Bipedal leaping Jurassic vertebrates in Southern Africa: proposed new ichnotaxon and inferred palaeoenvironment

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Abstract

The Lower Jurassic Clarens Formation (Stormberg Group, Karoo Supergroup, Main Karoo basin) contains relatively common vertebrate trackways impressed into apparently soft to firm, fine sediment beds preserved within the succession. At least three known ichnotaxa are interpreted as leaping bipedal vertebrates. Here we provide a generic description of a proposed new ichnotaxon to add to this small group of the oldest known bipedal hopping vertebrates in Africa and globally. *Saltirecarpipes* Genus Nova (Type Species *tinleyi*) (*saltus* – leap; *carpe* – seize; *pes* – foot) has been identified from tracks at Giants Castle in the KwaZulu-Natal Drakensberg. The type specimen in the National Museum Bloemfontein exhibits two adjacent tetradactyl impressions with four digits extended from metatarsal pads, comprising three inner digits grouped closer together and facing forwards, the fourth digit being much longer and curved outwards and slightly backwards. The digits are all strongly curved with claw impressions being preserved in several cases. These were small vertebrates, a leap length of ca. 180 mm being inferred. Being found in association with trace fossils of *Equisitales* (horse tails) a wet palaeoenvironment of small ponds is postulated. These appear to have been associated with distal fan sheetflood deposits of fine sediment at Giants Castle, which pass laterally into more central-basinal palaeodune deposits which characterise the Clarens Formation across the Main Karoo depository. The new ichnotaxon appears to have been restricted to wet desert marginal settings, feeding immature sediment to the desert basin, and which retreated proximally as aridification of the Clarens palaeoenvironment progressed.

Keywords: bipedal, leaping, vertebrates, Jurassic, South Africa, Clarens Formation, Karoo Supergroup, wet desert, sheetfloods

INTRODUCTION

While plant fossils typify the lower Molteno Formation (e.g., Johnson *et al.*, 2006), reptilian remains occur within the medial Elliot Formation and lower part of the upper Clarens Formation (the three formations comprising the informal Stormberg Group, Karoo Supergroup, Main Karoo basin), with dinosaurs of the Ornithischia and Saurischia, as well as Thecodontia and Crocodilia predominating (Kitching and Raath, 1984; Johnson *et al.*, 2006). Recently, Viglietti *et al.* (2020a) reviewed Elliot Formation biostratigraphy and defined a new *Scalenodontoides* Assemblage Zone in the lower part of that formation. This contains the oldest tetrapod fossils of the Stormberg Group and the oldest dinosaurs of the entire Main

Karoo basin succession (Viglietti *et al.*, 2020a). In a companion paper (Viglietti *et al.*, 2020b), the *Massospondylus* Assemblage Zone is defined, which was a dinosaur-dominated ecosystem equating to the upper Elliot Formation and the Clarens Formation; it possibly extended beyond stratigraphically, into the sedimentary strata found within the lowermost part of the succeeding and essentially volcanogenic Drakensberg Group. It is within the Lower Jurassic (Bordy *et al.*, 2020) Clarens Formation, and specifically within its basal sedimentary deposits that the proposed new ichnotaxon forming the subject of this short paper is found.

Due to cliffs typifying the Clarens Formation in most areas, common caves at their base (or within a few tens of metres thereof) offer the best access to the relevant stratigraphy and it is here that most fossils are reported: body and trace fossils of freshwater fish and crustaceans, insects, crocodylomorphs, cynodonts, sauropodomorphs and ornischian dinosaurs (Bordy and Head, 2018, and references therein). In contrast, in the uppermost part of the Clarens Formation near the contact with Drakensberg Group volcanics, plant fragments and more abundant petrified tree trunks occur (Haughton, 1924; Ellenberger, 1970; Bordy and Catuneanu, 2002; Bamford, 2004). Invertebrate trace fossils and inferred termitaria occur in the Lower Clarens beds while vertebrate trackways (particularly of dinosaurs) have been found in both the upper and lower parts of this formation (Haughton, 1924; van Eeden and Keyser, 1971; van Dijk, 1978; Olsen and Galton, 1984; Eriksson, 1986; Bordy and Catuneanu, 2002; Raath and Yates, 2005; Knoll, 2005; Bordy and Head, 2018; Abrahams *et al.*, 2020; Viglietti *et al.*, 2020a, 2020b).

The Giants Castle area of the KwaZulu-Natal Drakensberg has a well-established record of quadrupedal and bipedal vertebrate tracks, detailed below. Mr Ken Tinley found such trace fossils in the Clarens Formation in this area in 1966, encompassing ten different types of tracks (van Dijk, 1978). Following a conference in Stellenbosch that same year where the trace fossils were reported, photographs thereof were sent to a Southern African expert in Lesotho, Reverend Dr Paul Ellenberger. He proposed several new taxa in his presentation at the 2nd Gondwana Symposium in Cape Town, 1970, details being published in the relevant proceedings volume, and including: *Dinopentadiscus vandijki*, *D. lentus*, *Molapopentapodiscus (Dipodiscus) saltator*, *M. supersaltator*, *Malutitetrapodiscus saltator* and *Vandijkopentapus giantcastlensis* (Ellenberger, 1970, p. 350; p. 354; pI. XI, figs. 114, 115, 118 and 119). Ellenberger (1970) interpreted *Molapopentapodiscus (Dipodiscus) saltator*, *M. supersaltator* and *Malutitetrapodiscus saltator* as bipedal hopping dinosaurs (van Dijk, 2001). Figure 1 shows tracks of *M. supersaltator* and of the new ichnotaxon proposed in this paper, at Giants Castle.

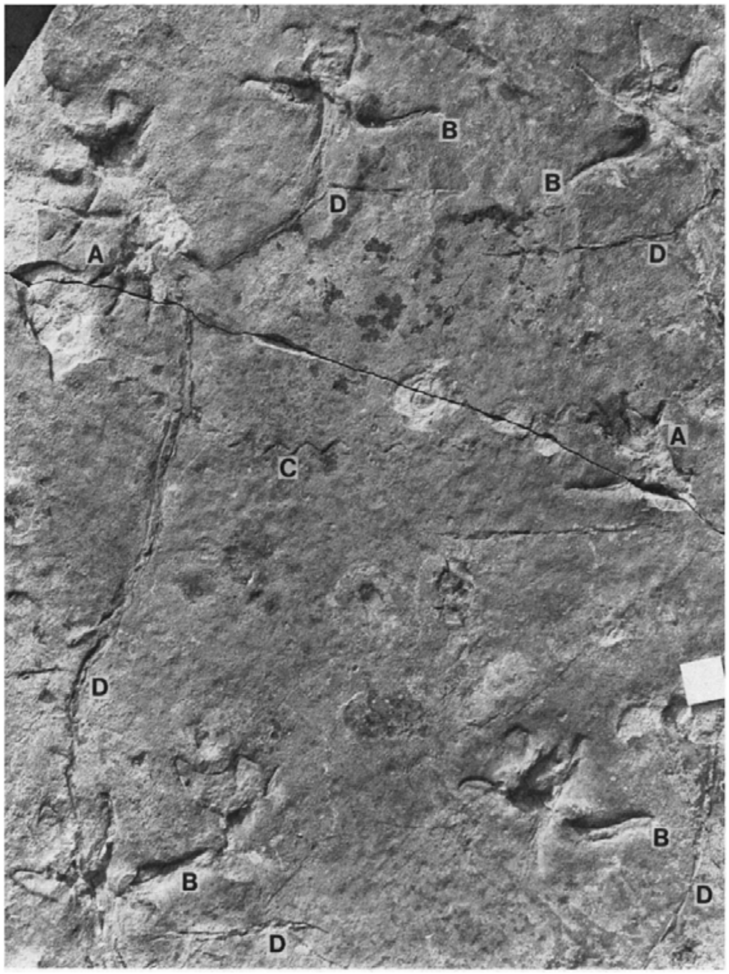

Figure 1. Sedimentary rock slab from Giants Castle which was reassembled from scree fragments, which shows prints from two inferred hopping vertebrates on its upper surface: (1) those attributed to *Molapopentapodiscus supersaltator* (three distinct digits visible, with small interdigit angles, and denoted by A: single print at top left, facing down to the left, and at middle right, another single print facing upwards) and (2) those of another hopper, the new ichnotaxon described here. This is, characterised by three strongly curved toes which are directed forwards and another toe directed to the side and angled somewhat backwards (denoted by B: right footprints occur at bottom right and at middle top, in each case with longer outer digit extending to the "B"; left footprint at the bottom left is obscured by a superimposed right footprint ("B" is between two prints); another left footprint is visible at the top right). Desiccation cracks (D) also occur in the slab, and a sinuous trail (denoted by C) cuts across the middle of the photograph. (White square for scale = 1 cm^2).

Several of the trackways at Giants Castle had been impressed into a soft yet cohesive (thus supposedly wet) sediment substrate. In some cases, when exposed, especially in cave roofs (e.g., Figure 5) the lower surfaces of such preserved sedimentary beds also exhibit a less clear impression of the surface prints; locally, due to sedimentary reworking of the upper surfaces, the lower impressions may appear to be clearer (van Dijk, 1978). However, this can be confusing as such undertracks (Gatesy, 2003) are normally distinctly less well defined. This author distinguishes between true tracks (made and preserved on the upper surface of a sediment bed) and undertracks that are made in subsurface layers (whether top or base thereof); deep tracks can make this distinction difficult as they tend to cut through a surface sediment layer in place of just disturbing them (Gatesy, 2003). The latter discusses some Late

Triassic theropod tracks found in Greenland, which indicate foot movement in complex and three-dimensional paths through the sediment. Gatesy *et al.* (1999) established that far more useful data on possible foot and even limb movements could be garnered from deeper, more indistinct tracks, as in the Greenland examples, where it could be demonstrated that while the theropod foot entered the soft sediment with toes splayed out, it left the sediment on moving forward, with the toes drawn together. Finally, regarding trackway preservation, there is the very valid point that a trackway may be formed initially with poor anatomical fidelity, but there is subsequently good preservation of an initially poorly defined set of tracks (Marchetti *et al.*, 2019; Falkingham and Gatesy, 2020).

Relating these findings to the Lower Jurassic tracks from Giants Castle, some of these double-sided trackways, assigned to *Molapopentapodiscus supersaltator* Ellenberger, exhibited relatively deep skid marks behind the individual prints in the upper surface, features which were absent on the lower impressions, thus supporting low angle skid marks rather than an alternative interpretation of a possible heel-like projection behind the print (van Dijk, 1978). Van Dijk (2001) described a unique mode of locomotion detectable from bipedal vertebrates, in the lower part of the Clarens Formation, at Giants Castle in the KwaZulu-Natal Drakensberg; these tracks are, to our knowledge, the oldest recorded example of leaping vertebrates known from the (Jurassic) global rock record. This paper proposes a new ichnotaxon for this animal, based on specimen NMQR 3949 from the National Museum Bloemfontein (Figure 2). It will also explore the postulated palaeoenvironment within which these leaping dinosaurs may have lived.

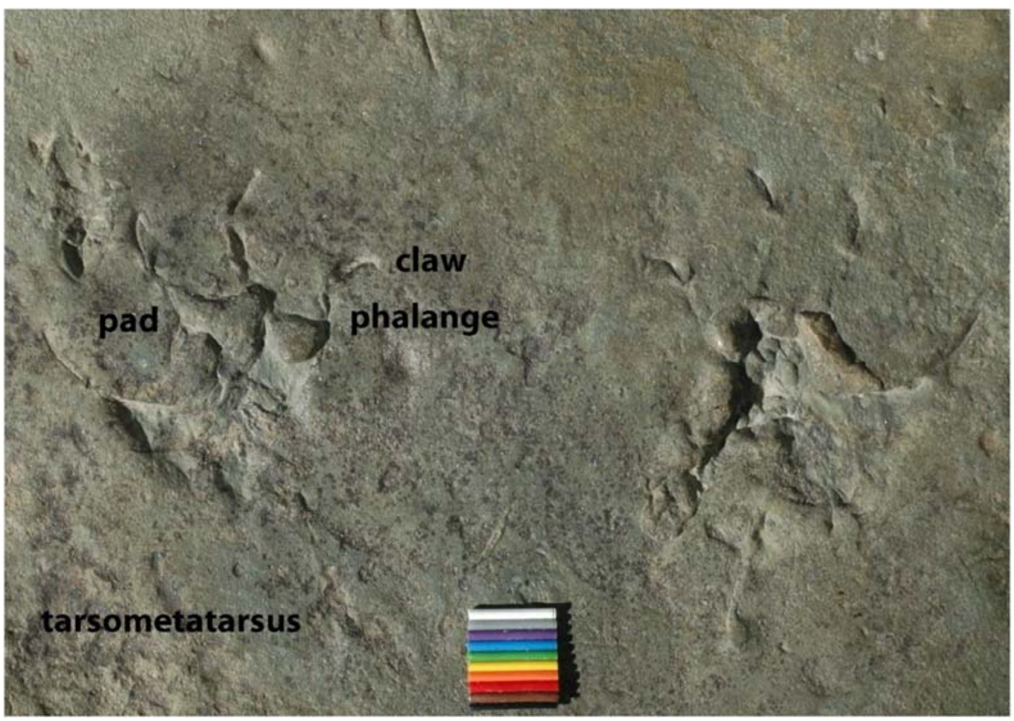

Figure 2. A pair of prints of the inferred bipedal hopper, *Saltirecarpipes* Genus Nova. Note that all the digits, comprising a phalange and a claw, curve towards the "trackway" midline, with three digits directed forwards and closer together than the remaining one, which is the outer digit in each case and whose pad is almost transverse in orientation. The claws are clearly shown on most of the digits. Each of the feet reflects fusion of the foot bones (metatarsals) with an ankle (tarsal element), giving a tarsometatarsus (inferred position shown, not impressed into substrate). Scale is 10 mm wide.

CLARENS FORMATION IN THE MAIN KAROO BASIN; PALAEOENVIRONMENTAL SETTINGS

The Karoo basins have a wide distribution across Africa (and equivalents across many parts of Gondwana) and are seen as directly related to a first-cycle geodynamic evolution encompassing the assembly and the breakup of the Pangea supercontinent (Catuneanu *et al.*, 2005). The Main Karoo basin-fill of South Africa provides a Late Carboniferous to Middle Jurassic reference stratigraphy of the Karoo Supergroup: Dwyka, Ecca, Beaufort, Stormberg (informal) and Drakensberg lithostratigraphic subdivisions, in ascending order, reflecting a generally observed evolution from cold, semi-arid, through warmer, humid times and ending with hot conditions allied to ephemeral rainfall prior to terminal volcanism (e.g., Johnson *et al.*, 2006). In contrast to the tectonic controls on Karoo basin evolution, the relatively uniform palaeoclimatic transitions led to a shared similarity in basin-fills, seen irrespective of geodynamic settings (Catuneanu *et al.*, 2005).

The Lower Jurassic Clarens Formation is the uppermost sedimentary unit of the Stormberg Group and of the entire Karoo Supergroup in the Main basin; it conformably overlies the Elliot Formation fluvial-loessic red beds, and is succeeded by the Drakensberg Group lavas (e.g., Catuneanu *et al.*, 2005; Bordy and Head, 2018; Bordy *et al.*, 2020). The Clarens Formation in the Main Karoo basin is dominated by fine sandy beds of aeolian origin, forming part of a very extensive desert sand sea which extended regionally within Africa (Catuneanu *et al.*, 2005; Bordy and Head, 2018). Du Toit (1918) first suggested an aeolian genesis for the Clarens Formation, and extensive studies since have supported this widely accepted interpretation, while also adding subordinate settings reflecting (probably ephemeral) rivers and fans, as well as lakes (playa and desert) within the Main basin (e.g., Johnson, 1966, 1976; Beukes, 1969, 1970; Eriksson, 1981, 1983, 1986; Eriksson *et al.*, 1994; Holzförster, 2007; Bordy and Head, 2018; Bordy *et al.*, 2020). Widespread studies of aeolian cross-bedding have always produced a consistent palaeowind direction, essentially from west to east, with variations from both northwestern and southwestern quadrants (e.g., Bordy and Head, 2018 and references therein).

The rather variable preserved thickness of Clarens strata in the Main Karoo basin varies from c. 10 – over 300 m (lacunae excluded; Bordy and Head, 2018 and references therein). The nature of the essentially gradational upper and lower contacts of the Clarens Formation make accurate thickness measurements open to interpretation. At some localities within the Main basin, wet desert deposits (which generally occur in the basal Clarens succession) occur in its uppermost portion again where they may also be associated locally with volcanic deposits of the lowermost Drakensberg Group (Beukes, 1969, 1970; Holzförster, 2007; Bordy and Head, 2018; Bordy *et al.*, 2020). The vertical zonation with lower and upper more massive sandstones, spatially associated with subordinate shallow water deposits, and a medial zone dominated by wind-related cross-bedding, commonly found in northern and western parts of the Clarens Formation in the Main basin are attributed to the palaeoclimatic change from initially semi-arid conditions, passing into arid and once more, semi-arid, vertically (e.g., Beukes 1969, 1970; Bordy and Head, 2018; Bordy *et al.*, 2020). Where upper Clarens Formation deposits are associated with early volcanism, largely in the southern Clarens outcrops, relatively small local depocentres characterised by pyroclastic and lacustrine deposits appear to have replaced widespread wind-deposited palaeo-dune sedimentary rocks

(Holzförster, 2007). A crater lake, phreatomagmatic model to their genesis and a wetter palaeoclimate is inferred with storms locally affecting lake sediments (Holzförster, 2007).

In the KwaZulu-Natal Drakensberg area, alluvial fan deposits pass laterally into distal sheetflood elements and localised mass-flow sedimentary units, which transition laterally and vertically into dry desert aeolian facies with localised, relatively small playa lake lenses therein (Figure 3) (Eriksson, 1983, 1986). Here, Eriksson (1981, 1983, 1986) recognised four facies, a predominant aeolian dune facies and three spatially associated wet desert facies, comprising inferred distal fan deposits, lowermost distal sheetflood sediments, and localised debris flow deposits, the latter three facies being found in the southeastern parts of the region (Figure 3). At several of the study sites in the southeast, distal channelised fan deposits make up the entire preserved thickness of the Clarens Formation, while the Giants Castle valley which forms the field site of this palaeontological study, is characterised by sheetflood deposits only, containing the bipedal vertebrate tracks focussed upon here, passing proximally into channelised lower fan sediments and distally into aeolian facies (Eriksson, 1979, 1981, 1983, 1986) (Figure 3).

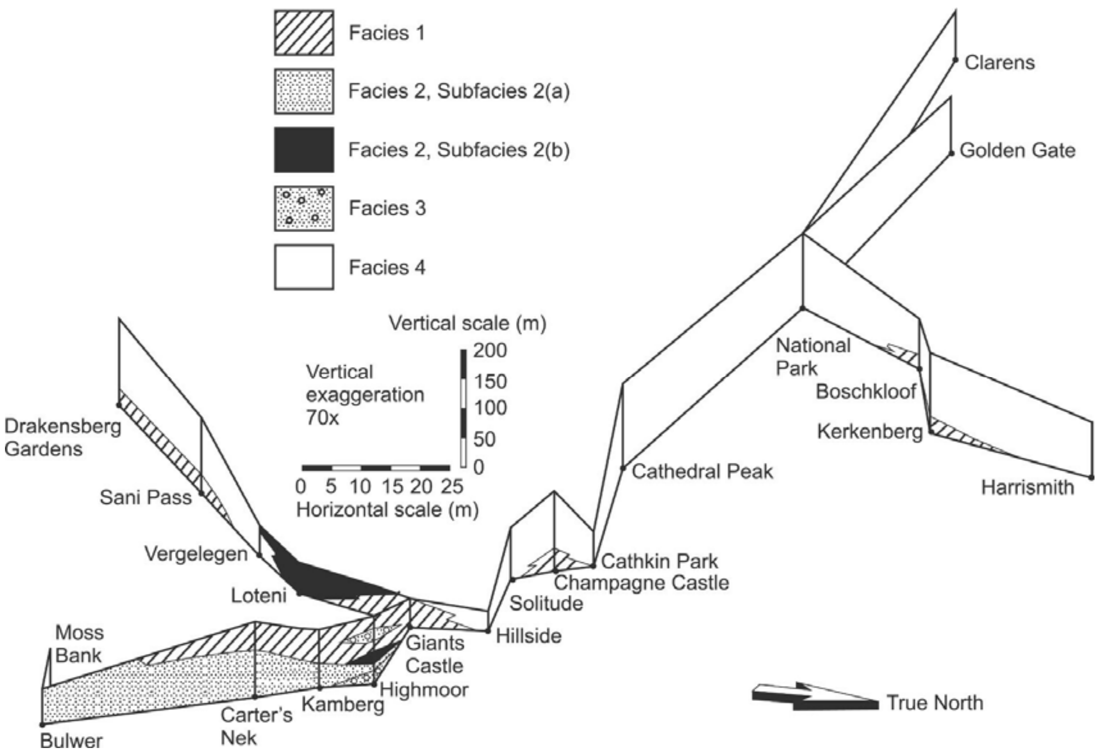

Figure 3. Fence diagram showing facies relationships for the Clarens Formation in the KwaZulu-Natal Drakensberg region. Facies are as follows: 1 = lowermost distal sheetflood sediments; 2 = distal fan deposits; 3 = localised debris flow deposits (1–3 together make up the inferred wet desert facies); 4 = predominant aeolian dune facies. Note that the Giants Castle area is characterised only by the distal sheetflood facies. Redrawn from Eriksson (1983, 1986).

Overall observed facies relationships suggest that aeolian deposits succeeded wet desert sediments, and within the latter three facies, the facies relationships point to fan retreat, with lowermost distal sheetflood sediments overlying fan channel sediments, with inverse thickness relations: sheetflood deposits replace fan channel deposits downcurrent (basinward), and then thin up-fan where they overlie the channelised sediments (Eriksson, 1983, 1986) (Figure 3). Thorough petrographic studies on Clarens sandstones have been limited; through point-counting 130 stained thin sections, Eriksson *et al.* (1994) determined that feldspathic wackes predominate. They inferred that the immature character of these sandstones indicated a relatively abundant alluvial sediment supply and rapid burial thereof, with these processes outstripping aeolian reworking of detritus. The implication is thus that influxes of wet desert sediments were relatively frequent during Clarens sedimentation, with wind reworking sufficing to form dunes from distal alluvial deposits but not being extensive or long-lasting enough to result in mineralogically mature aeolian deposits (Eriksson *et al.*, 1994). This interpretation applied to the KwaZulu-Natal Drakensberg region, the lack of detailed petrographic data elsewhere in the preserved basin precluding any larger scale interpretations.

Clarens formation sedimentology and inferred palaeoenvironment at Giants Castle ichnotaxon site

A vertical sedimentary profile measured in the immediate vicinity of the vertebrate tracks discussed in this paper, comprises 60 m of exposure in the field, the lower 31 m consisting essentially of partly calcareous siltstone in its basal three quarters, and of siltstone above that (Figure 4). Sedimentary structures in this lower 31 m are dominated by mud clasts, compaction features, with minor cross-laminations and localised erosive surfaces (Figure 4). Taken together, these features suggest rapid deposition of fine material under relatively elevated energy levels rather than the suspension sedimentation which typically is associated with siltstones in most settings (Eriksson 1979, 1983; references therein). The subordinate calcareous content in the lower three quarters of this interval, bearing in mind the overall desert palaeoenvironment envisaged for this formation (e.g., Eriksson, 1986; Bordy and Head, 2018; Bordy *et al.*, 2020), probably reflect localised evaporites developed as standing water desiccated.

This lower part of the profile is succeeded by 29 m of predominantly poorly sorted, muddy very fine-grained sandstones, characterised by fine (Figure 4) and convolute laminations and small scale planar cross-bedding (Figure 4). While the cross-bedding, and some minor ripple marks point to low energy directed current flows, the horizontal laminae (poorly sorted; soft sediment deformation thereof) suggest distal, fine-grained sheetflood deposits laid down through terminal flooding within alluvial fan systems (Eriksson, 1983, 1986). Minor rill marks and runzel marks (Figure 4), found together with vertebrate tracks on the upper surfaces of pervasive planar thin beds and laminae of fine sandstones (with localised undertracks also; Figure 5), suggest intermittent emergence of shallow water sheetflood settings (Eriksson, 1979, 1983, 1986; references therein).

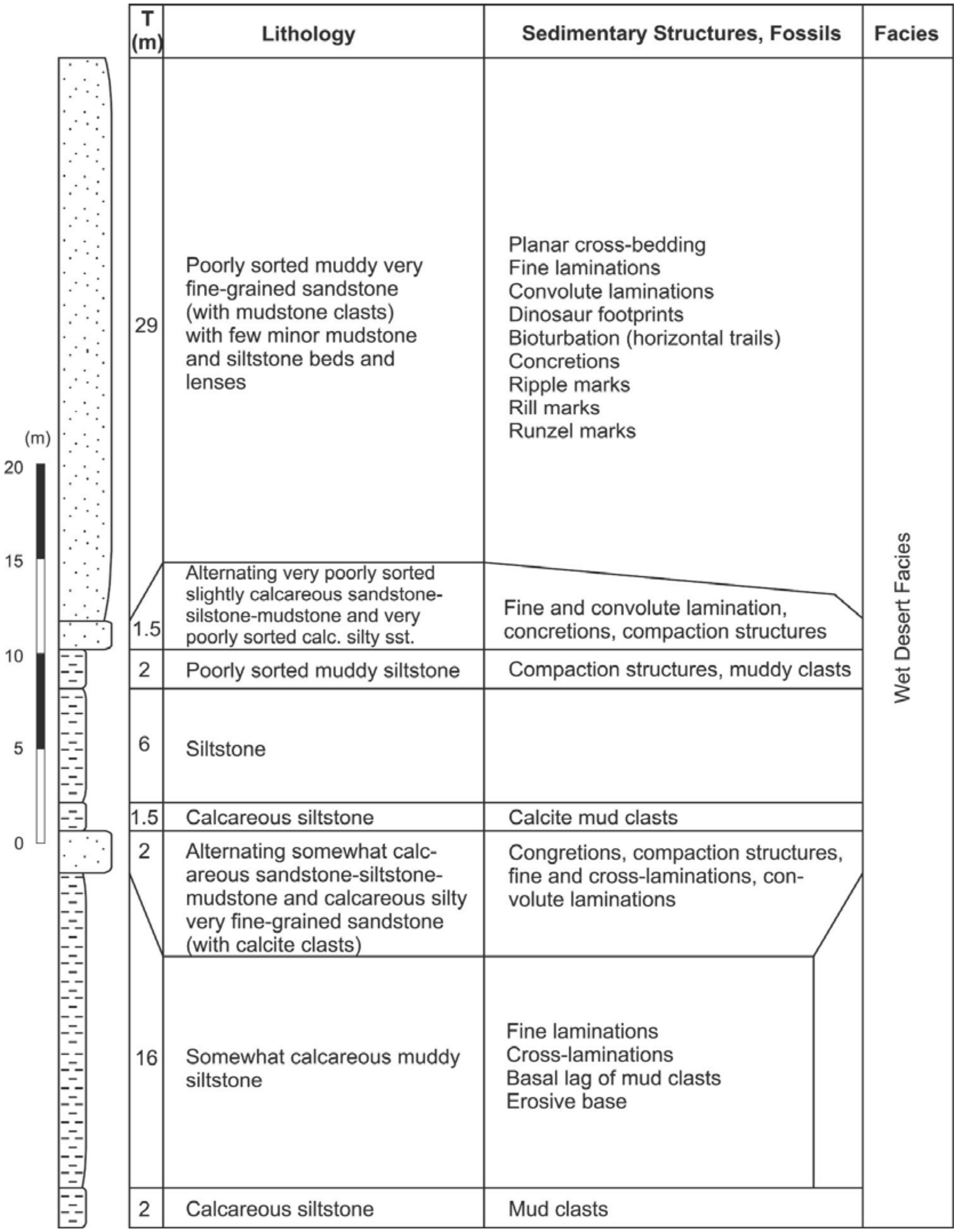

Figure 4. Vertical sedimentary profile measured through the Clarens Formation, Giants Castle, in the same location as the vertebrate footprints were discovered. Abbreviations: T = thickness; sst = sandstone. Redrawn from Eriksson (1979).

Figure 5. Photograph inside cave in lower part of Clarens Formation (a small part of the upper 29 m of partial profile shown in Figure 4) at Giants Castle. Surveying staff divisions = 20 cm, for scale. Note pervasive thin beds and laminae of fine-grained muddy sandstone, and dinosaur undertracks on cave roof at upper left. Other sedimentary features discussed in the text are found on upper bed/laminae surfaces exposed elsewhere on site.

Other profiles were measured in the Giants Castle valley within several kilometres of where Figure 4 was recorded, and just as at the locality of the vertebrate foorprints cave, exhibit predominantly fine material with fine laminations and thin planar bedding (about 25% of planar laminae/beds display soft sediment deformation features); additional structures found in these associated profiles and not seen at the Figure 4 site, include horizontal *Planolites* burrows (and inferred associated coprolites) on several planar laminae surfaces, minor localised small erosion channels, very minor plant fossils and trace fossils, and sand-filled mudcracks (Eriksson, 1983). All the profiles at Giants Castle, while dominated by generally fine sedimentary rocks, also exhibit upward-coarsening trends; this suggests that the postulated distal fan sheetflood settings were still advancing basinwards and palaeoclimate thus remained wet enough to support the observed fauna and flora. Overall, the Giants Castle area appears to have been subject to (most likely) episodic sheetflood events, leading to shallow water bodies, which dried out intermittently; however, it is unlikely that desiccation was ever complete before a subsequent sheetflood event brought in new fine sediment and sufficient water to sustain life. This reasoning underpins the “wet desert” facies interpretation applied to these fine, largely laminated sediments, at Giants Castle and several adjacent study sites by Eriksson (1979, 1983, 1986).

BIPEDAL LEAPING JURASSIC VERTEBRATES IN SOUTHERN AFRICA

The inferred mode of locomotion of bipedal Jurassic vertebrates from the Giants Castle region of South Africa, deduced from preserved trackways ascribed to *Molapopentapodiscus supersaltator*, suggested that long outer digits laterally, thrust the animal forwards and inwards, with the feet then diverging between leaps (van Dijk, 2001). These were, and remain, the oldest recorded leaping vertebrates in the world. However, the slab demonstrating this, was one of the ichnological specimens lost (destroyed or stolen) during rebuilding of a wing of the KwaZulu-Natal Museum, Pietermaritzburg. Some other specimens which showed feet with strong claws escaped this loss by being under study in Stellenbosch at the time. Impressions from vertebrate feet bearing paired digits, but none with long digits, had been illustrated in an earlier paper (van Dijk, 1978). This led, to feet with paired long digits being described as a "New Genus" (van Dijk, 2001, p. 374). Numerous photographs of all the specimens with clawed digits were subsequently taken.

One of the sedimentary rock slabs bearing trackways, reconstructed from scree fragments at Giants Castle while showing clear *Molapopentapodiscus supersaltator* tracks (denoted with A in Figure 1), also exhibited other tracks indicating a hopping mode of locomotion. This second group of tracks is characterised by a very long outer digit and three inner digits grouped closer together, the tips of all digits being strongly curved (denoted with B in Figure 1). Later on, a second, small slab from the Giants Castle site was found amongst those kept at the National Museum Bloemfontein, showing a pair of tracks (Figure 2) ascribed to this second, as yet unnamed ichnotaxon. This is inferred to be a new ichnotaxon, as is discussed here.

SYSTEMATIC ICHNOLOGY

Saltirecarpipes, new ichnogenus

Figures 1 and 2

Unassigned ichnogenus (van Dijk, 1978, p. 119; van Dijk, 2001, p. 374)

Type ichnospecies: *Saltirecarpipes tinleyi* n. isp.

Etymology: From the Latin *Saltus* "leap", "leaping"; *carpe* – "seize", *pes* – "foot". This name was chosen to reflect the apparently hopping (leaping) bipedal locomotion of the ichnospecies proposed, combined with claw impressions which strongly suggest the feet being capable of grasping as well (in vegetation?)

Distribution: Lower Jurassic Lower Clarens Formation, Stormberg Group, Karoo Supergroup, South Africa

Diagnosis: A symmetrical pair of tracks making up a step is represented by two adjacent tetradactyl impressions registered on the upper surface of a very fine layer of sediment on an isolated slab (Figure 2). The four digits extend from the metatarsal pads of each of these impressions. Because it cannot be determined whether a digit is absent on the inner or outer side of each pes, the digits cannot be numbered. Also, because the digit impressions are curved and the tips appear to be directed into the substrate, the individual digit lengths cannot be accurately measured. The interdigit angles vary from 16° – 40° – 73°, from the innermost to the outermost digits. The total span of the tips of the digits of each pes is 40 mm. The total span of the two track impressions (equivalent of trackway width if there were a trackway rather than just two tracks) is 108 mm.

All the digits are curved towards the "trackway" midline, with a distinctly larger interdigit angle between the inner three digits and the outer digit of each track. The digital pads of the outermost digits are almost transverse. Claw impressions are clearly visible on most of the digits of both individual tracks. The deeper tips of several of the digits suggest that they had claws directed into the substrate. Slight bends in the digits and accumulation of sediment are indications of two elements (phalange and claw) in each of the narrow digits.

No clear trackways of these paired feet have been discovered. Figure 1, however does show two clear impressions of a right foot, which may be judged to represent a leap or stride of about 180 mm for that foot. Two left foot tracks are also visible in this same figure, one reasonably clear and the other partially obscured by a further right foot track.

Discussion: *Saltirecarpipes* appears to have been a bipedal hopping dinosaur, which is a characteristic shared by three other known taxa from the Giants Castle site, *Molapopentapodiscus (Dipodiscus) saltator*, *M. supersaltator* and *Malutitetrapodiscus saltator* (Ellenberger, 1970; van Dijk, 2001). However, *Saltirecarpipes* tracks show clearly that each digit was made up of a phalange and a claw, curving towards the midline between two adjacent tracks, and commonly also with claws directed into the soft substrate sediment. It is the fourth, outermost digit seen in the *Saltirecarpipes* tracks that is very different from any of the other inferred hopping taxa, as it is considerably longer than the other three, forward-facing digits, and separated from those by a much larger interdigit angle such that it curves outwards and even slightly backwards. It would appear that this dinosaur possibly had grasping digits (curved, with terminal claws) but was also capable of a hopping locomotion on the ground, at least in soft substrates where the curved digits and their claws could sink into the sediment, which would not be possible on a hard substrate where this creature would most likely have struggled to move effectively. A superficial comparison of *Saltirecarpipes* in Figures 1 and 2 may give an initial impression that the two examples are morphologically distinct; however the tracks are more deeply impressed into the substrate in Figure 1 than those shown in Figure 2, and those in Figure 1 are also shown along with the other tracks, of *Molapopentapodiscus supersaltator*, which can confuse the eye at first glance.

A playa lacustrine palaeoenvironment of the sediments of the new ichnotaxon was discussed in Van Dijk (2001). It was not mentioned in that paper that plant trace fossils bearing a resemblance to *Equisitales* ("Scour = Rushes" or "Horse-Tails") occurred on the edges of the inferred playa-lakes or ponds, and could have served as night- or seasonal refuges for small clawed creatures. More detailed sedimentological modelling discussed above rather suggests an episodic sheetflood dominated setting, related to distal alluvial systems, and this would then logically have produced common pond settings.

Saltirecarpipes tinleyi new ichnospecies

Figures 1 and 2

Holotype: NMQR 3949, National Museum Bloemfontein, South Africa; as Figure 2.

Type locality: Giants Castle Reserve

Other localities: Giants Castle Reserve (and Highmoor [Figure 3] a likely locality needing more research); Lesotho specimens (Ellenberger, 1970) are not subsumed into the new ichnogenus and ichnospecies as yet.

Age: Lower Jurassic

Etymology: From Tinley – The specific name has been chosen in recognition of Ken Tinley, and the Tinley family of the Giants Castle Reserve

Diagnosis: As for ichnogenus.

Description: Morphological features that distinguish this as the ichnospecies are the outermost digit on each of the two tracks (Figure 2), which are much longer and unlike the other three curved digits, are oriented approximately transversely to the forward-directed other three digits. While it is difficult to make a definitive statement thereon, due to claw impressions being incomplete as a result of direction of claws into the soft substrate during hops/leaps, the claw impressions at the ends of the longer, outermost digits are not as well visible in the tracks (also the *Saltirecarpipes tinleyi* tracks in Figure 1) as they are for the three forward-directed digits (Figure 2).

DISCUSSION

Problems of stratigraphic placement of track-bearing succession at Giants Castle

The c. 60 m measured in the profile where the trackways were found is approximately the same thickness found in several other profiles measured at Giants Castle. The Giants Castle and adjacent study sites have the lowest thickness for the formation in the KwaZulu-Natal Drakensberg region (Figure 3). This could reflect a gentle palaeohigh rising gradually as sedimentation proceeded. When the wet desert sheetflood deposits of Facies 1 elsewhere in the region are examined, in five sites they are succeeded vertically by aeolian deposits (Figure 3). Elsewhere in the Clarens basin (eastern and northern parts thereof) the typical vertical succession comprises wet desert deposits at the base, followed by thick aeolian sediments and finally relatively thin wet facies again at the top (e.g., Beukes, 1969, 1970; Bordy and Head, 2018; Bordy *et al.*, 2020). When the three dimensional regional facies relationships in the KwaZulu-Natal Drakensberg region are seen in that framework, the Giants Castle deposits with the trackways can be interpreted as lower Clarens Formation stratigraphically.

However, when the sheetflood deposits at Giants Castle are seen within the framework of the wet desert, and specifcally the distal fan deposits of Facies 2, which thicken in an up-palaeocurrent direction (towards Bulwer, Figure 3), the trackway-bearing Giants Castle sheetflood deposits can be interpreted as upper Clarens Formation. The only real clarity in modelling the three-dimensional facies relationships for the Drakensberg region shown in Figure 3, is that the southeastern (Bulwer to Giants Castle transect) channelised distal fan deposits of the wet desert association, being more proximal would logically have formed first, followed by the laterally and vertically succeeding sheetflood sediments, including those at Giants Castle, next in chronological succession. The pervasive aeolian deposits which characterise much of the Clarens Formation in the KwaZulu-Natal Drakensberg region, laterally and vertically succeed the sheetflood deposits and in chronological framework must be the youngest facies in that region (Figure 3).

While uppermost Clarens wet desert deposits are not common in the Drakensberg region of KwaZulu-Natal, they do exist locally and are thin, but they are much better developed in northern, western and southern parts of the preserved basin (Beukes, 1969, 1970; Holzförster, 2007; Bordy and Head, 2018; Bordy *et al.*, 2020). These upper wet desert units would then, chronologically speaking, comprise the youngest Clarens facies overall. Within this interpretation, then, the track-bearing sheetflood deposits at Giants Castle, while not at the base of the overall sedimentation system, can be seen as within the upper part of the initial wet desert sedimentation systems on a basinal scale.

Palaeoenvironmental setting of Giants Castle tracks and implications of inferred palaeoclimate

The Giants Castle Clarens Formation deposits are unique within the formation, as the only area within the preserved basin where the entire exposed section of Clarens sediments is of inferred sheetflood origin. In addition, at Giants Castle, the site lies distally to a linear pattern of sites (Highmoor to Bulwer and Moss Bank) which are interpreted as distal alluvial fan deposits (Figure 3); the latter thus reflect a postulated set of partially channelised alluvial systems which entered the preserved basin from the southeast, and which presumably fed the distal sheetflood sediments at Giants Castle (Eriksson, 1979, 1983, 1986). No comparable set of deposits nor modelled palaeoenvironment has been found or proposed elsewhere around the preserved basin. The uppermost Clarens wet desert deposits are of regional extent in the west, north and south of the basin (e.g., Beukes, 1969, 1970; Holzförster, 2007; Bordy and Head, 2018; Bordy *et al.*, 2020), relatively thin compared to the wet desert deposits along the Bulwer – Giants Castle transect in the KwaZulu-Natal Drakensberg, and have no known spatial or genetic relationship with channelised fan systems. While it is somewhat speculative, it can be postulated, that clawed dinosaur trackways on wet soft sediment, as at Giants Castle represent a unique palaeoenvironment within the overall Clarens desert setting; here palaeogeographic placement enabled development of a possibly unique mode of locomotion for small dinosaurs, using curved and clawed digits on wet substrates, and also possibly in vegetation where they may have pursued either a dominant or parallel lifestyle to locomotion on the ground. The upper wet sediment settings and their dinosaur trackways elsewhere in the preserved basin (north, west and south thereof) possibly owed their origin more to palaeoclimatic change. That said, similar change may also have affected the envisaged palaeoenvironment for the Giants Castle area. Upward coarsening successions in the Giants Castle Clarens succession (Figure 4) suggest an advancing sheetflood system, while overall large scale three dimensional facies relationships (Figure 3) suggest that the fan systems feeding the sheetfloods were gradually retreating. Palaeoclimate might thus have been becoming wetter in the proximal alluvial fan – distal sheetflood system.

Comparable ichnotaxa

The ichnotaxa from Lesotho (e.g., Ellenberger, 1970, and later workers, e.g., Wilson *et al.*, 2009) in general do not appear to be junior synonyms of the proposed new ichnogenus. While Ellenberger (1970) interpreted *Molapopentapodiscus (Dipodiscus) saltator*, *M.*

supersaltator and *Malutitetrapodiscus saltator* as bipedal hopping dinosaurs (van Dijk, 2001), the first- and third-named ichnotaxa have straight digits, and only *M. supersaltator* which alone amongst the three is also found at Giants Castle (e.g. Figure 1) has curved digits analogous to *Saltirecarpipes* Genus nova. However, the curved digits of *M. supersaltator* as shown in Figure 1 are smaller than those of the proposed new ichnotaxon, lack a visible fourth digit, and also have much smaller interdigit angles than *Saltirecarpipes*; finally, the digits of the latter show greater curvature, also of the terminal claw impressions on each digit. It is particularly the long outer digit of *Saltirecarpipes* oriented almost transverse to the three forward-directed digits in the tracks and angled backwards even, relative to the forward movement direction, that defines the proposed new ichnotaxon.

Careful comparison of the proposed new ichnotaxon tracks with the extensive illustrations provided in Ellenberger (1970) suggests only two tracks that bear some resemblance to *Saltirecarpipes*: *Trisauropodiscus superaviforma* and *Sauroeidepus quthingensis* (numbered as tracks 48 and 129 in the Ellenberger, 1970 figures, respectively). They are placed in what is termed “Cave Sandstone inferieur, zone b/5” by Ellenberger (1970), which equates to lower but not the basal strata of the Clarens Formation, analogous to the stratigraphic level inferred for *Saltirecarpipes*. *Sauroeidepus quthingensis* is characterised by four thin digits with claws, but neither digits nor claws are curved, and the interdigital angles are significantly lower than for *Saltirecarpipes.* For *Trisauropodiscus superaviforma* the resemblance is closer, there being four thin digits, with high interdigital angles, but a claw appears to be present on only one digit (could be due to preservation); however, once more the digits and the one claw are not curved.

Mode of movement of trackmaker and mode of formation of tracks

Wilson *et al.* (2009) in a paper dealing with some of the best preserved tracks described from Moyeni in southern Lesotho, originally by Ellenberger (1970), define two diverse track-makers at the relevant site: a basal ornischian and a theropod dinosaur. The former apparently could alter trackway gauge (wider spacing of tracks gave greater stability for locomotion), position of the pes relative to trackway midline, and change from quadrupedal to bipedal gait as substrate types and slopes required. They further suggest that the theropod dinosaur inferred for the Lesotho trackways (which line later gave rise to birds) appears not to have been able to facilitate the change to quadrupedal walking achieved by the basal ornischian trackway-maker; instead, the theropod made use of its claws to provide grip in the substrate. The inferred palaeoenvironment interpreted from the trackway location and component sedimentary rocks present, comprised a basal rippled sandstone surface adjacent to the smooth slope of a fluvial scroll bar and finally an algal-matted, level bar top. It was these changing substrate conditions laterally, as the dinosaur proceeded, making the trackways that led to changes in locomotion methods (Wilson *et al.*, 2009). While the latter see them as Upper Elliot Formation features, these trackways have been dated as having a Lower Jurassic maximum depositional age (Bordy *et al.*, 2020).

Although the Lower Moyeni trackways are largely ascribed to Grallator or Anomopoes (Wilson *et al.*, 2009) and do not resemble the *Saltirecarpipes* tracks shown in Figure 2, a comparison with the Giants Castle tracks is useful, as they seem to share gripping claws. As yet no extensive *Saltirecarpipes* trackways are known, only a few tracks, at best reflecting a single step, and a single possible stride with clear evidence only for one foot, as presented in Figures 1 and 2. Sheetfloods by definition are essentially flat-lying sedimentation systems, depositing widespread, thin sheets of sediment, of variable calibres; at best they may exhibit slopes of a very few degrees (Eriksson, 1983 and references therein). The changes in locomotion style noted by Wilson *et al.* (2009) in their study would thus not be expected within the inferred Giants Castle palaeoenvironment. Sheetfloods would also not encourage extensive and robust algal mats to form (e.g., Schieber *et al.*, 2007, a major treatise on algal mats and their sedimentary features), as mats require essentially quiet periods lacking sedimentation to form and expand. Regular deposition such as in sheetfloods fed by relatively wet distal fan systems, that could support both vegetation and dinosaur populations, as at Giants Castle, would thus not favour algal (or rather microbial; Schieber *et al.*, 2007) mats. The most relevant aspect of Wilson *et al.*'s (2009) work would thus appear to be the Giants Castle track-makers' use of claws to grip the wet substrate, as also found for the Lesotho theropod trackway. Cohesion for this would also have been provided by the muddy component of sediment commonly present at Giants Castle (Figure 4), about 5–10% mud within sandstones providing enough cohesion, which is similar in achieving binding of sand particles as is achieved by microbial mats (Schieber *et al.*, 2007 and references therein).

Gatesy *et al.* (1999) studied theropod trackways from Greenland, of Late Triassic age, and stress that tracks reflect foot behaviour as a specific locomotion mode interacts with the nature of the substrate. While deep trackways might provide individual tracks that are much less clear than shallow trackway impressions, in softer sediment where the less distinct, deeper tracks form, there is evidence preserved often of the entry and exit of the foot from the soft sediment (Gatesy *et al.*, 1999). In the Greenland examples, the digits of the foot appear to have been drawn together as the dinosaur lifted the foot from the sediment, whereas they were spread out as the foot impacted the substrate. However, in the Giants Castle tracks, there is no evidence for "stirring" of the sediment through the pes sinking too deep into a soft and wet substrate and then being drawn forward, dragging through the sediment. Sediment seems to have been pushed ahead of the longer, outer digits (Figures 1 and 2) and, to a lesser extent, between the other three digits. There is also some indication of skidding behind the tracks (Figure 1, also to a lesser extent in Figure 2) or at least a forward movement component in addition to a more vertically oriented indentation mechanism related to the inferred hopping locomotion. The essentially sandy rather than muddy substrates provided by the sheetfloods inferred for Giants Castle, with enough mud to provide cohesion of the sand particles, thus favoured preservation of relatively clear tracks and only shallow impression into the sediment beds. In the context of preservation of tracks vis-à-vis the original anatomical fidelity of the track (cf. Marchetti *et al.*, 2019; Falkingham and Gatesy, 2020), for the *Saltirecarpipes* tracks both would appear to have been of good quality. Estimation of the relative importance for this substrate stability and a possibly more vertical impact and take-off for the inferred hopping motion of the Drakensberg tracks is difficult, and the weight of the dinosaur also would have played a role therein. A tentative hopping mode of locomotion is thus proposed for the Giants Castle tracks, partially comparable to modern birds; this might even be an indication of the proposed new ichnotaxon lying along an early pre-avian trend in dinosaur evolution.
The *Saltirecarpipes* tracks (Figure 1) can be described as birdlike, having narrow digits and a wide divarication between the second and fourth digits. Ellenberger (1970) also inferred birdlike tracks for *Trisauropodiscus* in the Clarens Formation, discussed briefly under comparable ichnotaxa above; Abrahams *et al.* (2017) similarly described this ichnotaxon from the upper Elliot Formation, as having been birdlike.

Potential trackmaker

It can be speculated from the *Saltirecarpipes* tracks that each foot represents the fusion of the bones of the feet (metatarsals = "beyond ankle") with an ankle (tarsal) element, yielding a tarsometatarsus (Figure 2). This would then, in life, articulate with a lower limb element composed in part with one or more tarsal elements, forming a tibiotarsus. This is what is seen in such reptiles as Archosaurs, including dinosaurs, and birds. While it is always challenging and seldom possible to make any confident suggestions of track-makers for an ichnogenus, none of the known body fossils from the Clarens Formation (e.g. Bordy *et al.*, 2020; Viglietti *et al.*, 2020b) can be linked to these tracks with any conviction. Archosaurs represent possible relevant trackmakers and on a speculative note, perhaps basal Pterosaurs may have been responsible. The latter being capable of flight, with greatly lengthened fourth digits (cf., outermost digits) and also seen as effective climbers in vegetation, at least provide a plausible speculative suggestion.

CONCLUSIONS

A proposed new ichnotaxon, *Saltirecarpipes* found at the Giants Castle Reserve in the KwaZulu-Natal Drakensberg is one of four track-makers from the Clarens Formation (Stormberg Group of the Karoo Supergroup in the Main Karoo basin) inferred to have been bipedal hoppers: *Molapopentapodiscus (Dipodiscus) saltator*, *M. supersaltator* and *Malutitetrapodiscus saltator* (van Dijk, 2001). The first- and third-named ichnotaxa have straight digits, and only *M. supersaltator* which alone amongst the three is also found at Giants Castle (e.g. Figure 1) has curved digits analogous to *Saltirecarpipes* Genus nova. The latter in turn is distinguished from *M. supersaltator* by an outermost long and distinctly curved digit orientated almost transverse to the forward directed set of three digits, which also have lower interdigit angles than that separating the outermost one from its nearest neighbour. Curved claw impressions occur at the termination of the *Saltirecarpipes* digits. The inferred mode of locomotion of these two bipedal hoppers at Giants Castle probably encompassed the claws providing grip in a soft substrate. A possibly unique locomotion and inferred arboreal to ground habitat for the two ichnotaxa were possibly directly related to an apparently unique palaeoenvironment inferred from the sedimentary beds at Giants Castle. The latter are related to a setting characterised by numerous successive sheetflood beds, deposited distally to channelised lower fan systems, which characterises the entire preserved thickness of the Clarens Formation at the site, unlike any other site in the preserved basin. Muddy sandstones enhanced cohesion thereby helping clear tracks to form, and also enhanced substrate stability for a hopping dinosaur. The track-maker of *Saltirecarpipes* may, speculatively, have belonged to the Archosaurs, and more specifically the Pterosaurs.

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