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Large theropod dinosaur footprint associations in western Gondwana: Behavioural and palaeogeographic implications

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In modern terrestrial ecosystems, the population size of large predators is low, and a similar pattern has usually been assumed for dinosaurs. However, fossil finds of monospecific, large theropod accumulations suggest that population dynamics were more complex. Here, we report two Early Cretaceous tracksites dominated by large theropod footprints, in Querulpa Chico (Peru) and Chacarilla (Chile). The two sites correspond to distinct depositional environments—tidal basin/delta (Querulpa Chico) and meandering river (Chacarilla)—with both subject to extensive arid or semiarid palaeoclimatic conditions. Although most trackways show no preferred orientation, a clear relationship between two trackmakers is observed in one instance. This observation, coupled with the high abundance of trackways belonging to distinct large theropods, and the exclusion of tracks of other animals, suggests some degree of grouping behaviour. The presence of freshwater sources in a dry climate and perhaps social behaviour such as pair bonding may have promoted interactions between large carnivores. Further, the occurrence of these two tracksites confirms that large theropod dinosaurs, possibly spinosaurids and/or carcharodontosaurids, existed on the western margin of Gondwana as early as the earliest Cretaceous.

Key words: Theropoda, footprints, behaviour, palaeogeography, Early Cretaceous, Gondwana, Chile, Peru.

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Introduction

In general, population densities of large, carnivorous animals are expected to be low in any terrestrial environment, especially for animals with high metabolic rates (Colinvaux 1978). Indeed, if large predators were abundant, they would need such large amounts of prey biomass that any given ecosystem could not be maintained for long. Their feeding reserves (mainly primary consumers: herbivores) would be reduced and they would be driven to extinction. This is why trophic webs are often represented as pyramids with predators at the top, primary consumers (potential prey items) at intermediate levels, and primary producers at the base (e.g., Gotelli 2008). Many assumptions have been made on how faunal equilibrium constrains variables such as population growth, climate, geography, and behaviour. One example is the sustainability of predatory packs compared to isolated hunters (Farlow 1993), in which large carnivorous animals are unlikely to hunt as packs because the resources demanded would negatively impact the population size of the prey and require a larger home range for the pack.

Non-avian theropod dinosaurs, which were presumably predatory, may have exhibited similar ecological dynamics. Cretaceous theropods include the largest (up to 14 m long) terrestrial predators of all time, such as *Carcharodontosaurus* (Stromer 1931), *Spinosaurus* (Stromer 1915, 1934; Sereno et al. 1996), *Giganotosaurus* (Coria and Salgado 1995; Calvo and Coria 1998), *Mapusaurus* (Coria and Currie 2006), and *Tyrannotitan* (Novas et al. 2005). Such extremely large carnivorous dinosaurs have been found nearly worldwide, and palaeoecological inferences for them are diverse and often contradictory, mainly because of the lack

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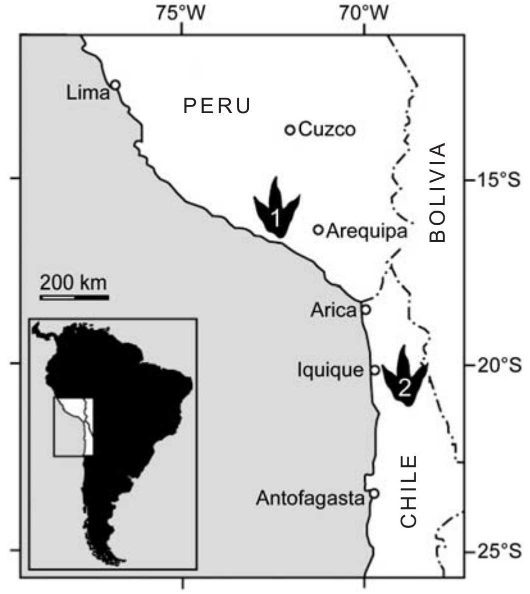

Fig. 1. Location of the large theropod trackbeds: track 1 indicates the Querulpa Chico locality while track 2 indicates the Chacarilla locality.

of modern analogues. Even though potential prey animals for these large theropods were abundant (sauropod and ornithopod dinosaurs, pterosaurs, fish, etc.), statistical estimates based on fossil bones indicate low abundances of these carnivore dinosaurs in most Mesozoic faunas (e.g., White et al. 1998). However, rare, almost monospecific bone accumulations of large theropods suggest that at least some of these animals were probably gregarious (Currie 1998; Porfiri et al. 2007; Currie and Eberth 2010), contradicting initial assumptions of faunal equilibrium. To explain this disparity, scavenging, rather than predation, has been hypothesized as a food-gathering strategy for the theropods (Ruxton and Houston 2003).

Dinosaur tracksite data provide useful complementary constraints on the problem of population density and behaviour of large predators (e.g., Lockley and Hunt 1995). Vertebrate footprints are abundant in the fossil record, more than body fossils, because they are generated repeatedly during the daily activities of an animal. Also, footprints cannot be transported or significantly reworked, and therefore they capture behaviours in environments in which the trackmakers lived. Dinosaur herding or other group behaviours have been inferred from several tracksites worldwide. However, the majority of these findings pertain to sauropods, basal iguanodontians and hadrosaurids (e.g., Ostrom 1972; Thulborn and Wade 1984; Farlow et al. 1989; Lockley et al. 1994; Lockley and Hunt 1995; Farlow and Chapman 1997; Lockley 1998; Day et al. 2002; Lockley et al. 2002). Almost defined pack structures of small and medium theropods have also been observed (e.g., Ostrom 1972; Lockley and Matsukawa 1999; Rogers 2002, Barco et al. 2006, Li et. al 2007). Recent morphological analyses of skulls indicate that a large number of these small-medium theropod families may have been herbivorous (Zanno and Makovicky 2011), which would have favoured gregarious behaviour. In contrast, large theropod footprints (anteroposterior length >0.3 m) and trackways are usually sparse in comparison with ichnites from any other dinosaur (e.g., Alonso and Marquillas 1986; Calvo 1991; Leonardi and Spezzamonte 1994; Lockley and Hunt 1994; Thulborn 2001; Mossman et al. 2003; Leonardi and Santos 2004; Boutakiout et al. 2009). Yet, theropod trackways are occasionally found associated with herbivorous dinosaur trackways with a configuration that suggests hunters following preys (Bird 1985; Farlow et al. 1989, Lockley and Hunt 1995).

To document further the behaviour of large theropod dinosaurs, we describe in this contribution two South American tracksites located in Querulpa Chico (Peru) and about 500 km away in Chacarilla (Chile) (Fig. 1). The two sites are estimated to date from the Early Cretaceous. As we discuss below, our observations reveal some level of grouping behaviour for large theropod dinosaurs. Moreover, the occurrence of these two tracksites confirms previous evidence for a geographic distribution of large theropod dinosaurs on the western margin of Gondwana (Moreno et al. 2004). In the absence of bones in the fossil record, these tracksites are the sole indication for the presence in this region of spinosaurids and carcharodontosaurids, the potential trackmakers known in South America during the Cretaceous (e.g., Coria and Salgado 1995; Kellner and Campos 1996; Coria and Currie 2002, 2006; Candeiro et al. 2004; Novas et al. 2005; Medeiros 2006; Salgado et al. 2009).

Institutional abbreviations.—MUSM, Museo Nacional de Historia Natural, Departamento de Paleontología, Lima, Peru; SGOPV, Museo Nacional de Historia Natural Santiago, Chile; SNGM, Servicio Nacional de Geología y Minería (SERNAGEOMIN), Santiago, Chile.

Geological setting

During the Early and Middle Jurassic, the deposition of marine sequences in northern Chile (Tarapacá Basin) and southern Peru (Arequipa Basin) was controlled by post-rift thermal subsidence and global sea-level fluctuations (Ardill et al. 1998). In contrast, during the Late Jurassic and Early Cretaceous, the Pacific plate converged and subducted against the western margin of Gondwana (Coira et al. 1982; Ramos and Kay 1991; Mpodozis and Allmendinger 1992). This event caused regional uplift in the southern Andes and back-arc basin extension of the northern and central Andes (Eppinger and Rosenfeld 1996; Ardill et al. 1998). As a result of this tectonic evolution, northern Chile and southern Peru experienced a widespread marine regression near the end of the Jurassic, followed by deposition of continental red-bed sequences during the Early Cretaceous (Rutland 1971; Bogdanic 1990). It was during this last phase of basin sedimentation that the large theropod trackways investigated in this study were recorded.

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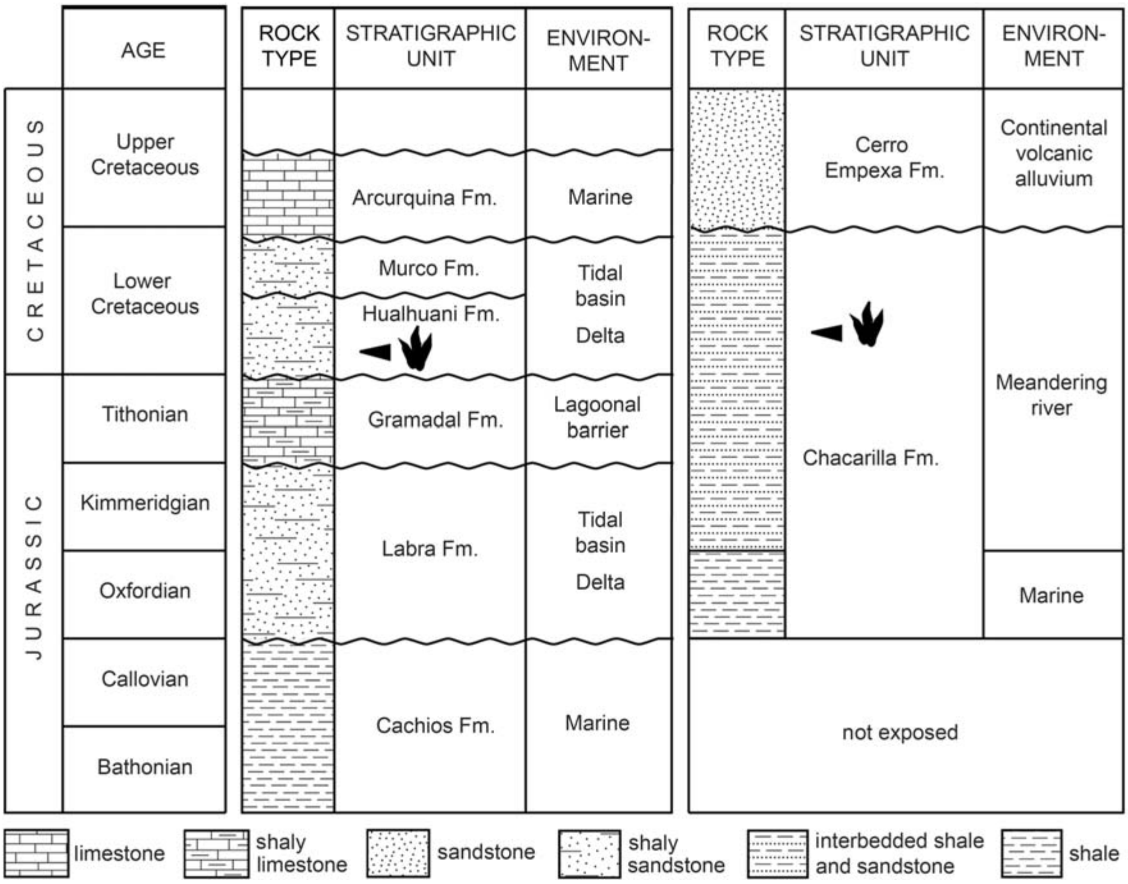

Fig. 2. Schematic Mesozoic chronostratigraphy for the Hualhuani and Chacarilla formations, with the expected relative positions of the track-bearing strata.

Querulpa Chico tracksite, Peru.—The Querulpa Chico tracksite is located about 70 km northwest of the city of Arequipa, southern Peru (Fig. 1). The track-bearing beds belong to the sedimentary Hualhuani Formation, which is among the uppermost units of the Yura Group (e.g., Sempere et al. 2004). The 1500 m-thick Hualhuani Formation is dominated by cross-bedded quartzose sandstones and shales (Guizado 1968; Rodriguez et al. 2005). These sediments were deposited along a beach that included both extensive tidal flats and deltaic environments (Jacay et al. 2006). The Hualhuani Formation unconformably overlies the Gramadal Formation, which is Tithonian (Late Jurassic) in age (Benavides 1962). Since it is overlain by the Murco Formation, which is late Early Cretaceous in age (Jenks 1948; Rodriguez et al. 2005), the Hualhuani Formation is most likely Neocomian, i.e., Early Cretaceous (e.g., Sempere et al. 2004; Jacay et al. 2006). The strata at the tracksite are oriented 70° NE and tilted 36° SE as a consequence of north-northwestward tectonic deformation. There are three track-bearing levels within a 20 m-thick sequence in the lower part of the unit. As shown in Fig. 2, preliminary data about the local palaeoenvironment are indicative of a tidal basin (Jacay et al. 2006).

Chacarilla tracksite, Chile.—The Chacarilla tracksite investigated here is one of several tracksites located in the Chacarilla Formation in an eponymous canyon about 40 km southeast of the town of Pica (Galli and Dingman1962; Fig. 1). Galli and Dingman (1962) referred to this particular tracksite as their "second locality" with theropod and ornithopod footprints. Rubilar-Rogers et al. (2008) recently described in detail the theropod tracks from this site and referred to it as "Chacarilla III". The Chacarilla Formation is entirely sedimentary with a minimum exposed thickness of 1100 m. It is divided in two unnamed units: a lower marine unit (Oxfordian; Galli and Dingman 1962), and an upper continental unit, in which the dinosaur footprints are recorded. This last unit is overlain by clastic sedimentary and volcanic rocks of the Cerro Empexa Formation (Late Cretaceous–Paleocene; Galli and Dingman 1962; Tomlinson et al. 2001) in an angular unconformity. The continental unit is intruded by Cenomanian-age dikes and plutons (99–94 Ma; Hammerschmidt et al. 1992). In addition, an unpublished Ar40/Ar39 plateau age on hornblende from an andesite lava, of 114.3 ± 2.0 Ma (2-sigma), taken at the sedimentary sequence of Cuesta de Montecristo Sequence (unpublished data, AJT) which conformably overlies Chacarilla-correlative, continental red-beds northeast of Antofagasta (Moreno et al. 2004), suggests that the Chacarilla Formation is not younger than Aptian. Combined, these observations indicate an age range of Late Jurassic to late Early Cretaceous for the entire Chacarilla Formation. The track-bearing beds are located near the top of the formation. They constitute a 140-m

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thick layer of interbedded shale and red sandstone (Fig. 2), which were deposited in point bars and floodplains of a meandering river environment (Blanco et al. 2000). Given the presence of large ornithopod footprints, the track-bearing unit has been assigned a maximum Early Cretaceous age (Blanco et al. 2000). The dinosaur footprints are in mudstone of the floodplain facies and occur along with plant remains and rooted stump casts. Sedimentary structures in this unit, such as complex channels, indicate palaeoflow toward the west-southwest.

Material and methods

All tracks from the Querulpa Chico and Chacarilla localities are preserved as negative epichnia (concave impressions). We took the following in situ measurements: pace and stride length, pace angulation, trackway direction, and footprint anteroposterior length and mediolateral width (Fig. 3, Table 1). In addition, we made latex molds and plaster casts of the best-preserved footprints. A cast of a Peruvian footprint is stored in MUSM (MUSM 1679); casts of the Chilean footprints are stored at SERNAGEOMIN (SNGM-311 to 317) and at SGOPV (SGOPV 1042 to 1047). The theropod identities of the trackmakers were established using traits that distinguish theropod from ornithopod tracks as outlined by Thulborn (1990) and Farlow and Chapman (1997).

Theropod dinosaur footprints.—Typically tridactyl, mesaxonic, with the impression of digit III considerably larger than either digit II or IV; digits divergent; presence of claw marks with sharp edges that are medially directed for digits II and III and laterally directed for digit IV; presence of an indentation along the medial margin of the footprint (at the base of digit II). Occasionally, theropod footprints exhibit tarsometatarsal impressions, which elongate the posterior margin of the ichnites, and/or hallux (digit I) impressions as a narrow mark at the base of digit II.

Large ornithopod dinosaur footprints.—Tridactyl, mesaxonic, with the lengths of digits II, III, and IV only slightly different; wide digits with rounded ends; digits converge proximally into a broad metatarsophalangeal impression ("heel pad"). Ornithopod ichnites are similar in anteroposterior and mediolateral dimensions, and their general shapes resemble a clover.

Description of the theropod dinosaur footprints

Querulpa Chico tracksite, Peru.—Eleven trackways, labelled A to K, comprising at least 67 footprints are exposed in the main trackbed (Figs. 4, 5; Table 1). Seven of the trackways (A, B, D–G, and I) consist of large theropod footprints, most of them well preserved. Footprints in these trackways are tridactyl or tetradactyl and mesaxonic, with length and width ranging between 51–65 cm and 41–54 cm, respectively. When present, hallux impressions are laterally directed. Almost all digits bear claw marks but lack clear digital pad impressions. The stride length ranges between 230 and 297 cm while the pace angulation varies between 133° and 166°. The other four trackways (C, H, J, and K) consist of smaller tridactyl theropod footprints, most of which are poorly preserved; a notable exception is footprint C4 (Fig. 5). These footprints are almost as wide as long (25–28 cm long and 26–28 cm wide). Although, the absence of morphological details precludes a confident description of the tracks, it is clear that they belong to theropod dinosaurs given the presence of claw marks and the fact that digit III is about 20–30% longer than digit II and IV. The average divarication angle between digits II and IV is 62°, ranging from 46° to 77°, which is also typical of theropods. The trackways are relatively narrow and have high pace angulations (166–173°); the stride length varies between 210 and 285 cm. Eight of the eleven trackways exhibit a preferred east-west orientation. Trackways B, C, D, and E head eastward and trackways F, H, I, and K head westward. In contrast, trackways A and G head south and trackway J heads north.

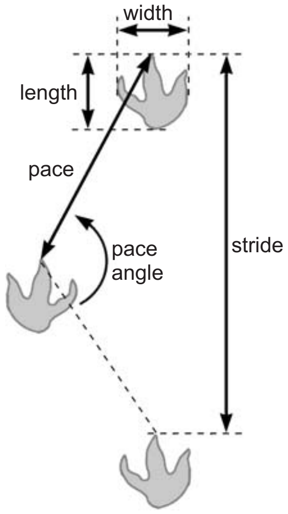

Fig. 3. Measurements taken in situ on footprints and trackways. Anteroposterior track length: distance between the distal tip of digit III and the proximal boundary of the sole; mediolateral track width: distance between the distal tip of lateral digits measured perpendicular to the track axis; pace angle: angle formed by the two segments joining three consecutive tracks; pace, distance between two consecutive tracks; stride length: distance between two consecutive tracks on the same side (left or right) of the trackway.

There are variations in footprint morphology between different trackways, but also within the same trackway due to differences in substrate consistency (Jackson et al. 2010), pedal kinematics, and timing between the passings of trackmakers. For example, in trackway A, the longest trackway (12 footprints), the first eight footprints (A1–A8) are deeper than the subsequent footprints and have hallux impressions. Footprints A1–A4 have wide digit impressions, while footprints A5–A8 have digit impressions about a third narrower.

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Table 1. Measurements of theropod footprints and trackways from Querulpa Chico and Chacarilla. Hip height calculated as 4.5 and 4.9 times the footprint length for small and large theropods, respectively (Thulborn, 1989). Speed estimated according to Alexander (1976): speed (km/h) = 2.817 × (stride in m) $^{1.67}$ × (hip height in m) $^{-1.17}$. N, the number of footprints in the trackway; SD, standard deviation.

Trackway	N	Length (cm)	Width (cm)	Pace (cm)	Pace angle (°)	Stride (cm)	Hip height (cm)	Stride/Hip height	Speed (km/h)
Querulpa Chico									
Large theropods									
A	12	58	45	130	133	230	284	0.8	3
B	6	65	45	148	166	297	319	0.9	4
D	7	64	54	130	148	250	314	0.8	3
E	7	59	41	124	150	234	289	0.8	3
F	5	59	46	139	161	271	289	0.9	4
G	5	58	50	139	162	271	284	1.0	4
I	7	51	45	147	166	283	250	1.1	5
Average ±1SD		59 ±5	47 ±4	134 ±9	155 ±12	262 ±25	290 ±23	0.9 ±0.1	4 ±1
Small theropods									
J	4	26	28	110	166	210	117	1.8	8
K	4	25	27	114	171	224	113	2.0	9
H	5	28	26	127	173	264	126	2.1	11
C	5	25	28	142	168	285	113	2.5	14
Average ±1SD		26 ±1	27 ±1	123 ±14	170 ±3	246 ±35	117 ±6	2.1 ±0.3	11 ±3
Chacarilla									
Large theropods									
3	8	33	21	117	180	234	162	1.4	7
4	8	34	27	120	180	241	167	1.4	7
5	6	31	29	117	178	234	152	1.5	7
6	1	55	37		176		270		
8	3	50	44	155	176	285	245	1.2	6
10	6	35	25	115	180	230	172	1.3	6
12	9	40	36	132	180	252	196	1.3	6
13	5	63	46	138	180	265	309	0.9	4
15	7	60	45	160	180	307	294	1.0	5
16	6	65	45	125	180	273	319	0.9	4
Average ±1SD		47 ±13	36 ±9	131 ±17	179 ±2	258 ±27	228 ±66	1.2 ±0.3	6 ±1
Small theropods									
17	6	23	22	116	180	232	104	2.2	11
18	2	16	13	61			72		
Average ±1SD		19 ±5	17 ±7	89 ±39			88 ±22		

The remaining A9–A12 footprints are tridactyl and display wide, posterior imprints (Figs. 4, 5). Track overprinting indicates that trackway A was later crossed by trackway D, which is also composed of footprints with hallux impressions. Trackway D displays long, deep tarsometatarsal impressions (Figs. 4, 5), a feature that is absent from the other trackways. Trackway F, which was registered later (based on track overprinting), is composed of shallow and narrow tridactyl footprints (Figs. 4, 5). The presence of displacement rims on some of the footprints (Fig. 5) indicates that the trackbed was one of the closest layers to the surface on which the animals walked (Allen 1997; Gatesy 2003). However, further confirmation of the layer as actual track surface is lacking due to the absence of other key indicators, such as skin impressions or sediment ejections.

We estimated the speed of theropod locomotion using the equation by Alexander (1976) derived from observations of modern animals and the conversion factor between foot length and hip height recommended by Thulborn (1989) for theropods. The results of the calculation shown in Table 1 indicate that large theropods were probably walking (3 to 5 km/h), while small theropods were moving about 2–3 times faster (8 to 14 km/h).

Chacarilla tracksite, Chile.—The fourteen trackways of the Chacarilla III tracksite consist of 76 individual footprints (Fig. 6). Two of the trackways (numbered 1 and 7) consist of large ornithopod footprints (average footprint length 39 cm and average width 32 cm). Two other trackways (17 and 18) consist of small theropod footprints (<25 cm long). The other ten trackways (3–6, 8, 10, 12, 13, 15, 16) were made by large

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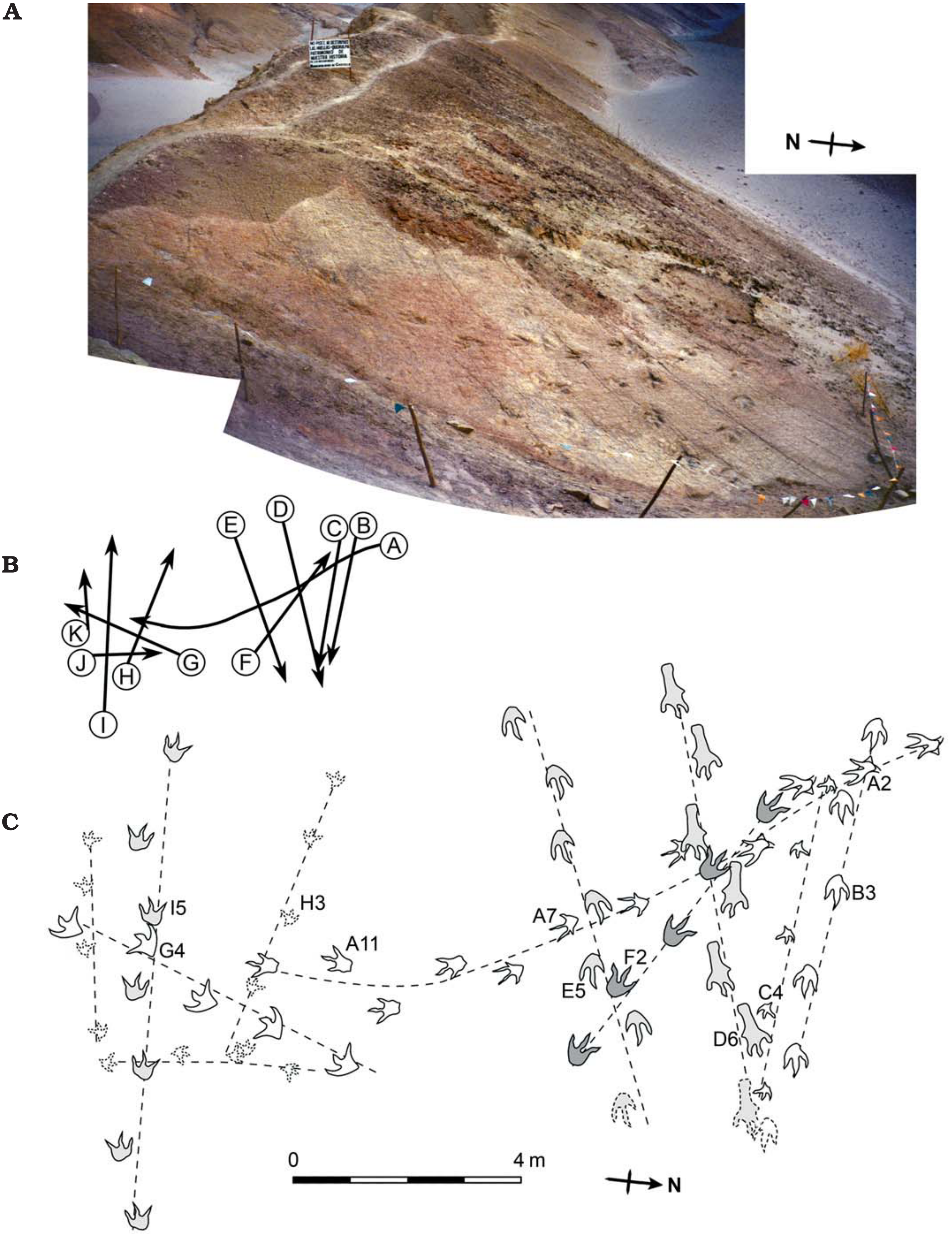

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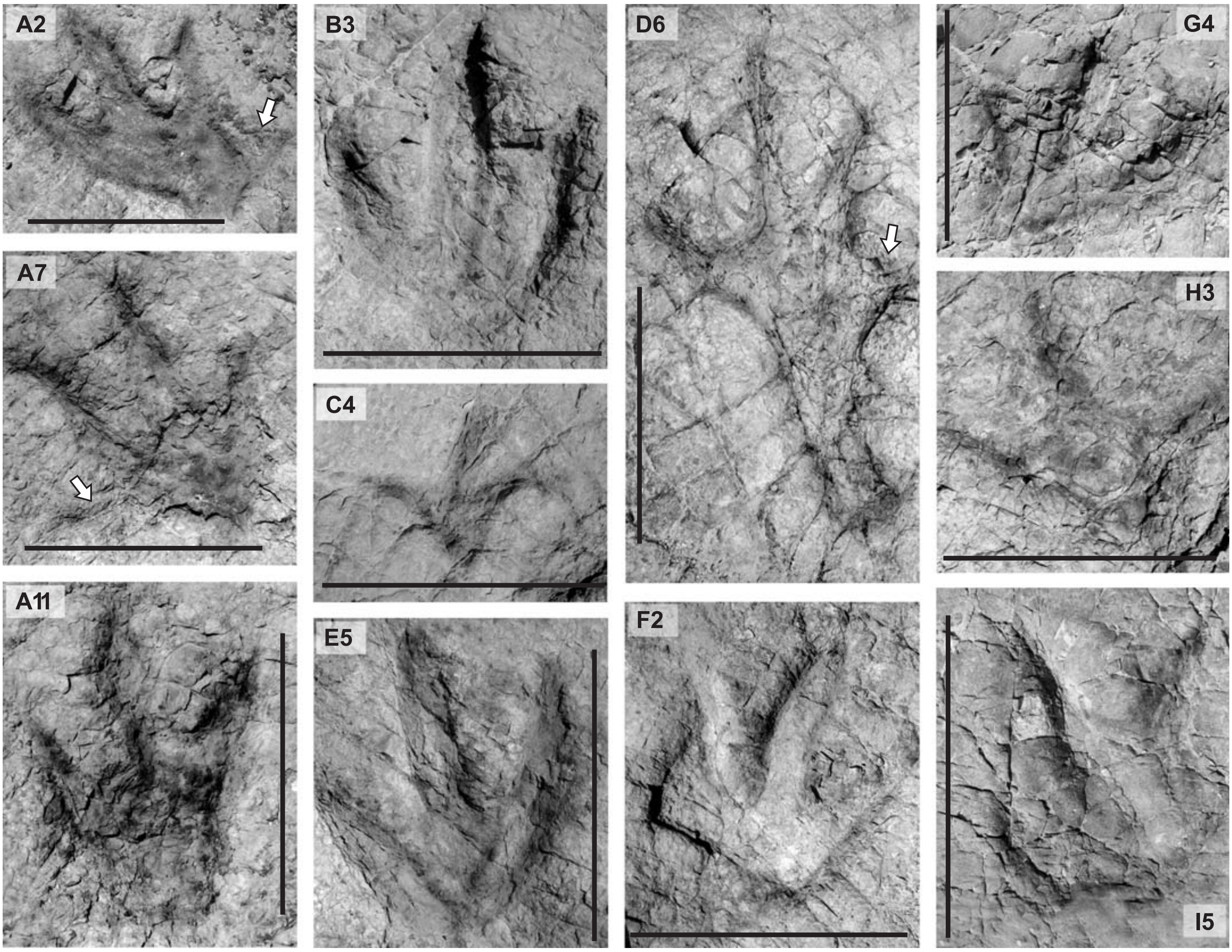

Fig. 5. Photographs of Early Cretaceous theropod footprints from the Querulpa Chico tracksite, Peru. A–I refer to the individual trackways in Fig. 4, and the number to the particular print in the trackway. Arrows point to hallux impressions. Scale bars 0.5 m.

theropods (footprint length >30 cm). The large theropod tracks are tri- and tetradactyl, mesaxonic, and have length and width between 31–65 cm and 21–46 cm, respectively. As with the theropod tracks from Peru, nearly all digit impressions possess claw marks, but they lack clear impressions of digital pads. The stride length varies between 230–307 cm, a range that is similar to the one derived for large theropods in the Querulpa Chico tracksite. The pace angle is 179 ± 2°, which is about 10% higher than the average pace angle for large theropods in the Peruvian site. This slight difference may be linked to the fact that the large theropods of the Chacarilla site were, on average, slightly smaller animals (hip 20% shorter) and were walking faster (4–7 km/h; Table 1).

← Fig. 4. Querulpa Chico tracksite, Peru. **A**. Panoramic photograph of the Querulpa Chico tracksite. **B**. Schematic map of the trackway directions and their relative positions. **C**. Distribution of the trackways in the main Querulpa Chico trackbed. A–K refer to particular trackways, and the associated numbers to the individual prints in the trackways.

Most of the trackways show no preferred orientation, with the exception of trackways 3 and 4, which are parallel and about 0.8 m away from one another. Interestingly, these two trackways exhibit similar pace lengths and footprint morphologies (Table 1; Fig. 6). In both trackways, the impression of digit III constitutes about 50% of the total footprint length. As shown in Fig. 6, both trackways were later crossed perpendicularly by three other trackways (1, 2, 5). Dinoturbation of the track surface is high in some areas (Fig. 6) and sediment consistency of the trackbed appears to have varied over time. For example, trackway 15, which consists of deep footprints, was later crossed by the shallower trackways 16 and 17. The continuity of trackways is also occasionally broken by multiple intersections of trackways (e.g., trackway 6). Some footprints were altered by overprinting, such as the second footprint of trackway 13, which overlapped and modified the edge of the second footprint of trackway 12. Ripple marks are present not only all across the trackbed, but also inside some of the footprints. This indi-

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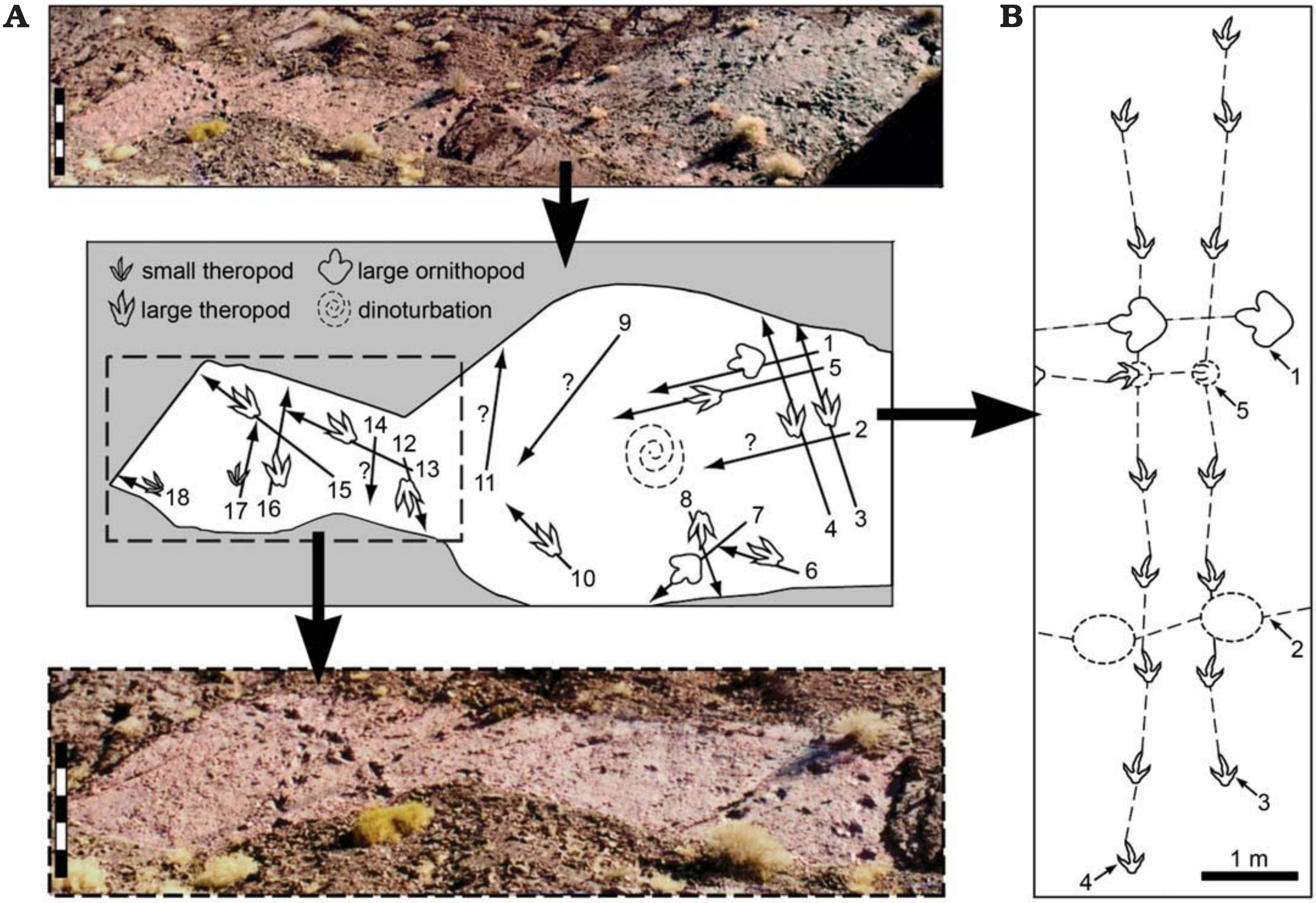

Fig. 6. Early Cretaceous Chacarilla tracksite, Chile. **A**. Line drawing and photographs of the Chacarilla theropod tracksite, showing orientations and distribution of trackways. **B**. Schematic map of trackways 3 and 4, crossed perpendicularly by trackways 1, 5 and 2 (unidentified trackway). Scale bars in A 5 m.

cates that moving water was present during and/or after the incursions of the trackmakers. This observation, together with the presence of displacement rims, suggests that the trackbed was the actual layer on which dinosaurs walked or a layer located right beneath it.

Discussion

The relatively high abundance of trackways of large theropods in Querulpa Chico and Chacarilla suggests that these dinosaurs had overlapping home ranges in the surrounding areas of each site. The morphological differences among footprints and trackways indicate that the tracks cannot be attributed to just one individual repeatedly visiting the site. Although uncertainties remain concerning the time interval over which the trackways were recorded, our study pinpoints the likelihood that distinct large carnivores frequently visited the studied areas. The inferred frequency seems unlikely for single hunters with exclusive territorial behaviour. It is, however, difficult to relate observed trackways to grouping behaviour. Indeed, the trackways investigated here do not display typical patterns of gregariousness such as those observed for herds of herbivorous dinosaurs: parallel trackways, approximately constant distances between trackways, same direction of movements (e.g., Ostrom 1972; Lockley et al. 2002). Instead, the orientation of the large theropod trackways appears mostly random, suggesting limited interactions between the trackmakers. However, strong relationships between trackways have been observed in one instance, i.e., between trackways 3 and 4 of the Chacarilla III locality (Fig. 6). The geometry of these two trackways supports pairing of two equally large theropods. Overall, our observations indicate that trackmakers were either solitary hunters with no exclusive territoriality or disorganized groups of gregarious individuals attached to one territory. Supporting evidence for the second hypothesis comes from recent skeletal and footprint studies in Argentina (Porfiri et al. 2007), North America (Varriccio et al. 2008; Currie and Eberth 2010), and Africa (Lingham-Soliar et al. 2003).

Fluctuating water levels in the tidal basin environment of the Querulpa Chico tracksite and inundation events in the floodplain environment of the Chacarilla tracksite likely facilitated the preservation of the footprints, and probably provided a preferential habitat for these animals. Palaeoclimatic studies indicate that southern Peru and northern Chile experienced arid to semiarid conditions at least since the Late Ju-

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rassic (Hartley et al. 2005) and that a wet-summer climatic belt was limited to areas further north (Philippe et al. 2003). It is likely that the presence of water in these dry areas would have attracted the fauna. This way, climatic and perhaps geographical constraints may have favoured interactions between non-gregarious large theropods. Although many of the other tracksites displaying large theropod footprints were recorded in similar depositional environments worldwide, none shows a high density of large theropod trackways (e.g., Alonso and Marquillas 1986; Calvo 1991; Leonardi and Spezzamonte 1994; Lockley and Hunt 1994; Thulborn 2001; Moreno and Pino 2002; Moreno and Benton 2005; Mossman et al. 2003; Mateus and Milàn 2010). Interestingly, climatic conditions corresponding to these other tracksites range from subtropical to temperate, hence not as arid as the conditions at Querulpa Chico and Chacarilla. This comparison further suggests a possible link between climate and the observed concentration of theropods.

Large (>0.3 m long) theropod dinosaur footprints are known from several Late Jurassic–Cretaceous localities in South America, including Argentina (e.g., Alonso and Marquillas 1986; Calvo 1991; Calvo and Mazzetta 2004), Brazil (e.g., Leonardi and Spezzamonte 1994; Leonardi and Santos 2004), Chile (Moreno et al. 2004; Rubilar-Rogers et al. 2008), and recently in Bolivia (Apesteguía and Gallina 2011) (see also reviews by Leonardi 1994 and Weishampel et al. 2004). The Peruvian Querulpa Chico trackways now expand that list. Moreover, our observations from the Querulpa Chico and Chacarilla tracksites confirms a previous report by Moreno et al. (2004) from a tracksite located near Calama 270 km south of Chacarilla that large theropods were living on the western border of the Gondwana supercontinent during the Late Jurassic–Early Cretaceous period. The Querulpa Chico site, therefore, expands the geographic distribution of large theropods almost 800 km to the north. In the absence of bone remains in the fossil record, the Querulpa Chico, Chacarilla and Calama tracksites are the sole indication for the presence in western Gondwana of large theropod dinosaurs.

Large carnivorous dinosaurs in South America with sizes comparable to those of the Peruvian and Chilean trackmakers, as estimated from the footprint length (hip height up to 3 m), pertain to spinosaurids and carcharodontosaurids, for which bone remains are known from the Aptian to the Santonian of Argentina and Brazil (e.g., Coria and Salgado 1995; Kellner and Campos 1996; Coria and Currie 2002, 2006; Candeiro et al. 2004; Novas et al. 2005; Medeiros 2006; Salgado et al. 2009). We should mention that known abelisauroids from the Early Cretaceous have feet smaller than 0.3 m and therefore could not have produced the large footprints recorded in the Querulpa Chico, Chacarilla and Calama tracksites (e.g., Coria et al. 2002, Calvo et al. 2004). Because these three tracksites are slightly older than the bone record of spinosaurids and carcharodontosaurids, they suggest an earlier arrival of such large theropods in western Gondwana. This confirms previous hypotheses of Apesteguía and Gallina (2011) and Rauhut (2004). Therefore, the Querulpa Chico, Chacarilla and Calama tracksites are together with the Berriasian–Barremian tracksites from Northestern Brazil (e.g., Leonardi and Spezzamonte 1994; Leonardi and Santos 2004) the oldest sites in South America evidencing the presence of large theropods. This observation contrasts with findings from Africa, where large theropods were already present during the Middle and Late Jurassic (e.g., Lingham-Soliar et al. 2003; Belvedere et al. 2010, Wagensommer et al. 2010).

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