A comparison between dinosaur footprints from the Middle Jurassic of the Isle of Skye, Scotland, UK, and Shell, Wyoming, USA

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Synopsis

Measurements of Middle Jurassic tridactyl dinosaur tracks from the Bathonian, Lealt Shale, Valtos Sandstone, Duntulm and Kilmaluag formations of the Isle of Skye, UK, are compared to the same measurements taken for dinosaur footprints from the Bajocian, Gypsum Spring and the Bathonian, Sundance Formation of the Bighorn Basin, Wyoming, USA. Principal component analysis of the data suggests that the smaller footprints from the Valtos Sandstone and Kilmaluag formations are indistinguishable from the footprints of the Sundance Formation. The single footprint from the Lealt Shale Formation is similar to the larger footprints from the Valtos Sandstone Formation. The footprints from the Duntulm and Gypsum Springs formations form distinct groupings from all other footprints. Four different groupings of dinosaur footprints can be recognized from the principal component analysis that may represent at least four different types of dinosaur.

Introduction

Dinosaur footprints are well known from the Middle Jurassic rocks of the Isle of Skye, Scotland, UK (Clark & Barco Rodriguez 1998; Andrews & Hudson 1984; Clark *et al.* 2004, 2005; Marshall 2005) and the Big Horn Basin, Wyoming, USA (Kvale *et al.* 2001, 2004; Breithaupt *et al.* 2004) (Fig. 1).

The first recorded occurrence of dinosaur remains on the Isle of Skye was the discovery of a large 49 cm long footprint from the Lealt Shale Formation (Bathonian) at Rubha nam Brathairean in 1982 (Andrews & Hudson 1984; Delair & Sarjeant 1985) (Fig. 2(1)). In 1996, further footprints were found on a fallen block of the overlying Valtos Sandstone Formation (Bathonian) near to the original locality (Clark & Barco Rodriguez 1998; Clark 2001*a*, 2004, 2005). Other footprints from the Valtos Sandstone Formation have been found at Dun Dearg and Kilt Rock, near Valtos (Clark *et al.* 2005) (Fig. 2(2, 3)) and from a locality north of Elgol in the southern part of the Isle of Skye (Marshall 2005) (Fig. 2(6)). The footprints from both these locations are much smaller (<30 cm length) and have triangular claw impressions rather than the broad spatulate digits of the first recorded footprint from the Lealt Shale Formation. Further footprints have been found since then in the Duntulm Formation (Bathonian) at An Corran, Staffin Bay (Fig. 2(4)) and the Kilmaluag Formation (Bathonian) at Score Bay, north of Uig (Clark 2003, 2005; Clark *et al.* 2004, 2005) (Fig. 2(5)). The Duntulm Formation footprints are all large footprints up to 53 cm in length with narrow digits and triangular claw impressions (Clark *et al.* 2004). These also differ from the Lealt Shale Formation footprint and are thought to have been produced by a large theropod. In late 2002, dinosaur footprints from the Kilmaluag Formation were discovered on loose blocks of sandstone, as well as *in situ,* on the foreshore at Lub Score, NW Trotternish Peninsula, Isle of Skye. The majority of these footprints are less than 14 cm long, and are closely associated with larger footprints (about 22 cm long) of what seems likely to be the same ichnospecies (Clark *et al.* 2005). These footprints are stratigraphically younger than any other dinosaur remains found in Scotland.

Dinosaur bones are also known from Scotland. A theropod tibia was found in the Broadford Beds Formation (Hettangian) in the Strathaird Peninsula, southern Isle of Skye (Benton *et al.* 1995), a thyreophoran ulna and radius came from the Bearreraig Sandstone Formation (Bajocian) at Bearreraig Bay, northern Isle of Skye (Clark 2001*b*), and cetiosaur bones and a coelophysoid-grade tail bone were discovered in the Valtos Sandstone Formation (Bathonian) at Dun Dearg near Staffin (Clark *et al.* 1995, 2004; Liston 2004). The latest discovery has been of a sauropod tooth from the Kilmaluag Formation (Bathonian) near Glen Scaladal, north of Elgol, Isle of Skye (Barrett 2006).

In Wyoming, footprints from the Middle Jurassic are known from the Gypsum Springs Formation (Bajocian) and the Sundance Formation (Bathonian) in the Bighorn Basin, northern Wyoming (Kvale *et al.* 2001, 2004; Mickelson *et al.* 2006) (Fig. 3). The best known tracksite is the Sundance Formation Red Gulch Dinosaur Tracksite (discovered by Cliff Manuel of Shell) (Fig. 3(2)) between Greybull and Shell on Bureau of Land Management property, Wyoming (Breithaupt 2001),

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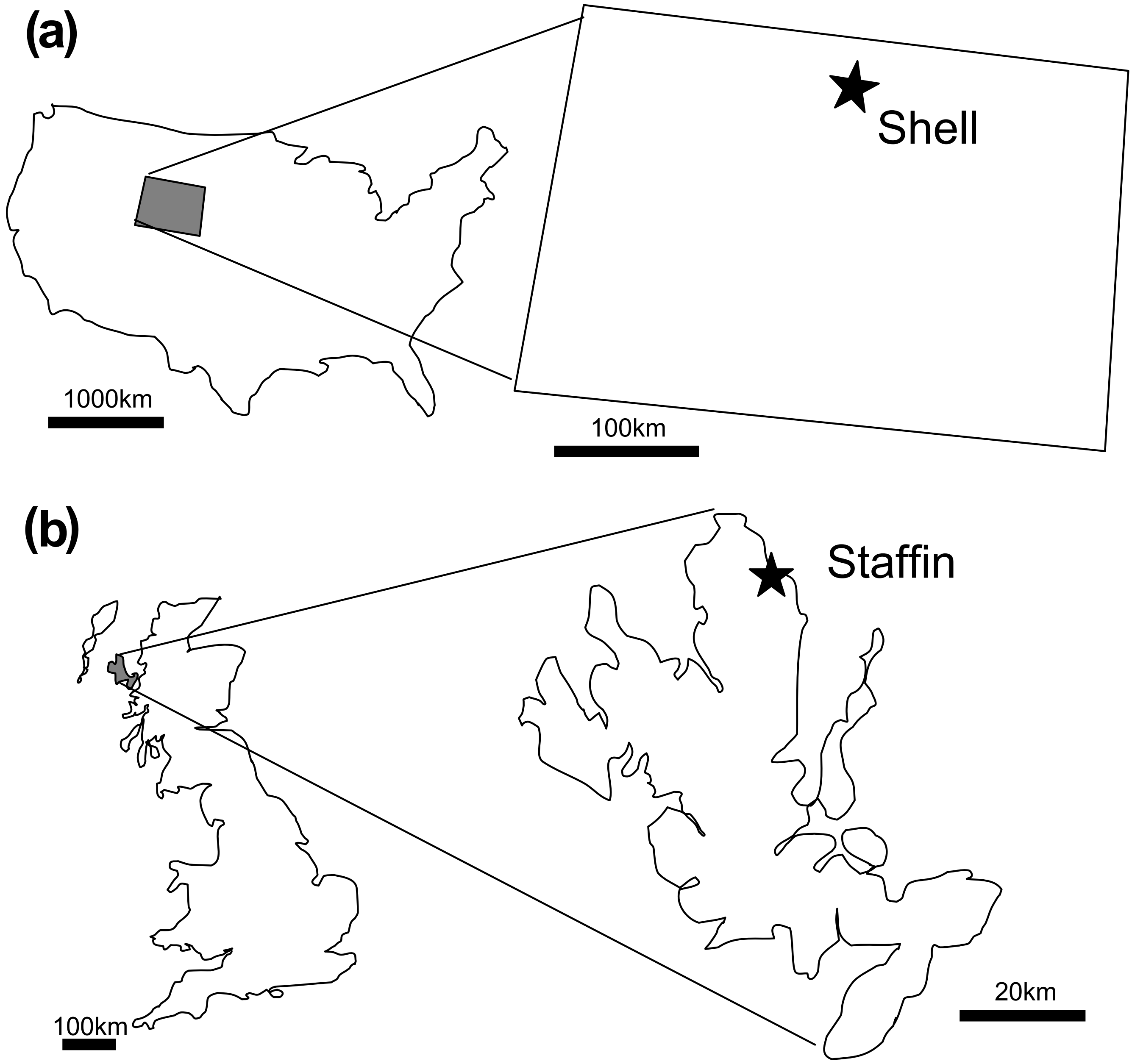

FIG. 1. (a) Map of the United States of America showing location of Shell, Wyoming. (b) Map of Great Britain showing location of Staffin, Isle of Skye.

although further localities also include the 'Yellow Brick Road' (which is on Wyoming State land and was discovered by Rowena Manuel of Shell (Fig. 3(4)) (Adams & Breithaupt 2003) and Flitner Ranch (which is on private land (Fig. 3(3)) tracksites. All the Sundance Formation tracksites seem to occur in the Canyon Creek Member if the basal Sundance Formation (Harris & Lacovara 2004; Kvale *et al.* 2004). There are other equivalent horizons to the Sundance Formation in Utah from which dinosaur footprints are also known (Lockley *et al.* 1998; Hamblin & Foster 2000; Kvale *et al.* 2004).

The Gypsum Spring Formation footprints are similar sized tridactyl dinosaur footprints although the hallux impression is sometimes visible (Kvale *et al.* 2001) are Bajocian in age. The northernmost Gypsum Spring Formation site was discovered by Erik Kvale in about 1997 (Fig. 3(1)).

Methods

The footprints used in this analysis are from the Trotternish Peninsula, Isle of Skye and include examples from the Lealt Shale, Valtos Sandstone, Duntulm, and Kilmaluag formations. The footprints from the Valtos Sandstone Formation included two sizes and varieties (one less than 15 cm in length with narrow digits and triangular terminations and the other over 25 cm in length with broad digits with rounded terminations) that were included separately in the analysis to see if they would plot differently. All dinosaur footprints from the Isle of Skye were measured from photographs taken in the field, or from photographs of samples in the Staffin Museum and Hunterian Museum collections.

Photographs of footprints used in this study from the Red Gulch, Yellow Brick Road and Flitner Ranch

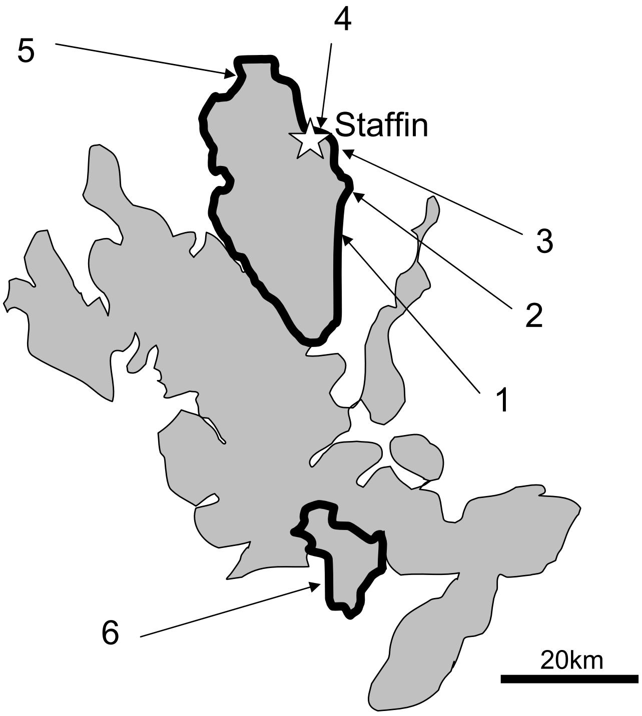

FIG. 2. Map showing the Middle Jurassic dinosaur localities of the Isle of Skye (1–5 are in the Trotternish Peninsula and 6 is in the Strathaird Peninsula; both are outlined). (1) Bearreraig Bay; (2) Rubha nam Brathairean; (3) Dun Dearg; (4) An Corran; (5) Score Bay; (6) Elgol.

dinosaur tracksite were photographed during the 2006 summer season in the field, as well as a single footprint from the Flitner tracksite at the Draper Museum of Natural History in Cody, Wyoming (the Smithsonian Institution has a mould of a six-track sequence of which footprint no. 1 is in the Draper Museum and footprint no. 4 was also collected (USNM 508544)). There are track sequences of more than six footprints at both Red Gulch and Flitner sites, but the majority of the rest are individual footprints.

A landmark analysis was carried out on the footprints using five points (Fig. 4a). The landmarks chosen were the tips of the digits, not including claw impressions, the back of the ‘heel’ (back end of the footprint produced in the plantigrade posture (Thulborn 1990, fig. 4.6a), not including any hallux impressions, and the posterior of the proximal node of digit III. Landmark data were produced from the photographs using tpsDig version 2 (Rohlf 2004). The resulting polygons were analysed by flipping the left-handed footprints to allow a direct shape comparison, and performing a 2D procrustes transform to eliminate orientation and size anomalies using PAST version 1.57 (Hammer *et al.* 2001, 2007). The polygons were then subjected to principal component analysis using PAST version 1.57 (Hammer *et al.* 2001, 2007) to compare the footprints from the different localities.

Principal component analysis was also carried out on five different measurements using PAST version 1.57 (Hammer *et al.* 2001, 2007) (Fig. 4b). A 2D procrustes transform was also done to eliminate size anomalies. The measurements included the width between the distal points of digits II and IV ($W_{II–IV}$); the length from the line between the distal points of digits II and IV and the distal point of digit III (h_{III}); the length between the ‘heel’ impression and the line between the distal points of digit III (pL); the length between the posterior point of the proximal phalange of digit III and the distal point of digit III (L_{III}); and the angle between the distal points of digits II, III and IV (α) (Fig. 4b, Tables 1, 2, 3). None of these measurements included the claws as the length of the claw impressions can vary greatly depending on the amount of drag as the animal moves, and is less reliable in differentiating between different trackmakers (Clark 2005). The lengths of the digit impressions and α can also be affected by drag, but do not seem to vary as much as is evidenced by the tight correlation between width/length and α in footprints from the Kilmaluag Formation (Clark 2005).

Palaeogeography and palaeoenvironments

During the Middle Jurassic, the dinosaur-bearing localities in Wyoming have been estimated as being within 15° to 20°N latitude (Kvale *et al.* 2001). In

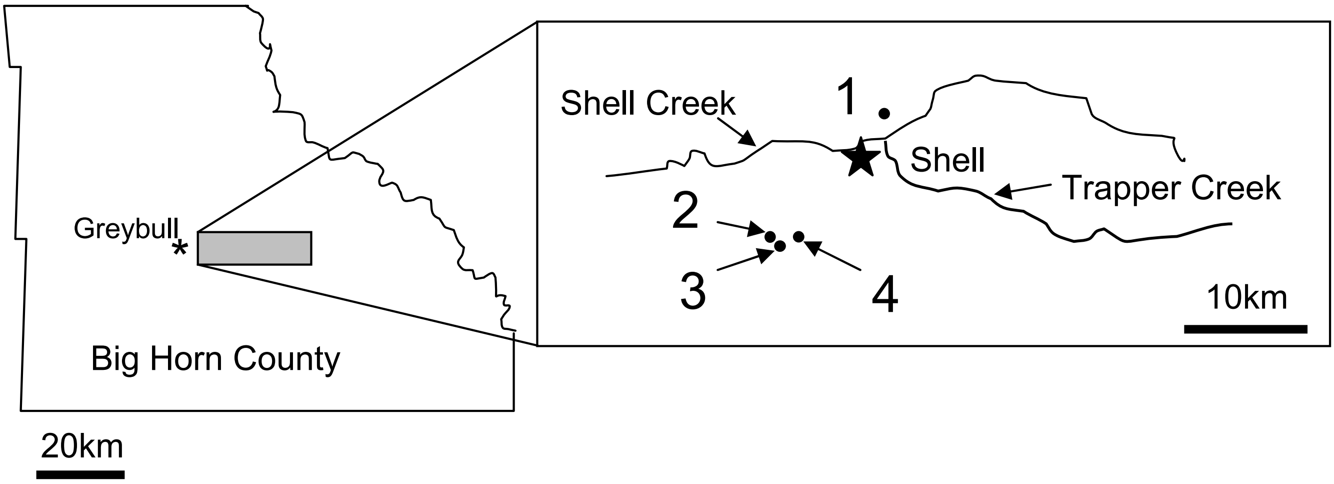

FIG. 3. Middle Jurassic footprint localities near Shell in Big Horn County, Wyoming. (1) Gypsum Springs Formation; (2) Red Gulch Tracksite; (3) Flitner Ranch Tracksite; (4) Yellow Brick Road.

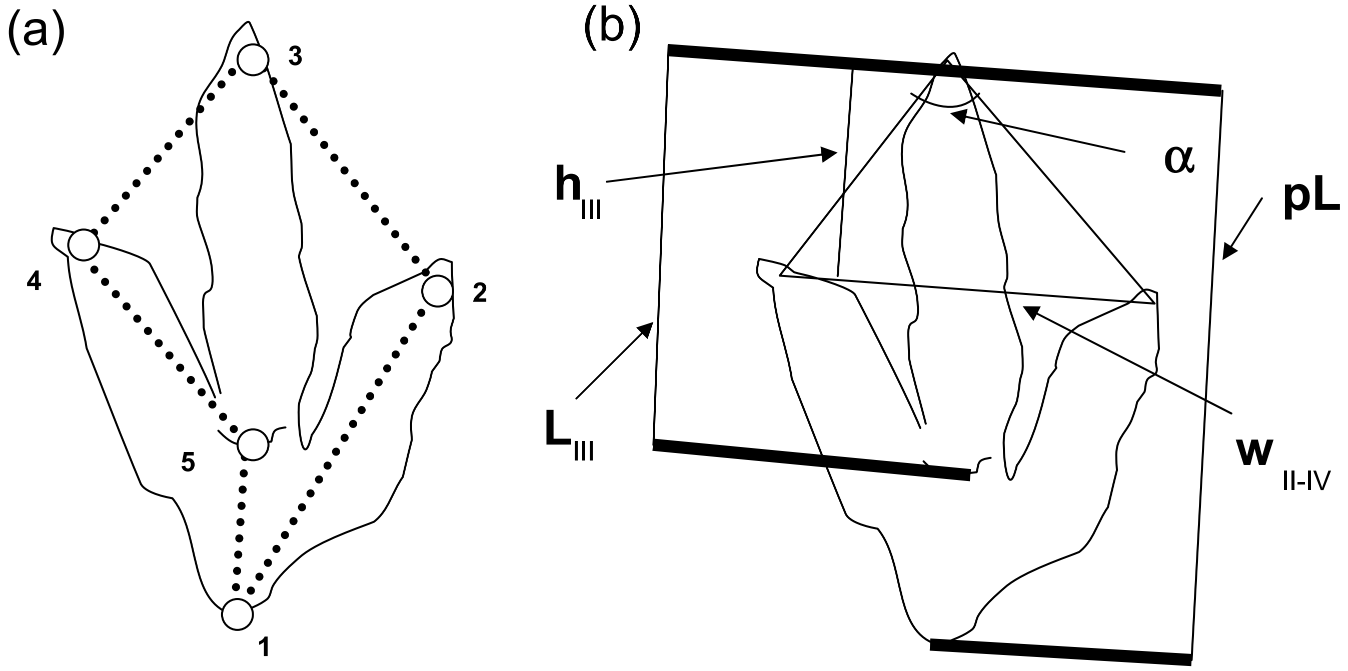

FIG. 4. (a) Points used for landmark analysis. (b) Measurements taken of footprints for comparison: h_{III}, perpendicular length of digit III from $W_{II–IV}$; L_{III}, length of digit III; $W_{II–IV}$, distance between the apices of digits II and IV; pL, footprint length; α, angle between digits II, III and IV.

Scotland, the palaeolatitude was probably between latitude 35° and 45°N (Callomon 2003; Cecca *et al.* 2005). The distance between the localities in Scotland and those in Wyoming, during the Middle Jurassic, was approximately 4000 km (Fig. 5).

In Wyoming the palaeoenvironment was warm and dry. Although many of the footprint-bearing horizons are biomicrites with ripples suggesting the presence of water, there are also large halite pseudomorphs, especially at the Flitner Ranch site, indicating periods, perhaps seasonal, of evaporation (Kvale *et al.* 2001). *Rhyzocorallium* and *Diplocraterion*, from the overlying sediments, disturb the footprint surface at the Red Gulch tracksite locality (Kvale *et al.* 2001). These trace fossils are also found associated with the Duntulm and Kilmaluag Formation footprints on the Isle of Skye (Clark *et al.* 2004). The dinosaurs in Wyoming lived in a seasonally arid environment during the Middle Jurassic of both the Gypsum Springs and Sundance formations (Kvale *et al.* 2001).

In Scotland, the depositional environment during the Lealt Shale Formation, as well as the Duntulm Formation, is interpreted as being dominated by brackish marine lagoon conditions (Harris & Hudson 1980; Andrews & Walton 1990). The Valtos Sandstone Formation is thought to have been more fluvio-deltaic with the footprints associated with a period of emergent desiccation indicated by mudcracks. The footprint-bearing sediments of the Valtos Sandstone Formation are calcareous sandstones containing abundant bivalves (Clark & Barco Rodriguez 1998). The Kilmaluag Formation footprint-bearing sediments were deposited in a more freshwater lagoonal setting with abundant marls and mudstones; the footprints are found at two horizons within a single sandstone unit at two localities (Clark *et al.* 2005). The footprints at the base of the unit are impressed into a mud-cracked mudstone which was covered with a sandsheet. The second level is 14 cm above the base where the dinosaur footprints occur in a ripple-bedded sandstone (Clark *et al.* 2005).

The sediments and palaeontology at the Wyoming localities appear to suggest that the dinosaurs lived closer to a marine shoreline in a seasonally arid environment, whereas the dinosaurs at the Scottish localities lived in a deltaic environment with brackish and freshwater lagoons that were prone to occasional reduction in size due to desiccation (Kvale *et al.* 2001; Clark *et al.* 2005).

Results

It was hoped that, using landmark analysis, it would be possible to distinguish between tridactyl dinosaur footprints on the basis of five landmarks. All the landmark data from Wyoming (n=58) and Scotland (n=48) were analysed using principal component analysis, but it was not possible to distinguish between the different forms with confidence (Fig. 6). All the 95% confidence circles overlap substantially and the 95% confidence circles for the Kilmaluag and Sundance formations contain over 96% of the data. It was hoped that the larger footprints of the Duntulm (Fig. 7c), Lealt Shale (Fig. 7a) and Valtos Sandstone formations would plot differently to the smaller Sundance (Fig. 8a–c), Gypsum Spring (Fig. 8d), Kilmaluag (Fig. 7d), and Valtos Sandstone (Fig. 7b) formations. Only the larger footprints from the Lealt Shale and Valtos Sandstone formations appeared to deviate slightly from the other footprints (Fig. 9d). Further discoveries of these larger footprints

TABLE 1

Measurements taken from the footprints of the Kilmaluag Formation. Each field identifier refers to an individual footprint (see Fig. 4 and text for definitions of measurements).

	$w_{II–IV}$ (cm)	h_{III} (cm)	pL (cm)	L_{III} (cm)	α (degrees)
KF1a	7.6	5	11.7	8.1	70
KF1b	7.5	4.8	11.3	8	78
KF1c	8.1	5.4	11.4	8.1	74
K2a	14.5	8.5	20.8	14.3	83
K2b	6.6	3.4	9.2	8.6	90
K2c	6.3	2.8	8.4	6.1	72
K2d	4.7	3.1	7.4	5.4	75
K2e	5.8	3.7	8.4	5.8	77
K2f	5.4	3.5	8.3	6.3	78
K2g	6.1	4.5	9.9	7.8	75
K2h	5.9	3.3	8.1	5.9	82
K2i	6.2	3.6	9.3	6.5	80
K2j	6.5	5	10.7	7.2	80
K2k	10.7	6.5	13.5	10.4	80
K2l	5.6	3.6	8.2	5.4	83
K2m	6.2	4.4	9.6	6.5	75
K2n	6.1	3.6	8.8	6.1	78
K2o	6.3	3.9	9.2	6.7	78
K2p	6.5	4	9.8	6.2	77
K2q	6.8	3.5	9.5	5.9	84
K2r	8.9	5	13.8	9.3	85
K2t	5	3.1	8.5	6	77
K2u	5.2	3.9	8.7	7	72
K2v	6.2	4.1	8	6.7	78
K2w	5.4	3.4	9.4	6.3	76
K2x	6.6	4.3	9.6	7.3	82
KF3a	6.2	2.8	7.6	6.5	94
KF3b	1.2	0.7	1.8	1.6	78
KF3c	1	0.7	1.8	1.5	70
KF4	9.7	6	16.7	11.1	78
KF5	10.4	5.6	17.8	12.1	80
KF6	6	3.5	8.4	6.2	82
KF7	13.1	7.6	22.4	14.7	82
KF9a	19.2	12.6	27	20	92
KF9b	4.8	2.9	6.8	5.1	82
KF9c	5.6	3.6	10.7	7.4	80
KF9d	5.6	3.7	9.2	6.9	77
KF9e	7.7	4.2	11.4	8	84

TABLE 2

Measurements taken from the footprints of the Sundance Formation. Each field identifier refers to an individual footprint (SI refers to footprints in the collections of the Smithsonian Institution, Washington) (see Fig. 4 and text for definitions of measurements).

	$w_{II–IV}$ (cm)	h_{III} (cm)	pL (cm)	L_{III} (cm)	α (degrees)
YBR1	10.18	6.79	14.69	9.27	74
YBR2	10.25	9.45	17.85	13.09	83
YBR3	15.23	8.34	20.97	12.94	85
YBR4	8.76	5.81	13.29	9.24	76
YBR5	11.98	7.75	18.34	13.05	76
YBR6	8.74	6.83	13.99	10.73	68
YBR7	17.51	9.33	21.56	19.94	86
YBR8	14.44	8.75	18.77	17.67	77
YBR9	11.58	6.22	17.78	13.12	84
YBR10	17.07	8.81	20.27	15.84	86
YBR11	20.9	10.62	22.96	19.56	88
YBR12	12.71	9.29	17.97	14	82
YBR14	3.99	2.55	4.98	6.38	78
YBR15	10.47	8.31	19.45	14.57	66
YBR16	13.14	9.31	18.52	12.96	78
YBR17	10.74	7.81	19.68	15.28	74
YBR18	9.33	5.5	13.31	10.32	85
YBR19	14.36	7.68	20.82	13.87	85
YBR20	11.72	6.06	16.8	12.08	88
YBR21	9.64	6.06	13.91	11.47	82
YBR22	12.08	7.51	15.73	11.82	82
YBR24	5.72	3.85	8.75	6.55	73
YBR26	6.66	3.77	8.88	6.47	85
YBR27	14.8	7.03	16.23	12.87	91
YBR28	16.92	6.7	20.91	15.34	98
YBR29	15.38	6.6	15.9	11.89	98
YBR30	6.85	3.9	9.29	7.4	83
YBR31	14.85	8.7	17.5	15.36	82
YBR32	14.5	8.14	17.75	14.6	83
YBR33	10.94	5.04	13.72	10.69	92
YBR34	12.01	8.18	17.34	12.51	66
YBR35	7.06	3.05	9.4	7.98	98
YBR36	11.1	3.98	12.81	8.56	98
YBR37	13.58	8.16	17.76	12.94	80
YBR38	8.45	4.98	11.3	8.48	78
YBR39	10.56	5.51	13.98	10.42	88
YBR40	11.9	8.6	15.54	12.21	81
YBR41	10.5	4.17	13.8	10	98
CodyFR	16.82	9.53	19.87	15.58	92
FR1	15.48	9.05	21.11	16.34	86
FR2	20.26	9.18	19.24	14.98	93
FR3	21.87	10.31	23.93	17.98	88
FR4	26.16	8.72	28.1	18.27	91
SI508524a	12.72	7.78	18.49	13.87	84
SI508524b	10.59	6.5	14.45	10.99	77
SI508524c	11.44	7.97	17.92	12.9	76
SI508524d	10.33	6.6	13.23	11.56	84
RGTS1	16.31	12.09	26.59	19.35	77
RGTS2	9.54	7.42	17.7	12.74	74
RGTS3	14.89	10.11	25.08	16.25	78
RGTS4	13.67	7.92	23.15	14.61	88
RGTS5	18.38	8.76	29.08	22.04	98
RGTS6	20.46	10.66	26.6	21.65	84

would need to be made and added to the data for this deviation to be confirmed.

Principal component analysis of the measurements of the footprints, however, seems to be more useful in distinguishing between footprints from the various formations (Tables 4, 5, 6). The footprints of the Sundance, Kilmaluag Formation, and the smaller footprints of the Valtos Sandstone Formation, all plot in a similar position with nearly all the data from these three formations contained within the 95% confidence circle for the Sundance Formation. Briethaupt *et al.* (2007a, b) suggested that the Sundance Formation preserved a monotaxonomic community of carnivorous dinosaurs as the footprints exhibit a similar growth trend to modern emu footprints. The tight correlation of the principal component analysis of the footprints examined here

TABLE 3

Measurements taken from the footprints of the Gypsum Springs Formation (GS2–3), Duntulm Formation (DF1–8, DFs1); Lealt Shale Formation (LSF) and the Valtos Sandstone Formation (VSF). LSF1, VSF and VSF1 were similar large footprints with rounded broad digits and were analysed together. Each field identifier refers to an individual footprint (see Fig. 4 and text for definitions of measurements).

	$w_{II–IV}$ (cm)	h_{III} (cm)	pL (cm)	L_{III} (cm)	α (degrees)
GS2a	11.97	13.06	25.73	17.57	49
GS2b	9.03	10.12	19.74	14.56	50
GS3	10.19	8.92	22.39	17.11	61
DF1	26.9	16.73	39.21	32.2	86
DF2	35.7	14.69	48.07	36.5	88
DF3	22.8	15.29	37.4	25	81
DF4	29.4	23.01	54.32	33.5	72
DF5	27.2	21.52	52.44	32.8	82
DF6	27	18.36	42.12	30.2	81
DF7	29.6	17.88	52.48	38.7	82
DF8	27.1	17.06	48.13	34.3	80
DFs1	20.2	12.76	26.87	19.7	75
LSF1	44.57	13.71	49	35.95	115
VSF	39.8	13.54	47.67	34.12	111
VSF1	27.06	10.41	36.11	24.31	102
VSF2a	9	6.16	12.2	11.9	69
VSF2b	9	6.16	12	11.9	67
VSF2c	11.6	8.26	16.5	16.59	66
VSF2d	11.1	5.67	13.3	13.3	87
VSF2e	15.1	10.85	17.6	18.13	69
VSF2f	9.2	6.3	12.6	12.88	65
VSF2g	9.1	6.3	13.9	13.51	61
VSF3	5.1	3.72	10.8	6.41	72
VSF4	11.9	7.02	20.4	13.25	88
VSF5a	14.93	5.58	22	13.76	100
VSF5b	14.5	5.77	17	12.38	109

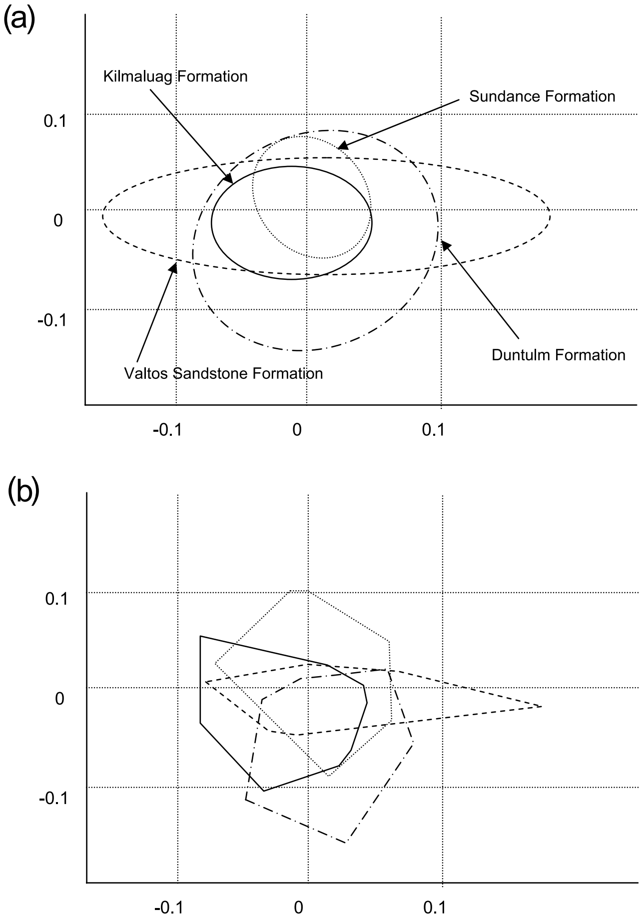

FIG. 6. Centred principal component analysis of the landmark data: (a) 95% confidence circles; (b) convex hulls.

supports this view. The data from the older Gypsum Spring Formation plot above the Sundance Formation 95% confidence circle, and the large footprints from the Duntulm, Valtos Sandstone and Lealt Shale formations

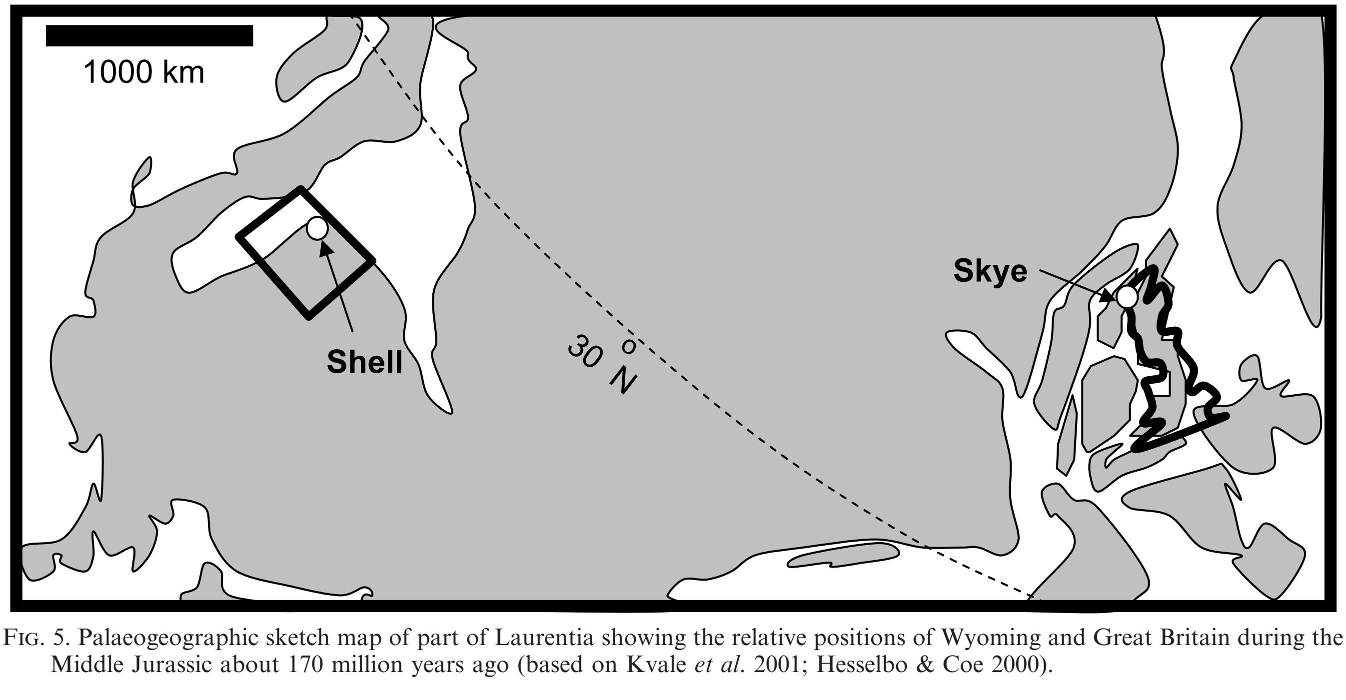

FIG. 5. Palaeogeographic sketch map of part of Laurentia showing the relative positions of Wyoming and Great Britain during the Middle Jurassic about 170 million years ago (based on Kvale *et al.* 2001; Hesselbo & Coe 2000).

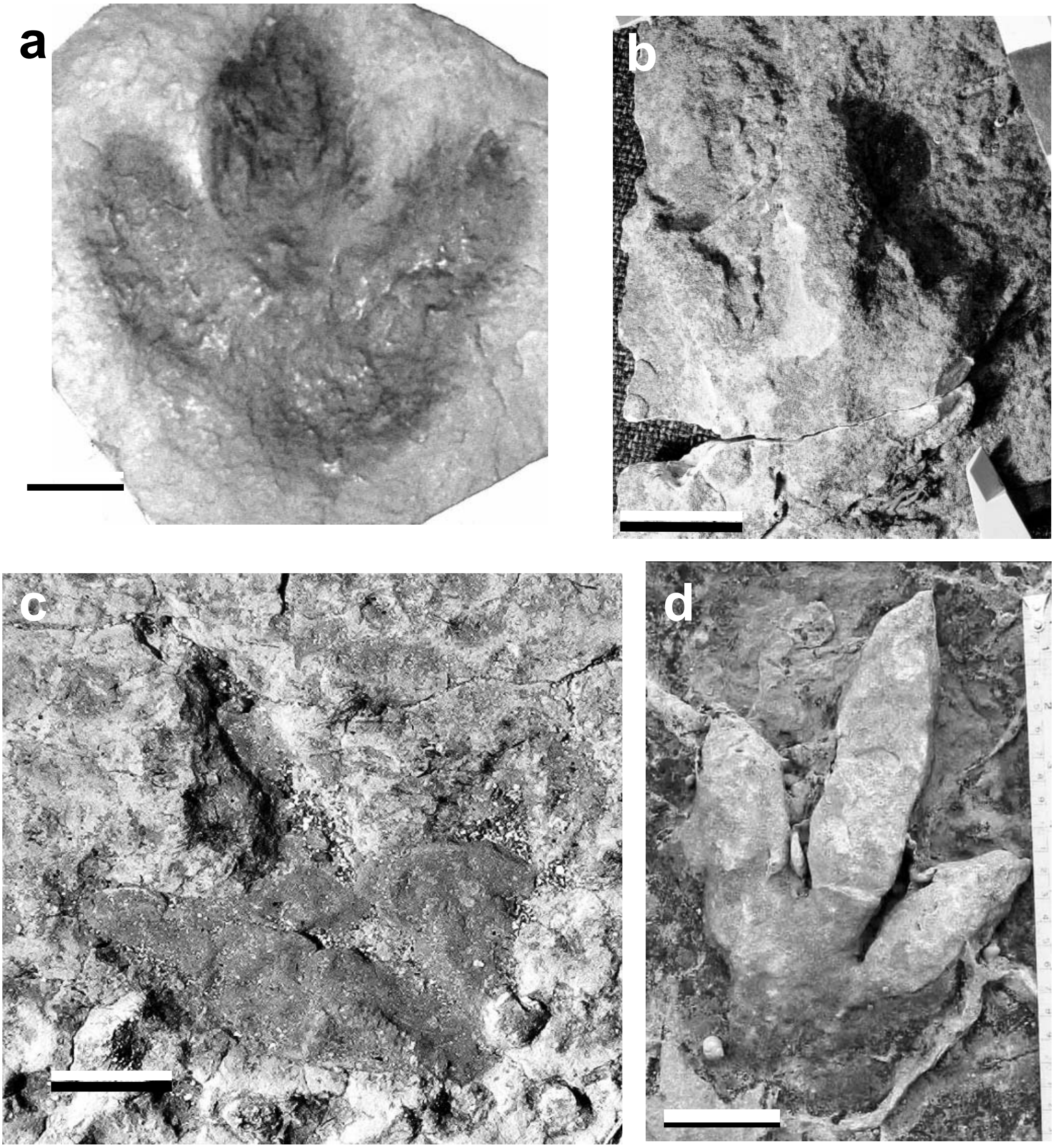

FIG. 7. Typical dinosaur footprints from the Middle Jurassic of the Isle of Skye: (a) from the Lealt Shale Formation of Rubha nam Brathairean (scale bar 10 cm); (b) from the Valtos Sandstone Formation at Dun Dearg (scale bar 2 cm); (c) from the Duntulm Formation at An Corran (scale bar 10 cm); (d) from the Kilmaluag Formation at Score Bay (scale bar 5 cm).

plot in different space to the right of the Sundance Formation (Fig. 10a). This is more easily seen when using the convex hull plots of the data from the various formations (Fig. 10b).

The measurements used in this analysis may provide a more useful means of distinguishing between different types of dinosaurs on the basis of their footprints (adapted from Clark *et al.* 2005). The sediments were similar between the tracksite localities, and the tracks were either surface tracks or shallow transmission tracks, resulting in a good correlation between similar tracks. Studies looking at more distinct sediment types and variations in track shape and dimensions with transmission depth would help determine whether these measurements may be more widely useful. This method is not used here to distinguish between dinosaur ichnospecies which may vary as a result of transmission, sediment type, water content of the sediment, as well as the size, weight and type of trackmaker. The width of the digits, claw impressions, and digit divergence from

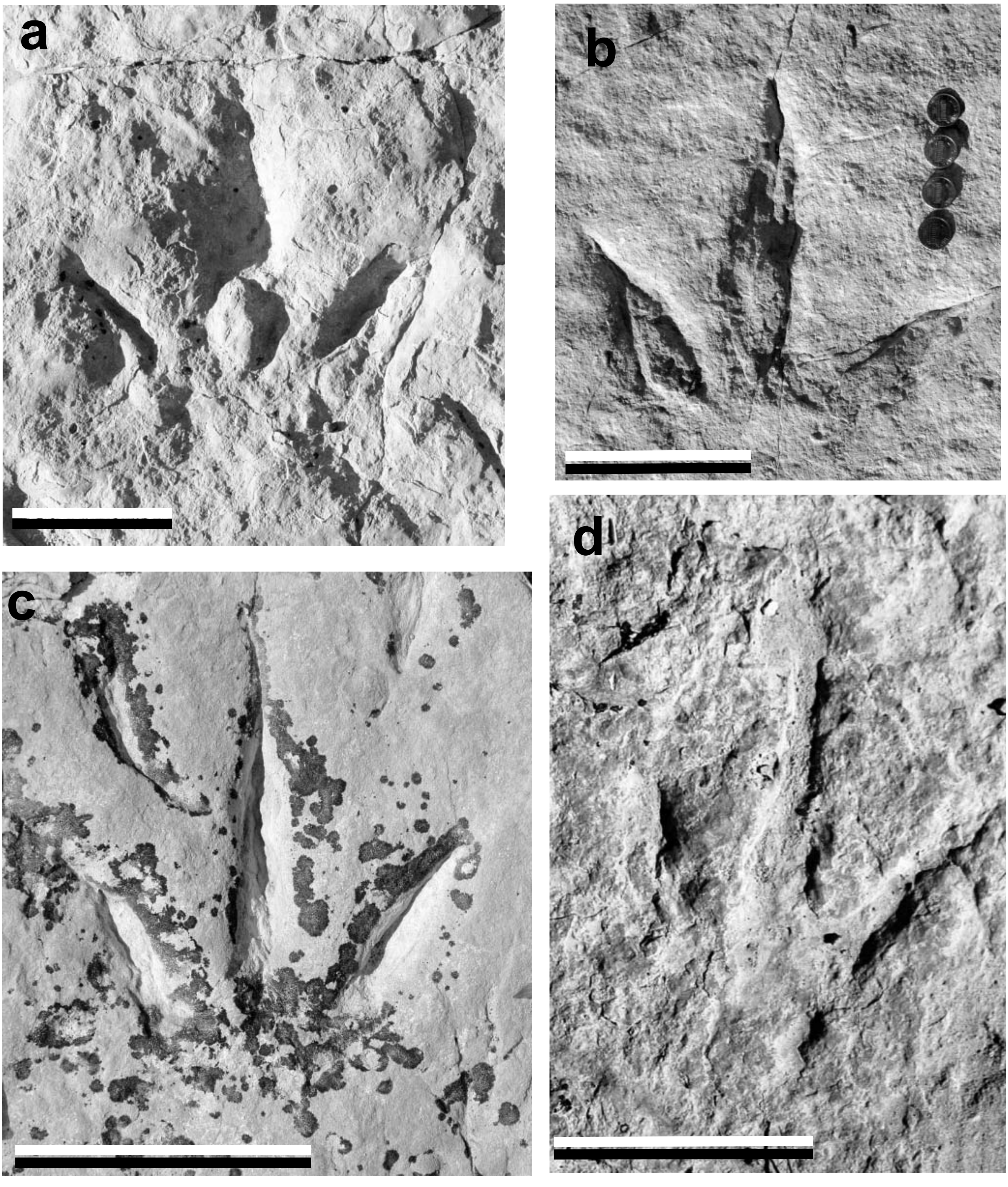

FIG. 8. Typical dinosaur footprints from the Middle Jurassic of Wyoming (a–c are from the Sundance Formation): (a) from the Red Gulch Tracksite; (b) from the Flitner Ranch Tracksite (USNM 508544); (c) from the Yellow Brick Road Tracksite; (d) from the Gypsum Springs Formation. (scale bars 10 cm).

the rear of the footprint may vary as a result of these factors (Clark *et al.* 2005).

Conclusions

It is possible to distinguish between different dinosaur footprints on the basis of morphometric analysis using measurements of the width between the distal ends of digits II and IV, various lengths and the angle between the distal ends of digits II, III and IV. A landmark analysis of the same footprints did not allow any distinction between footprints from different formations. Perhaps the use of more landmarks on the pad impressions would produce better results, but better preservation

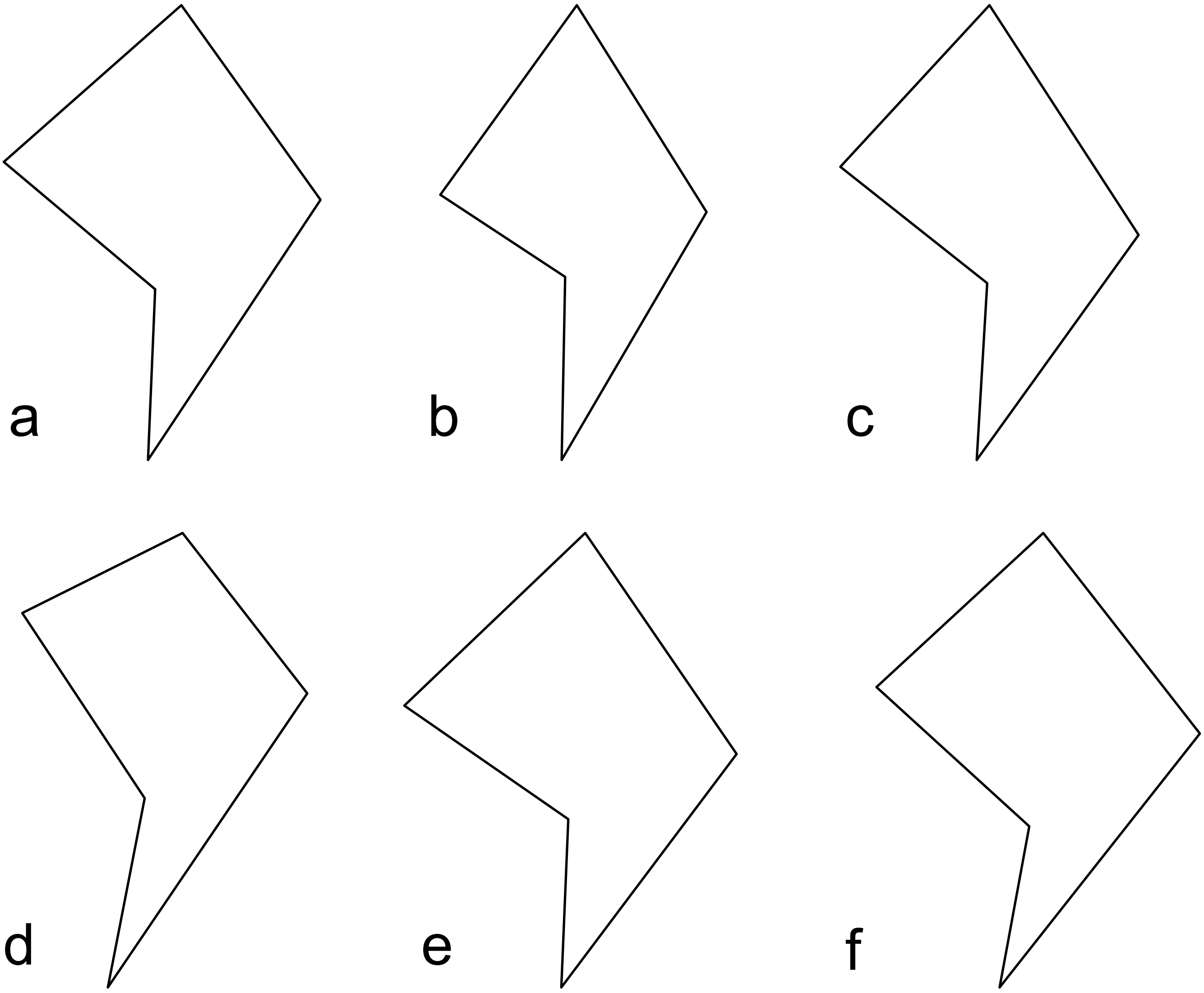

FIG. 9. Mean shapes of landmark data of footprints: (a) Kilmaluag Formation; (b) Valtos Sandstone Formation; (c) Duntulm Formation; (d) large footprints from Valtos Sandstone Formation and Lealt Shale Formation; (e) Sundance Formation; (f) Gypsum Springs Formation.

TABLE 4

Correlation eigenvalues as a percentage of their sum for the measured variables (with a Jolliffe cut off of 0.7, only the first two principal components are considered to be significant).

Principal component	Eigenvalues	Variance (%)
1	3.87	77.57
2	1.00	20.03
3	0.06	1.29
4	0.03	0.71
5	0.02	0.40

TABLE 5

Correlation loadings of the measured variables for the first two principal components.

Variable	Loading (PC1)	Loading (PC2)
w_{II-IV}	0.97	−0.14
h_{III}	0.93	0.29
pL	0.99	0.09
L_{III}	0.99	0.10
α	0.34	−0.94

would be required to be able to introduce further landmarks.

The footprints from the Sundance, Valtos Sandstone and Kilmaluag formations are indistinguishable and it is thought that they may have been produced by a similar type of dinosaur. The sharp claw impressions on prints from both these localities and the discovery of a coelophysoid-grade caudal vertebra from the Valtos Sandstone Formation, indicates that the animal that produced these footprints may have been a small theropod morphologically similar to a coelophysoid (Clark 2001b, 2004, 2005; Clark *et al.* 2004). The high density of footprints from the same level in the Sundance Formation (probably over 150 000 footprints per square kilometre; Kvale *et al.* 2001) are represented by a range of sizes from about 8 cm to nearly 30 cm from the Sundance Formation near Shell. In Scotland, the equivalent footprints from the Kilmaluag Formation range in size from less than 2 cm in length to about 25 cm. This

TABLE 6

Eigenvalues as a percentage of their sum for the first five principal components using landmark data (with a Jolliffe cut-off of 0.00018, only the first five principal components are considered significant).

Principal component	Eigenvalues	Variance (%)
1	0.00094	30.00
2	0.00075	24.05
3	0.00054	17.37
4	0.00044	14.03
5	0.00032	10.21
6	0.00011	3.63

suggests that the dinosaur was gregarious and may even have moved in family groups (Clark *et al.* 2005; Breithaupt *et al.* 2007*a*, *b*), although this is disputed by Roach & Brinkman (2007).

If the trackmaker genus in Wyoming is the same as the trackmaker for the similar footprints in Scotland, then its presence at these two distant locations needs to be explained. One hypothesis is that they may have migrated between these two locations following sauropods which certainly existed in Scotland at this time (Clark *et al.* 1995; Barrett 2006; Liston 2004). It has been suggested that some Cretaceous hadrosaur dinosaurs migrated, but this has been disputed (Fiorillo & Gangloff 2001; Lockley 1995). Caribou migrate about 700 km from their wintering grounds to their calving grounds (Zalatan *et al.* 2006) and can accumulate up to more than 5000 km in a year (Fancy *et al.* 1989) for the round journey. It is unlikely that the individual trackmakers migrated between the two sites, but it may represent the full range of the dispersed trackmaker genus. It is therefore suggested that this represents a wider Laurasian distribution for this theropod trackmaker.

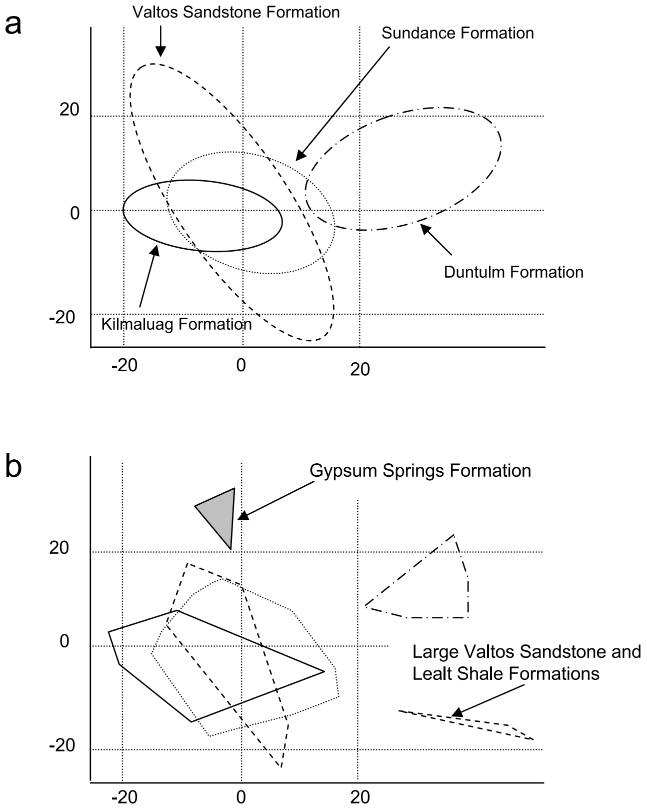

FIG. 10. Centred principal component analysis of the measured data: (a) 95% confidence circles; (b) convex hulls.

The other question to be considered is where all the herbivores are, if these footprints are considered to be of a theropod trackmaker. It is possible that they are living further inland amongst the vegetation rather than close to the inland sea or saline lagoons of Wyoming. In Scotland there do appear to be herbivore remains, but the footprints are rarely associated with those of theropods. Only in the Valtos Sandstone Formation are large spatulate digits on tridactyl footprints found in close association with footprints with small narrow digits. Similar patterns have been observed where there is a bias towards the footprints of carnivorous dinosaurs by eight to two (Leonardi 1989). It may also be that the carnivorous dinosaurs feed on near-shore aquatic prey such as fish, which would also explain why there is a predominance of carnivorous dinosaur footprints in arid near-shore environments such as those found at both the Wyoming and Scottish sites. The existence of herbivorous dinosaurs in the Scottish localities can be due to the variety and greater abundance of vegetation derived from a nearby source into the fluvio-deltaic and near-shore marine depositional environments (Dower *et al.* 2004). The other possibility is that there is just not enough exposure of the track-bearing surfaces to have a fully representative ichnofauna. If the trackways represent only a short period of emergence, it is likely that only a few species will be represented on the shores of receding lagoons or seas.

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