 1986), as has been suggested for South America by Carballido et al. (2015).

The ornithopod ichnofauna of the Broome Sandstone indicates that the abundance and diversity of these ornithischians in the Australian mid-Cretaceous extended into the Valanginian–Barremian. Small- to medium-bodied trackmaker taxa similar to those responsible for *Wintonopus latimorum* tracks in the Cenomanian–Turonian of the Eromanga Basin were already part of Australia's ornithischian fauna at the time the Broome Sandstone was deposited, along with larger-bodied forms that displayed a comparable subunguligrade pedal stance (*Win. middletonae*). The high diversity of these small- to medium-bodied bipedal ornithopods in the Broome Sandstone—most likely basal iguanodontians—parallels that of dryosaurids and non-styracosternan ankylopollexians in the Upper Jurassic and Lower Cretaceous of North America and Europe (Norman, 2004). Other large- and very large-bodied forms (represented by tracks assigned to *Amblydactylus* cf. *A. kortmeyeri* and *Walmadanyichnus hunteri*, respectively) may be indicative of large-bodied non-hadrosauroid styracosternans similar to *Muttaborrasaurus* (Bartholomai and Molnar, 1981; Molnar, 1996a; Agnolín et al., 2010). However, the very large size and unusual, near-circular morphology resulting from short and broad digital impressions displayed by tracks assigned to *Walmadanyichnus hunteri* is unlike large ornithopod tracks from the Eromanga Basin known to contain *Muttaborrasaurus* body fossil remains (see Romilio and Salisbury, 2011, 2014). In many respects, these tracks are reminiscent of those typically attributed to large-bodied hadrosauroids such as *Hadrosauropodus* or *Caririchnium* (see Díaz-Martínez et al., 2015).

Accounting for the presence of large-bodied hadrosauroids in Australia during the Early Cretaceous is difficult. Hadrosauroids first diversified in uppermost Lower Cretaceous of Asia and to a lesser extent North America (Prieto-Márquez, 2010; Shibata et al., 2015). Thus far, the only confirmed record of hadrosauroids from the Gondwanan landmasses are four taxa of 'kritosaurs' from the upper Campanian–Maastrichtian of Argentina (Bonaparte et al., 1984; Bonaparte and Rougier, 1987; Coria, 2011; Coria et al., 2012): *Secernosaurus koerneri*, '*Kritosaurus australis*', *Willinakaqe salitralensis*, and *Lapampasaurus cholinoi*, along with some indeterminate specimens of lambeosaurines (Brett-Surman, 1979; Bonaparte et al., 1984; Juárez Valieri et al., 2010; Prieto-Márquez and Salinas, 2010; Coria, 2011). The precise number of hadrosauroids in this assemblage seems to be in a state of flux. Prieto-Márquez and Salinas (2010) have proposed that '*Kritosaurus australis*' is a junior synonym of *S. koerneri*, whereas Cruzado-Caballero and Coria (2016) have shown that *Willinakaqe salitralensis* may not be diagnostic, and that the hypodigm probably belongs to at least two different taxa. Notwithstanding these issues, scant remains of likely hadrosaurids are also known from the Upper Cretaceous (upper Maastrichtian) of the Antarctic Peninsula (Rich et al.,

1999; Case et al., 2000). All these taxa are currently regarded as Late Cretaceous immigrants from North America (Bonaparte and Rougier, 1987; Prieto-Márquez and Salinas, 2010).

*Hadrosauropodus* has a temporal range that spans the Aptian–Maastrichtian (Díaz-Martínez et al., 2015), with tracks known from numerous sites in North America, Europe, and Asia, closely corresponding to the fossil record of hadrosauroids (Horner et al., 2004; Prieto-Márquez, 2010). Ornithopod tracks assigned to *Caririchnium* are known from sites that span the Lower Cretaceous in South America, North America, Europe, and Asia (Díaz-Martínez et al., 2015). The oldest record of *Caririchnium* is that of *C. magnificum*, which comes from the Berriasian–Hauterivian Antenor Navarro Formation of Brazil (Leonardi, 1984; Díaz-Martínez et al., 2015). Given their age, Novas (2007), Coria and Cambiaso (2007), and Díaz-Martínez et al. (2015) have speculated that these tracks may have been made by a basal iguanodontian, basal ankylopollexian, or non-hadrosauroid styracosternan, despite the fact that there is no body fossil record of large-bodied representatives of these clades in the Lower Cretaceous of South America. Although tracks assignable to *Caririchnium* have not been recorded in Africa (Díaz-Martínez et al., 2015), there are two large-bodied non-hadrosauroid styracosternans from the Aptian portion of the Elrhaz Formation of Niger, Africa (*Ouranosaurus nigeriensis* and *Lurdusaurus arentus*; Taquet, 1976; Taquet and Russell, 1999), thus consistent with the idea that large-bodied ornithopods were part of Lower Cretaceous dinosaurian faunas in Gondwana. Whether tracks assigned to *Walmadanyichnus hunteri* pertain to a similar type of non-hadrosauroid iguanodontid is difficult to ascertain in the absence of body fossil material from the Lower Cretaceous of Australia. Although seemingly rare during the Early Cretaceous in other Gondwanan dinosaurian faunas, the ichnological evidence from the Broome Sandstone indicates that, at least in Australia, these large herbivores were relatively abundant, surpassed only by sauropods.

The high diversity of thyreophorans in the ichnofauna of the Broome Sandstone indicates that these herbivorous ornithischians formed an important part of Australia's Early Cretaceous dinosaurian faunas. Body fossils of thyreophorans are now known from all the Gondwanan landmasses (Galton and Upchurch, 2004; Vickaryous et al., 2004; Ridgwell and Sereno, 2010; Pereda Suberbiola et al., 2013). During the Cretaceous, the most substantial skeletal remains of Gondwanan thyreophorans come from Australia, where two medium-bodied ankylosaurian taxa are known: *Minmi paravertebra* from the lower Aptian portion of the Bungil Formation of the Surat Basin (Molnar, 1980b) and *Kunbarrasaurus ieveri* from the upper Albian Allaru Mudstone of the Eromanga Basin (Molnar, 1996b; Leahey et al., 2015). Indeterminate and undescribed ankylosaurian remains further indicate that additional taxa may have been present in the Eromanga (Molnar, 1991; Rich and Vickers-Rich, 2003a; Leahey and Salisbury, 2013) and Otway and Gippsland (Barrett et al., 2010b) basins. Other evidence for Gondwanan ankylosaurs is limited to fragmentary remains from the Campanian Tahora Formation of New Zealand (Molnar and Wiffen, 1994), the middle Campanian–lower Maastrichtian Allen Formation of Argentina (Ankylosauria indet.; Coria and Salgado, 2001), and the Campanian Snow Hill Island Formation of Antarctica (*Antarctopelta oliveroi*; Gasparini et al., 1996; Salgado and Gasparini, 2006). Isolated teeth from the Cenomanian–Turonian of Madagascar assigned to '*Stegosaurus madagascariensis*' by Piveteau (1926) have recently been reinterpreted as pertaining to an indeterminate ankylosaurid (Maidment, 2010; Pereda Suberbiola et al., 2013). The ichnofauna of the Broome Sandstone shows that the diversity of thyreophorans in the Australian part of eastern Gondwana was even greater during the Valanginian–Barremian, and that in addition to likely basal ankylosaurian trackmakers (represented by tracks assigned to Broome

thyreophoran morphotype A and possibly Broome thyreophoran morphotype B), stegosaurians formed an important part of the ornithischian fauna (represented by tracks assigned to *Garbina roeorum*, cf. *Garbina*, *Luluichinus mueckeii*, and cf. *Luluichnus*). Indeed, tracks that can be assigned to *Garbina roeorum* are considerably more abundant and widespread across tracksites in the Yanijarri–Lurujarri section of the Dampier Peninsula than other thyreophoran tracks, suggesting a higher abundance of this stegosaurian trackmaker. Although stegosaurian body fossils are not known from Australia, skeletal remains of stegosaurians are known from the Cretaceous of other Gondwanan landmasses. *Paranthodon africanus*, from the Berriasian–Hauterivian Kirkwood Formation of South Africa, represents one of the historically earliest discovered stegosaurians (Atherstone, 1857; Galton, 1981b; Galton and Coombs, 1981; Maidment et al., 2008). Indeterminate stegosaurian remains have been also been described from the Barremian–lower Aptian La Amarga Formation of Argentina (Bonaparte, 1996; Pereda Suberbiola et al., 2013). In contrast, *Dravidosaurus blanfordi* from the Coniacian Trichinopoly Group of southern India, initially thought to represent a stegosaurian by Yadagiri and Ayyasami (1979), has recently been considered a nomen dubium, with most of the material likely belonging to a plesiosaur (Chatterjee and Rudra, 1996).

During the Late Jurassic, stegosaurians were abundant, very diverse, and occurred on all continents except South America, Australia, and Antarctica (Dong, 1990; Galton and Upchurch, 2004; Maidment and Wei, 2006; Maidment et al., 2008; Galton, 2012). The assignment herein of the probable stegosaurian manual track from the Walloon Coal Measures of Balgowan (Hill et al., 1966) to cf. *Garbina* further suggests that stegosaurians may have been present in Australia during the Middle Jurassic. As is the case with sauropods, the high diversity of thyreophorans, including likely stegosaurians, represented in the Broome Sandstone ichnofauna is reminiscent of the Late Jurassic dinosaurian body fossil faunas of North America and Laurasia. Ichnological evidence from the Upper Jurassic–Lower Cretaceous La Puerta Formation of Bolivia hints at potentially the same situation in South America (Apesteeguía and Gallina, 2011). However, given that all four of the La Puerta Formation thyreophoran trackmakers left tetradactyl pedal tracks, we are not convinced that any can unambiguously be assigned to stegosaurians, which typically have a tridactyl pes (e.g., *Kentrosaurus* and *Stegosaurus*; Galton and Upchurch, 2004). As a consequence, it seems more likely that the Bolivian tracks pertain to ankylosaurians or basal thyreophorans. Other tracks from the Berriasian–Hauterivian Antenor Navarro Formation of Brazil, initially assigned to the ichnotaxon *Carrichnium magnificum* and attributed to a stegosaurian by Leonardi (1984), most likely belong to a quadrupedal ornithomimid (Lockley, 1987; Lockley and Wright, 2001; Díaz-Martínez et al., 2015). That being the case, evidence for stegosaurians in South America is probably limited to the aforementioned skeletal remains from the La Amarga Formation. Leanza et al. (2004), Apesteeguía (2007), Novas (2007), and Pereda Suberbiola et al. (2013) all considered the occurrence of stegosaurians alongside diplodocoids sauropods in the Barremian–lower Aptian of South America to be reminiscent of the dinosaurian faunas from the Late Jurassic of East Africa (specifically the upper Kimmeridgian–Tithonian Tendaguru Beds of Tanzania), and that such a fauna might be characteristic for Gondwana during this time. The same type of fauna also appears to have extended into the Berriasian–Hauterivian Kirkwood Formation of South Africa (McPhee et al., 2016). The occurrence of tracks that can be assigned to stegosaurians and other thyreophorans in the Broome Sandstone is consistent with this idea and suggests that the range of this type of dinosaurian fauna extended into eastern Gondwana until at least the Barremian.

The absence of evidence for stegosaurians from the mid-Cretaceous of Australia is suggestive of some kind of faunal turnover between the Barremian and Aptian, with ankylosaurians persisting as the dominant quadrupedal ornithischians. Although body fossil evidence for stegosaurians in the Lower Cretaceous of Gondwana is rare (Galton, 1981b; Galton and Coombs, 1981; Maidment et al., 2008; Pereda Suberbiola et al., 2013), the ichnological evidence from Broome suggests that this might be an artifact of an incomplete body fossil record, and that after diversifying and becoming broadly distributed globally during the Late Jurassic, stegosaurians and perhaps also some non-eurypodan thyreophorans became an important component of Gondwanan dinosaurian faunas during the Early Cretaceous. The rise in diversity and abundance of other types of thyreophorans—namely, ankylosaurians—as well as various bipedal ornithomimids and sauropods may be part of the reason that stegosaurians did not persist into the mid-Cretaceous in Australia and other Gondwanan landmasses. Whether the Upper Cretaceous record of ankylosaurian thyreophorans seen in Antarctica (Gasparini et al., 1996; Salgado and Gasparini, 2006; Arbour and Currie, 2016) and South America (Coria and Salgado, 2001) is a holdover from a mid-Cretaceous Gondwanan basal thyreophoran radiation or representative of an invasion of more derived taxa from North America remains to be thoroughly tested, pending the discovery of more complete body fossil remains, but at the moment the latter scenario seems the most likely (Bonaparte, 1986). Tracks indicative of large-bodied ankylosaurians from the ?Maastrichtian El Molino Formation of Bolivia support this idea (McCrea et al., 2001).

Overall, the ichnofauna of the Broome Sandstone reinforces the idea that Australia's Early Cretaceous dinosaurian fauna was not too different from what would be expected for a Gondwanan landmass at that time. Most aspects of Australia's mid-Cretaceous dinosaurian faunas were already in place, with both sauropods and bipedal ornithomimids being diverse and abundant, and thyreophorans being the only type of quadrupedal ornithischian. There is no unambiguous evidence for the presence of marginocephalians, particularly anything that could suggest a neoceratopsian (contra Rich and Vickers-Rich, 1994). Important aspects of the fauna that are not seen in the Australian mid-Cretaceous body fossil record are the presence of stegosaurians and an overall higher diversity of thyreophorans and theropods, and the presence of large-bodied hadrosauroid-like ornithomimids and very large-bodied sauropods. In many respects, these differences suggest a holdover from the Late Jurassic, when the majority of dinosaurian clades had a more cosmopolitan distribution prior to the fragmentation of Pangea (Apesteeguía, 2002; Leanza et al., 2004). The presence of stegosaurians and a high diversity of sauropods is reminiscent of the Late Jurassic African faunas of the upper Kimmeridgian–Tithonian Tendaguru beds (Janensch, 1914, 1925, 1929a, 1929b, 1935–1936; Bonaparte, 1986; Weishampel et al., 2004; Rauhut, 2005a, 2006b; Allain et al., 2007; Rauhut, 2011). Although the record for the Lower Cretaceous of Gondwana is sparse, a similar mix of taxa occurs in the Barremian–lower Aptian La Amarga Formation of Argentina (Bonaparte, 1996; Pereda Suberbiola et al., 2013) and the Berriasian–Hauterivian Kirkwood Formation of South Africa (Atherstone, 1857; Galton, 1981b; Galton and Coombs, 1981; Maidment et al., 2008; MCPhee et al., 2016). The persistence of this fauna across the Jurassic–Cretaceous boundary in South America, Africa, and Australia might characterize Gondwanan dinosaurian faunas more broadly, as has been proposed by Bonaparte (1986), Salgado and Bonaparte (1991), Leanza et al. (2004), and Apesteeguía (2007). It further suggests that the extinction event that affected the Laurasian dinosaurian faunas across the Jurassic–Cretaceous boundary (Raup and Sepkoski, 1986) may not have been extreme in Gondwana, and that this difference may have foreshadowed the onset of Laurasian–Eurogondwanan

provincialism (Bonaparte, 1979, 1986; Apesteguía, 2007; Ezcurra and Agnolin, 2012). The disappearance of stegosaurians and the apparent drop in diversity of theropods by the mid-Cretaceous suggest that, similar to South America (Leanza et al., 2004; Apesteguía, 2007; Novas, 2009), Australia passed through a period of faunal turnover between the Valanginian and Aptian.

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#### LITERATURE CITED

- Adams, T. L., C. Strganac, M. J. Polcyn, and L. L. Jacobs. 2010. High resolution three-dimensional laser-scanning of the type specimen of *Eubrontes (?) glenrosensis* Shuler, 1935, from the Comanchean (Lower Cretaceous) of Texas: implications for digital archiving and preservation. *Palaeontologia Electronica* 13(3):1T. [http://palaeo-electronica.org/2010\\_3/226/index.html](http://palaeo-electronica.org/2010_3/226/index.html).
- Agnolin, F. L., M. D. Ezcurra, D. F. Pais, and S. W. Salisbury. 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Journal of Systematic Palaeontology* 8:257–300.
- Agnolin, F. L., J. E. Powell, F. E. Novas, and M. Kundrát. 2012. New alvarezsaurid (Dinosauria, Theropoda) from uppermost Cretaceous of north-western Patagonia with associated eggs. *Cretaceous Research* 35:33–56.
- Akerman, K. 1975. Aboriginal camp sites on the western coast of Dampier Land, Western Australia. *Occasional Papers in Anthropology* 4:93–104.
- Akerman, K. 1976. Horde Areas and Mythological Sites between James Price Point and Coconut Well on the West Coast of Dampierland, WA. Kimberley Land Council, Broome, Western Australia.
- Akerman, K. 1981. The dinosaur footprints. *Broome News*, November 1981:30–31.
- Alexander, R. M. 1976. Estimates of speeds of dinosaurs. *Nature* 261:129–130.
- Allain, R., and N. Aquesbi. 2008. Anatomy and phylogenetic relationships of *Tazoudasaurus naimi* (Dinosauria, Sauropoda) from the late Early Jurassic of Morocco. *Geodiversitas* 30:345–424.
- Allain, R., R. S. Tykoski, N. Aquesbi, N.-E. Jalil, M. Monbaron, D. A. Russell, and P. Taquet. 2007. An abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the radiation of ceratosaurs. *Journal of Vertebrate Paleontology* 27:610–624.
- Allen, J. P., and C. R. Fielding. 2007. Sedimentology and stratigraphic architecture of the Late Permian Betts Creek Beds, Queensland, Australia. *Sedimentary Geology* 202:5–34.
- Allen, J. R. L. 1983. Studies in fluvial sedimentation; bar complexes and sandstone sheets (low sinuosity braided streams) in the

- Brownstones, Lower Devonian, Welsh Borders. *Sedimentary Geology* 55:233–262.
- Anonymous. 1935. Guiding in the West. *The Age* November 5, 1935:4.
- Anonymous. 1946. Broome natives knew of dinosaur tracks. *The Daily News* (Perth, Western Australia, 1882–1950) Saturday 5 January 1946:15.
- Anonymous. 1952. Dinosaur's footprints. *Queensland Government Mining Journal* 53:949–950.
- Anonymous. 1996. Thieves walk off with sacred dinosaur footprints. *CN/Reuters news story* October 15.
- Anonymous. 1999. *Heritage Trail. Lurujarri—Retracing the Song Cycle from Minarriny to Yinara*. Heritage Council of Western Australia, East Perth, Australia, 9 pp.
- Antunes, M. T. 1976. *Dinosaurios Eocretácicos de Lagosteriros*. Universidade Nova de Lisboa. *Ciências da Terra* 1:1–36.
- Apesteuguía, S. 2002. Successional structure in continental tetrapod faunas from Argentina along the Cretaceous; pp. 135–141 in *Realização UNESP (ed.), Boletim do VI Simpósio sobre o Cretáceo do Brasil/2º Simpósio sobre o Cretáceo de América del Sur*, (Sao Pedro, Brasil), resumos. Sao Pedro, Brazil.
- Apesteuguía, S. 2005. Evolution of the titanosaur metacarpus; pp. 321–345 in V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Apesteuguía, S. 2007. The sauropod diversity of the La Amarga Formation (Barremian), Neuquén (Argentina). *Gondwana Research* 12:533–546.
- Apesteuguía, S., and J. F. Bonaparte. 2004. Bajada Colorada (Valanginian) dinosaurs from Neuquén: note on the oldest Cretaceous dinosaurs from the Neuquén basin. *Ameghiniana* 41:34R.
- Apesteuguía, S., and P. A. Gallina. 2011. Tunasniyoj, a dinosaur tracksite from the Jurassic-Cretaceous boundary of Bolivia. *Anais da Academia Brasileira de Ciências* 83:267–277.
- Arbour, V. M., and P. J. Currie. 2016. Systematics, phylogeny and palaeobiogeography of the ankylosaurid dinosaurs. *Journal of Systematic Palaeontology* 14:385–444.
- Atherstone, W. G. 1857. *Geology of Uitenhage*. The Eastern Province Monthly Magazine 1:518–532.
- Avanzini, M., G. Leonardi, and P. Mietto. 2003. *Lavinipies cheminii* ichnogen., *ichnosp. nov.*, a possible sauropodomorph track from the Lower Jurassic of the Italian Alps. *Ichnos* 10:179–193.
- Avanzini, M., L. Piñuela, and J. C. Garcia-Ramos. 2012. Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. *Lethaia* 45:238–252.
- Avanzini, M., S. Frisia, K. Van Den Driessche, and E. Keppens. 1997. A dinosaur tracksite in an early Liassic tidal flat in northern Italy: paleoenvironmental reconstruction from sedimentology and geochemistry. *Palaios* 12:538–551.
- Avanzini, M., D. Piubelli, P. Mietto, G. Roghi, R. Romano, and D. Masetti. 2006. Lower Jurassic (Hettangian-Sinemurian) dinosaur track megasites, southern Alps, northern Italy. *New Mexico Museum of Natural History and Science Bulletin* 37:207–216.
- Baird, D. 1957. Triassic reptile footprint faunules from Milford, New Jersey. *Bulletin of the Museum of Comparative Zoology* 117:449–520.
- Baird, D. 1980. A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona; pp. 219–230 in L. L. Jacobs (ed.), *Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert*. Museum of Northern Arizona Press, Flagstaff, Arizona.
- Baird, D. 1989. Medial Cretaceous carnivorous dinosaur and footprints from New Jersey. *The Mosasaur* 4:53–63.
- Bakker, R. T. 1996. The real Jurassic Park: dinosaurs and habitats at Como Bluff, Wyoming. *Museum of Northern Arizona, Bulletin* 60:35–49.
- Balme, B. E. 1963. Appendix 10: Palynological reports on samples from BMR 4A; pp. 71–74 in S. D. Henderson, M. A. Condon, and L. V. Bastian (eds.), *Stratigraphic Drilling. Canning Basin, Western Australia*. Report of the Bureau of Mineral Resources, Geology and Geophysics, Australia. No. 60. Perth, Australia.
- Barrett, P., A. Milner, and J. Hooker. 2014. A new ornithomimid dinosaur from the latest Cretaceous of the Antarctic Peninsula. *Journal of Vertebrate Paleontology* 34(Programs and Abstracts):85–86.
- Barrett, P. M., B. P. Kear, and R. B. J. Benson. 2010a. Opalized archosaur remains from the Bulldog Shale (Aptian: Lower Cretaceous) of South Australia. *Alcheringa* 34:292–301.
- Barrett, P. M., R. B. J. Benson, T. H. Rich, and P. Vickers-Rich. 2011. First spinosaurid dinosaur from Australia and the cosmopolitanism of Cretaceous dinosaur faunas. *Biology Letters* 7:933–936.
- Barrett, P. M., T. H. Rich, P. Vickers-Rich, T. A. Tumanova, M. Inglis, D. Pickering, L. Kool, and B. P. Kear. 2010b. Ankylosaurian dinosaur remains from the Lower Cretaceous of southeastern Australia. *Alcheringa* 34:205–217.
- Bartholomai, A. 1966. Fossil footprints in Queensland. *Australian Natural History* 15:147–150.
- Bartholomai, A., and R. E. Molnar. 1981. *Muttaborrasaurus*, a new iguanodontid (Ornithischia: Ornithomimidae) dinosaur from the Lower Cretaceous of Queensland. *Memoirs of the Queensland Museum* 20:319–349.
- Bates, D. M. 1929. Warragunna, Jindabirrbirr, and Joogajooga. A legend of Broome. *The Australasian*, Melbourne 9 March 1929:6.
- Bates, K. T., P. L. Manning, B. Vila, and D. Hodgetts. 2008. Three-dimensional modelling and analysis of dinosaur trackways. *Palaeontology* 51:999–1010.
- Beaton, B. (ed.) 1992. *The Great Dinosaur Hunt. Reel Images and Location Equipment*, Victoria Park, Western Australia, Australia.
- Bell, P. R., A. Cau, F. Fanti, and E. T. Smith. 2016. A large-clawed theropod (Dinosauria: Tetanurae) from the Lower Cretaceous of Australia and the Gondwanan origin of megaraptorid theropods. *Gondwana Research* 36:473–487.
- Belvedere, M. 2009. *Ichnological researches on the Upper Jurassic dinosaur tracks in Iouaridène area (Demnat, central High-Atlas, Morocco)*. Ph.D. dissertation, Università Degli Studi di Padova, Padua, Italy, 130 pp.
- Belvedere, M., and P. Mietto. 2010. First evidence of stegosaurian *Deltaopodus* footprints in North Africa (Iouaridène Formation, Upper Jurassic, Morocco). *Palaeontology* 53:233–240.
- Benson, R. B. J., P. M. Barrett, T. H. Rich, and P. Vickers-Rich. 2010a. A southern tyrant reptile. *Science* 327:1613.
- Benson, R. B. J., T. H. Rich, P. Vickers-Rich, and M. Hall. 2012. Theropod fauna from southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. *PLoS ONE* 7:e37122. doi: 10.1371/journal.pone.0037122.
- Benson, R. B. J., P. M. Barrett, T. H. Rich, P. Vickers-Rich, D. Pickering, and T. Holland. 2010b. Response to comment on “A southern tyrant reptile”. *Science* 329:1013–d.
- Benrerrak, K., S. Muecke, and P. Roe. 1996. *Reading the Country: Introduction to Nomadology*, second edition. Freemantle Arts Centre Press, Fremantle, Western Australia, Australia, 280 pp.
- Bird, R. T. 1939. Thunder in his footsteps. *Natural History* 43:254–261, 302.
- Bird, R. T. 1941. A dinosaur walks into the museum. *Natural History* 47:74–81.
- Bird, R. T. 1944. Did *Brontosaurus* ever walk on land? *Natural History* 53:60–67.
- Bird, R. T. 1985. *Bones for Barnum Brown: adventures of a dinosaur hunter*. Texas Christian University Press, Fort Worth, Texas, 225 pp.
- Bock, W. 1952. Triassic reptilian tracks and trends of locomotive evolution, with remarks on correlation. *Journal of Paleontology* 26:395–433.
- Boggs, S., Jr. 2009. *Petrology of Sedimentary Rocks*, second edition. Cambridge University Press, Cambridge, U.K., 610 pp.
- Boggs, S., Jr. 2011. *Principles of Sedimentology and Stratigraphy*, fifth edition. Prentice Hall, Upper Saddle River, New Jersey, 600 pp.
- Bonaparte, J. F. 1979. Dinosaurs: a Jurassic assemblage from Patagonia. *Science* 205:1377–1379.
- Bonaparte, J. F. 1986. History of the terrestrial Cretaceous vertebrates of Gondwana; pp. 63–95 in J. F. Bonaparte (ed.), *Simpósio Evolucion de los Vertebrados Mesozoicos*. Actas IV Congreso Argentino de Paleontología y Biostratigrafía. Mendoza, Noviembre 23–27, 1986. Editorial Inca, Mendoza, Argentina.
- Bonaparte, J. F. 1991. The Gondwanian theropod families Abelisauridae and Noasauridae. *Historical Biology* 5:1–25.
- Bonaparte, J. F. 1996. Cretaceous tetrapods of South America. *Münchner Geowissenschaftliche Abhandlungen A* 30:73–130.
- Bonaparte, J. F. 1999. Evolución de las vertebras presacras en Sauropodomorpha. *Ameghiniana* 36:115–187.
- Bonaparte, J. F., and R. A. Coria. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Rio Limay (Albiano-Cenomaniano) de la Provincia del Neuquén, Argentina. *Ameghiniana* 30:271–282.

- Bonaparte, J. F., and Z. Kielan-Jaworowska. 1987. Late Cretaceous dinosaur and mammal faunas of Laurasia and Gondwana; pp. 24–29 in P. J. Currie and E. H. Koster (eds.), Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. Occasional Papers of the Tyrrell Museum of Palaeontology. Drumheller, Alberta, Canada.
- Bonaparte, J. F., and G. W. Rougier. 1987. The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Part VII—the hadrosaurs. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* 3:155–161.
- Bonaparte, J. F., M. R. Franchi, J. E. Powell, and E. G. Sepulveda. 1984. La formación Los Alamitos (Campaniano-Maastrichtiano) del sudeste de Río Negro, con descripción de *Kritosaurus australis* n. sp. (Hadrosauridae). Significado paleogeográfico de los vertebrados. *Asociación Geológica Argentina, Revista* 39:284–299.
- Bonnan, M. F. 2005. Pes anatomy in sauropod dinosaurs: implications for functional morphology, evolution, and phylogeny; pp. 346–380 in V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Bose, M. N., and M. L. Kasat. 1972. The genus *Ptilophyllum* in India. *The Palaeobotanist* 19:115–145.
- Botsman, P. 2012. Law Below the Top Soil; Walmadany (James Price Point) and the Question of the Browse Basin Gas Resource of North West Australia. Save the Kimberley, Broome, Western Australia, Australia, 108 pp.
- Boutakiout, M., J. Nouri, L. Ladel, I. Díaz-Martínez, and F. Pérez-Lorente. 2012. El yacimiento de icnitas de dinosaurio 34IGR. Iouaridène, Alto Atlas Central. Marruecos. *Geogaceta* 51:43–46.
- Bradshaw, E., and R. Fry. 1989. A Management Report for the Lurujarri Heritage Trail, Broome, Western Australia. Department of Aboriginal Sites, Western Australian Museum, Perth, Australia, 36 pp.
- Bradshaw, M. T., A. N. Yeates, R. M. Beynon, A. T. Brakel, R. P. Langford, J. M. Totterdell, and M. Yeung. 1988. Palaeogeographic evolution of the North West Shelf region; pp. 29–54 in P. G. Purcell and R. R. Purcell (eds.), *The North West Shelf Australia*. Petroleum Exploration Society of Australia, Western Australian Branch, Perth, Australia.
- Brett-Surman, M. K. 1979. Phylogeny and palaeobiogeography of hadrosaurian dinosaurs. *Nature* 277:560–562.
- Brown, S. A., I. M. Boserio, K. S. Jackson, and K. W. Spence. 1984. The geological evolution of the Canning Basin—implications for petroleum exploration; pp. 85–96 in P. G. Purcell (ed.), *The Canning Basin*, W.A. Geological Society of Australia and Petroleum Exploration Society of Australia, Perth, Australia.
- Brunschweiler, R. O. 1957. The geology of Dampier Peninsula, Western Australia. *BMR Journal of Australian Geology & Geophysics* 13:1–19.
- Brusatte, S. L., T. J. Challands, D. A. Ross, and M. Wilkinson. 2016. Sauropod dinosaur trackways in a Middle Jurassic lagoon on the Isle of Skye, Scotland. *Scottish Journal of Geology* 52:1–9.
- Bryan, S. E., A. E. Constantine, C. J. Stephens, A. Ewart, R. W. Schon, and J. Parianos. 1997. Early Cretaceous volcano-sedimentary successions along the eastern Australian continental margin: implications for the break-up of eastern Gondwana. *Earth and Planetary Science Letters* 153:85–102.
- Bryan, S. E., A. G. Cook, C. M. Allen, C. Siegel, D. J. Prudy, J. S. Green-tree, and I. T. Uysal. 2012. Early-mid Cretaceous tectonic evolution of eastern Gondwana: from silicic LIP magmatism to continental rapture. *Episodes* 35:142–152.
- Buffetaut, E., and G. Cuny. 1995. African dinosaur discoveries [comment on Sereno et al 1994]. *Science* 267:1750–1752.
- Calvo, J. O. 1991. Huellas de dinosaurios en la Formación Río Limay (Albiano-Cenomaniano?), Picum Leufu, Provincia de Neuquén, República Argentina. (Ornithischia-Saurischia: Sauropoda-Theropoda). *Ameghiniana* 28:241–258.
- Calvo, J. O., and G. V. Mazzetta. 2004. Nuevos hallazgos de huellas de dinosaurios en la Formación Río Limay (Albiano-Cenomaniano), Picum Leufu, Neuquén, Argentina. *Ameghiniana* 41:545–554.
- Calvo, J. O., and L. Salgado. 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Alban-Cenomanian of Argentina: new evidence on the origin of the Diplodocidae. *Gaia* 11:13–33.
- Calvo, J. O., J. D. Porfiri, and F. E. Novas. 2007a. Discovery of a new ornithomimid dinosaur from the Portezuelo Formation (Upper Cretaceous), Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro* 65:471–483.
- Calvo, J. O., J. D. Porfiri, B. J. González Riga, and A. W. A. Kellner. 2007b. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais da Academia Brasileira de Ciências* 79:529–541.
- Cantrill, D. J., and J. A. Webb. 1987. A reappraisal of *Phyllopteroides* Medwell (Osmundaceae) and its stratigraphic significance in the Lower Cretaceous of eastern Australia. *Alcheringa* 11:59–85.
- Carballido, J. L., A. C. Garrido, J. I. Canudo, and L. Salgado. 2010. Redescription of *Rayososaurus agrioensis* Bonaparte (Sauropoda, Diplodocoidea), a rebbachisaurid from the early Late Cretaceous of Neuquén. *Geobios* 43:493–502.
- Carballido, J. L., D. Pol, M. L. Parra Ruge, S. P. Bernal, M. E. Páramo-Fonseca, and F. Etayo-Serna. 2015. A new Early Cretaceous brachiosaurid (Dinosauria, Neosauropoda) from northwestern Gondwana (Villa de Leiva, Colombia). *Journal of Vertebrate Paleontology*. doi: 10.1080/02724634.2015.980505.
- Cariou, E., N. Olivier, B. Pittet, J.-M. Mazin, and P. Hantzpergue. 2014. Dinosaur track record on a shallow carbonate-dominated ramp (Loule section, Late Jurassic, French Jura). *Facies* 60:229–253.
- Carrano, M. T., and S. D. Sampson. 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 6:183–236.
- Carrano, M. T., S. D. Sampson, and C. A. Forster. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria, Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 22:510–534.
- Carvalho, I. d. S., L. S. Avilla, and L. Salgado. 2003. *Amazonsaurus maranhensis* gen. et sp. nov. (Sauropoda, Diplodocoidea) from the Lower Cretaceous (Aptian-Albian) of Brazil. *Cretaceous Research* 24:697–713.
- Case, J. A., J. E. Martin, D. S. Chaney, M. Reguero, S. A. Marensi, S. M. Santillana, and M. O. Woodburne. 2000. The first duck-billed dinosaur (family Hadrosauridae) from Antarctica. *Journal of Vertebrate Paleontology* 20:612–614.
- Castanera, D., C. Pascual, and J. I. Canudo. 2013. Primera evidencia de morfología del pie en saurópodos en el grupo Urbión de la Cuenca de Cameros (Cretácico Inferior, Soria, España). *Geogaceta* 53:13–16.
- Castanera, D., C. Pascual, J. I. Canudo, N. Hernandez Medrano, and J. L. Barco. 2012. Ethological variations in gauge in sauropod trackways from the Berriasian of Spain. *Lethaia* 45:476–489.
- Castanera, D., J. L. Barco, I. Díaz-Martínez, J. H. Gascon, F. Pérez-Lorente, and J. I. Canudo. 2011. New evidence of a herd of titanosauriform sauropods from the Lower Berriasian of the Iberian Range (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 307:218–231.
- Castanera, D., M. Boutakiout, L. Latifa, I. Díaz-Martínez, E. García-Ortiz de Landaluce, and F. Pérez Lorente. 2010. New sauropod trackway from Iouaridène Formation (Kimmeridgian, Upper Jurassic) in the High Atlas, Morocco; pp. 47–50 in P. Huerta and F. Torcida Fernández-Baldor (eds.), *V Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. Salas de los Infantes (Burgos, España), 16–18 de Septiembre de 2010, Libro de Resúmenes. Colectivo Arqueológico y Paleontológico de Salas, C. A. S., Burgos, Spain.
- Castanera, D., B. Vila, N. L. Razzolini, V. F. dos Santos, C. Pascual, and J. I. Canudo. 2014. Sauropod trackways of the Iberian Peninsula: palaeoethological and palaeoenvironmental implications. *Journal of Iberian Geology* 40:49–59.
- Chatterjee, S., and D. K. Rudra. 1996. KT events in India: impact, rifting, volcanism and dinosaur extinction. *Memoirs of the Queensland Museum* 39:489–532.
- Chatwin, B. 1987. *The Songlines*. Jonathan Cape, London, U.K., 293 pp.
- Choiniere, J. N., C. A. Forster, and W. J. de Klerk. 2012. New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous Kirkwood Formation of South Africa. *Journal of African Earth Sciences* 71–72:1–17.
- Chure, D. J. 1998. A reassessment of the Australian *Allosaurus* and its implications for the Australian refugium concept. *Journal of Vertebrate Paleontology* 18(3, Supplement):34A.
- Chure, D. J., B. B. Britt, J. A. Whitlock, and J. A. Wilson. 2010. First complete sauropod dinosaur skull from the Cretaceous of the Americas and the evolution of sauropod dentition. *Naturwissenschaften* 97:379–391.
- Cobos, A., R. Royo-Torres, L. Luque, L. Alcalá, and L. Mampel. 2010. An Iberian stegosaurus paradise: the Villar del Arzobispo Formation

- (Tithonian–Berriasian) in Teruel (Spain) Palaeogeography, Palaeoclimatology, Palaeoecology 293:223–236.
- Colbert, E. H. 1968. Men and Dinosaurs. Evans Brothers Limited, London, U.K., 283 pp.
- Colbert, E. H., and D. Merrilees. 1967. Cretaceous dinosaur footprints from Western Australia. Journal of Royal Society of Western Australia 50:21–25.
- Commonwealth of Australia. 2011. Environment Protection and Biodiversity Conservation Act 1999—inclusion of a place in the National Heritage List—the West Kimberley. Commonwealth of Australia Gazette S132:1–19.
- Cook, A. G., N. Saini, and S. A. Hocknull. 2010. Dinosaur footprints from the Lower Jurassic of Mount Morgan, Queensland. Memoirs of the Queensland Museum 55:135–146.
- Coombs, W. P., Jr., and R. E. Molnar. 1981. Sauropoda (Reptilia, Saurischia) from the Cretaceous of Queensland. Memoirs of the Queensland Museum 20:351–373.
- Coria, R. A. 1999. Ornithopod dinosaurs from the Neuquén Group, Patagonia, Argentina: phylogeny and biostratigraphy. National Science Museum Monographs 15:47–60.
- Coria, R. A. 2011. South American hadrosaurs: considerations on their diversity; pp. 28–32 in D. Braman, D. A. Eberth, D. C. Evans, and W. Taylor (eds.), International Hadrosaur Symposium at Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, September 22–23, 2011. Abstract Volume. Royal Tyrrell Museum of Palaeontology, Drumheller.
- Coria, R. A., and J. O. Calvo. 2002. A new iguanodontian ornithopod from Neuquén Basin, Patagonia, Argentina. Journal of Vertebrate Paleontology 22:503–509.
- Coria, R. A., and A. V. Cambiaso. 2007. Ornithischia; pp. 167–187 in Z. B. d. Gasparini, L. Salgado, and R. A. Coria (eds.), Patagonian Mesozoic Reptiles. Indiana University Press, Bloomington, Indiana.
- Coria, R. A., and L. Salgado. 2001. South American ankylosaurs; pp. 159–168 in K. Carpenter (ed.), The Armored Dinosaurs. Indiana University Press, Bloomington, Indiana.
- Coria, R. A., A. V. Cambiaso, and L. Salgado. 2007. New records of basal ornithopod dinosaurs in the Cretaceous of North Patagonia. Ameghiniana 44:473–477.
- Coria, R. A., B. J. González Riga, and S. Casadío. 2012. Un nuevo hadrosáurido (Dinosauria, Ornithopoda) de la Formación Allen, provincia de La Pampa, Argentina. Ameghiniana 49:552–572.
- Coria, R. A., J. J. Moly, M. Reguero, S. Santilana, and S. Marensi. 2013. A new ornithopod (Dinosauria; Ornithischia) from Antarctica. Cretaceous Research 41:186–193.
- Crane, S. 2013. First Footprints: The Epic Story of the First Australians. Allen & Unwin, Sydney, Australia, 316 pp.
- Cruzado-Caballero, P., and R. A. Coria. 2016. Revisiting the hadrosaurid (Dinosauria: Ornithopoda) diversity of the Allen Formation: a re-evaluation of *Willinkaque salitralensis* from Salitral Moreno, Río Negro Province, Argentina. Ameghiniana 53:231–237.
- Currie, P. J. 1983. Hadrosaur trackways from the Lower Cretaceous of Canada. Acta Palaeontologica Polonica 28:63–73.
- Currie, P. J. 1995. Ornithopod trackways from the Lower Cretaceous of Canada; pp. 431–443 in W. A. S. Sarjeant (ed.), Vertebrate Fossils and Scientific Concepts: A Tribute to L. Beverly Halstead. Gordon and Breach Publishers, Amsterdam, The Netherlands.
- Currie, P. J., and W. A. S. Sarjeant. 1979. Lower Cretaceous dinosaur footprints from the Peace River Canyon, British Columbia, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 11:287–301.
- Currie, P. J., G. C. Nadon, and M. G. Lockley. 1991. Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Colorado. Canadian Journal of Earth Sciences 28:102–115.
- Currie, P. J., P. Vickers-Rich, and T. H. Rich. 1996. Possible oviraptorosaur (Theropoda, Dinosauria) specimens from the Early Cretaceous Otway Group of Dinosaur Cove, Australia. Alcheringa 20:73–79.
- Curry Rogers, K. A., and C. A. Forster. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. Nature 412:530–534.
- Curry Rogers, K. A., and C. A. Forster. 2004. The skull of *Rapetosaurus krausei* (Sauropoda, Titanosauria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 24:121–144.
- D’Emic, M. D. 2012. Early evolution of titanosauriform sauropod dinosaurs. Zoological Journal of the Linnean Society 166:624–671.
- D’Emic, M. D. 2013. Revision of the sauropod dinosaurs of the Lower Cretaceous Trinity Group, southern USA, with the description of a new genus. Journal of Systematic Palaeontology 11:707–726.
- D’Orazi Porchetti, S., H. B. Mocke, M. Latiano, and A. Wagensommer. 2015. First record of *Otozoum* from Namibia. Lethaia 48:72–82.
- Dalla Vecchia, F. M. 1994. Jurassic and Cretaceous sauropod evidence in the Mesozoic carbonate platforms of the the southern Alps and Dinarids. Gaia 10:65–73.
- Dalla Vecchia, F. M., and A. Tarlao. 2000. New dinosaur track sites in the Albian (Early Cretaceous) of the Istrian peninsula (Croatia). Part II—palaeontology. Memorie di Scienze Geologiche 52:227–292.
- Day, J. J., P. Upchurch, D. B. Norman, A. S. Gale, and H. P. Powell. 2002. Sauropod trackways, evolution, and behavior. Science 296:1659.
- Dayton, L. 1991. Missing dinosaurs turn up in Australia. New Scientist 131:20.
- de Klerk, W. J., C. A. Forster, S. D. Sampson, A. Chinsamy-Turan, and C. F. Ross. 2000. A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. Journal of Vertebrate Paleontology 20:324–332.
- Dettmann, M. E., R. E. Molnar, J. G. Douglas, D. Burger, C. R. Fielding, H. T. Clifford, J. Francis, P. A. Jell, T. H. Rich, M. J. Wade, P. Vickers-Rich, N. S. Pledge, A. Kemp, and A. Rozefeld. 1992. Australian Cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications. Cretaceous Research 13:207–262.
- Díaz-Martínez, I., X. Pereda Suberbiola, F. Pérez-Lorente, and J. I. Canudo. 2015. Ichnotaxonomic review of large ornithopod dinosaur tracks: temporal and geographic implications. PLoS ONE 10: e0115477. doi: 10.1371/journal.pone.0115477.
- Diedrich, C. G. 2004. New important iguanodontid and theropod trackways of the tracksite Obernkirchen in the Berriasian of NW Germany and megatracksite concept of central Europe. Ichnos 11:215–228.
- Diedrich, C. G. 2011. Upper Jurassic tidal flat megatracksites of Germany—coastal dinosaur migration highways between European islands, and a review of the dinosaur footprints. Palaeobiodiversity and Palaeoenvironments 91:129–155.
- Dodson, P., D. W. Krause, C. A. Forster, S. D. Sampson, and F. Ravoavy. 1998. Titanosaurid (Sauropoda) osteoderms from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 18:563–568.
- Doeglas, D. J.. 1968. Grain-size indices, classification and environment. Sedimentology 10:83–100.
- Dong, Z. 1990. Stegosaurs of Asia; pp. 255–268 in K. Carpenter and P. J. Currie (eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, U.K.
- Douglas, J. G. 1969. The Mesozoic floras of Victoria, 1 and 2. Geological Survey of Victoria, Memoir 28:1–310.
- Drummond, B. J., M. J. Sexton, T. J. Barton, and R. D. Shaw. 1991. The nature of faulting along the margins of the Fitzroy Trough, Canning Basin, and implications for the tectonic development of the trough. Exploration Geophysics 22:111–116.
- Du, Y.-s., D. Li, B. Peng, R. Lei, and Z. Bai. 2002. Large scale dinosaur footprints of sauropod from Yanguoxia, Yongjing County, Gansu Province. Earth Science—Journal of China University of Geosciences 27:367–372.
- Durack, E. 1946. Time and tide: the story in pictures of Roebuck Bay N. W. Australia; commentary by Mary Durack. Imperial Print, Perth, 18 pp.
- Dutuit, J.-M., and A. Ouazzou. 1980. Découverte d’une de dinosaure sauropode sur le site d’empreintes de Demnat (Haut-Atlas Marocain). Mémoires de la Société Géologique de France (Nouvelle Serie) 139:95–102.
- Ellenberger, P. 1972. Contribution à la classification des pistes de vertébrés du Trias: les types du Stormberg d’Afrique du Sud (I), Paleovertebrata, Mémoire Extraordinaire. Laboratoire de Paléontologie des Vertébrés, Montpellier, France, 152 pp.
- Environmental Protection Authority, Western Australia. 2012. Browse Liquefied Natural Gas Precinct: Report and Recommendations of the Environmental Protection Authority. Report 1444. Department of State Development, Government of Western Australia, Perth, 165 pp + appendices.
- Ezcurra, M. D., and F. L. Agnolin. 2012. A new global palaeobiogeographical model for the late Mesozoic and early Tertiary. Systematic Biology 61:553–566.
- Ezquerro, R., S. Doublet, L. Costeur, P. M. Galton, and F. Pérez-Lorente. 2007. Were non-avian theropod dinosaurs able to swim?

- Supportive evidence from an Early Cretaceous trackway, Cameros Basin (La Rioja, Spain). *Geology* 35:507–510.
- Falkingham, P. L., K. T. Bates, and J. O. Farlow. 2014. Historical photogrammetry: Bird's Paluxy River dinosaur chase sequence digitally reconstructed as it was prior to excavation 70 years ago. *PLoS ONE* 9:e93247. doi: 10.1371/journal.pone.0093247.
- Falkingham, P. L., K. T. Bates, and P. D. Mannion. 2012. Temporal and palaeoenvironmental distribution of manus- and pes-dominated sauropod trackways. *Journal of the Geological Society, London* 169:365–370.
- Fanti, F., P. R. Bell, and R. L. Sissons. 2013. A diverse, high-latitude ichnofauna from the Late Cretaceous Wapiti Formation, Alberta, Canada. *Cretaceous Research* 41:256–269.
- Fanti, F., A. Cau, L. Cantelli, M. Hassine, and M. Auditore. 2015. New information on *Tataouinea hannibalis* from the Early Cretaceous of Tunisia and implications for the tempo and mode of rebbachisaurid sauropod evolution. *PLoS ONE* 10:e0123475. doi: 10.1371/journal.pone.0123475.
- Farlow, J. O. 1981. Estimates of dinosaur speeds from a new trackway site in Texas. *Nature* 294:747–748.
- Farlow, J. O. 1987. A Guide to Lower Cretaceous Dinosaur Footprints and Tracksites of the Paluxy River Valley, Somervell County, Texas. South Central Section Geological Society of America, and Baylor University, Houston, Texas, 50 pp.
- Farlow, J. O. 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. *Zubia* 10:89–138.
- Farlow, J. O. 2001. *Acrocantiosaurus* and the maker of Comanchean large theropod footprints; pp. 408–427 in D. H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie*. Indiana University Press, Bloomington, Indiana.
- Farlow, J. O., and R. E. Chapman. 1997. The scientific study of dinosaur footprints; pp. 519–553 in J. O. Farlow and M. K. Brett-Surman (eds.), *The Complete Dinosaur*. Indiana University Press, Bloomington, Indiana.
- Farlow, J. O., and M. G. Lockley. 1993. An osteometric approach to the identification of the makers of early Mesozoic tridactyl dinosaur footprints. *New Mexico Museum of Natural History and Science Bulletin* 3:123–132.
- Farlow, J. O., J. G. Pittman, and J. M. Hawthorne. 1989. *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the U.S. Gulf Coastal Plain; pp. 371–394 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.
- Farlow, J. O., T. R. J. Holtz, T. H. Worthy, and R. E. Chapman. 2013. Feet of the fierce (and not so fierce): pedal proportions in large theropods, other non-avian dinosaurs, and large ground birds; pp. 88–132 in J. M. Parrish, R. E. Molnar, P. J. Currie, and E. B. Koppelhus (eds.), *Tyrannosaurid Paleobiology*. Indiana University Press, Bloomington, Indiana.
- Farlow, J. O., M. O. Brien, G. J. Kuban, B. F. Dattilo, K. T. Bates, P. L. Falkingham, L. Piñuela, A. Rose, A. Freels, C. Kumagai, C. Libben, and J. Whitcraft. 2012. Dinosaur tracksites of the Paluxy River valley (Glen Rose Formation, Lower Cretaceous), Dinosaur Valley State Park, Somervell County, Texas; pp. 41–69 in P. Huerta Hurtado, F. Torcida Fernández-Baldor, and J. I. Canudo Sanagustín (eds.), *Actas de los V Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, Salas de los Infantes, Burgos, España, 16–18 de Septiembre de 2010*. Colectivo Arqueológico y Paleontológico de Salas, C. A. S., Burgos, Spain.
- Fitzgerald, E. M. G., M. T. Carrano, T. Holland, B. E. Wagstaff, D. Pickering, T. H. Rich, and P. Vickers-Rich. 2012. First ceratopsian dinosaur from Australia. *Naturwissenschaften* 99:397–405.
- Flannery, T. F., and T. H. Rich. 1981. Dinosaur digging in Victoria. *Australian Natural History* 20:195–198.
- Folk, R. L., P. B. Andrews, and D. Lewis. 1970. Detrital sedimentary rock classification and nomenclature for use in New Zealand. *New Zealand Journal of Geology and Geophysics* 13:937–968.
- Forman, D. J., and D. W. Wales (eds.). 1981. *Geological Evolution of the Canning Basin, Western Australia*. Australian Government Publishing Service, Canberra, Australia, viii + 91 pp.
- Forster, C. A., A. A. Farke, J. A. McCartney, W. J. de Klerk, and C. F. Ross. 2009. A “basal” tetanuran from the Lower Cretaceous Kirkwood Formation of South Africa. *Journal of Vertebrate Paleontology* 29:283–285.
- Foster, J. R., and M. G. Lockley. 1995. Tridactyl dinosaur footprints from the Morrison Formation (Upper Jurassic) of northeast Wyoming. *Ichnos* 4:35–41.
- Foster, J. R., and M. G. Lockley. 2006. The vertebrate ichnological record of the Morrison Formation (Upper Jurassic, North America). *New Mexico Museum of Natural History and Science Bulletin* 36:203–216.
- Fraas, E. 1908. Ostafrikanische Dinosaurier. *Palaeontographica* 55:105–144.
- Garbuniya, L. K. 1951. [Dinosaur footprints from the Lower Cretaceous of Georgia]. *Doklady Akademiyi Nauk SSSR* 81:917–919.
- Garbuniya, L. K., and V. V. Kurbatov. 1982. Jurassic dinosaur tracks of Tashkurgan (Uzbekistan SSR); pp. 20–22 in Abstracts and Proceedings of the 23rd Scientific Session, Academy of Sciences of the Georgian Soviet Socialist Republic, Tbilisi, Georgia.
- Gallina, P. A., S. Apesteguía, A. Haluza, and J. I. Canale. 2014. A diplodocid sauropod survivor from the Early Cretaceous of South America. *PLoS ONE* 9:e97128. doi: 10.1371/journal.pone.0097128.
- Gallup, M. R. 1989. Functional morphology of the hindfoot of the Texas sauropod *Pleurocoelus* sp. indet. *Geological Society of America, Special Paper* 238:71–74.
- Galton, P. M. 1981a. *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and Africa. *Postcranial skeleton*. *Paläontologische Zeitschrift* 55:271–312.
- Galton, P. M. 1981b. *Craterosaurus pottonensis* Seeley, a stegosaurian dinosaur from the Lower Cretaceous of England, and a review of Cretaceous stegosaurs. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 161:28–46.
- Galton, P. M. 1983. The cranial anatomy of *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and East Africa, with a review of hypsilophodontids from the Upper Jurassic of North America. *Geologica et Palaeontologica* 17:207–243.
- Galton, P. M. 2012. Stegosauria; pp. 483–504 in M. K. Brett-Surman, T. R. Holtz, and J. O. Farlow (eds.), *The Complete Dinosaur*, second edition. Indiana University Press, Bloomington, Indiana.
- Galton, P. M., and W. P. Coombs Jr. 1981. *Paranthodon africanus* (Broom), a stegosaurian dinosaur from the Lower Cretaceous of South Africa. *Geobios* 14:299–309.
- Galton, P. M., and P. Upchurch. 2004. Stegosauria; pp. 343–362 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- García-Ramos, J. C., L. Piñuela, and J. I. Ruiz-Omenaca. 2006. Vertebrate tracks from the Late Jurassic (Kimmeridgian) of Asturias (north Spain). *Journal of Vertebrate Paleontology* 26(3, Supplement):65A.
- Gardello, M. 1946. Time and tide. *Western Mail*, 15 August 1946:8.
- Gasparini, Z., R. A. Coria, and L. Salgado. 2007. Reptilian faunal succession in the Mesozoic of Patagonia: an updated overview; pp. 335–358 in Z. B. d. Gasparini, L. Salgado, and R. A. Coria (eds.), *Patagonian Mesozoic Reptiles*. Indiana University Press, Bloomington, Indiana.
- Gasparini, Z., E. B. Olivero, R. A. Scasso, and C. A. Rinaldi. 1987. Un anquilosaurio (Reptilia, Ornithischia) Campaniano en el continente Antártico; pp. 131–141 in J. A. Moura and H. M. N. Gilson (eds.), *Anais do X Congresso Brasileiro de Paleontologia, Rio de Janeiro, 19–25 De Julho, 1987*. Sociedade Brasileira de Paleontologia, Brasília.
- Gasparini, Z. B. d., X. Pereda Suberbiola, and R. E. Molnar. 1996. New data on the ankylosaurian dinosaur from the Late Cretaceous of the Antarctic Peninsula. *Memoirs of the Queensland Museum* 39:583–594.
- Gheerbrant, E., and J.-C. Rage. 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology* 241:224–246.
- Gianechini, F. A., and S. Apesteguía. 2011. Unenlagiinae revisited: dromaeosaurid theropods from South America. *Anais da Academia Brasileira de Ciências* 83:163–195.
- Gibson, D. L. 1983. Broome, W.A. Sheet SE/51-6. Geological Survey of Western Australia, 1:250 000 Geological Series Explanatory Notes:25.

- Gierlinski, G. D. 1991. New dinosaur ichnotaxa from the Early Jurassic of the Holy Cross Mountains, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 85:137–148.
- Gierlinski, G. D. 1997. Sauropod tracks in the Early Jurassic of Poland. *Acta Palaeontologica Polonica* 42:533–538.
- Gierlinski, G. D. 1999. Tracks of a large thyreophoran dinosaur from the Early Jurassic of Poland. *Acta Palaeontologica Polonica* 44:231–234.
- Gierlinski, G. D. 2008. Late Cretaceous dinosaur tracks from the Roztocze Hills of Poland; p. 44 in A. Uchman (ed.), *Second International Congress on Ichnology, Abstract Book and the Intracongress Field Trip Guidebook, Cracow, Poland, August 29–September 8, 2008*. Polish Geological Institute, Warsaw, Poland.
- Gierlinski, G. D. 2009. A preliminary report on new dinosaur tracks in the Triassic, Jurassic and Cretaceous of Poland; pp. 75–90 in *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, Salas de los Infantes (Burgos, España), 13–15 de Septiembre de 2007. Colectivo Arqueológico y Paleontológico de Salas, C. A. S., Burgos, Spain*.
- Gierlinski, G. D., and G. Pienkowski. 1999. Dinosaur track assemblages from the Hettangian of Poland. *Geological Quarterly* 43:329–346.
- Gierlinski, G. D., and A. Potemka. 1987. Lower Jurassic dinosaur footprints from Gliniany Las, northern slope of the Holy Cross Mountains, Poland. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 175:107–120.
- Gierlinski, G. D., and K. Sabath. 2008. Stegosaurian footprints from the Morrison Formation of Utah and their implications for interpreting other ornithischian tracks. *Oryctos* 8:29–46.
- Gierlinski, G. D., and G. Sawicki. 1998. New sauropod tracks from the Lower Jurassic of Poland. *Geological Quarterly* 42:477–480.
- Gierlinski, G. D., G. Pienkowski, and G. Niedźwiedzki. 2004. Tetrapod track assemblage in the Hettangian of Sołtyków, Poland, and its paleoenvironmental background. *Ichnos* 11:195–213.
- Gierlinski, G. D., P. Menducki, K. Janiszewska, I. Wick, and B. Andrzej. 2009. A preliminary report on dinosaur track assemblages from the Middle Jurassic of the Imilchil area, Morocco. *Geological Quarterly* 53:477–482.
- Gilmore, C. W. 1914. Osteology of the armored Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus*. *Bulletin of the United States National Museum* 89:1–143.
- Gilmore, C. W. 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum* 11:175–300.
- Glauert, L. 1952. Dinosaur footprints near Broome. *Western Australian Naturalist* 3:82–83.
- González Riga, B. J. 2011. Speeds and stance of titanosaur sauropods: analysis of *Titanopodus* tracks from the Late Cretaceous of Mendoza, Argentina. *Anais da Academia Brasileira de Ciências* 83:279–290.
- González Riga, B. J., and J. O. Calvo. 2009. A new wide-gauge track site from the Late Cretaceous of Mendoza, Neuquén Basin, Argentina. *Palaeontology* 52:631–640.
- González Riga, B. J., M. C. Lamanna, L. Ortiz David, D., J. O. Calvo, and J. P. Coria. 2016. A gigantic new dinosaur from Argentina and the evolution of the sauropod hind foot. *Scientific Reports* 6:19165. doi: 10.1038/srep19165.
- González Riga, B. J., L. D. O. David, M. B. Tomaselli, C. R. A. Candeiro, J. P. Coria, and M. Prámparo. 2015. Sauropod and theropod dinosaur tracks from the Upper Cretaceous of Mendoza (Argentina): trackmakers and anatomical evidences. *Journal of South American Earth Sciences* 61:134–141.
- Gradstein, F. M., J. G. Ogg, M. D. Schmitz, and G. M. Ogg (eds.) 2012. *The geologic time scale 2012*. Cambridge University Press, Cambridge, 1144 pp.
- Grant-Mackie, J. A., Y. Aita, B. E. Balme, H. J. Campbell, A. B. Challinor, D. A. B. MacFarlan, R. E. Molnar, G. R. Stevens, and R. A. Thulborn. 2000. Jurassic palaeobiogeography of Australasia; pp. 311–354 in A. J. Wright and G. C. Young (eds.), *Palaeobiogeography of Australian Faunas and Floras*. Association of Australasian Palaeontologists, Canberra, Australia.
- Haines, P. W. 2011. *Geology, Exploration History, and Petroleum Prospectivity of State Acreage Release Area L11-5, Canning Basin, Western Australia*. Geological Survey of Western Australia, Perth, Australia, 10 pp.
- Haines, P. W., and D. Wingate. 2007. Contrasting depositional histories, detrital zircon provenance and hydrocarbon system: did the Larapintine Seaway link the Canning and Amedee basins during the Ordovician?; pp. 36–51 in T. J. Munson and G. J. Ambrose (eds.), *Proceedings of the Central Australian Basins Symposium (CABS), Alice Springs, Northern Territory, 16–18 August 2005*. Northern Territory Geological Survey, Special Publication 2.
- Haubold, H. 1971. *Ichnia amphibiorum et reptiliorum fossilium*; in O. Kuhn (ed.), *Handbuch der Paläoherpetologie, Volume 18*. Gustav Fischer Verlag, Stuttgart, Germany, 124 pp.
- Haughton, S. H. 1915. On some dinosaur remains from Bushmanland. *Transactions of the Royal Society of South Africa* 5:259–264.
- Hawthorne, J. M. 1990. Dinosaur track-bearing strata of the Lampasas cut plain and Edwards Plateau, Texas. *Baylor Geological Studies, Bulletin* 49:1–47.
- Heckert, A. B., and S. G. Lucas. 1998. A new dinosaur track locality from the Dakota Sandstone (Upper Cretaceous: Cenomanian) in west-central New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 14:169–171.
- Heilmann, G. 1926. *The Origin of Birds*. Witherby, London, U.K., 208 pp.
- Heinrich, W.-D. 1999. The taphonomy of dinosaurs from the Upper Jurassic of Tendaguru (Tanzania) based on field sketches of the German Tendaguru Expedition (1909–1913). *Fossil Record* 2:25–61.
- Henderson, R. A., J. S. Crampton, W. E. Dettmann, J. G. Douglas, D. Haig, S. Shafik, J. D. Stilwell, and R. A. Thulborn. 2000. Biogeographical observations on the Cretaceous biota of Australasia; pp. 355–404 in G. C. Young, J. A. Talent, and J. R. Laurie (eds.), *Palaeobiogeography of Australian Faunas and Floras*. Association of Australasian Palaeontologists, Canberra, Australia.
- Hendricks, A. 1981. *Die saurierfährte von MÜNCHENHAGEN bei REHBURG-LOCUM (NW-DEUTSCHLAND)*. *Abhandlungen des Landesmuseum für Naturkunde Münster* 43:1–22.
- Herne, M. C. 2009. Postcranial osteology of *Leaellynasaura amicagraphica* (Dinosauria: Ornithischia) from the Early Cretaceous of south-eastern Australia. *Journal of Vertebrate Paleontology* 29(3, Supplement):113A.
- Herne, M. C. 2013. *Anatomy, systematics and phylogenetic relationships of the Early Cretaceous ornithopod dinosaurs of the Australian-Antarctic rift system*. Ph.D. dissertation. The University of Queensland, Brisbane, Queensland, Australia, 464 pp.
- Herne, M. C., and S. W. Salisbury. 2009. The status of *Leaellynasaura amicagraphica* (Dinosauria: Ornithischia) from the Early Cretaceous of south-eastern Australia; p. 35 in K. J. Travouillon, T. H. Worthy, S. Hand, and P. Creaser (eds.), *Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics 2009, The University of New South Wales, Sydney, 22–25 June 2009*. Geological Society of Australia, Sydney, Australia.
- Herne, M. C., J. P. Nair, and S. W. Salisbury. 2010. Comment on “A southern tyrant reptile”. *Science* 329:1013–c.
- Hill, D., G. Playford, and J. T. Woods. 1966. *Jurassic Fossils of Queensland*. Queensland Palaeontographical Society, Brisbane, Queensland, Australia, 32 pp.
- Hill, E. 1973. ‘Kabbarli’. *A Personal Memoir of Daisy Bates*. Angus and Robertson, Sydney, Australia, 173 pp.
- Hocknull, S. A., and A. G. Cook. 2008. Hypsilophodontid (Dinosauria: Ornithischia) from latest Albian, Winton Formation, central Queensland. *Memoirs of the Queensland Museum* 52:212.
- Hocknull, S. A., M. A. White, T. R. Tischler, A. G. Cook, N. D. Calleja, T. Sloan, and D. A. Elliott. 2009. New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS ONE* 4:e6190. doi: 10.1371/journal.pone.0006190.
- Holliday, C. M., R. C. Ridgely, J. C. Sedlmayr, and L. M. Witmer. 2010. Cartilaginous epiphyses in extant archosaurs and their implications for reconstructing limb function in dinosaurs. *PLoS ONE* 5:e13120. doi:10.1371/journal.pone.0013120.
- Holtz, T. R., Jr., R. E. Chapman, and M. C. Lamanna. 2004. *Mesozoic biogeography of Dinosauria*; pp. 627–642 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- Hooker, J. J., A. C. Milner, and S. E. K. Sequeira. 1991. An ornithopod dinosaur from the Late Cretaceous of West Antarctica. *Antarctic Science* 3:331–332.

- Horner, J. R., D. B. Weishampel, and C. A. Forster. 2004. Hadrosauridae; pp. 438–463 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- Hornung, J. J., and M. Reich. 2014. *Metatetrapous valdensis* Nopcsa, 1923 and the presence of ankylosaur tracks (Dinosauria: Thyreophora) in the Berriasian (Early Cretaceous) of northwestern Germany. *Ichnos* 21:1–18.
- Hu, D., L. Hou, L. Zhang, and X. Xu. 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* 461:640–643.
- Hübner, T. R. 2007. *Dryosaurus lettowvorbecki*—a hoard of options. *Hallesches Jahrbuch für Geowissenschaften, Beiheft* 23:137–139.
- Hübner, T. R. 2011. Ontogeny in *Dysalotosaurus lettowvorbecki*. Ph.D. dissertation, Ludwig-Maximilians-Universität, Munich, Germany, 338 pp.
- Hübner, T. R., and O. W. M. Rauhut. 2010. A juvenile skull of *Dysalotosaurus lettowvorbecki* (Ornithischia: Iguanodontia), and implications for cranial ontogeny, phylogeny, and taxonomy in ornithopod dinosaurs. *Zoological Journal of the Linnean Society* 160:366–396.
- Huene, F. F. v. 1929. Los saurisquios y ornitisquios del Cretaceo Argentino. *Anales del Museo de la Plata (Series 2)* 3:1–194.
- Huh, M., K.-G. Hwang, I. S. Paik, C. H. Chung, and B. Kim. 2003. Dinosaur tracks from the Cretaceous of South Korea: distribution, occurrences and paleobiological significance. *The Island Arc* 12:132–144.
- Hwang, K.-G., M. G. Lockley, M. Huh, and I. S. Paik. 2008. A reinterpretation of dinosaur footprints with internal ridges from the Upper Cretaceous Uhangri Formation, Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 258:59–70.
- Ibircu, L. M., R. D. Martínez, and G. A. Casal. 2014. Reappraisal of *Notohypsilophodon comodorensis* (Ornithischia: Ornithopoda) from the Late Cretaceous of Patagonia, Argentina. *Zootaxa* 3786:401–422.
- Ibircu, L. M., G. A. Casal, R. D. Martínez, M. C. Lamanna, and L. Salgado. 2015. New material of *Katpensaurus goicoecheai* (Sauropoda: Diplodocoidea) and its significance for the morphology and evolution of Rebbachisauridae. *Ameghiniana* 52:430–446.
- Ibircu, L. M., G. A. Casal, M. C. Lamanna, R. D. Martínez, J. D. Harris, and K. J. Lacovara. 2012. The southernmost records of Rebbachisauridae (Sauropoda: Diplodocoidea), from early Late Cretaceous deposits in central Patagonia. *Cretaceous Research* 34:220–232.
- Ibircu, L. M., R. D. Martínez, M. C. Lamanna, G. A. Casal, M. Luna, J. D. Harris, and K. J. Lacovara. 2010. A medium-sized ornithopod (Dinosauria: Ornithischia) from the Upper Cretaceous Bajo Barreal Formation of Lago Colhué Huapi, southern Chubut Province, Argentina. *Annals of Carnegie Museum* 79:39–50.
- Ingersoll, R. V., T. F. Bullard, R. L. Ford, J. P. Grimm, J. D. Pickle, and S. W. Sares. 1984. The effect of grain size on detrital modes: a test of the Grazzi-Dickinson point-counting method. *Journal of Sedimentary Research* 54:103–116.
- Irby, G. V. 1995. Posterolateral markings on dinosaur tracks, Cameron Dinosaur Tracksite, Lower Jurassic Moenave Formation, northeastern Arizona. *Journal of Paleontology* 69:779–784.
- Ishigaki, S. 1986. Morocco no Kyouryu. Tsukiji Shokan, Tokyo, Japan.
- Ishigaki, S. 1988. Les empreintes de dinosaures du Jurassique inférieur du Haut Atlas central Marocain. *Notes du Service Géologique du Maroc* 44:79–86.
- Ishigaki, S. 1989. Footprints of swimming sauropods from Morocco; pp. 83–86 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.
- Ishigaki, S., and Y. Matsumoto. 2009. “Off-tracking”—like phenomenon observed in the turning sauropod trackway from the Upper Jurassic of Morocco. *Fukui Prefectural Dinosaur Museum Memoir* 8:1–10.
- Jain, S. L., and S. Bandyopadhyay. 1997. New titanosaurid (Dinosauria: Sauropoda) from the Late Cretaceous of central India. *Journal of Vertebrate Paleontology* 17:114–136.
- Janensch, W. 1914. Übersicht über die Wirbeltierfauna der Tendaguruschichten, nebst einer kurzen charakterisierung der neu aufgeführten arten von sauropoden. Sonderabdruck aus dem Archiv für Biontologie 3:81–110.
- Janensch, W. 1925. Ein aufgestelltes skelett des stegosauriers *Kentrosaurus aethiopicus* E. Hennig aus den Tendaguru-schichten Deutsch-Ostafrikas. *Palaeontographica (Supplement 7)* 1:255–276.
- Janensch, W. 1929a. Magensteine bei sauropoden der Tendaguruschichten. *Palaeontographica (Supplement 7)* 2:135–143.
- Janensch, W. 1929b. Die wirbelsäule der gattung *Dicraeosaurus*. *Palaeontographica (Supplement 7)* 2:35–133.
- Janensch, W. 1935–1936. Die schädel der sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica (Supplement 7)* 2:145–298.
- Janensch, W. 1955. Der ornithopode *Dysalotosaurus* der Tendaguruschichten. *Palaeontographica (Supplement 7)* 3:105–176.
- Janensch, W. 1961a. Die gliedmaszen und gliedmaszengürtel der sauropoden der Tendaguru-Schichten. *Palaeontographica (Supplement 7)* 3:177–235.
- Janensch, W. 1961b. Skelettrekonstruktion von *Dysalotosaurus lettowvorbecki*. *Palaeontographica (Supplement 7)* 3:237–240.
- Jenny, J., and J.-A. Jossen. 1982. Decouverte d’empreintes de pas de Dinosauriens dans le Jurassique inférieur (Pliensbachien) du Haut-Atlas central (Maroc). *Comptes Rendus Hebdomadaires des Séances de l’Académie des Sciences, Série IIA (Sciences de la Terre et des planètes)* 294:223–226.
- Jones, W. S., and L. Glauert. 1945–1946. Walter S. Jones and Ludwig Glauert letters, 26 September 1945–5 January 1946. Archives of the Western Australian Museum, Perth, Australia, 15 pp.
- Juárez Valieri, R. D., J. A. Haro, L. E. Fiorelli, and J. O. Calvo. 2010. A new hadrosauroid (Dinosauria: Ornithopoda) from the Allen Formation (Late Cretaceous) of Patagonia, Argentina. *Revista del Museo Argentino de Ciencias Naturales, n.s.* 12:217–231.
- Kaever, M., and A. F. Lapparent. 1974. Les traces de pas de dinosaures du Jurassique de Barkhausen (Basse Saxe, Allemagne). *Bulletin de la Société Géologique de France (série 7)* 16:516–525.
- Kear, B. J., and R. J. Hamilton-Bruce. 2011. *Dinosaurs in Australia*. CSIRO Publishing, Collingwood, Victoria, Australia, 190 pp.
- Kennard, J. M., M. J. Jackson, K. K. Romine, R. D. Shaw, and P. N. Southgate. 1994. Depositional sequences and associated petroleum systems of the Canning Basin, W.A.; pp. 657–676 in P. G. Purcell and R. R. Purcell (eds.), *The Sedimentary Basins of Western Australia*. Petroleum Exploration Society of Australia, Western Australian Branch, Perth, Australia.
- Kenneally, K. F., D. C. Edinger, and T. Willing. 1996. *Broome and Beyond: Plants and People of the Dampier Peninsula, Kimberley, Western Australia*. Department of Conservation and Land Management, Como, Western Australia, Australia, iv + 256 pp.
- Kennedy, W. J., H. C. Klinger, and N. J. Mateer. 1987. First record of an Upper Cretaceous sauropod dinosaur from Zululand, South Africa. *South African Journal of Science* 83:173–174.
- Kim, J. Y., and M. G. Lockley. 2012. New sauropod tracks (*Brontopodus pentadactylus* ichnosp. nov.) from the Early Cretaceous Haman Formation of Jinju area, Korea: implications for sauropods manus morphology. *Ichnos* 19:84–92.
- Kim, J. Y., M. G. Lockley, H. M. Kim, J.-D. Lim, and K.-S. Kim. 2009. New dinosaur tracks from Korea, *Ornithopodichnus masanensis* ichnogen. et ichnosp. nov. (Jindong Formation, Lower Cretaceous): implications for polarities in ornithopod foot morphology. *Cretaceous Research* 30:1387–1397.
- Kingdon, J. 1974. Pangolins; pp. 353–375 in *East African Mammals: An Atlas of Evolution of Africa. Insectivora and Bats*. The University of Chicago, Chicago, Illinois.
- Kool, L. 2006. *Dinosaur Dreaming 2006 Field Report*. Monash University, Clayton, Victoria, Australia.
- Kool, L. 2007. *Dinosaur Dreaming 2007 Field Report*. Monash University, Clayton, Victoria, Australia.
- Kurtz, W. J., M. G. Lockley, and D. J. Engard. 2001. Dinosaur tracks in the Plainview Formation, Dakota Group (Cretaceous, Albian) near Canon City, Colorado: a preliminary report on another “Dinosaur Ridge”. *The Mountain Geologist* 38:155–164.
- Lacovara, K. J., M. C. Lamanna, L. M. Ibircu, J. C. Poole, E. R. Schroeter, P. V. Ullmann, K. K. Voegele, Z. M. Boles, A. M. Carter, E. K. Fowler, V. M. Egerton, A. E. Moyer, C. L. Coughenour, J. P. Schein, J. D. Harris, R. D. Martínez, and F. E. Novas. 2014. A gigantic, exceptionally complete titanosaurian sauropod dinosaur from southern Patagonia, Argentina. *Scientific Reports* 4:6196. doi: 10.1038/srep06196.
- Lallensack, J. N., P. M. Sander, N. Knötschke, and O. Wings. 2015. Dinosaur tracks from the Langenberg Quarry (Late Jurassic, Germany) reconstructed with historical photogrammetry: evidence for large theropods

- soon after insular dwarfism. *Palaeontologia Electronica* 18(2):31A. <http://palaeo-electronica.org/content/2015/1166-langenberg-tracks>.
- Lamanna, M. C., R. D. Martínez, M. Luna, G. Casal, P. Dodson, and J. Smith. 2001. Sauropod faunal transition through the Cretaceous Chubut Group of central Patagonia. *Journal of Vertebrate Paleontology* 21(3, Supplement):70A.
- Langston, W., Jr. 1974. Nonmammalian Comanchean tetrapods. *Geoscience and Man* 8:77–102.
- Lapparent, A. F. 1951. Découverte de dinosauriens, associés à une faune de reptiles et de poissons, dans le Crétacé inférieur de l'extrême Sud Tunisien. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* 239:1430–1432.
- Le Loeuff, J., C. Gourrat, P. Landry, L. Hautier, R. Liard, C. Soullat, E. Buffetaut, and R. Enay. 2006. A Late Jurassic sauropod tracksite from southern Jura (France). *Comptes Rendus Palevol* 5:705–709.
- Leahey, L., R. E. Molnar, and S. W. Salisbury. 2008. The cranial osteology of *Minmi* sp., a basal ankylosauromorph (Ornithischia: Dinosauria) from the Early Cretaceous (Albian) Allaru Formation of Richmond, north-western Queensland, Australia. *Journal of Vertebrate Paleontology* 28(3, Supplement):104A.
- Leahey, L., R. E. Molnar, and S. W. Salisbury. 2010. Postcranial osteology of *Minmi* sp., a basal ankylosauromorph (Dinosauria: Ornithischia) from the Early Cretaceous (Albian) Allaru Mudstone of Queensland, Australia. *Journal of Vertebrate Paleontology* 30(3, Supplement):121A.
- Leahey, L., R. E. Molnar, K. Carpenter, L. M. Witmer, and S. W. Salisbury. 2015. Cranial osteology of the ankylosaurian dinosaur formerly known as *Minmi* sp. (Ornithischia: Thyreophora) from the Lower Cretaceous Allaru Mudstone of Richmond, Queensland, Australia. *PeerJ* 3:e1475. doi: 10.7717/peerj.1475.
- Leahey, L. G., and S. W. Salisbury. 2013. First evidence of ankylosaurian dinosaurs (Ornithischia: Thyreophora) from the 'mid'-Cretaceous (late Albian–Cenomanian) Winton Formation of Queensland, Australia. *Alcheringa* 37:249–257.
- Leanza, H. A., S. Apesteguía, F. E. Novas, and M. S. de la Fuente. 2004. Cretaceous terrestrial beds from the Neuquen Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research* 25:61–87.
- Lee, Y.-N. 1997. Bird and dinosaur footprints in the Woodbine Formation (Cenomanian), Texas. *Cretaceous Research* 18:849–864.
- Lee, Y.-N., and H.-J. Lee. 2006. A sauropod trackway in Donghae-Myeon, Goseong County, south Gyeongsang Province, Korea and its paleobiological implications of Uhangri manus-only sauropod tracks. *Journal of the Paleontological Society of Korea* 22:1–14.
- Leonardi, G. 1984. Le impronte fossile di dinosauri; pp. 165–186 in J. F. Bonaparte, E. H. Colbert, P. J. Currie, A. J. de Ricqlès, Z. Kielan-Jaworowska, G. Leonardi, N. Morello, and P. Taquet (eds.), *Sulle Orme dei Dinosauri*. Erizzo Editrice, Venice, Italy.
- Leonardi, G. (ed.). 1987. *Glossary and Manual of Tetrapod Footprint Palaeoichnology*. Departamento Nacional da Producao Mineral, Brasilia, Brazil, 117 pp.
- Leonardi, G. 1994. Annotated Atlas of South America Tetrapod Footprints (Devonian to Holocene), with an Appendix on Mexico and Central America. Companhia de Pesquisa de Recursos Minerais, Brasilia, Brazil, 248 pp.
- Leonardi, G., and I. d. S. Carvalho. 2007. Dinosaur ichnocoenosis from Sousa and Uirauna-Brejo das Freiras basis, northeast Brazil; pp. 355–369 in I. d. S. Carvalho, R. C. T. Cassab, C. Schwanke, M. A. Carvalho, A. C. S. Fernandes, M. A. Rodrigues, M. S. S. Carvalho, M. Arai, and M. E. Q. Oliverira (eds.), *Paleontologia: Cenários de Vida*. Interciencias, Rio de Janeiro, Brazil.
- Leslie, R. B., H. J. Evans, and C. L. Knight. 1976. *Economic Geology of Australia and Papua New Guinea*. Volume 3, Petroleum. Australasian Institute of Mining and Metallurgy, Parkville, Victoria, Australia, xi + 541 pp.
- Lessertisseur, J. 1955. Traces fossiles d'activité animal et leur signification paléobiologique. *Memoires de la Société Géologique de France*, (Nouvelle Serie) 74:1–150.
- Li, J., M. G. Lockley, Y. Zhang, S. Hu, M. Matsukawa, and Z. Bai. 2012. An important ornithischian tracksite in the Early Jurassic of the Shenmu Region, Shaanxi, China. *Acta Geologica Sinica* 86:1–10.
- Lim, J.-D., M. G. Lockley, and D. Y. Kong. 2012. The trackway of a quadrupedal ornithopod from the Jindong Formation (Cretaceous) of Korea. *Ichnos* 19:101–104.
- Lim, S.-K., S.-Y. Yang, and M. G. Lockley. 1989. Large dinosaur footprint assemblages from the Cretaceous Jindong Formation of Korea; pp. 333–336 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.
- Lipar, M., and J. A. Webb. 2014. Middle–late Pleistocene and Holocene chronostratigraphy and climate history of the Tamala Limestone, Cooloongup and Safety Bay Sands, Nambung National Park, south-western Western Australia. *Australian Journal of Earth Sciences* 61:1023–1039.
- Lires, J., J. C. Garcia-Ramos, and L. Piñuela. 2002. Icnias de estegosaurios en los del Jurásico Superior de Asturias; pp. 30–31 in F. Perez-Lorente (ed.), *Dinosaurios y otros reptiles Mesozoicos en España*. Resúmenes de las comunicaciones ponencias y panels. Instituto de Estudios Riojanos, Universidad de La Rioja, Logroño, Spain.
- Lires, J., L. Piñuela, and J. C. García-Ramos. 2001. Nuevos datos y reinterpretación del yacimiento Jurásico de icnitas de dinosaurio de la playa de La Griega (Colunga, Asturias); pp. 342–347 in G. Meléndez, Z. Herrera, G. Delvene, and B. Azanza (eds.), *Los Fósiles y la Paleogeografía (XVII Jornadas de la Sociedad Española de Paleontología 5)*. Volumen I. Sociedad Española de Paleontología, Universidad de Zaragoza, Zaragoza.
- Lockley, M. G. 1987. Dinosaur footprints from the Dakota Group of eastern Colorado. *The Mountain Geologist* 24:107–122.
- Lockley, M. G. 1991. *Tracking Dinosaurs: A New Look at an Ancient World*. Cambridge University Press, Cambridge, U.K., 238 pp.
- Lockley, M. G. 2000a. Philosophical perspectives on theropod track morphology: blending qualities and quantities in the science of ichnology. *Gaia* 15:279–300.
- Lockley, M. G. 2000b. An amended description of the theropod footprint *Bueckeburgichnus maximus* Kuhn 1958, and its bearing on the megalosaur tracks debate. *Ichnos* 7:217–225.
- Lockley, M. G., and J. R. Foster. 2006. Dinosaur and turtle tracks from the Morrison Formation (Upper Jurassic) of Colorado National Monument, with observations on the taxonomy of vertebrate swim tracks. *New Mexico Museum of Natural History and Science Bulletin* 36:193–198.
- Lockley, M. G., and A. P. Hunt. 1995. Ceratopsid tracks and associated ichnofauna from the Laramie Formation (Upper Cretaceous: Maastrichtian) of Colorado. *Journal of Vertebrate Paleontology* 15:592–614.
- Lockley, M. G., and A. P. Hunt. 1998. A probable stegosaur track from the Morrison Formation of Utah. *Modern Geology* 23:331–342.
- Lockley, M. G., and C. A. Meyer. 2000. *Dinosaur Tracks and Other Fossil Footprints of Europe*. Columbia University Press, New York, New York, 323 pp.
- Lockley, M. G., and V. F. Santos. 1993. A preliminary report on sauropod trackways from the Avelino site, Sesimbra region, Upper Jurassic, Portugal. *Gaia* 6:38–42.
- Lockley, M. G., and J. L. Wright. 2001. Trackways of large quadrupedal ornithopods from the Cretaceous: a review; pp. 428–442 in D. H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie*. Indiana University Press, Bloomington, Indiana.
- Lockley, M. G., J. O. Farlow, and C. A. Meyer. 1994a. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia* 10:135–145.
- Lockley, M. G., K. J. Houck, and N. K. Prince. 1986. North America's largest dinosaur trackway site: implications for Morrison Formation paleoecology. *Geological Society of America, Bulletin* 97:1163–1176.
- Lockley, M. G., M. Huh, and B. S. Kim. 2012. *Ornithopodichnus* and pes-only sauropod trackways from the Hwasun tracksite, Cretaceous of Korea. *Ichnos* 19:93–100.
- Lockley, M. G., S. G. Lucas, and A. P. Hunt. 2006a. *Eosauropus*, a new name for a Late Triassic track: further observations on the Late Triassic ichnogenus *Tetrasauropus* and related forms, with notes on the limits of interpretation. *New Mexico Museum of Natural History and Science Bulletin* 37:192–198.
- Lockley, M. G., C. A. Meyer, and V. F. Santos. 1996a. *Megalosauripus*, *Megalosaropus* and the concept of megalosaur footprints. *Museum of Northern Arizona, Bulletin* 60:113–118.
- Lockley, M. G., C. A. Meyer, and V. F. Santos. 2000. *Megalosauripus* and the problematic concept of megalosaur footprints. *Gaia* 15:313–337.
- Lockley, M. G., G. C. Nadon, and P. J. Currie. 2003. A diverse dinosaur-bird footprint assemblage from the Lance Formation, Upper Cretaceous, Eastern Wyoming: implications for ichnotaxonomy. *Ichnos* 11:229–249.

- Lockley, M. G., J. L. Wright, and M. Matsukawa. 2001a. A new look at *Magnoavipes* and so-called “big-bird” tracks from Dinosaur Ridge (Cretaceous, Colorado). *The Mountain Geologist* 38:137–146.
- Lockley, M. G., J. C. Garcia-Ramos, L. Piñuela, and M. Avanzini. 2008a. A review of vertebrate track assemblages from the Late Jurassic of Asturias, Spain with comparative notes on coeval ichnofaunas from the western USA: implications for faunal diversity in siliciclastic facies assemblages. *Oryctos* 8:53–70.
- Lockley, M. G., K. M. Hups, K. Cart, and S. Gerwe. 2011. A zone of sauropodomorph footprints in the basal Wingate Sandstone (latest Triassic) of western Colorado and eastern Utah: is *Eosauropus* a common ichnogenus in this region? *New Mexico Museum of Natural History and Science Bulletin* 53:337–343.
- Lockley, M. G., M. King, S. Howe, and T. Sharp. 1996b. Dinosaur tracks and other archosaur footprints from the Triassic of South Wales. *Ichnos* 5:23–41.
- Lockley, M. G., C. A. Meyer, A. P. Hunt, and S. G. Lucas. 1994b. The distribution of sauropod tracks and trackmakers. *Gaia* 10:233–248.
- Lockley, M. G., C. A. Meyer, R. Schultz-Pittman, and G. Forney. 1996c. Late Jurassic dinosaur tracksites from Central Asia: a preliminary report on the world’s longest trackways. *Museum of Northern Arizona, Bulletin* 60:137–140.
- Lockley, M. G., J. L. Wright, A. P. Hunt, and S. G. Lucas. 2001b. The Late Triassic sauropod track record comes into focus: old legacies and new paradigms; pp. 181–190 in S. G. Lucas and D. Ulmer-Scholle (eds.), *New Mexico Geological Society Guidebook*, 52nd Field Conference, *Geology of the Llano Estacado*.
- Lockley, M. G., L. Xing, J. Y. Kim, and M. Matsukawa. 2014. Tracking Lower Cretaceous dinosaurs in China: a new database for comparison with ichnofaunal data from Korea, the Americas, Europe, Africa and Australia. *Biological Journal of the Linnean Society* 113:770–789.
- Lockley, M. G., K. J. Houck, S.-Y. Yang, M. Matsukawa, and S.-K. Lim. 2006b. Dinosaur-dominated footprint assemblages from the Cretaceous Jindong Formation, Hallyo Haesang National Park area, Goseong County, South Korea: evidence and implications. *Cretaceous Research* 27:70–101.
- Lockley, M. G., J. Lires, J. C. García-Ramos, L. Piñuela, and M. Avanzini. 2007. Shrinking the world’s largest dinosaur tracks: observations on the ichnotaxonomy of *Gigantosauropus asturiensis* and *Hispanosauropus hauboldi* from the Upper Jurassic of Asturias, Spain. *Ichnos* 14:247–255.
- Lockley, M. G., A. S. Schulp, C. A. Meyer, G. Leonardi, and D. Kerumba Mamani. 2002a. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research* 23:383–400.
- Lockley, M. G., J. L. Wright, D. White, M. Matsukawa, J. Li, L. Feng, and H. Li. 2002b. The first sauropod trackways from China. *Cretaceous Research* 23:363–381.
- Lockley, M. G., S. H. Kim, J. Y. Kim, K.-S. Kim, M. Matsukawa, R. Li, J. Li, and S.-Y. Yang. 2008b. *Minisauripus*—the track of a diminutive dinosaur from the Cretaceous of China and South Korea: implications for stratigraphic correlation and theropod foot morphodynamics. *Cretaceous Research* 29:115–130.
- Long, J. A. 1990. *Dinosaurs of Australia and Other Animals of the Mesozoic Era*. Reed Books, Balgowlah, New South Wales, Australia, 87 pp.
- Long, J. A. 1992a. Cretaceous dinosaur ichnofauna from Broome, western Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 9:262.
- Long, J. A. 1992b. First dinosaur bones from Western Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 9:21–28.
- Long, J. A. 1993. Dinosaurs down under. *Australian Natural History* 24:30–39.
- Long, J. A. 1995. A theropod dinosaur bone from the Late Cretaceous Molecap Greensand, Western Australia. *Records of the Western Australian Museum* 17:143–146.
- Long, J. A. 1998. *Dinosaurs of Australia and New Zealand and Other Animals of the Mesozoic Era*. UNSW Press, Sydney, Australia, 188 pp.
- Long, J. A. 2002. *The Dinosaur Dealers*. Allen and Unwin, Sydney, Australia, 220 pp.
- Long, J. A., and A. R. I. Cruickshank. 1996. First record of an Early Cretaceous theropod dinosaur bone from Western Australia. *Records of the Western Australian Museum* 18:219–222.
- Long, J. A., and R. E. Molnar. 1998. A new Jurassic theropod dinosaur from Western Australia. *Records of the Western Australian Museum* 19:121–129.
- Longman, H. A. 1933. A new dinosaur from the Queensland Cretaceous. *Memoirs of the Queensland Museum* 10:131–144.
- Lü, J., L. Xu, X. Zhang, W. Hu, Y. Wu, S. Jia, and Q. Ji. 2007. A new gigantic sauropod dinosaur with the deepest known body cavity from the Cretaceous of Asia. *Acta Geologica Sinica* 81:167–176.
- Lucas, A. M., and P. R. Stettenheim. 1972. *Avian Anatomy, Integument*. United States Department of Agriculture Handbook 362. United States Government Printing Office, Washington, D.C., 750 pp.
- Lydekker, R. 1889. Notes on new and other dinosaurian remains. *Geological Magazine (Series 3)* 6:352–356.
- Mack, G. H., W. C. James, and H. C. Monger. 1993. Classification of paleosols. *Geological Society of America Bulletin* 105:129–136.
- Maidment, S. C. R. 2010. Stegosauria: a historical review of the body fossil record and phylogenetic relationships. *Swiss Journal of Geosciences* 103:199–210.
- Maidment, S. C. R., and G. Wei. 2006. A review of the Late Jurassic stegosaurs (Dinosauria, Stegosauria) from the People’s Republic of China. *Geological Magazine* 143:621–634.
- Maidment, S. C. R., D. B. Norman, P. M. Barrett, and P. Upchurch. 2008. Systematics and phylogeny of Stegosauria (Dinosauria: Ornithischia). *Journal of Systematic Palaeontology* 6:367–407.
- Major, A., and W. A. S. Sarjeant. 2001. The folklore of footprints in stone: from Classical to Antiquity to the Present. *Ichnos* 8:143–163.
- Makovicky, P. J., S. Apesteguía, and F. L. Agnolín. 2005. The earliest dromaeosaurid theropod from South America. *Nature* 437:1007–1011.
- Mannion, P. D., and A. Otero. 2012. A reappraisal of the Late Cretaceous Argentinean sauropod dinosaur *Argyrosaurus superbus*, with a description of a new titanosaur genus. *Journal of Vertebrate Paleontology* 32:614–638.
- Mannion, P. D., and P. Upchurch. 2010. A quantitative analysis of environmental associations in sauropod dinosaurs. *Paleobiology* 36:253–282.
- Mannion, P. D., P. Upchurch, R. N. Barnes, and O. Mateus. 2013. Osteology of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atalaiensis* (Macronaria) and the evolutionary history of basal titanosauriforms. *Zoological Journal of the Linnean Society* 168:98–206.
- Marsh, O. C. 1877. A new order of extinct Reptilia (Stegosauria) from the Jurassic of the Rocky Mountains. *American Journal of Science (Series 3)* 14:513–514.
- Marsh, O. C. 1880. Principal characters of American Jurassic dinosaurs. Part III. *American Journal of Science (Series 3)* 19:253–259.
- Martin, A., P. Vickers-Rich, T. H. Rich, and L. Kool. 2007. Polar dinosaur tracks in the cretaceous of Australia: though many were cold, few were frozen. *Journal of Vertebrate Paleontology* 27(3, Supplement):112A.
- Martin, A. J., T. H. Rich, M. Hall, P. Vickers-Rich, and G. M. Vazquez-Prokopec. 2012. A polar dinosaur-track assemblage from the Eumeralla Formation (Albian), Victoria, Australia. *Alcheringa* 36:171–188.
- Martínez, R. D. 1998. *Notohypsilophodon comodorensis*, gen. et sp. nov., un Hypsilophodontidae (Ornithischia: Ornithopoda) del Cretácico Superior de Chubut, Patagonia central, Argentina. *Acta Geológica Leopoldensia* 21:119–135.
- Marty, D. 2008. Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez-Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology. *GeoFocus* 21:1–278.
- Marty, D., C. A. Meyer, M. Belvedere, J. Ayer, and K. L. Schäfer. 2013. Rochefort-Les Grattes: an Early Tithonian dinosaur tracksite from the Canton Neuchâtel, Switzerland. *Revue de Paléobiologie* 32:373–384.
- Marty, D., W. A. Hug, A. Iberg, L. Cavin, C. A. Meyer, and M. G. Lockley. 2003. Preliminary report on the Courtedoux dinosaur tracksite from the Kimmeridgian of Switzerland. *Ichnos* 10:209–219.
- Marty, D., M. Belvedere, C. A. Meyer, P. Mietto, G. Paratte, C. Lovis, and B. Thüring. 2010. Comparative analysis of Late Jurassic sauropod trackways from the Jura Mountains (NW Switzerland) and the central High Atlas Mountains (Morocco): implications for sauropod ichnotaxonomy. *Historical Biology* 22:109–133.

- Mateus, O., and J. Milàn. 2010. A diverse Upper Jurassic dinosaur ichnofauna from central-west Portugal. *Lethaia* 43:245–257.
- Mateus, O., J. Milàn, M. Romano, and M. A. Whyte. 2011. New finds of stegosaur tracks from the Upper Jurassic Lourinhã Formation, Portugal. *Acta Palaeontologica Polonica* 56:651–658.
- Matsukawa, M., M. G. Lockley, and J. Li. 2006. Cretaceous terrestrial biotas of East Asia, with special reference to dinosaur-dominated ichnofaunas: towards a synthesis. *Cretaceous Research* 27:3–21.
- Matsukawa, M., K. Shibata, R. Kukiham, K. Koarai, and M. G. Lockley. 2005. Review of Japanese dinosaur track localities: implications for ichnotaxonomy, paleogeography and stratigraphic correlation. *Ichnos* 12:201–222.
- McAllister, J. A. 1989. Dakota Formation tracks from Kansas: implications for the recognition of tetrapod subaqueous traces; pp. 343–348 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.
- McCrea, R. T., M. G. Lockley, and C. A. Meyer. 2001. Global distribution of purported ankylosaur track occurrences; pp. 413–454 in K. Carpenter (ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- McCrea, R. T., M. G. Lockley, P. W. Haines, and N. Draper. 2012. Palaeontology Survey of the Broome Sandstone—Browse LNG Precinct Report (November 2011). Appendix 6, Browse Liquefied Natural Gas Precinct: Report and Recommendations of the Environmental Protection Authority (Report 1444). Department of State Development, Government of Western Australia, Perth, Australia, 120 pp.
- McGregor, W. 1988. A survey of the languages of the Kimberley region—Report from the KLRC. *Australian Aboriginal Studies* 2:92–102.
- McIntosh, J. S., W. P. Coombs Jr., and D. A. Russell. 1992. A new diplodocid sauropod (*Dinosauria*) from Wyoming, U.S.A. *Journal of Vertebrate Paleontology* 12:158–167.
- McLoughlin, S. 1996. Early Cretaceous macrofloras of Western Australia. *Records of the Western Australian Museum* 18:19–65.
- McPhee, B., A. M. Yates, J. N. Choiniere, and F. Abdala. 2014. The complete anatomy and phylogenetic relationships of *Antetonitrus ingenipes* (Sauropodiformes, Dinosauria): implications for the origins of Sauropoda. *Zoological Journal of the Linnean Society* 171:151–205.
- McPhee, B. W., P. D. Mannion, W. J. de Klerk, and J. N. Choiniere. 2016. High diversity in the sauropod dinosaur fauna of the Lower Cretaceous Kirkwood Formation of South Africa: Implications for the Jurassic–Cretaceous transition. *Cretaceous Research* 59:228–248.
- McWhae, J. R. H., P. E. Playford, A. W. Lindner, B. F. Glenister, and B. E. Balme. 1956. The stratigraphy of western Australia. *Journal of the Geological Society of Australia* 4:1–153.
- Meijide Fuentes, F., C. Fuentes Vidarte, and M. Meijide Calvo. 2001. Primeras huellas de saurópodo en el Weald de Soria (España). *Parabrontopodus distercii*, nov. ichnosp; pp. 407–415 in *Actas de las I Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*, Salas de los Infantes (Burgos, España), 21 al 25 de Septiembre de 1999. Colectivo Arqueológico y Paleontológico de Salas, C. A. S., Burgos, Spain.
- Meijide Fuentes, F., C. Fuentes Vidarte, M. Meijide Calvo, and M. Meijide Fuentes Jr. 2004. Rastro de un dinosaurio saurópodo en el Weald de Soria (España). *Brontopodus oncalensis* nov. icnsp. *Celtiberia* 54:501–516.
- Mensink, H., and D. Mertmann. 1984. Dinosaurier-Faehrtten (*Gigantosauropus asturiensis* n.g. n.sp.; *Hispanosauropus hauboldi* n.g. n.sp.) im Jura Asturiens bei la Griega and Ribadesella (Spanien). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1984:405–415.
- Mesa, V., and D. Perea. 2015. First record of theropod and ornithopod tracks and detailed description of sauropod trackways from the Tacuarembó Formation (Late Jurassic–?Early Cretaceous) of Uruguay. *Ichnos* 22:109–121.
- Meyer, C. A. 1990. Sauropod tracks from the Upper Jurassic Reuchenette Formation (Kimmeridgian, Lommiswil, Kt. Solothurn) of northern Switzerland. *Eclogae Geologicae Helvetiae* 83:389–397.
- Meyer, C. A. 1993. A sauropod dinosaur megatracksite from the Late Jurassic of northern Switzerland. *Ichnos* 3:29–38.
- Meyer, C. A., and J. G. Pittman. 1994. A comparison between the *Brontopodus* ichnofacies of Portugal, Switzerland and Texas. *Gaia* 10:125–133.
- Meyer, C. A., and B. Thüring. 2003a. Dinosaurs of Switzerland. *Comptes Rendus Palevol* 2:103–117.
- Meyer, C. A., and B. Thüring. 2003b. The first iguanodontid dinosaur tracks from the Swiss alps (Schrattenkalk Formation, Aptian). *Ichnos* 10:221–228.
- Meyer, C. A., M. G. Lockley, J. W. Robinson, and V. F. Santos. 1994. A comparison of well-preserved sauropod tracks from the Late Jurassic of Portugal and the western United States: evidence and implications. *Gaia* 10:57–64.
- Miall, A. D. 1977. A review of the braided-river depositional environment. *Earth Science Reviews* 13:1–62.
- Miall, A. D. 1985. Architectural-element analysis, a new method of facies analysis applied to fluvial deposits. *Earth Science Reviews* 22:261–308.
- Miall, A. D. 1988. Architectural elements and bounding surfaces in fluvial deposits: anatomy of the Kayenta Formation (Lower Jurassic), southwest Colorado. *Sedimentary Geology* 55:233–262.
- Miall, A. D. 2010. *The Geology of Stratigraphic Sequences*, second edition. Springer-Verlag, Berlin, Germany, 522 pp.
- Miall, A. D. 2014. *Fluvial Depositional Systems*. Springer, Heidelberg, Germany, 316 pp.
- Milàn, J., and R. G. Bromley. 2008. The impact of sediment consistency on track and undertrack morphology: experiments with emu tracks in layered cement. *Ichnos* 15:18–24.
- Milàn, J., and L. M. Chiappe. 2009. First American record of the Jurassic ichnospecies *Deltapodus brodricki* and a review of the fossil record of stegosaurian footprints. *Journal of Geology* 117:343–348.
- Milàn, J., P. Christiansen, and O. Mateus. 2005. A three-dimensionally preserved sauropod manus impression from the Upper Jurassic of Portugal: implications for sauropod manus shape and locomotor mechanics. *Kaupia* 14:47–52.
- Milàn, J., D. B. Loope, and R. G. Bromley. 2008. Crouching theropod and *Navahopus* sauropodomorph tracks from the Early Jurassic Navajo Sandstone of USA. *Acta Palaeontologica Polonica* 53:197–205.
- Milner, A. R. C., M. G. Lockley, and J. I. Kirkland. 2006. A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah. *New Mexico Museum of Natural History and Science Bulletin* 37:315–328.
- Mohabey, D. M. 1986. Note on dinosaur foot print from Kheba District, Gujarat. *Journal of the Geological Society of India* 27:456–459.
- Molnar, R. E. 1980a. Australian late Mesozoic terrestrial tetrapods: some implications. *Memoires de la Société Géologique de France, (Nouvelle Série)* 139:131–143.
- Molnar, R. E. 1980b. An ankylosaur (*Ornithischia: Reptilia*) from the Lower Cretaceous of southern Queensland. *Memoirs of the Queensland Museum* 20:77–87.
- Molnar, R. E. 1981. Reflections on the Mesozoic of Australia; pp. 47–60 in G. Olshevsky (ed.), *Mesozoic Vertebrate Life*. No. 1: New Mesozoic Faunas. George Olshevsky publishing, San Diego, USA.
- Molnar, R. E. 1984. Ornithischian dinosaurs in Australia; pp. 151–157 in W.-E. Reif and F. Westphal (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Attempto Verlag, Tübingen, Germany.
- Molnar, R. E. 1989. Terrestrial tetrapods in Cretaceous Antarctica. *Geological Society, London, Special Publications* 47:131–140.
- Molnar, R. E. 1991. Fossil reptiles in Australia; pp. 605–702 in P. Vickers-Rich, J. M. Monaghan, R. F. Baird, T. H. Rich, E. M. Thompson, and C. Williams (eds.), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio, and Monash University Publications Committee, Melbourne, Australia.
- Molnar, R. E. 1992. Paleozoogeographic relationships of Australian Mesozoic tetrapods; pp. 259–266 in S. Chatterjee and N. Hotton III (eds.), *New Concepts in Global Tectonics*. Texas Tech University Press, Lubbock, Texas.
- Molnar, R. E. 1996a. Observations on the Australian ornithopod dinosaur *Muttaborrasaurus*. *Memoirs of the Queensland Museum* 39:639–652.
- Molnar, R. E. 1996b. Preliminary report on a new ankylosaur from the Early Cretaceous, Australia. *Memoirs of the Queensland Museum* 39:653–668.
- Molnar, R. E. 2001a. A reassessment of the phylogenetic position of Cretaceous sauropod dinosaurs from Queensland, Australia; pp. 139–144 in H. A. Leanza (ed.), *VII International Symposium on Mesozoic Terrestrial Ecosystems*, Buenos Aires, Argentina, September 26–October 1, 1999. *Asociacion Paleontologica Argentina*, Buenos Aires, Argentina.

- Molnar, R. E. 2001b. Armour of the small ankylosaur *Minmi*; pp. 341–362 in K. Carpenter (ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Molnar, R. E. 2010. Taphonomic observations on eastern Australian Cretaceous sauropods. *Alcheringa* 34:421–429.
- Molnar, R. E. 2011. New morphological information about Cretaceous sauropod dinosaurs from the Eromanga Basin, Queensland, Australia. *Alcheringa* 35:329–339.
- Molnar, R. E., and H. T. Clifford. 2000. Gut contents of a small ankylosaur. *Journal of Vertebrate Paleontology* 20:194–196.
- Molnar, R. E., and H. T. Clifford. 2001. An ankylosaurian cololite from the Lower Cretaceous of Queensland, Australia; pp. 399–412 in K. Carpenter (ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Molnar, R. E., and E. Frey. 1987. The paravertebral elements of the Australian ankylosaur *Minmi* (Reptilia: Ornithischia, Cretaceous). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 175:19–37.
- Molnar, R. E., and P. M. Galton. 1986. Hypsilophodontid dinosaurs from Lightning Ridge, New South Wales, Australia. *Geobios* 19:231–243.
- Molnar, R. E., and N. S. Pledge. 1980. A new theropod dinosaur from South Australia. *Alcheringa* 4:281–287.
- Molnar, R. E., and S. W. Salisbury. 2005. Observations on Cretaceous sauropods from Australia; pp. 454–465 in V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Molnar, R. E., and J. Wiffen. 1994. A Late Cretaceous polar dinosaur fauna from New Zealand. *Cretaceous Research* 15:689–706.
- Molnar, R. E., T. F. Flannery, and T. H. Rich. 1981. An allosaurid theropod dinosaur from the Early Cretaceous of Victoria, Australia. *Alcheringa* 5:141–146.
- Molnar, R. E., T. F. Flannery, and T. H. Rich. 1985. Aussie *Allosaurus* after all. *Journal of Paleontology* 59:1511–1513.
- Moratalla, J. J. 2009. Sauropod tracks of the Cameros Basin (Spain): identification, trackway patterns and changes over the Jurassic-Cretaceous. *Geobios* 42:797–811.
- Moreno, K., and M. J. Benton. 2005. Occurrence of sauropod dinosaur tracks in the Upper Jurassic of Chile (redescription of *Iguanodonichnus frenki*). *Journal of South American Earth Sciences* 20:253–257.
- Moreno, K., M. T. Carrano, and R. Snyder. 2007. Morphological changes in pedal phalanges through ornithomimid dinosaur evolution: a bio-mechanical approach. *Journal of Morphology* 268:50–63.
- Mossbrucker, M. T., R. T. Bakker, M. G. Lockley, G. D. Gierlinski, and K. M. Hups. 2009. Probable stegosaur tracks from the Jurassic Morrison Formation, Colorado and Utah. *Dinosaur Ridge Report* 20:26–29.
- Mountford, C. P. 1973. European folk-lore in Australian mythology; pp. 360–371 in K. Tauchmann (ed.), *Festschrift zum 65. Geburtstag von Helmut Petri*. Bohlau Verlag, Köln, Germany.
- Muller, R. D., M. Gurnis, and T. Torsvik. 2012. GPlates. 1.2.0. EarthByte Project (part of AuScope) in the School of Geosciences at the University of Sydney, Sydney, Australia; Division of Geological and Planetary Sciences (GPS) at CalTech, Pasadena, California; Center for Geodynamics at the Norwegian Geological Survey (NGU), Trondheim, Norway.
- Nair, J. P., and S. W. Salisbury. 2012. New anatomical information on *Rhoetosaurus brownei* Longman, 1926, a gravisaurian sauropodomorph dinosaur from the Middle Jurassic of Queensland, Australia. *Journal of Vertebrate Paleontology* 32:369–394.
- Nath, T. T., P. Yadagiri, and A. K. Moitra. 2002. First record of armoured dinosaur from the Lower Jurassic Kota Formation, Pranhita-Godavari Valley, Andhra Pradesh. *Journal of the Geological Society of India* 59:575–577.
- Nicoll, R. S., J. R. Laurie, A. P. Kelman, D. J. Mantel, P. W. Haines, A. J. Mory, and R. M. Hocking. 2009. Canning Basin Biozonation and Stratigraphy, Chart 31. Commonwealth of Australia (Geoscience Australia), Canberra, A.C.T., Australia.
- Nicosia, U., F. M. Petti, G. Perugini, S. D’Orazi Porchetti, E. Sacchi, M. A. Conti, N. Mariotti, and A. Zarattini. 2007. Dinosaur tracks as paleogeographic constraints: new scenarios for the Cretaceous geography of the Periadriatic region. *Ichnos* 14:69–90.
- Norman, D. B. 2004. Basal Iguanodontia; pp. 413–437 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- Norman, J. E. d., and G. V. Norman. 2007. *A Pearling Master’s Journey; in the Wake of the Schooner Mist*. BPA Print Group, Burwood, Victoria, Australia, xiii + 338 pp.
- Nouri, J., I. Díaz-Martínez, and F. Pérez-Lorente. 2011. Tetradactyl footprints of an unknown affinity theropod dinosaur from the Upper Jurassic of Morocco. *PLoS ONE* 6:e26882. doi: 10.1371/journal.pone.0026882.
- Novas, F. E. 2007. Evolution of South American dinosaurs; pp. 333–353 in I. d. S. Carvalho, R. C. T. Cassab, C. Schwanke, M. A. Carvalho, A. C. S. Fernandes, M. A. Rodrigues, M. S. S. Carvalho, M. Arai, and M. E. Q. Oliverira (eds.), *Paleontologia: Cenários de Vida*. Interciencias, Rio de Janeiro, Brazil.
- Novas, F. E. 2009. The age of dinosaurs in South America. Indiana University Press, Bloomington, Indiana, 452 pp.
- Novas, F. E., A. V. Cambiaso, and A. Ambrosio. 2004. A new basal iguanodontian (Dinosauria, Ornithischia) from the Upper Cretaceous of Patagonia. *Ameghiniana* 41:75–82.
- Novas, F. E., S. Chatterjee, D. K. Rudra, and P. M. Datta. 2010. *Rahiolisaurus gujaratensis*, n. gen. n. sp., a new abelisaurid theropod from the Late Cretaceous of India; pp. 45–62 in S. Bandyopadhyay (ed.), *New Aspects of Mesozoic Biodiversity*. Springer, Heidelberg, Germany.
- Novas, F. E., L. Salgado, J. O. Calvo, and F. L. Agnolín. 2005. Giant titanosaur (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia. *Revista del Museo Argentino de Ciencias Naturales*, n.s. 7:37–41.
- Novas, F. E., F. L. Agnolín, M. D. Ezcurra, J. D. Porfiri, and J. I. Canale. 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. *Cretaceous Research* 45:174–215.
- O’Leary, M. A., E. M. Roberts, J. J. Head, F. Sissoko, and M. L. Bouare. 2004. Titanosaurian (Dinosauria, Sauropoda) remains from the “Continental Intercalaire” of Mali. *Journal of Vertebrate Paleontology* 24:923–930.
- O’Connor, P. M. 2007. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir* 8. *Journal of Vertebrate Paleontology* 27(2, Supplement):127–162.
- Olivero, E. B., Z. B. d. Gasparini, C. A. Rinaldi, and R. A. Scasso. 1991. First record of dinosaurs in Antarctica (Upper Cretaceous, James Ross Island): palaeogeographical implications; pp. 617–622 in M. R. Thomson, J. A. Crane, and J. W. Thomson (eds.), *Geological evolution of Antarctica*. Cambridge University Press, Cambridge, U.K.
- Olsen, J., M. Durack, G. Dutton, V. Serventy, and A. Bortignon. 1984. *The Land Beyond Time: A Modern Exploration of Australia’s North-West Frontiers*. The Macmillan Company of Australia, Melbourne, Australia, 112 pp.
- Olsen, P. E., J. B. Smith, and N. G. McDonald. 1998. Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). *Journal of Vertebrate Paleontology* 18:586–601.
- Ösi, A., and E. Buffetaut. 2011. Additional non-avian theropod and bird remains from the early Late Cretaceous (Santonian) of Hungary and a review of the European abelisauroid record. *Annales de Paléontologie* 97:35–49.
- Page, D. 1998. Stegosaur tracks and the persistence of facies—the Lower Cretaceous of Western Australia. *Geology Today* 14:75–77.
- Parker, L. R., and R. L. Rowley Jr. 1989. Dinosaur footprints from a coal mine in east central Utah; pp. 361–366 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.
- Parliament of the Commonwealth of Australia. 1991. *The Injured Coastline: Protection of the Coastal Environment*. Report of the House of Representatives Standing Committee on Environment, Recreation and the Arts. Australian Government Publishing Service, Canberra, Australia, xviii + 126 pp.
- Partridge, A. D. 2006. Jurassic–Early Cretaceous spore-pollen and dinocyst zonation for Australia; pp. 1–4 in E. Monteil (ed.), *Australian Mesozoic and Cenozoic Palynology Zonations—Updated from the 2004 Geologic Time Scale*. Commonwealth of Australia (Geoscience Australia), Canberra, A.C.T., Australia.
- Pascual Arribas, C., and N. Hernández Medrano. 2010. Nuevos datos sobre el yacimiento icnítico de Las Cuestas I (Santa Cruz

- de Yanguas, Soria, España). *Studia Geologica Salmanticensis* 46:121–157.
- Pascual Arribas, C., N. Hernández Medrano, P. Latorre Macarrón, and E. Sanz Pérez. 2009. Estudio de un rastro de huellas de saurópodo del yacimiento de Las Cuestas I (Santa Cruz de Yanguas, Soria, España). Implicaciones taxonómicas. *Studia Geologica Salmanticensis* 44:13–40.
- Peabody, F. E. 1948. Reptile and amphibian trackways from the Lower Triassic Moenkopi Formation of Arizona and Utah. *Bulletin of the Department of Geological Sciences, University of California* 27:295–468.
- Peabody, F. E. 1955. Taxonomy and the footprints of tetrapods. *Journal of Paleontology* 29:915–918.
- Pearson, N. J., M. G. Mangano, L. A. Buatois, S. Casadio, and M. R. Raising. 2012. Ichnology, sedimentology, and sequence stratigraphy of outer-estuarine and coastal-plain deposits: implications for the distinction between allogenic and autogenic expressions of the *Glossifungites* Ichnofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 333:192–217.
- Pereda Suberbiola, X., P. M. Galton, H. Mallison, and F. E. Novas. 2013. A plated dinosaur (Ornithischia, Stegosauria) from the Early Cretaceous of Argentina, South America: an evaluation. *Alcheringa* 37:65–78.
- Piñuela, L., J. C. Garcia-Ramos, and J. Lires. 2002. Comportamiento gregario de ornitópodos en el Jurásico de Asturias; pp. 44–45 in F. Perez-Lorente (ed.), *Dinosaurios y otros reptiles Mesozoicos en España. Resúmenes de las comunicaciones ponencias y panels*. Instituto de Estudios Riojanos, Universidad de La Rioja, Logroño, Spain.
- Pittman, J. G. 1989. Stratigraphy, lithology, depositional environment, and track type of dinosaur track-bearing beds of the Gulf Coastal Plain; pp. 135–153 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.
- Pittman, J. G., and D. D. Gillette. 1989. The Briar site: a new sauropod dinosaur tracksite in Lower Cretaceous beds of Arkansas; pp. 313–332 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.
- Pittman, J. G., and M. G. Lockley. 1994. A review of sauropod dinosaur tracksites of the Gulf of Mexico Basin. *Gaia* 10:95–108.
- Piveteau, J. 1926. Contribution à l'étude des formations lagunaires du nordouest de Madagascar. *Bulletin de la Société Géologique de France (Series 4)* 26:33–38.
- Platt, B. F., and S. T. Hasiotis. 2006. Newly discovered sauropod dinosaur tracks with skin and foot-pad impressions from the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, U.S.A. *Palaios* 21:249–261.
- Playford, P. E., R. N. Cope, A. E. Cockbain, G. H. Low, and D. C. Lowry. 1975. Phanerozoic; pp. 223–433 in *The Geology of Western Australia*. Australian Government Publishing Service, Canberra, Australia.
- Plumb, K. A. 1979. The tectonic evolution of Australia. *Earth Science Reviews* 14:205–249.
- Poropat, S. F., P. D. Mannion, P. Upchurch, S. A. Hocknull, B. P. Kear, and D. A. Elliot. 2015a. Reassessment of the non-titanosaurian somphospondylan *Wintonotitan watsi* (Dinosauria: Sauropod: Titanosauriformes) from the mid-Cretaceous Winton Formation, Queensland, Australia. *Papers in Palaeontology* 1:59–106.
- Poropat, S. F., P. M. Upchurch, P. D. Mannion, S. A. Hocknull, J. P. Nair, B. P. Kear, and D. A. Elliot. 2013. Tall shoulders, wide hips and strange front feet: a reassessment of Queensland's Cretaceous sauropod fauna; p. 69 in G. Prideaux (ed.), *CAVEPS 2013: 14th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics*, Flinders University, Adelaide, 30th September–4th October 2013. Flinders University, Adelaide, Australia.
- Poropat, S. F., P. Upchurch, P. D. Mannion, S. A. Hocknull, B. P. Kear, T. Sloan, G. H. K. Sinapius, and D. A. Elliot. 2015b. Revision of the sauropod dinosaur *Diamantinasaurus matildae* Hocknull et al. 2009 from the mid-Cretaceous of Australia: implications for Gondwanan titanosauriform dispersal. *Gondwana Research* 27:995–1033.
- Prieto-Márquez, A. 2010. Global historical biogeography of hadrosaurid dinosaurs. *Zoological Journal of the Linnean Society* 159:503–525.
- Prieto-Márquez, A., and G. C. Salinas. 2010. A re-evaluation of *Secernosaurus koernerii* and *Kritosaurus australis* (Dinosauria, Hadrosauridae) from the Late Cretaceous of Argentina. *Journal of Vertebrate Paleontology* 30:813–837.
- Rabbitt, E. 1989. Dinosaur prints evidence of ancient life. *North West Telegraph (Port Hedland, W.A.)*, 1986–1989 (date uncertain), 2 pp.
- Rainforth, E. C. 2003. Revision and re-evaluation of the Early Jurassic dinosaurian ichnogenus *Otozoum*. *Palaeontology* 46:803–838.
- Rauhut, O. W. M. 2005a. Post-cranial remains of “coelurosaur” (Dinosauria, Theropoda) from the Late Jurassic of Tanzania. *Geological Magazine* 142:97–107.
- Rauhut, O. W. M. 2005b. Osteology and relationships of a new theropod dinosaur from the Middle Jurassic of Patagonia. *Palaeontology* 48:87–110.
- Rauhut, O. W. M. 2006a. A brachiosaurid sauropod from the Late Jurassic Canadian Calcáreo Formation of Chubut, Argentina. *Fossil Record* 9:226–237.
- Rauhut, O. W. M. 2006b. Theropod dinosaurs from the Late Jurassic of Tanzania and the origin of Cretaceous Gondwanan theropod faunas. *Journal of Vertebrate Paleontology* 26(3, Supplement):113A.
- Rauhut, O. W. M. 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Special Papers in Palaeontology* 86:131–163.
- Rauhut, O. W. M., and C. Werner. 1997. First record of a Maastrichtian sauropod dinosaur from Egypt. *Palaeontologia africana* 34:63–67.
- Rauhut, O. W. M., J. L. Carballido, and D. Pol. 2015. A diplocidid sauropod dinosaur from the Late Jurassic Cañadón Calcáreo Formation of Chubut, Argentina. *Journal of Vertebrate Paleontology*. doi: 10.1080/02724634.2015.982798.
- Raup, D. M., and J. R. Sepkoski. 1986. Periodic extinction of families and genera. *Science* 231:833–836.
- Remes, K. 2009. Taxonomy of Late Jurassic diplocidid sauropods from Tendaguru (Tanzania). *Fossil Record* 12:23–46.
- Rich, T., B. P. Kear, R. Sinclair, B. Chinnery, K. Carpenter, M. McHugh, and P. Vickers-Rich. 2014. *Serendipaceratops arthurclarkei* Rich & Vickers-Rich, 2003 is an Australian Early Cretaceous ceratopsian. *Alcheringa* 38:1–25.
- Rich, T. H. 1996. Significance of polar dinosaurs in Gondwana. *Memoirs of the Queensland Museum* 39:711–717.
- Rich, T. H. 2007. Polar Dinosaurs of Australia. *Museum Victoria Nature Series*. Museum Victoria, Melbourne, Australia, 40 pp.
- Rich, T. H., and P. Vickers-Rich. 1988. A juvenile dinosaur brain from Australia. *National Geographic Research* 4:148.
- Rich, T. H., and P. Vickers-Rich. 1989. Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia. *National Geographic Research* 5:15–53.
- Rich, T. H., and P. Vickers-Rich. 1994. Neoceratopsians and ornithomimosaurs: dinosaurs of Gondwana origin? *National Geographic Research and Exploration* 10:129–131.
- Rich, T. H., and P. Vickers-Rich. 1999. The Hypsilophodontidae from southeastern Australia. *National Science Museum Monographs* 15:167–180.
- Rich, T. H., and P. Vickers-Rich. 2000. *Dinosaurs of Darkness*. Indiana University Press, Bloomington, Indiana, 222 pp.
- Rich, T. H., and P. Vickers-Rich. 2003a. *A Century of Australian Dinosaurs*. Queen Victoria Museum and Art Gallery, Launceston, and Monash Science Centre, Monash University, Clayton, Victoria, Australia, 125 pp.
- Rich, T. H., and P. Vickers-Rich. 2003b. Protoceratopsian? ulnae from Australia. *Records of the Queen Victoria Museum, Launceston* 113:1–12.
- Rich, T. H., and G. C. Young. 1996. Vertebrate biogeographic evidence for connections of the east and southeast Asian blocks with Gondwana. *Australian Journal of Earth Sciences* 43:625–634.
- Rich, T. H., R. A. Gangloff, and W. R. Hammer. 1997. Polar dinosaurs; pp. 562–573 in P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego, California.
- Rich, T. H., P. Vickers-Rich, M. Fernandez, and S. Santillana. 1999. A probable hadrosaur from Seymour Island, Antarctic Peninsula. *National Science Museum Monographs* 15:219–222.
- Rich, T. H., P. Vickers-Rich, B. E. Wagstaff, J. R. C. M. Mason, C. B. Douthitt, and R. T. Gregory. 1989. Early Cretaceous biota from the northern side of the Australo-Antarctic rift valley. *Geological Society, London, Special Publications* 47:121–130.
- Rich, T. H., P. Vickers-Rich, B. E. Wagstaff, J. R. C. M. Mason, T. F. Flannery, M. Archer, R. E. Molnar, and J. A. Long. 1992. Two possible chronological anomalies in the Early Cretaceous tetrapod assemblages of southeastern Australia; pp. 165–176 in N. J. Mateer

- and P. Chen (eds.), *Aspects of Nonmarine Cretaceous Geology*. China Ocean Press, Beijing, China.
- Ridgwell, N., and P. C. Sereno. 2010. A basal thyreophoran (Dinosauria, Ornithischia) from the Tiouraren Formation of Niger. *Journal of Vertebrate Paleontology* 30(Programs and Abstracts):150A–151A.
- Roberts, E. M. 2007. Facies architecture and depositional environments of the Upper Cretaceous Kaiparowits Formation, southern Utah. *Sedimentary Geology* 197:207–233.
- Roe, J., and C. Shaw. 2008. Joseph Roe and Cyril Shaw on behalf of the Goolarabooloo and Jabirr Jabirr Peoples/Western Australia/Kimberley Quarry Pty Ltd. Application No. WO07/803. National Native Title Tribunal Hearing Report 118 (25 August 2008). National Native Title Tribunal of Australia, available at [www.austlii.edu.au/au](http://www.austlii.edu.au/au). Accessed 30 November 2013.
- Roe, P. 1983. *Gularabulu*. Freemantle Arts Centre Press, Fremantle, Western Australia, Australia, 98 pp.
- Romano, M., and M. A. Whyte. 2003. Jurassic dinosaur tracks and trackways of the Cleveland Basin, Yorkshire: preservation, diversity and distribution. *Proceedings of the Yorkshire Geological Society* 54:185–215.
- Romano, M., and M. A. Whyte. 2012. Information on the foot morphology, pedal skin texture and limb dynamics of sauropods: evidence from the ichnological record of the Middle Jurassic of the Cleveland Basin, Yorkshire, UK. *Zubia* 30:45–92.
- Romano, M., M. A. Whyte, and S. J. Jackson. 2007. Trackway ratio: a new look at trackway gauge in the analysis of quadrupedal dinosaur trackways and its implications for ichnotaxonomy. *Ichnos* 14:257–270.
- Romano, M., M. A. Whyte, and P. L. Manning. 1999. New sauropod dinosaur prints from the Saltwick Formation (Middle Jurassic) of the Cleveland Basin, Yorkshire. *Proceedings of the Yorkshire Geological Society* 52:361–369.
- Romilio, A., and S. W. Salisbury. 2011. A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: a case for mistaken identity. *Cretaceous Research* 32:135–142.
- Romilio, A., and S. W. Salisbury. 2013. Three-dimensional analysis of the largest tracks from the Lark Quarry dinosaur tracksite, central-western Queensland; pp. 74–75 in G. Prideaux (ed.), *CAVEPS 2013: 14th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics*, Flinders University, Adelaide, 30th September–4th October 2013. Flinders University, Adelaide, Australia.
- Romilio, A., and S. W. Salisbury. 2014. Large dinosaurian tracks from the Upper Cretaceous (Cenomanian–Turonian) portion of the Winton Formation, Lark Quarry, central-western Queensland, Australia: 3D photogrammetric analysis renders the ‘stampede trigger’ scenario unlikely. *Cretaceous Research* 51:186–207.
- Romilio, A., S. W. Salisbury, and J. P. Nair. 2014. Ichnological evidence for diverse pedal postures in ornithopodan dinosaurs. *Journal of Vertebrate Paleontology* 34(Program and Abstracts):216.
- Romilio, A., R. T. Tucker, and S. W. Salisbury. 2013. Re-evaluation of the Lark Quarry dinosaur tracksite (late Albian–Cenomanian Winton Formation, central-western Queensland, Australia): no longer a stampede? *Journal of Vertebrate Paleontology* 33:102–120.
- Royo-Torres, R., A. Cobos, and L. Alcalá. 2006. A giant European dinosaur and a new sauropod clade. *Science* 314:1925–1927.
- Royo-Torres, R., A. Cobos, L. Luque, A. Aberasturi, E. Espilez, I. Fierro, A. Gonzalez, L. Mampel, and L. Alcalá. 2009. High European sauropod dinosaur diversity during Jurassic–Cretaceous transition in Riodeva (Teruel, Spain). *Palaeontology* 52:1009–1027.
- Rozadilla, S., F. L. Agnolin, F. E. Novas, A. M. Aranciaga Rolando, M. J. Motta, J. M. Lirio, and M. P. Isasi. 2016. A new ornithopod (Dinosauria, Ornithischia) from the Upper Cretaceous of Antarctica and its palaeobiogeographical implications. *Cretaceous Research* 57:311–324.
- Salgado, L., and J. F. Bonaparte. 1991. Un nuevo saurópodo Dicraeosauridae, *Amargasaurus cazaui* gen. et sp. nov., de la Formación La Amarga, Neocomiano de la Provincia del Neuquén, Argentina. *Ameghiniana* 28:333–346.
- Salgado, L., and Z. B. d. Gasparini. 2004. Revisión del primer dinosaurio Antártico (Ornithischia, Ankylosauria): implicancia paleobiogeográfica; 5 pp. in Instituto Nacional del Antártico Argentino, V Simposio Argentino y I° Latinoamericano sobre Investigaciones Antárticas, Actas. Buenos Aires, 30 August–3 September, 2004. Resumen Expandido N° 101GP (5 pp; CD ROM). Instituto Nacional del Antártico Argentino (Dirección Nacional del Antártico), Buenos Aires, Argentina.
- Salgado, L., and Z. B. d. Gasparini. 2006. Reappraisal of an ankylosaurian dinosaur from the Upper Cretaceous of James Ross Island (Antarctica). *Geodiversitas* 28:119–135.
- Salgado, L., I. d. S. Carvalho, and A. C. Garrido. 2006. *Zapalasaurus bonapartei*, un nuevo dinosaurio saurópodo de La Formación La Amarga (Cretácico Inferior), noroeste de Patagonia, Provincia de Neuquén, Argentina. *Geobios* 39:695–707.
- Salgado, L., A. C. Garrido, S. E. Cocca, and J. R. Cocca. 2004. Lower Cretaceous rebbachisaurid sauropods from Cerro Aguada del Leon (Lohan Cura Formation), Neuquén Province, northwestern Patagonia, Argentina. *Journal of Vertebrate Paleontology* 24:903–912.
- Salisbury, S. W., M. C. Lamanna, and R. E. Molnar. 2006. A new titanosauriform sauropod from the mid-Cretaceous (Albian–Cenomanian) Winton Formation of central-western Queensland, Australia. *Journal of Vertebrate Paleontology* 26(3, Supplement):118A.
- Salisbury, S. W., T. H. Rich, P. Vickers-Rich, and P. J. Currie. 2011. Australian Cretaceous non-avian theropod dinosaur teeth; p. 73 in K. Trinajstić, M. Bunce, N. Warburton, C. Hadley, A. Baynes, and M. Siversson (eds.), *CAVEPS Perth 2011: 13th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics*, Perth, April 27th–30th. Geological Survey of Western Australia, Perth, Australia.
- Sampson, S. D., M. T. Carrano, and C. A. Forster. 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. *Nature* 409:504–506.
- Sampson, S. D., L. M. Witmer, C. A. Forster, D. W. Krause, P. M. O’Connor, P. Dodson, and F. Ravoavy. 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science* 280:1048–1051.
- Santos, V. F., C. M. Silva, and L. A. Rodrigues. 2008. Dinosaur track sites from Portugal: scientific and cultural significance. *Oryctos* 8:77–88.
- Santos, V. F., J. J. Moratalla, and R. Royo-Torres. 2009. New sauropod trackways from the Middle Jurassic of Portugal. *Acta Palaeontologica Polonica* 54:409–422.
- Santos, V. F., M. G. Lockley, J. J. Moratalla, and A. M. G. Carvalho. 1992. The longest dinosaur trackway in the world? Interpretation of Cretaceous footprints from Carenque, near Lisbon, Portugal. *Gaia* 5:18–27.
- Santos, V. F., V. F. Santos, M. G. Lockley, C. A. Meyer, J. Carvalho, and A. M. Galopim de Carvalho. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia* 10:5–13.
- Sarjeant, W. A. S. 1970. Fossil footprints from the Middle Triassic of Nottinghamshire and the Middle Jurassic of Yorkshire. *Mercian Geologist* 3:269–282.
- Sarjeant, W. A. S., J. B. Delair, and M. G. Lockley. 1998. The footprints of *Iguanodon*: a history and taxonomic study. *Ichnos* 6:183–202.
- Scanlon, J. D. 2006. Dinosaurs and other Mesozoic reptiles of Australasia; pp. 265–290 in J. R. Merrick, M. Archer, G. M. Hickey, and M. S. Y. Lee (eds.), *Evolution and Biogeography of Australian Vertebrates*. Australian Scientific Publishing, Sydney, Australia.
- Schumacher, B. A., and M. G. Lockley. 2014. Newly documented trackways at “Dinosaur Lake,” the Purgatoire Valley Dinosaur Tracksite. *New Mexico Museum of Natural History and Science Bulletin* 62:261–267.
- Semeniuk, V. 2008. Holocene sedimentation, stratigraphy, biostratigraphy, and history of the Canning Coast, north-western Australia. *Journal of the Royal Society of Western Australia* 91(Supplement):53–148.
- Senter, P. J. 2010. Evidence for a sauropod-like metacarpal configuration in stegosaurian dinosaurs. *Acta Palaeontologica Polonica* 55:427–432.
- Sereno, P. C., J. A. Wilson, and J. L. Conrad. 2004. New dinosaurs link southern landmasses in the mid-Cretaceous. *Proceedings of the Royal Society of London B, Biological Sciences* 271:1325–1330.
- Sereno, P. C., J. A. Wilson, H. C. E. Larsson, D. B. Dutheil, and H.-D. Sues. 1994. Early Cretaceous dinosaurs from the Sahara. *Science* 266:267–271.
- Sereno, P. C., A. L. Beck, D. B. Dutheil, H. C. E. Larsson, G. H. Lyon, B. Moussa, R. W. Sadleir, C. A. Sidor, D. J. Varricchio, G. P. Wilson, and J. A. Wilson. 1999. Cretaceous sauropods from the Sahara and

- the uneven rate of skeletal evolution among dinosaurs. *Science* 286:1342–1347.
- Serventy, V. 1954. Tracks of giant reptile exposed by the sea. *The West Australian*, Tuesday 19 October 1954:3.
- Serventy, V. 1955. Schools are for children. *Western Mail* Friday 23 December 1955:15–17.
- Serventy, V. 1964. Footprints of the Dreamtime dinosaur. *Australian Women's Weekly* Wednesday 15 July 1964:9.
- Serventy, V. 1967. *Nature Walkabout*. A.H. & A.W. Reed, Artarmon, Sydney, Australia, 137 pp.
- Shibata, K., P. Jintasakul, Y. Azuma, and H.-L. You. 2015. A new basal hadrosauroid dinosaur from the Lower Cretaceous Khok Kruat Formation in Nakhon Ratchasima Province, northeastern Thailand. *PLoS ONE* 10:e0145904. doi: 10.1371/journal.pone.0145904.
- Shuler, E. W. 1935. Dinosaur track mounted in the band stand at Glen Rose, Texas. *Field and Laboratory* 4:9–13.
- Siverson, M. 2010a. Preliminary Report upon the Palaeontology (Including Dinosaur Footprints) of the Broome Sandstone in the James Price Point Area, Western Australia. Document No. 60103995-0000-GE-REP-0009. AECOM Australia Pty Ltd, Perth, Australia, 19 pp.
- Siverson, M. 2010b. Report on Macro-fossils in Intertidal Outcrops of the Broome Sandstone, 1.2–2.7 km South of James Price Point (Proposed Marine Infrastructure Shore Crossing) and 6.2–7.5 km South of James Price Point (Proposed Southern Pipeline Shore Crossing). Western Australian Museum, Perth, Australia, 14 pp.
- Smith, E. 1999. *Black Opal Fossils of Lightning Ridge*. Kangaroo Press (Simon and Schuster), Sydney, Australia, 112 pp.
- Smith, J. B., and J. O. Farlow. 2003. Osteometric approaches to trackmaker assignment for the Newark Supergroup ichnogenera *Grallator*, *Anchisauripus*, and *Eubrontes*; pp. 273–292 in P. M. LeTourneau and P. E. Olsen (eds.), *The Great Rift Valleys of Pangea in Eastern North America. Volume 2: Sedimentology, Stratigraphy, and Paleontology*. Columbia University Press, New York, New York.
- Smith, J. B., M. C. Lamanna, A. S. Askar, K. A. Bergig, S. O. Tshakreen, M. M. Abugares, and D. T. Rasmussen. 2010. A large abelisauroid theropod dinosaur from the Early Cretaceous of Libya. *Journal of Paleontology* 84:927–934.
- Smith, J. B., M. C. Lamanna, K. J. Lacovara, P. Dodson, J. R. Smith, J. C. Poole, R. Giegengack, and Y. S. Attia. 2001. A giant sauropod dinosaur from an Upper Cretaceous mangrove deposit in Egypt. *Science* 292:1704–1706.
- Smith, J. G. 1968. Tectonics of the Fitzroy wrench trough, Western Australia. *American Journal of Science* 266:766–776.
- Smith, N. D., P. J. Makovicky, F. L. Agnolín, M. D. Ezcurra, D. F. Pais, and S. W. Salisbury. 2008. A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the mid-Cretaceous. *Proceedings of the Royal Society of London B, Biological Sciences* 275:2085–2093.
- Smith, S. D., W. S. Persons IV, and L. Xing. 2016. A tyrannosaur trackway at Glenrock, Lance Formation (Maastrichtian), Wyoming. *Cretaceous Research* 61:1–4.
- Smith, T. E., D. S. Edwards, A. P. Kelman, J. R. Laurie, S. le Poidevi, R. S. Nicoll, A. J. Mory, P. W. Haines, and R. M. Hocking. 2013. *Canning Basin Biozonation and Stratigraphy, 2013, Chart 31, Commonwealth of Australia (Geoscience Australia)*, Canberra, ACT, Australia.
- Soto-Acuña, S., R. A. Otero, D. Rubilar-Rogers, and A. O. Vargas. 2015. Arcosaurios no avianos de Chile. *Museo Nacional de Historia Natural de Chile, Publicación Ocasional* 63:209–263.
- Staines, H. R. E., and J. T. Woods. 1964. Recent discovery of Triassic dinosaur footprints in Queensland. *Australian Journal of Science* 27:55.
- Stanford, R., R. Weems, and M. G. Lockley. 2004. A new dinosaur ichnotaxon from the Lower Cretaceous Patuxent Formation of Maryland and Virginia. *Ichnos* 11:251–259.
- Stanner, W. E. H. 1979. *White Man Got No Dreaming: Essays, 1938–1973*. Australian National University Press, Canberra, Australia, 389 pp.
- Sternberg, C. M. 1932. Dinosaur tracks from Peace River, British Columbia. *Canada National Museum Bulletin* 68:59–85.
- Stokes, B., and W. B. McGregor. 2003. Classification and subclassification of the Nyalnyulan languages; pp. 29–74 in N. Evans (ed.), *The Non-Pama–Nyungan Languages of Northern Australia: Comparative Studies of the Continent's Most Linguistically Complex Region*. Pacific Linguistics, Canberra, Australia.
- Sweeney, R. C. H. 1974. *Naturalist in the Sudan*. Taplinger Publishing, New York, New York, 240 pp.
- Tapley, I. J. 1988. The reconstruction of palaeodrainage and regional structures in Australia's Canning and Officer Basins using NOAA-AVHRR satellite imagery. *Earth Science Reviews* 25:409–425.
- Taquet, P. 1976. Géologie et paléontologie du gisement de Gadoufaoua (Aptien du Niger). *Cahiers de Paléontologie*. Éditions du Centre National de la Recherche Scientifique, Paris, France, 191 pp.
- Taquet, P., and D. A. Russell. 1999. A massively-constructed iguanodont from Gadoufaoua, Lower Cretaceous of Niger. *Annales de Paléontologie* 85:85–96.
- Thom, J. H. 1975. Remaining Precambrian areas—Kimberley Region; pp. 160–193 in *The Geology of Western Australia*. Australian Government Publishing Service, Canberra, Australia.
- Thulborn, A. 1999. New dinosaur tracks from the Walloon Coal Measures (Middle Jurassic) of Queensland. *Records of the Western Australian Museum* 57(Supplement):419.
- Thulborn, R. A. 1986. Early Triassic tetrapod faunas of southeastern Gondwana. *Alcheringa* 10:297–313.
- Thulborn, R. A. 1989. The gaits of dinosaurs; pp. 39–50 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.
- Thulborn, R. A. 1994. Ornithopod dinosaur tracks from the Lower Jurassic of Queensland. *Alcheringa* 18:247–258.
- Thulborn, R. A. 2013. Lark Quarry revisited: a critique of methods used to identify a large dinosaurian track-maker in the Winton Formation (Albian–Cenomanian), western Queensland, Australia. *Alcheringa* 37:312–330.
- Thulborn, R. A., and M. J. Wade. 1979. Dinosaur stampede in the Cretaceous of Queensland. *Lethaia* 12:275–279.
- Thulborn, R. A., and M. J. Wade. 1984. Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. *Memoirs of the Queensland Museum* 21:413–517.
- Thulborn, T. 1990. *Dinosaur Tracks*. Chapman and Hall, London, U.K., 410 pp.
- Thulborn, T. 1998. Dinosaur tracks at Broome, Western Australia. *Geology Today* 14:139.
- Thulborn, T. 2000. Australia's earliest theropods: footprint evidence in the Ipswich coal measures (Upper Triassic) of Queensland. *Gaia* 15:301–311.
- Thulborn, T. 2001. History and nomenclature of the theropod dinosaur tracks *Bueckeburgichnus* and *Megalosauripus*. *Ichnos* 8:207–222.
- Thulborn, T. 2002. Giant dinosaur tracks in the Broome Sandstone (Lower Cretaceous) of Western Australia; pp. 154–155 in G. A. Brock and J. A. Talent (eds.), *First International Palaeontological Congress (IPC2002)*, 6–10 July, 2002, Macquarie University, N.S.W., Australia. Geological Society of Australia, Sydney, Australia.
- Thulborn, T. 2003. Comment on “Ascent of dinosaurs linked to an Iridium anomaly at the Triassic–Jurassic boundary”. *Science* 301:169b.
- Thulborn, T. 2004. Extramorphological features of sauropod dinosaur tracks in the Uhangri Formation (Cretaceous), Korea. *Ichnos* 11:295–298.
- Thulborn, T. 2009. *Megalosauropus broomensis* and the many misconceptions of megalosaur tracks; pp. 89–90 in A. D. Buscalioni and M. A. Fregenal-Martinez (eds.), *Abstracts Tenth International Symposium on Mesozoic Terrestrial Ecosystems and Biota*, Teruel, 17–19 September 2009. Universidad Autónoma de Madrid, Madrid, Spain.
- Thulborn, T. 2012. Impact of sauropod dinosaurs on lagoonal substrates in the Broome Sandstone (Lower Cretaceous), Western Australia. *PLoS ONE* 7:e36208. doi: 10.1371/journal.pone.0036208.
- Thulborn, T., T. L. Hamley, and P. Foulkes. 1994. Preliminary report on sauropod dinosaur tracks in the Broome Sandstone (Lower Cretaceous) of Western Australia. *Gaia* 10:85–94.
- Tidwell, V., K. Carpenter, and W. Brooks. 1999. New sauropod from the Lower Cretaceous of Utah, USA. *Oryctos* 2:21–37.
- Tidwell, V., K. Carpenter, and S. Meyer. 2001. New titanosauriform (Sauropoda) from the Poison Strip member of the Cedar Mountain Formation (Lower Cretaceous), Utah; pp. 139–165 in D. H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie*. Indiana University Press, Bloomington, Indiana.

- Tindale, N. B. 1974. *Aboriginal Tribes of Australia: Their Terrain, Environmental Controls, Distribution, Limits, and Proper Names*. University of California Press, Berkeley, California, 404 pp.
- Torcida Fernández-Baldor, F., I. Díaz-Martínez, R. Contreras, P. Huerta, D. Montero, and V. Urién. 2015. Unusual sauropod tracks in the Jurassic-Cretaceous interval of the Cameros Basin (Burgos, Spain). *Journal of Iberian Geology* 41:141–154.
- Towner, R. R., and D. L. Gibson. 1983. Geology of the onshore Canning Basin, Western Australia. Bureau of Mineral Resources, Geology and Geophysics, Australia, Bulletin 215:1–51.
- Tschopp, E., O. Wings, T. Frauenfelder, and W. Brinkmann. 2015. Articulated bone sets of manus and pedes of *Camarasaurus* (Sauropoda, Dinosauria). *Palaeontologia Electronica* 18(2):44A. <http://palaeo-electronica.org/content/2015/1284-manus-and-pes-of-camarasaurus>.
- Tucker, R. T. 2011. Taphonomy of Sheridan College Quarry 1, Buffalo, Wyoming: implications for reconstructing historic dinosaur localities including Utterback's 1902–1910 Morrison dinosaur expeditions. *Geobios* 44:527–541.
- Tucker, R. T., E. M. Roberts, and S. W. Salisbury. 2011. New information on the stratigraphy, depositional environment and taphonomy of the mid-Cretaceous Winton Formation, central-western Queensland, Australia; p. 84 in K. Trinajstić, M. Bunce, N. Warburton, C. Hadley, A. Baynes, and M. Siversson (eds.), *CAVEPS Perth 2011: 13th Conference on Australasian Vertebrate Evolution*, Palaeontology and Systematics, Perth, April 27th–30th. Geological Survey of Western Australia, Perth, Australia.
- Tucker, R. T., E. M. Roberts, Y. Hu, A. I. S. Kemp, and S. W. Salisbury. 2013. Detrital zircon age constraints for the Winton Formation, Queensland: contextualizing Australia's Late Cretaceous dinosaur faunas. *Gondwana Research* 24:767–779.
- Turner, S., L. B. Bean, M. E. Dettmann, J. L. McKellar, S. McLoughlin, and R. A. Thulborn. 2009. Australian Jurassic sedimentary and fossil successions: current work and future prospects for marine and non-marine correlation. *GFF* 131:49–70.
- Upchurch, P., P. M. Barrett, and P. Dodson. 2004. Sauropoda; pp. 259–322 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- Veevers, J. J. 1967. The Phanerozoic geological history of northwest Australia. *Journal of the Geological Society of Australia* 14:253–272.
- Veevers, J. J., and A. T. Wells. 1961. The geology of the Canning Basin, Western Australia. Bureau of Mineral Resources, Geology and Geophysics, Bulletin 60:1–323.
- Vickaryous, M. K., T. Maryanska, and D. B. Weishampel. 2004. Ankylosauria; pp. 363–392 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- Vickers-Rich, P. 1996. Early Cretaceous polar tetrapods from the great southern rift valley, southeastern Australia. *Memoirs of the Queensland Museum* 39:719–723.
- Vickers-Rich, P., and T. H. Rich. 1993. Australia's polar dinosaurs. *Scientific American* 269:50–55.
- Vickers-Rich, P., and T. H. Rich. 1997. The polar dinosaurs of southeastern Australia; pp. 253–257 in D. L. Wolberg, G. D. Rosenberg, and E. Stump (eds.), *Dinofest™ International*. Proceedings of a Symposium Sponsored by Arizona State University, April, 1996, Tempe, Arizona. Academy of Natural Sciences, Philadelphia, Pennsylvania.
- Vila, B., O. Oms, Á. Galobart, and K. T. Bates. 2013a. Dynamic similarity in titanosaur sauropods: ichnological evidence from the Fumanya Dinosaur Tracksite (southern Pyrenees). *PLoS ONE* 8:e57408. doi: 10.1371/journal.pone.0057408.
- Vila, B., O. Oms, J. Marmi, and Á. Galobart Lorente. 2008. Tracking Fumanya footprints (Maastrichtian, Pyrenees): historical and ichnological overview. *Oryctos* 8:115–130.
- Vila, B., O. Oms, V. Fondevilla, R. Gaete, Á. Galobart, V. Riera, and J. I. Canudo. 2013b. The latest succession of dinosaur tracksites in Europe: hadrosaur ichnology, track production and palaeoenvironments. *PLoS ONE* 8:e72579. doi: 10.1371/journal.pone.0072579.
- Voigt, S., D. S. Berman, and A. C. Henrici. 2007. First well-established track-trackmaker association of Paleozoic tetrapods based on *Ichnoterium* trackways and diadectid skeletons from the Lower Permian of Germany. *Journal of Vertebrate Paleontology* 27:553–570.
- Wagstaff, B. E., and J. R. C. McEwen Mason. 1989. Palynological dating of Lower Cretaceous coastal vertebrate localities, Victoria, Australia. *National Geographic Research* 5:54–63.
- Wagstaff, B. E., A. E. Constantine, and J. R. C. M. Mason. 1997. Palynological dating of Strzelecki Group sediments associated with Lower Cretaceous labyrinthodont fossils, Victoria, Australia. *Palaeontographica Abteilung A* 247:19–22.
- Wandres, A., and J. Bradshaw. 2005. New Zealand tectonostratigraphy and implications for conglomeratic rocks for the configuration of the SW Pacific margin of Gondwana. Geological Society London Special Publication 2005 246:176–216.
- Weems, R. E., and J. M. Bachman. 2015. The Lower Cretaceous Patuxent Formation ichnofauna of Virginia. *Ichnos* 22:208–219.
- Weishampel, D. B., P. M. Barrett, R. A. Coria, J. Le Loeuff, X. Xing, Z. Xijin, A. Sahni, E. M. P. Goman, and C. R. Noto. 2004. Dinosaur distribution; pp. 517–606 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- Welles, S. P. 1983. *Allosaurus* (Saurischia, Theropoda) not yet in Australia. *Journal of Paleontology* 57:196.
- White, M. A., P. R. Bell, A. G. Cook, S. F. Poropat, and D. A. Elliot. 2015a. The dentary of *Australovenator wintonensis* (Theropoda, Megaraptoridae); implications for megaraptorid dentition. *PeerJ* 3:e1512. doi: 10.7717/peerj.1512.
- White, M. A., A. G. Cook, S. A. Hocknull, T. Sloan, G. H. K. Sinapius, and D. A. Elliot. 2012. New forearm elements discovered of holotype specimen *Australovenator wintonensis* from Winton, Queensland, Australia. *PLoS ONE* 7:e39364. doi: 10.1371/journal.pone.0039364.
- White, M. A., P. R. Bell, A. G. Cook, D. G. Barnes, T. R. Tischler, B. J. Bassam, and D. A. Elliot. 2015b. Forearm range of motion in *Australovenator wintonensis* (Theropoda, Megaraptoridae). *PLoS ONE* 10:e0137709. doi: 10.1371/journal.pone.0137709.
- White, M. A., R. B. J. Benson, T. R. Tischler, S. A. Hocknull, A. G. Cook, D. G. Barnes, S. F. Poropat, S. J. Wooldridge, T. Sloan, G. H. K. Sinapius, and D. A. Elliot. 2013. New *Australovenator* hind limb elements pertaining to the holotype reveal the most complete neovenatorid leg. *PLoS ONE* 8:e68649. doi: 10.1371/journal.pone.0068649.
- White, M. E. 1961. Plant fossils from the Canning Basin, Western Australia. Appendix 6; pp. 291–320 in J. J. Veevers and A. T. Wells (eds.), *The Geology of the Canning Basin, Western Australia*, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 60. Australian Government Publishing Service, Canberra, Australia.
- Whyte, M. A., and M. Romano. 1994. Probable sauropod footprints from the Middle Jurassic of Yorkshire, England. *Gaia* 10:15–26.
- Whyte, M. A., and M. Romano. 2001a. A dinosaur ichnocoenosis from the Middle Jurassic of Yorkshire, UK. *Ichnos* 8:223–234.
- Whyte, M. A., and M. Romano. 2001b. Probable stegosaurian dinosaur tracks from the Saltwick Formation (Middle Jurassic) of Yorkshire, England. *Proceedings of the Geologists' Association* 112:45–54.
- Whyte, M. A., M. Romano, and D. J. Elvidge. 2007. Reconstruction of Middle Jurassic dinosaur-dominated communities from the vertebrate ichnofauna of the Cleveland Basin of Yorkshire, UK. *Ichnos* 14:117–129.
- Willis, P., and A. Thomas. 2005. *Digging up Deep Time: Fossils, Dinosaurs and Megabeasts from Australia's Distant Past*. ABC Books, Sydney, Australia, 294 pp.
- Wilson, J. A. 2005. Integrating ichnofossil and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach. *Paleobiology* 31:400–423.
- Wilson, J. A., and R. Allain. 2015. Osteology of *Rebbachisaurus garasbae* Lavocat, 1954, a diplodocoid (Dinosauria, Sauropoda) from the early Late Cretaceous-aged Kem Kem beds of southeastern Morocco. *Journal of Vertebrate Paleontology*. doi: 10.1080/02724634.2014.1000701.
- Wilson, J. A., and M. T. Carrano. 1999. Titanosaurs and the origin of “wide-gauge” trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* 25:252–267.
- Wilson, J. A., D. M. Mohabey, S. E. Peters, and J. J. Head. 2010. Predation upon hatchling dinosaurs by a new snake from the Late Cretaceous of India. *PLoS Biology* 8:e1000322. doi:10.1371/journal.pbio.1000322.
- Wilson, J. A., P. C. Sereno, S. Srivastava, D. K. Bhatt, A. Khosla, and A. Sahni. 2003. A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. Contributions from the Museum of Paleontology, University of Michigan 31:1–42.

- Woodroffe, S. A., and B. P. Horton. 2005. Holocene sea-level changes in the Indo-Pacific. *Journal of Asian Earth Sciences* 25:29–43.
- Worms, E. 1944. Aboriginal place names in Kimberley, Western Australia. *Oceania* 14:284–310.
- Wright, J. L. 2005. Steps in understanding sauropod biology: the importance of sauropod tracks; pp. 252–284 in K. A. Curry Rogers and J. A. Wilson (eds.), *The Sauropods: Evolution and Paleobiology*. University of California Press, Berkeley, California.
- Xing, L., J. D. Harris, and C. Jia. 2010. Dinosaur tracks from the Lower Cretaceous Mengtuan Formation in Jiangsu, China and morphological diversity of local sauropod tracks. *Acta Palaeontologica Sinica* 49:448–460.
- Xing, L., J. D. Harris, and P. J. Currie. 2011. First record of dinosaur trackway from Tibet, China. *Geological Bulletin of China* 30:173–178.
- Xing, L., P. R. Bell, J. D. Harris, and P. J. Currie. 2012. An unusual, three-dimensionally preserved, large hadrosaurid pes track from 'mid'-Cretaceous Jianguan Formation of Chongqing, China. *Acta Geologica Sinica* 86:204–312.
- Xing, L., F. Wang, S. Pan, and W. Chen. 2007. The discovery of dinosaur footprints from the middle Cretaceous Jiaguan Formation of Qijiang County, Chongqing City. *Acta Geologica Sinica* 81:1591–1602.
- Xing, L., J. D. Harris, S. Toru, F. Masato, and Z. Dong. 2009a. Discovery of dinosaur footprints from the Lower Jurassic Lufeng Formation of Yunnan Province, China and new observations on *Changpeipus*. *Geological Bulletin of China* 28:16–29.
- Xing, L., M. G. Lockley, R. T. McCrea, G. D. Gierliński, L. G. Buckley, and J. Zhang. 2013a. First record of *Deltapodus* tracks from the Early Cretaceous of China. *Cretaceous Research* 42:55–65.
- Xing, L., J. D. Harris, Z. Dong, Y. Lin, W. Chen, S. Guo, and Q. Ji. 2009b. Ornithopod (Dinosauria: Ornithischia) tracks from the Upper Cretaceous Zhutian Formation in the Nanxiong basin, Guangdong, China and general observations on large Chinese ornithopod footprints. *Geological Bulletin of China* 28:829–843.
- Xing, L., G. Peng, M. G. Lockley, Y. Ye, H. Klein, J. Zhang, and W. S. Persons IV. 2015a. Early Cretaceous sauropod and ornithopod trackways from a stream course in Sichuan Basin, southwest China. *New Mexico Museum of Natural History and Science Bulletin* 67:319–325.
- Xing, L., M. G. Lockley, Y. Tang, H. Klein, J. Zhang, W. S. Persons IV, H. Dai, and Y. Ye. 2015b. Theropod and ornithischian footprints from the Middle Jurassic Yanan Formation of Zizhou County, Shaanxi, China. *Ichnos* 22:1–11.
- Xing, L., M. G. Lockley, J. Zhang, H. Klein, D. Li, T. Miyashita, Z. Li, and S. B. Kümmell. 2016b. A new sauropodomorph ichnogenus from the Lower Jurassic of Sichuan, China fills a gap in the track record. *Historical Biology* 28:881–895.
- Xing, L., G. Peng, M. G. Lockley, Y. Ye, H. Klein, R. T. McCrea, J. Zhang, and W. S. Persons IV. 2016a. Saurischian (theropod–sauropod) track assemblages from the Jiaguan Formation in the Sichuan Basin, Southwest China: ichnology and indications to differential track preservation. *Historical Biology*.
- Xing, L., G. Peng, Y. Ye, M. G. Lockley, H. Klein, W. S. Persons IV, J. Zhang, C. Shu, and B. Hao. 2014. Sauropod and small theropod tracks from the Lower Jurassic Ziliujing Formation of Zigong City, Sichuan, China, with an overview of Triassic–Jurassic dinosaur fossils and footprints of the Sichuan Basin. *Ichnos* 21:119–130.
- Xing, L., D. Li, M. G. Lockley, D. Marty, J. Zhang, W. S. Persons IV, H. You, C. Peng, and S. B. Kümmell. 2015c. Dinosaur natural track casts from the Lower Cretaceous Hekou Group in the Lanzhou–Minhe Basin, Gansu, northwest China: ichnology, track formation, and distribution. *Cretaceous Research* 52:194–205.
- Xing, L., M. G. Lockley, M. F. Bonnan, D. Marty, H. Klein, Y. Liu, J. Zhang, H. Kuang, M. E. Burns, and N. Li. 2015d. Late Jurassic–Early Cretaceous trackways of small-sized sauropods from China: new discoveries, ichnotaxonomy and sauropod manus morphology. *Cretaceous Research* 56:470–481.
- Xing, L., M. G. Lockley, D. Marty, H. Klein, L. G. Buckley, R. T. McCrea, J. Zhang, G. D. Gierliński, J. D. Divay, and Q. Wu. 2013b. Diverse dinosaur ichnoassemblages from the Lower Cretaceous Dasheng Group in the Yishu fault zone, Shandong Province, China. *Cretaceous Research* 45:114–134.
- Xing, L., M. G. Lockley, F. Wang, X. Hu, S. Luo, J. Zhang, W. Du, W. S. Persons IV, X. Xie, and X. Wang. 2015e. Stone flowers explained as dinosaur undertracks: unusual ichnites from the Lower Cretaceous Jiaguan Formation, Qijiang District, Chongqing, China. *Geological Bulletin of China* 34:885–890.
- Xing, L., M. G. Lockley, G. Yang, A. Mayor, H. Klein, W. S. Persons IV, Y. Chen, G. Peng, Y. Ye, and J. Ebi. 2015f. Tracking a legend: an Early Cretaceous sauropod trackway from Zhaojue County, Sichuan Province, southwestern China. *Ichnos* 22:22–28.
- Xing, L., J. Zhang, M. G. Lockley, R. T. McCrea, H. Klein, L. Alcalá, L. G. Buckley, M. E. Burns, S. B. Kümmell, and Q. He. 2015g. Hints of the early Jehol Biota: important dinosaur footprint assemblages from the Jurassic–Cretaceous Boundary Tuchengzi Formation in Beijing, China. *PLoS ONE* 10:e0122715. doi: 10.1371/journal.pone.0122715.
- Xing, L., M. G. Lockley, D. Marty, H. Klein, G. Yang, J. Zhang, G. Peng, Y. Ye, W. S. Persons IV, X. Yin, and T. Xu. 2016c. A diverse saurischian (theropod–sauropod) dominated footprint assemblage from the Lower Cretaceous Jiaguan Formation in the Sichuan Basin, southwestern China: a new ornithischian ichnotaxon, pterosaur tracks and an unusual sauropod walking pattern. *Cretaceous Research* 60:176–193.
- Xing, L., D. Marty, K. Wang, M. G. Lockley, S. Chen, X. Xu, Y. Liu, H. Kuang, J. Zhang, H. Ran, and W. S. Persons IV. 2015h. An unusual sauropod turning trackway from the Early Cretaceous of Shandong Province, China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 437:74–84.
- Xing, L., M. G. Lockley, D. Marty, J. Zhang, Y. Wang, H. Klein, R. T. McCrea, L. G. Buckley, M. Belvedere, O. Mateus, G. D. Gierliński, L. Piñuela, W. S. Persons IV, F. Wang, H. Ran, H. Dai, and X. Xie. 2015i. An ornithopod-dominated tracksite from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of Qijiang, south-central China: new discoveries, ichnotaxonomy, preservation and palaeoecology. *PLoS ONE* 10:e0141059. doi: 10.1371/journal.pone.0141059.
- Yadagiri, P., and K. Ayyasami. 1979. A new stegosaurian dinosaur from Upper Cretaceous sediments of South India. *Journal of the Geological Society of India* 20:521–530.
- Yeates, A. N., R. W. A. Crowe, R. R. Towner, L. A. I. Wyborn, and V. L. Passmore. 1984. Regional geology of the on-shore Canning Basin, WA; pp. 23–55 in P. G. Purcell (ed.), *The Canning Basin*, W.A. Geological Society of Australia and Petroleum Exploration Society of Australia, Perth, Australia.
- Young, C.-C. 1960. Fossil footprints in China. *Vertebrata Palasiatica*. *Nature* 4:53–67.
- Zhang, F., Z. Zhou, X. Xu, X. Wang, and C. S. Sullivan. 2008. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature* 455:844–847.
- Zhang, J., D. Li, M. Li, M. G. Lockley, and Z. Bai. 2006. Diverse dinosaur-, pterosaur-, and bird-track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, northwest China. *Cretaceous Research* 27:44–55.
- Zhang, J., L. Xing, G. D. Gierliński, F. Wu, M. Tian, and P. J. Currie. 2012. First record of dinosaur trackways in Beijing, China. *Chinese Science Bulletin* 57:144–152.
- Zhen, S., J. Li, C. Rao, and S. Hu. 1986. Dinosaur footprints of Jinning, Yunnan. *Memoirs of the Beijing Natural History Museum* 33:1–18.
- Zhen, S., J. Li, C. Rao, N. J. Mateer, and M. G. Lockley. 1989. A review of dinosaur footprints in China; pp. 187–197 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.

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APPENDIX 1. Temporal distribution and taxonomic diversity of Australian Cretaceous dinosaurian faunas, arranged primarily by depositional basin and secondarily by stratum. Occurrences based on body fossil specimens are shown in plain font, while those based on tracks are shown in bold font. Taxonomic assignments for various specimens follow the most current literature; where we disagree with a proposed revision, we have deferred to an earlier assignment with which we concur. Track/trackmaker hip height size estimates correspond to categories shown in Table 1 and are based on the mean sizes for all assigned tracks. Equivalent hip height size estimates for body fossil taxa are based on type or referred specimens.

Depositional basin & stratum	Taxonomic assignment	Material and references	Size (see Table 1)
<b>CARNARVON BASIN</b> (Western Australia)			
Miria Formation (Maastrichtian)	Theropoda: Theropoda cf. Coelurosauria	Isolated partial humerus (Long, 1992; Agnolín et al., 2010)	Medium
Birdrong Sandstone (Valanginian–Aptian)	Theropoda: Theropoda indet.	Isolated caudal vertebra (Long and Cruickshank, 1996; Agnolín et al., 2010)	Medium
<b>PERTH BASIN</b> (Western Australia)			
Molecap Greensand (Cenomanian–lower Turonian)	Theropoda: Theropoda indet.	Isolated pedal phalanx (Long, 1995; Agnolín et al., 2010)	Medium
<b>EROMANGA BASIN</b> (Queensland and South Australia)			
Winton Formation (upper Albian–lower Turonian)	Theropoda: <i>Australovenator wintonensis</i>	(Hocknull et al., 2009; Agnolín et al., 2010; White et al., 2012; Novas et al., 2013; White et al., 2013b; White et al., 2015b; White et al., 2015a; Novas et al., 2016)	Large
	Theropoda: Megaraptora indet.	Isolated teeth (Salisbury et al., 2011)	Large
	Sauropoda: <i>Wintonotitan watti</i>	(Coombs and Molnar, 1981; Molnar, 2001a; Molnar and Salisbury, 2005; Hocknull et al., 2009; Agnolín et al., 2010; Poropat et al., 2013b; Poropat et al., 2015a)	Medium
	Sauropoda: <i>Diamantinasaurus matildae</i>	(Hocknull et al., 2009; Agnolín et al., 2010; Poropat et al., 2013a; Poropat et al., 2013b; Poropat et al., 2015b; Poropat et al., 2016)	Medium
	Sauropoda: <i>Savannasaurus elliotorum</i>	(Poropat et al., 2016)	Medium
	Other indeterminate and undescribed titanosauriform specimens	(Coombs and Molnar, 1981; Molnar, 2001a; Molnar and Salisbury, 2005; Salisbury et al., 2006; Molnar, 2010, 2011a; Poropat et al., 2013b)	–
	Ornithopoda: Ornithopoda indet.	Isolated tooth (Hocknull and Cook, 2008)	Small
	<b>Ornithopoda: cf. <i>Iguanodontipus</i> (Previously referred to as ‘<i>Amblydactylus</i> cf. <i>A. gethingi</i>’ and ‘cf. <i>Tyrannosauropus</i>’)</b>	<b>Lark Quarry tracks (Thulborn and Wade, 1984; Romilio and Salisbury, 2011, 2013; Thulborn, 2013; Romilio and Salisbury, 2014; Falkingham, 2016)</b>	<b>Large</b>
	<b>Ornithopoda: <i>Wintonopus latomorum</i></b>	<b>Lark Quarry tracks (Thulborn and Wade, 1979, 1984; Romilio and Salisbury, 2013; Romilio et al., 2013)</b>	<b>Small</b>
	Thyreophora: Ankylosauria indet.	Isolated teeth (Leahey and Salisbury, 2013)	Small
Mackunda Formation (upper Albian)	Ornithopoda: <i>Muttaborrasaurus langdoni</i>	(Bartholomai and Molnar, 1981; Molnar, 1995, 1996b; Cannon, 2006; Agnolín et al., 2010)	Very Large
Allaru Mudstone (upper Albian)	Sauropoda: <i>Austrosaurus mckillopi</i>	(Longman, 1933; Coombs and Molnar, 1981; Molnar, 2001a; Molnar and Salisbury, 2005; Agnolín et al., 2010; Molnar, 2011a; Poropat et al., 2013b; Poropat, 2016)	Medium
	Ornithopoda: <i>Muttaborrasaurus</i> sp.	(Molnar, 1996b; Agnolín et al., 2010)	Very large
	Thyreophora: <i>Kunbarrasaurus ierversi</i> .	(Molnar, 1996a; Molnar and Clifford, 2000; Molnar, 2001b; Molnar and Clifford, 2001; Leahey et al., 2008; Agnolín et al., 2010; Leahey et al., 2010; Leahey et al., 2015; Arbour and Currie, 2016)	Medium

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## APPENDIX 1. (Continued)

Depositional basin & stratum	Taxonomic assignment	Material and references	Size (see Table 1)
Toolebuc Formation (upper Albian)	Sauropoda: Titanosauria indet.	Distal humerus (Molnar and Salisbury, 2005)	Medium
	Sauropoda: Titanosauriformes indet.	Cervical vertebra ('Hughenden brachiosaur') (Molnar, 1991, 2001a; Molnar and Salisbury, 2005)	Medium
Bulldog Shale (Aptian)	Theropoda: <i>Kakuru kujani</i>	Cast of right tibia (Molnar and Pledge, 1980; Rauhut, 2005; Agnolín et al., 2010; Barrett et al., 2010a)	Small
<b>SURAT BASIN (NSW and Queensland)</b>			
Griman Creek Formation (lower–middle Albian)	Theropoda: Megaraptora indet.	Fragmentary postcranium (Bell et al., 2016)	Large
	Theropoda: Megaraptora indet. (' <i>Rapator ornitholestoides</i> ')	Metacarpal I (Huene, 1932; Molnar, 1980b, 1991; Agnolín et al., 2010; Novas et al., 2013; White et al., 2013a)	Medium
	Theropoda: Megaraptora indet.	Isolated teeth (Smith, 1999; Salisbury et al., 2011)	Medium
	Theropoda: Theropoda indet. (' <i>Walgettosuchus woodwardi</i> ')	Caudal vertebra (Woodward, 1910; Huene, 1932; Molnar, 1990, 1991; Smith, 1999; Agnolín et al., 2010)	Small
	Sauropoda: Neosauropoda indet.	Partial ischium (Molnar, 2011b)	Medium
	Other indeterminate isolated sauropod elements	Fragmentary vertebrae and isolated teeth (Smith, 1999; Molnar and Salisbury, 2005; Molnar, 2011b)	—
	Ornithopoda: Ornithopoda indet. (' <i>Fulgurotherium australe</i> ')	Partial femur (holotype of ' <i>F. australe</i> ') + other isolated teeth and postcranial elements (Molnar, 1984; Molnar and Galton, 1986; Long, 1998; Smith, 1999; Cannon, 2006; Agnolín et al., 2010)	Small
	Ornithopoda: Ornithopoda indet.	Isolated scapula and teeth (Long, 1998; Smith, 1999)	Large
	<b>Ornithopoda: Ornithopoda indet.</b>	<b>Les Price track (Molnar, 1991)</b>	<b>Large</b>
Bungil Formation: Minmi Member (lower Aptian)	Thyreophora: <i>Minmi paravertebra</i>	(Molnar, 1980a, 1981; Molnar and Frey, 1987; Agnolín et al., 2010; Arbour and Currie, 2016)	Small
<b>OTWAY BASIN (Victoria)</b>			
Eumeralla Formation (upper Aptian–lower Albian)	Theropoda: Megaraptora indet.	Paired pubic bones ('Australian tyrannosauroid'), ulna and teeth (Rich and Vickers-Rich, 2003b; Smith et al., 2008; Agnolín et al., 2010; Benson et al., 2010a; Benson et al., 2010b; Herne et al., 2010; Salisbury et al., 2011; Benson et al., 2012; Novas et al., 2013; Herne et al., 2016; Novas et al., 2016)	Medium
	Theropoda: Maniraptora indet.	Thoracic vertebra – 'Australian oviraptorosaurian' (Currie et al., 1996; Agnolín et al., 2010; Benson et al., 2012)	Medium
	Theropoda: Coelurosauria indet. (' <i>Timimus hermani</i> ')	Femur (Rich and Vickers-Rich, 1994; Agnolín et al., 2010; Benson et al., 2012; Novas et al., 2013)	Medium
	Theropoda: Averostra indet.	Astragalus – 'Australian ceratosaurian' (Fitzgerald et al., 2012; Novas et al., 2013)	Medium
	Theropoda: Orionides indet.	Cervical vertebra – 'Australian spinosaurid' (Barrett et al., 2011; Benson et al., 2012; Novas et al., 2013)	Medium
	Other indeterminate isolated theropod elements	Surangular and isolated postcranial elements (Currie et al., 1996; Agnolín et al., 2010; Benson et al., 2012; Novas et al., 2013)	—
		<b>Theropoda: Theropoda indet.</b>	<b>Milanesia Beach tracks (Martin et al., 2012)</b>

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## APPENDIX 1. (Continued)

Depositional basin & stratum	Taxonomic assignment	Material and references	Size (see Table 1)
	Ornithopoda: <i>Leaellynasaura amicagraphica</i>	Partial cranium (Rich and Vickers-Rich, 1988, 1989, 1999; Herne, 2009; Herne and Salisbury, 2009; Agnolín et al., 2010; Rich et al., 2010; Herne et al., 2016)	Small
	Ornithopoda: <i>Atlascopcosaurus loadsi</i>	Partial maxilla (Rich et al., 1989; Rich and Vickers-Rich, 1999; Agnolín et al., 2010)	Small
	Other indeterminate isolated ornithopod elements	(Rich and Vickers-Rich, 1989, 1999, 2003b; Agnolín et al., 2010)	—
	<b>Ornithopoda: Ornithopoda indet.</b>	<b>Skenes Creek track (Flannery and Rich, 1981; Kool, 2006, 2007; Martin, 2016)</b>	<b>Small</b>
	<b>Ornithopoda: Ornithopoda indet.</b>	<b>Knowledge Creek track (Flannery and Rich, 1981; Molnar, 1991; Rich and Vickers-Rich, 2000; Scanlon, 2006; Martin et al., 2007; Martin et al., 2012; Martin, 2016)</b>	<b>Small</b>
	Thyreophora: Ankylosauria indet	Teeth and fragmentary postcranial elements (Barrett et al., 2010b)	Small
<b>GIPPSLAND BASIN (Victoria)</b>			
Wonthaggi Formation (upper Aptian)	Theropoda: ?Megaraptora indet.	Astragalus – ‘Aussie <i>Allosaurus</i> ’ (Molnar et al., 1981; Welles, 1983; Molnar et al., 1985; Rich et al., 1992; Chure, 1998; Hocknull et al., 2009; Agnolín et al., 2010; Benson et al., 2012; Fitzgerald et al., 2012; Novas et al., 2013)	Medium
	Theropoda: Megaraptora indet.	Isolated teeth (Salisbury et al., 2011; Benson et al., 2012)	Medium
	Other indeterminate isolated theropod elements	(Woodward, 1906; Agnolín et al., 2010; Benson et al., 2012)	—
	<b>Theropoda: Theropoda indet.</b>	<b>Flat Rocks tracks (Kool, 2006, 2007; Martin et al., 2007)</b>	<b>Large</b>
	Genasauria indet. ( <i>‘Serendipaceratops arthurclarkae’</i> )	Ulna (Rich and Vickers-Rich, 1994, 2003b; Agnolín et al., 2010; Rich et al., 2014)	Small
	Ornithopoda: <i>Qantassaurus intrepidus</i>	Partial dentary (Rich and Vickers-Rich, 1999; Agnolín et al., 2010)	Small
	Other indeterminate isolated ornithopod elements	(Rich et al., 1989; Rich and Vickers-Rich, 1999; Agnolín et al., 2010)	—
	Thyreophora: Ankylosauria indet.	(Barrett et al., 2010b)	Small
<b>CANNING BASIN (Western Australia)</b>			
Broome Sandstone (Valanginian–Barremian)	<b>Theropoda: <i>Megalosauropus broomensis</i></b>	<b>(Glauert, 1952; Colbert and Merrillees, 1967; Thulborn, 2009)</b>	<b>Large</b>
	<b>Theropoda: <i>Yangtzepeus clarkei</i> ichnogen. et ichnosp. nov.</b>		<b>Large</b>
	<b>Theropoda: Broome theropod morphotype A</b>		<b>Small</b>
	<b>Theropoda: Broome theropod morphotype B</b>		<b>Large</b>
	<b>Theropoda: Broome theropod morphotype C</b>		<b>Large</b>
	<b>Sauropoda: <i>Oobardjidama foulkesi</i> ichnogen. et ichnosp. nov.</b>		<b>Medium</b>
	<b>Sauropoda: Broome sauropod morphotype A</b>		<b>Very large</b>
	<b>Sauropoda: Broome sauropod morphotype B</b>		<b>Large</b>

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Depositional basin & stratum	Taxonomic assignment	Material and references	Size (see Table 1)
	Sauropoda: Broome sauropod morphotype C		Large
	Sauropoda: Broome sauropod morphotype D		Large
	Sauropoda: Broome sauropod morphotype E		Medium
	Ornithopoda: <i>Wintonopus latomorum</i>	Tracks previously referred to 'cf. <i>Wintonopus</i> ' (Thulborn, 2012)	Small
	Ornithopoda: <i>Wintonopus middletonae</i> ichnosp. nov.		Medium
	Ornithopoda: <i>Walmadanyichnus hunteri</i> ichnogen. et ichnosp. nov.		Very large
	Ornithopoda: <i>Amblydactylus</i> cf. <i>A. kortmeyeri</i>		Large
	Thyreophora: <i>Garbina roeorum</i> ichnogen. et ichnosp. nov.		Large
	Thyreophora: cf. <i>Garbina roeorum</i>		Very large
	Thyreophora: <i>Luluichnus mueckeii</i> ichnogen. et ichnosp. nov.	Previously referred to as 'stegosaur pedal track' (Long, 1990, 1998)	Medium
	Thyreophora: cf. <i>Luluichnus mueckeii</i>	Previously referred to as 'stegosaur hind foot track' (Rich and Vickers-Rich, 2003a)	Medium
	Thyreophora: Broome thyreophoran morphotype A		Very large
	Thyreophora: Broome thyreophoran morphotype B	Previously referred to as 'stegosaur manual track' (Long, 1990, 1998)	Medium

## LITERATURE CITED: APPENDIX 1

- Agnolín, F. L., M. D. Ezcurra, D. F. Pais, and S. W. Salisbury. 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Journal of Systematic Palaeontology* 8:257–300.
- Arbour, V. M., and P. J. Currie. 2016. Systematics, phylogeny and palaeobiogeography of the ankylosaurid dinosaurs. *Journal of Systematic Palaeontology* 14:385–444.
- Barrett, P. M., B. P. Kear, and R. B. J. Benson. 2010a. Opalized archosaur remains from the Bulldog Shale (Aptian: Lower Cretaceous) of South Australia. *Alcheringa* 34:292–301.
- Barrett, P. M., R. B. J. Benson, T. H. Rich, and P. Vickers-Rich. 2011. First spinosaurid dinosaur from Australia and the cosmopolitanism of Cretaceous dinosaur faunas. *Biology Letters* 7:933–936.
- Barrett, P. M., T. H. Rich, P. Vickers-Rich, T. A. Tumanova, M. Inglis, D. Pickering, L. Kool, and B. P. Kear. 2010b. Ankylosaurian dinosaur remains from the Lower Cretaceous of southeastern Australia. *Alcheringa* 34:205–217.
- Bartholomai, A., and R. E. Molnar. 1981. *Muttaburrasaurus*, a new iguanodontid (Ornithischia: Ornithopoda) dinosaur from the Lower Cretaceous of Queensland. *Memoirs of the Queensland Museum* 20:319–349.
- Bell, P. R., A. Cau, F. Fanti, and E. T. Smith. 2016. A large-clawed theropod (Dinosauria: Tetanurae) from the Lower Cretaceous of Australia and the Gondwanan origin of megaraptorid theropods. *Gondwana Research*.
- Benson, R. B. J., P. M. Barrett, T. H. Rich, and P. Vickers-Rich. 2010a. A southern tyrant reptile. *Science* 327:1613.
- Benson, R. B. J., T. H. Rich, P. Vickers-Rich, and M. Hall. 2012. Theropod fauna from southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. *PLoS ONE* 7:e37122. doi: 10.1371/journal.pone.0037122.
- Benson, R. B. J., P. M. Barrett, T. H. Rich, P. Vickers-Rich, D. Pickering, and T. Holland. 2010b. Response to comment on “A southern tyrant reptile”. *Science* 329:1013–d.
- Cannon, L. 2006. The Muttaburra lizard. *Australian Age of Dinosaurs* 4:16–31.
- Chure, D. J. 1998. A reassessment of the Australian *Allosaurus* and its implications for the Australian refugium concept; pp. 34A, Society of Vertebrate Paleontology, Sixty-sixth annual meeting, Abstracts of papers.
- Colbert, E. H., and D. Merrilees. 1967. Cretaceous dinosaur footprints from Western Australia. *Journal of Royal Society of Western Australia* 50:21–25.
- Coombs, W. P., Jr., and R. E. Molnar. 1981. Sauropoda (Reptilia, Saurischia) from the Cretaceous of Queensland. *Memoirs of the Queensland Museum* 20:351–373.
- Currie, P. J., P. Vickers-Rich, and T. H. Rich. 1996. Possible oviraptorosaur (Theropoda, Dinosauria) specimens from the Early Cretaceous Otway Group of Dinosaur Cove, Australia. *Alcheringa* 20:73–79.
- Falkingham, P. L. 2016. Applying objective methods to subjective track outlines; pp. 72–81 in P. L. Falkingham, D. Marty, and A. Richter (eds.), *Dinosaur tracks: the next steps*. Indiana University Press, Bloomington & Indianapolis.
- Fitzgerald, E. M. G., M. T. Carrano, T. Holland, B. E. Wagstaff, D. Pickering, T. H. Rich, and P. Vickers-Rich. 2012. First ceratopsian dinosaur from Australia. *Naturwissenschaften* 99:397–405.
- Flannery, T. F., and T. H. Rich. 1981. Dinosaur digging in Victoria. *Australian Natural History* 20:195–198.
- Glauert, L. 1952. Dinosaur footprints near Broome. *Western Australian Naturalist* 3:82–83.
- Herne, M. C., A. M. Tait, and S. W. Salisbury. 2016. Sedimentological reappraisal of the *Leaellynasaura amicagraphica* (Dinosauria, Ornithopoda) holotype locality in the Lower Cretaceous of Victoria, Australia, with taphonomic implications for the taxon. *New Mexico Museum of Natural History and Science Bulletin* 71:121–148.
- Herne, M. C. 2009. Postcranial osteology of *Leaellynasaura amicagraphica* (Dinosauria: Ornithischia) from the Early Cretaceous of southeastern Australia; pp. 113A, Society of Vertebrate Paleontology, Sixty-ninth annual meeting, and the Fifty-seventh Symposium of Vertebrate Palaeontology and Comparative Anatomy (SVPCA), Programs and Abstracts.
- Herne, M. C., and S. W. Salisbury. 2009. The status of *Leaellynasaura amicagraphica* (Dinosauria: Ornithischia) from the Early Cretaceous of south-eastern Australia; p. 35 in K. J. Travouillon, T. H. Worthy, S. Hand, and P. Creaser (eds.), *Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics 2009*. Geological Society of Australia, Sydney, Australia.
- Herne, M. C., J. P. Nair, and S. W. Salisbury. 2010. Comment on “A southern tyrant reptile”. *Science* 329:1013–c.
- Hocknull, S. A., and A. G. Cook. 2008. Hypsilophodontid (Dinosauria: Ornithischia) from latest Albian, Winton Formation, central Queensland. *Memoirs of the Queensland Museum* 52:212.
- Hocknull, S. A., M. A. White, T. R. Tischler, A. G. Cook, N. D. Calleja, T. Sloan, and D. A. Elliott. 2009. New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS ONE* 4:e6190. doi: 10.1371/journal.pone.0006190.
- Huene, F. F. v. 1932. Die fossile reptil-ordnung Saurischia, ihre entwicklung und geschichte. *Monographien zur Geologie und Palaeontologie (Serie I)* 4:361 pp.
- Kool, L. 2006. Dinosaur Dreaming 2006 Field Report. Monash University, Clayton, Victoria, Australia.
- Kool, L. 2007. Dinosaur Dreaming 2007 Field Report. Monash University, Clayton, Victoria, Australia.
- Latham v The Queen. 2000. Appeal Judgement, Case No CCA:41/2000. Supreme Court of Western Australia WASCA 338:1–15.
- Leahey, L., R. E. Molnar, and S. W. Salisbury. 2008. The cranial osteology of *Minmi* sp., a basal ankylosauromorph (Ornithischia: Dinosauria) from the Early Cretaceous (Albian) Allaru Formation of Richmond, north-western Queensland, Australia. *Journal of Vertebrate Paleontology* 28(3, Supplement):104A.
- Leahey, L., R. E. Molnar, and S. W. Salisbury. 2010. Postcranial osteology of *Minmi* sp., a basal ankylosauromorph (Dinosauria: Ornithischia) from the Early Cretaceous (Albian) Allaru Mudstone of Queensland, Australia. *Journal of Vertebrate Paleontology* 30(3, Supplement):121A.
- Leahey, L., R. E. Molnar, K. Carpenter, L. M. Witmer, and S. W. Salisbury. 2015. Cranial osteology of the ankylosaurian dinosaur formerly known as *Minmi* sp. (Ornithischia: Thyreophora) from the Lower Cretaceous Allaru Mudstone of Richmond, Queensland, Australia. *PeerJ* 3:e1475. doi: 10.7717/peerj.1475.
- Leahey, L. G., and S. W. Salisbury. 2013. First evidence of ankylosaurian dinosaurs (Ornithischia: Thyreophora) from the ‘mid’-Cretaceous (late Albian–Cenomanian) Winton Formation of Queensland, Australia. *Alcheringa* 37:249–257.
- Long, J. A. 1990. *Dinosaurs of Australia and other animals of the Mesozoic Era*. Reed Books Pty Ltd, Balgowlah, 87 pp.
- Long, J. A. 1992. First dinosaur bones from Western Australia. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 9:21–28.
- Long, J. A. 1995. A theropod dinosaur bone from the Late Cretaceous Molecap Greensand, Western Australia. *Records of the Western Australian Museum* 17:143–146.
- Long, J. A. 1998. *Dinosaurs of Australia and New Zealand and Other Animals of the Mesozoic Era*. UNSW Press, Sydney, Australia, 188 pp.
- Long, J. A., and A. R. I. Cruickshank. 1996. First record of an Early Cretaceous theropod dinosaur bone from Western Australia. *Records of the Western Australian Museum* 18:219–222.
- Longman, H. A. 1933. A new dinosaur from the Queensland Cretaceous. *Memoirs of the Queensland Museum* 10:131–144.
- Martin, A., P. Vickers-Rich, T. H. Rich, and L. Kool. 2007. Polar dinosaur tracks in the cretaceous of Australia: though many were cold, few were frozen; pp. 112A in C. Bell, T. B. Rowe, A. B. Busbey, B. J. Chinnery-Allgeier, E. Ekdale, C. George, C. Jass, T. M. Lehman, E. Lund, L. K. Murray, and P. M. Sander (eds.), *Society of Vertebrate Paleontology, Sixty-seventh annual meeting, Program and Abstracts*.
- Martin, A. J. 2016. A close look at Victoria’s first known dinosaur tracks. *Memoirs of Museum Victoria* 74:63–71.
- Martin, A. J., T. H. Rich, M. Hall, P. Vickers-Rich, and G. M. Vazquez-Prokopec. 2012. A polar dinosaur-track assemblage from the Eumeralla Formation (Albian), Victoria, Australia. *Alcheringa* 36:171–188.
- Molnar, R. E. 1980a. An ankylosaur (Ornithischia: Reptilia) from the Lower Cretaceous of southern Queensland. *Memoirs of the Queensland Museum* 20:77–87.

- Molnar, R. E. 1980b. Australian late Mesozoic terrestrial tetrapods: some implications. *Memoires de la Societe Geologique de France*, (Nouvelle Serie) 139:131–143.
- Molnar, R. E. 1981. Reflections on the Mesozoic of Australia; pp. 47–60 in G. Olshevsky (ed.), *Mesozoic Vertebrate Life*. No. 1: New Mesozoic Faunas. George Olshevsky (private publishing), San Diego, USA.
- Molnar, R. E. 1984. Ornithischian dinosaurs in Australia; pp. 151–157 in W.-E. Reif and F. Westphal (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems*, Short Papers. Attempto Verlag, Tübingen, Germany.
- Molnar, R. E. 1990. Problematic Theropoda: “carnosaurs”; pp. 306–317 in D. B. Weishampel, P. Dodson, and H. Osmolska (eds.), *The Dinosauria*. University of California Press, Berkeley, California.
- Molnar, R. E. 1991. Fossil reptiles in Australia; pp. 605–702 in P. Vickers-Rich, J. M. Monaghan, R. F. Baird, T. H. Rich, E. M. Thompson, and C. Williams (eds.), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio, and Monash University Publications Committee, Melbourne, Australia.
- Molnar, R. E. 1995. Possible convergence in the jaw mechanisms of ceratopsians and *Muttaborrasaurus*; pp. 115–117 in A. Sun and Y. Wang (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, Short Papers. China Ocean Press, Beijing.
- Molnar, R. E. 1996a. Preliminary report on a new ankylosaur from the Early Cretaceous, Australia. *Memoirs of the Queensland Museum* 39:653–668.
- Molnar, R. E. 1996b. Observations on the Australian ornithopod dinosaur *Muttaborrasaurus*. *Memoirs of the Queensland Museum* 39:639–652.
- Molnar, R. E. 2001a. A reassessment of the phylogenetic position of Cretaceous sauropod dinosaurs from Queensland, Australia; pp. 139–144 in H. A. Leanza (ed.), *VII International Symposium on Mesozoic Terrestrial Ecosystems*. Asociacion Paleontologica Argentina, Buenos Aires, Argentina.
- Molnar, R. E. 2001b. Armour of the small ankylosaur *Minmi*; pp. 341–362 in K. Carpenter (ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Molnar, R. E. 2010. Taphonomic observations on eastern Australian Cretaceous sauropods. *Alcheringa* 34:421–429.
- Molnar, R. E. 2011a. New morphological information about Cretaceous sauropod dinosaurs from the Eromanga Basin, Queensland, Australia. *Alcheringa* 35:329–339.
- Molnar, R. E. 2011b. Sauropod (Saurischia: Dinosauria) material from the Early Cretaceous Griman Creek Formation of the Surat Basin, Queensland, Australia. *Alcheringa* 35:303–307.
- Molnar, R. E., and H. T. Clifford. 2000. Gut contents of a small ankylosaur. *Journal of Vertebrate Paleontology* 20:194–196.
- Molnar, R. E., and H. T. Clifford. 2001. An ankylosaurian cololite from the Lower Cretaceous of Queensland, Australia; pp. 399–412 in K. Carpenter (ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Molnar, R. E., and E. Frey. 1987. The paravertebral elements of the Australian Ankylosaur *Minmi* (Reptilia: Ornithischia, Cretaceous). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 175:19–37.
- Molnar, R. E., and P. M. Galton. 1986. Hypsilophodontid dinosaurs from Lightning Ridge, New South Wales, Australia. *Geobios* 19:231–243.
- Molnar, R. E., and N. S. Pledge. 1980. A new theropod dinosaur from South Australia. *Alcheringa* 4:281–287.
- Molnar, R. E., and S. W. Salisbury. 2005. Observations on Cretaceous sauropods from Australia; pp. 454–465 in V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Molnar, R. E., T. F. Flannery, and T. H. Rich. 1981. An allosaurid theropod dinosaur from the Early Cretaceous of Victoria, Australia. *Alcheringa* 5:141–146.
- Molnar, R. E., T. F. Flannery, and T. H. Rich. 1985. Aussie *Allosaurus* after all. *Journal of Paleontology* 59:1511–1513.
- Novas, F. E., A. M. Aranciaga Rolando, and F. E. Agnolín. 2016. Phylogenetic relationships of the Cretaceous Gondwanan theropods *Megaraptor* and *Australovenator*: the evidence afforded by their manual anatomy. *Memoirs of Museum Victoria* 74:49–61.
- Novas, F. E., F. L. Agnolín, M. D. Ezcurra, J. D. Porfiri, and J. I. Canale. 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. *Cretaceous Research* 45:174–215.
- Poropat, S. F. 2016. Eight decades of *Austrosaurus*. The discovery and rediscovery of Queensland’s first Cretaceous dinosaur. *Australian Age of Dinosaurs* 13:24–39.
- Poropat, S. F., S. A. Hocknull, B. P. Kear, and D. A. Elliot. 2013a. Paleobiogeographic implications of Australia’s Cretaceous sauropods. *Journal of Vertebrate Paleontology* 33(Programs and Abstracts): 193.
- Poropat, S. F., P. D. Mannion, P. Upchurch, S. A. Hocknull, B. P. Kear, and D. A. Elliot. 2015a. Reassessment of the non-titanosaurian somphospondylan *Wintonotitan watti* (Dinosauria: Sauropod: Titanosauriformes) from the mid-Cretaceous Winton Formation, Queensland, Australia. *Papers in Palaeontology* 1:59–106.
- Poropat, S. F., P. M. Upchurch, P. D. Mannion, S. A. Hocknull, J. P. Nair, B. P. Kear, and D. A. Elliot. 2013b. Tall shoulders, wide hips and strange front feet: a reassessment of Queensland’s Cretaceous sauropod fauna; p. 69 in G. Prideaux (ed.), *CAVEPS Flinders University, Adelaide 2013, 14th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics*, xx, 30th September–4th October 2013. Flinders University, Adelaide, Australia.
- Poropat, S. F., P. D. Mannion, P. Upchurch, S. A. Hocknull, B. P. Kear, M. Kundrát, T. R. Tischler, T. Sloan, G. H. K. Sinapius, J. A. Elliott, and D. A. Elliot. 2016. New Australian sauropods shed light on Cretaceous dinosaur palaeobiogeography. *Scientific Reports* 6: 34467. doi:10.1038/srep34467
- Poropat, S. F., P. M. Upchurch, P. D. Mannion, S. A. Hocknull, B. P. Kear, T. Sloan, G. H. K. Sinapius, and D. A. Elliot. 2015b. Revision of the sauropod dinosaur *Diamantinasaurus matildae* Hocknull et al. 2009 from the mid-Cretaceous of Australia: implications for Gondwanan titanosauriform dispersal. *Gondwana Research* 27:995–1033.
- Rauhut, O. W. M. 2005. Post-cranial remains of “coelurosaurs” (Dinosauria, Theropoda) from the Late Jurassic of Tanzania. *Geological Magazine* 142:97–107.
- Rich, T., B. P. Kear, R. Sinclair, B. Chinnery, K. Carpenter, M. McHugh, and P. Vickers-Rich. 2014. *Serendipaceratops arthurclarkae* Rich & Vickers-Rich, 2003 is an Australian Early Cretaceous ceratopsian. *Alcheringa* 38:456–479.
- Rich, T. H., and P. Vickers-Rich. 1988. A juvenile dinosaur brain from Australia. *National Geographic Research* 4:148.
- Rich, T. H., and P. Vickers-Rich. 1989. Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia. *National Geographic Research* 5:15–53.
- Rich, T. H., and P. Vickers-Rich. 1994. Neoceratopsians and ornithomimosaurs: dinosaurs of Gondwana origin? *National Geographic Research and Exploration* 10:129–131.
- Rich, T. H., and P. Vickers-Rich. 1999. The Hypsilophodontidae from southeastern Australia. *National Science Museum Monographs* 15:167–180.
- Rich, T. H., and P. Vickers-Rich. 2000. *Dinosaurs of Darkness*. Indiana University Press, Bloomington, Indiana, 222 pp.
- Rich, T. H., and P. Vickers-Rich. 2003. *A century of Australian dinosaurs*. Queen Victoria Museum and Art Gallery, Launceston, and Monash Science Centre, Monash University, 125 pp.
- Rich, T. H., and P. Vickers-Rich. 2003. Protoceratopsian? ulnae from Australia. *Records of the Queen Victoria Museum, Launceston* 113:1–12.
- Rich, T. H., P. M. Galton, and P. Vickers-Rich. 2010. The holotype individual of the ornithopod dinosaur *Leaellynasaura amicagraphica* Rich & Rich, 1989 (late Early Cretaceous, Victoria, Australia). *Alcheringa* 34:385–396.
- Rich, T. H., P. Vickers-Rich, B. E. Wagstaff, J. R. C. M. Mason, C. B. Douthitt, and R. T. Gregory. 1989. Early Cretaceous biota from the northern side of the Australo-Antarctic rift valley. *Geological Society, London, Special Publications* 47:121–130.
- Rich, T. H., P. Vickers-Rich, B. E. Wagstaff, J. R. C. M. Mason, T. F. Flannery, M. Archer, R. E. Molnar, and J. A. Long. 1992. Two possible chronological anomalies in the Early Cretaceous tetrapod assemblages of southeastern Australia; pp. 165–176 in N. J. Mateer and P. Chen (eds.), *Aspects of Nonmarine Cretaceous Geology*. China Ocean Press, Beijing.
- Romilio, A., and S. W. Salisbury. 2011. A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western

- Queensland, Australia: a case for mistaken identity. *Cretaceous Research* 32:135–142.
- Romilio, A., and S. W. Salisbury. 2013. Three-dimensional analysis of the largest tracks from the Lark Quarry dinosaur tracksite, central-western Queensland; pp. 74–75 in G. Prideaux (ed.), *CAVEPS Flinders University, Adelaide 2013*, 14th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, xx, 30th September–4th October 2013. Flinders University, Adelaide, Australia.
- Romilio, A., and S. W. Salisbury. 2014. Large dinosaurian tracks from the Upper Cretaceous (Cenomanian–Turonian) portion of the Winton Formation, Lark Quarry, central-western Queensland, Australia: 3D photogrammetric analysis renders the ‘stampede trigger’ scenario unlikely. *Cretaceous Research* 51:186–207.
- Romilio, A., R. T. Tucker, and S. W. Salisbury. 2013. Re-evaluation of the Lark Quarry dinosaur tracksite (late Albian–Cenomanian Winton Formation, central-western Queensland, Australia): no longer a stampede? *Journal of Vertebrate Paleontology* 33:102–120.
- Salisbury, S. W., M. C. Lamanna, and R. E. Molnar. 2006. A new titanosauriform sauropod from the mid-Cretaceous (Albian–Cenomanian) Winton Formation of central-western Queensland, Australia. *Journal of Vertebrate Paleontology* 26(3, Supplement):118A.
- Salisbury, S. W., T. H. Rich, P. Vickers-Rich, and P. J. Currie. 2011. Australian Cretaceous non-avian theropod dinosaur teeth; p. 73 in K. Trinajstić, M. Bunce, N. Warburton, C. Hadley, A. Baynes, and M. Siversson (eds.), *CAVEPS Perth 2011*, 13th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, Perth, April 27th–30th. Geological Survey of Western Australia, xx, Australia.
- Scanlon, J. D. 2006. Dinosaurs and other Mesozoic reptiles of Australasia; pp. 265–290 in J. R. Merrick, M. Archer, G. M. Hickey, and M. S. Y. Lee (eds.), *Evolution and Biogeography of Australian Vertebrates*. Australian Scientific Publishing, Sydney, Australia.
- Smith, E. 1999. *Black Opal Fossils of Lightning Ridge*. Kangaroo Press (Simon and Schuster), Sydney, Australia, 112 pp.
- Smith, N. D., P. J. Makovicky, F. L. Agnolín, M. D. Ezcurra, D. F. Pais, and S. W. Salisbury. 2008. A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the mid-Cretaceous. *Proceedings of the Royal Society of London, B* 275:2085–2093.
- Thulborn, R. A. 2013. Lark Quarry revisited: a critique of methods used to identify a large dinosaurian track-maker in the Winton Formation (Albian–Cenomanian), western Queensland, Australia. *Alcheringa* 37:312–330.
- Thulborn, R. A., and M. J. Wade. 1979. Dinosaur stampede in the Cretaceous of Queensland. *Lethaia* 12:275–279.
- Thulborn, R. A., and M. J. Wade. 1984. Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. *Memoirs of the Queensland Museum* 21:413–517.
- Thulborn, R. A., and M. J. Wade. 1984. Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. *Memoirs of the Queensland Museum* 21:413–517.
- Thulborn, T. 2009. *Megalosauropus broomensis* and the many misconceptions of megalosaur tracks; pp. 89–90 in Á. D. Buscalioni and M. A. Fregenal-Martinez (eds.), *Abstracts Tenth International Symposium on Mesozoic Terrestrial Ecosystems and Biota*, Teruel, 17–19 September, 2009. Universidad Autónoma de Madrid, Madrid, Spain.
- Thulborn, T. 2012. Impact of sauropod dinosaurs on lagoonal substrates in the Broome Sandstone (Lower Cretaceous), Western Australia. *PLoS ONE* 7:e36208. doi: 10.1371/journal.pone.0036208.
- Welles, S. P. 1983. *Allosaurus* (Saurischia, Theropoda) not yet in Australia. *Journal of Paleontology* 57:196.
- White, M. A., P. R. Bell, A. G. Cook, S. F. Poropat, and D. A. Elliot. 2015a. The dentary of *Australovenator wintonensis* (Theropoda, Megaraptoridae); implications for megaraptorid dentition. *PeerJ* 3:e1512. doi: 10.7717/peerj.1512.
- White, M. A., P. L. Falkingham, A. G. Cook, S. A. Hocknull, and D. A. Elliot. 2013a. Morphological comparisons of metacarpal I for *Australovenator wintonensis* and *Raptor ornitholestoides*: implications for their taxonomic relationships. *Alcheringa* 37:435–441.
- White, M. A., A. G. Cook, S. A. Hocknull, T. Sloan, G. H. K. Sinapius, and D. A. Elliot. 2012. New forearm elements discovered of holotype specimen *Australovenator wintonensis* from Winton, Queensland, Australia. *PLoS ONE* 7:e39364. doi: 10.1371/journal.pone.0039364.
- White, M. A., P. R. Bell, A. G. Cook, D. G. Barnes, T. R. Tischler, B. J. Bassam, and D. A. Elliot. 2015b. Forearm range of motion in *Australovenator wintonensis* (Theropoda, Megaraptoridae). *PLoS ONE* 10:e0137709. doi: 10.1371/journal.pone.0137709.
- White, M. A., R. B. J. Benson, T. R. Tischler, S. A. Hocknull, A. G. Cook, D. G. Barnes, S. F. Poropat, S. J. Wooldridge, T. Sloan, G. H. K. Sinapius, and D. A. Elliot. 2013b. New *Australovenator* hind limb elements pertaining to the holotype reveal the most complete neovenatorid leg. *PLoS ONE* 8:e68649. doi: 10.1371/journal.pone.0068649.
- Woodward, A. S. 1906. On a tooth of *Ceratodus* and a dinosaurian claw from the Lower Jurassic of Victoria, Australia. *Annals and Magazine of Natural History (Series 7)* 18:1–3.
- Woodward, A. S. 1910. On remains of a megalosaurian dinosaur from New South Wales. Report of the British Association for the Advancement of Science 79:482–483.

## APPENDIX 2: REMOVAL AND THEFT OF DINOSAURIAN TRACKS FROM THE BROOME SANDSTONE

During the 1990s, there was a series of incidents involving the removal and theft of dinosaurian tracks on the Dampier Peninsula. These events greatly affected and offended the Maja (Law Bosses) for this country and the Song Cycle, and caused immense damage to the working relationship between paleontologists, local dinosaur tracking enthusiasts, and members of the indigenous community. As a consequence, access to some tracksites became and continues to be very sensitive, and in the eyes of Goolarabooloo and many people in the Broome community, the professional reputation of the Western Australian Museum was severely damaged. In the course of this study, much in the way of new information came to light concerning what occurred during this period, and it is now apparent that the sequence in which events unfolded and the specific tracks involved became confused. Given the dark shadow these events have cast over the dinosaurian tracks of the Dampier Peninsula and Australian paleontology in general, we feel it is important to provide an update.

The first incident occurred in July 1991 during the ‘Great Dinosaur Hunt.’ Correspondence between Paul Foulkes and John Long during 1990 and 1991 shows that Long was expressly told to seek the consent of the then senior Goolarabooloo Maja, the late Paddy Roe, before visiting certain tracksites for the purpose of scientific research. Long did not follow through on this advice and proceeded with the expedition without liaising with Roe (also see T. Hamley quoted in Rich and Vickers-Rich, 2003a:85). Foulkes, Louise Middleton, and Goolarabooloo only learned of Long and his team’s visit after news footage of the ‘Great Dinosaur Hunt’ aired in late July–early August 1991. Some time later, it was realized that the boulder preserving the purported stegosaurian manual and pedal tracks (Fig. 54), first shown to Long in 1990 by Foulkes and reported in Long (1990, 1992a) and Thulborn et al. (1994), had been taken to Perth for further study at the Western Australian Museum (Long, 2002; Rich and Vickers-Rich, 2003a). The removal of this boulder occurred without the knowledge or consent of Foulkes or Goolarabooloo (although Long claims that he did have permission; Long, 2002:6) and caused Foulkes a great deal of stress, straining his relationship with Paddy Roe who had entrusted him with access to the tracksites. The boulder was returned to Broome in 1994 (Long, 2002:6) and placed safely back in country by Goolarabooloo.

One of the main concerns that Foulkes and Goolarabooloo had was that footage from the ‘Great Dinosaur Hunt’ would allow people to recognize the location of some of the tracksites, placing them in danger from vandalism or theft. Their fears were

realized in October 1996, when Paddy Roe's grandson, Phillip Roe (now a Maja), noticed a trace in the sand that he thought was consistent with a power cord at one of the tracksites featured in the documentary. Phillip states that the trace led to an overhanging portion of rock platform that had had its corner removed, and that this corner preserved an important tridactyl track linked to Marala. The power cord trace and freshly cut straight edge indicated to Phillip that an angle grinder or similar power tool had been used (P. Roe, pers. comm., April 2014). Phillip alerted his brother, the late Joseph Roe, who in turn reported the incident to the Broome police. The police were taken to the site not long after and photographed the cut platform. Apart from Goolarabooloo and the police, no one else went to the tracksite during this time to examine the cut platform. At this stage, it was not entirely clear to the Broome police which tracks had been stolen, if any, but Roe maintains that it was a medium-sized tridactyl theropod track. Correspondence between the Broome police, the Kimberley Land Council, John Long, Tony Thulburn, and Paul Foulkes led them to believe that the missing portion of rock platform contained one of the sets of tracks previously identified in 1990/1991 as potentially pertaining to a stegosaurian (Long, 2002:10–13, pl. 1) (Fig. 51). Aside from the boulder with the manual track (Fig. 54A–C) that had been removed during the 'Great Dinosaur Hunt,' at the time these were thought to be the only other stegosaurian tracks in Australia. News of the theft was soon made public, attracting international media attention and sending shockwaves through the paleontological, indigenous, and Broome communities alike (Holden, 1996; Pockley, 1996; O'Brien, 1998; Page, 1998; Thulborn, 1998; Long, 2002). No clues as to what happened would emerge for over two years.

On 4 November 1998, Michael Latham from Broome was charged with the theft of a theropod track from the Broome Sandstone and two ~7000-year-old human footprints from the Lombadina area, approximately 180 km north of Broome (Fang, 1998; O'Brien, 1998). When Broome police become aware of the thefts and that Latham might be involved, a search of his house was carried out, but nothing was found. It was later determined that after the search, Latham gave the tracks that were in his possession to other persons, and that some of the tracks were returned to their original locations. A theropod track was later handed to Broome police (Supreme Court of Western Australia, 2000) and Latham was implicated in its theft, while video footage seized during the police raid indicated that the human tracks were in the possession of Rodney Illingworth, at the time the manager of Roebuck Bay Station. Latham was found guilty and sentenced to two years' jail (Pockley, 2000; Supreme Court of Western Australia, 2000). Illingworth was initially acquitted (Pockley, 2000) but was later retried and found guilty of knowingly being in the possession of stolen artifacts (Anonymous, 2000). Latham pleaded guilty to having cut the theropod track from a rock platform using an angle grinder, and said that it came from a site on Roebuck Bay, southwest of Broome (Pockley, 2000; Latham v The Queen, 2000; Long, 2002). A second theropod track was returned to Goolarabooloo around the time of Latham's arrest (P. Roe, pers. comm., April 2014). Phillip Roe maintains that this was the tridactyl track that he had noticed was missing in 1996 and which subsequently became confused with the stegosaurian tracks (see below). Shortly after Latham's trial, the Roe brothers returned the theropod track to country.

The block preserving the theropod track from Roebuck Bay that Latham admitted to stealing is currently housed in the Broome Historical Museum. We agree with Long (2002:22) that the cut marks on this block are consistent with those that would have been made by an angle grinder. However, Long (2002:22–23) has stated that photographs taken at the northern site in 1996 (initially discovered by Phillip Roe) by Broome police

revealed that the missing portion of rock platform displayed "lines of plug and feathering," suggesting that hand chisels and possibly a drill had been used to remove it. This observation, along with Latham's testimony that the theropod track he was publicly accused of stealing came from Roebuck Bay, led Long and others to conclude that the purported stegosaurian tracks were still missing, possibly having been sold overseas (Fang, 1998; Thulborn, 1998; Pockley, 2000; Long, 2002). On the back of this supposition, a worldwide search for the missing stegosaurian tracks commenced in 2000 (Long, 2002). As a consequence of the 1996 thefts and the events of the 'Great Dinosaur Hunt' five years earlier, relations between Long and the Roe brothers were severely strained, and their knowledge of the second recovered theropod track from the northern site was not considered by Long, who continued the search for the supposedly missing stegosaurian tracks.

The recovered theropod track from Roebuck Bay is tentatively assignable to *M. broomensis*, as has been suggested elsewhere (Pockley, 2000; Long, 2002). The cut edges of the block show cross-sections through thinly (millimeter thin) laminated silts and sand consistent with those seen in track-bearing horizons in the Broome Sandstone of the Roebuck Bay area, which are quiet distinct from those farther north (see LFA-2 in Geological Setting; Figs. 9–11). After having examined the track along with video footage and photographs of the damaged rock platform discovered by Phillip Roe in 1996, we agree with the latter's observation that the broken edge on the platform is very clean and square and was probably sawn through with a large angle grinder. Contrary to the assertions of Long (2002:22–23), we could see no evidence for plug and feathering on this platform, which would have required a series of closely spaced, parallel, relatively deep drill holes to have been made prior to splitting. In our opinion, the possible pilot holes on the cut platform that Long (2002) refers to do not seem deep enough to have facilitated plug and feathers, and if these holes/cracks were indeed drilled, they were probably only done in order to get the initial cut with an angle grinder started. It is possible that a chisel may have been used to dislodge the sawn block after it had been cut, and in dislodging it, some parts of the edges may have broken. Both of these possibilities are distinctly different to plug and feathering. In addition, any broken edges on the cut block could easily have been cleaned up once it was removed (hence accounting for the apparent 'multiple masonry saw blade idea' outlined by Long, 2002:22). These observations lead us to conclude that: (1) the *M. broomensis* track that was in Latham's possession and which now resides in the Broome Historical Museum comes from an unknown locality on Roebuck Bay, and that this track has nothing to do with the cut platform discovered by Phillip Roe in 1996 farther north; (2) the tridactyl track that was stolen from the cut platform discovered by Phillip Roe was also a theropod track, and this track has also been recovered and has been returned to country; (3) both theropod track thefts were probably performed with an angle grinder, and neither involved the use of plug and feathering.

Significantly, during this study, we were able to relocate the supposedly missing 'stegosaurian' tracks (Fig. 51), which we have assigned to *Luluichnus mueckeii*. Photographs of these tracks taken by Foulkes in 1990 (Fig. 51A) show that they were preserved on the edge of a portion of rock platform. In the years since Foulkes' photograph was taken, that particular portion of rock platform has broken away, with the portion preserving the *L. mueckeii* tracks splitting in two, and the halves now a considerable distance from each other, presumably the result of wave action during subsequent storm and/or cyclone activity. No part of either half of the original rock platform or the two portions that preserve the tracks has been sawn with an angle grinder or split with a line of drill holes and/or plug and feathering, and

both are considerably thicker than the cut platform discovered in 1996 by Phillip Roe (which we now assume initially preserved the second theropod track, also removed by Latham). Each half of the platform preserving the *L. mueckeii* tracks would weigh several hundred kilograms, if not more, and the intact portion of platform with the tracks would easily weigh over a metric ton. It therefore seems highly unlikely that it could have been removed and then replaced without the use of heavy earth-moving machinery, which would have been noticed. We therefore suspect that these *L. mueckeii* tracks have been at the site all along, and that their continued presence there went unnoticed once the portion of rock platform on which they are preserved broke up.

So thankfully, but somewhat ironically, despite a nearly two-decade search (see Pockley, 1996; Fang, 1998; Pockley, 2000; Long, 2002), Australia's most infamous fossil theft appears never to have happened. With the 1994 repatriation of the 'stegosaurian' boulder from the Western Australian Museum, the recovery of the two theropod tracks stolen by Latham, and the rediscovery of the other 'missing' 'stegosaurian' tracks, all the tracks that were either thought or known to be missing can now be accounted for.

#### LITERATURE CITED: APPENDIX 2

- Anonymous. 2000. Man to be retried on receiving fossil. Australian Associated Press 21 December 2000.
- Fang, G. 1998. Dinosaur mystery has left not prints. The Western Australian, 7 November 1998.
- Holden, C. 1996. Australians seek to stem fossil thefts. Science 274:725.
- Long, J. A. 1990. Dinosaurs of Australia and Other Animals of the Mesozoic Era. Reed Books, Balgowlah, New South Wales, Australia, 87 pp.
- Long, J. A. 1992. Cretaceous dinosaur ichnofauna from Broome, Western Australia. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 9:262.
- Long, J. A. 2002. The Dinosaur Dealers. Allen and Unwin, Sydney, Australia, 220 pp.
- O'Brien, N. L. 1998. Following in stolen dinosaur footprints. The Australian, November 27, 1998.
- Page, D. 1998. Stegosaur tracks and the persistence of facies—the Lower Cretaceous of Western Australia. Geology Today 14:75–77.
- Pockley, P. 1996. Aboriginal relations strained by theft of dinosaur footprints. Nature 383:655.
- Pockley, P. 2000. Australian jailed for removal of fossilized footprints. Nature 404:4.
- Rich, T. H., and P. Vickers-Rich. 2003. A Century of Australian Dinosaurs. Queen Victoria Museum and Art Gallery, Launceston, and Monash Science Centre, Monash University, Clayton, Victoria, Australia, 125 pp.
- Supreme Court of Western Australia. 2000. Latham -v- The Queen. Appeal Judgement, Case No CCA:41/2000. Supreme Court of Western Australia, Court of Appeal (WASCA) 338:1–15.
- Thulborn, T. 1998. Dinosaur tracks at Broome, Western Australia. Geology Today 14:139.
- Thulborn, T., T. L. Hamley, and P. Foulkes. 1994. Preliminary report on sauropod dinosaur tracks in the Broome Sandstone (Lower Cretaceous) of Western Australia. Gaia 10:85–94.