Three age groups of ornithopods inferred from footprints in the mid-Cretaceous Dakota Group, eastern Colorado, North America

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Abstract

Ornithopod population structure is inferred from a large sample of footprints from the mid-Cretaceous Dakota Group of Colorado, New Mexico and Oklahoma. Allometric analyses and size-frequency distributions suggest size (age) classes or recruitments for tracks identified as *Caririchnium leonardii* (Ornithopoda) from sequence 3 of the mid-Cretaceous Dakota Group of the Rocky Mountain Front Range High Plains region. Five hundred ninety-eight footprints from 284 trackways were used in the statistical analysis. Tests were conducted that revealed no significant difference between analyses of right and left footprints or between casts and molds. Allometric analysis suggests a growth curve that can be subdivided into three segments, corresponding to foot lengths of 16.5–21.7, 21.7–29.3 and 29.3–55.0 cm, respectively. These are interpreted as juvenile (possibly yearlings), subadults and adults. The former two categories may correspond to animal recruitments (n, $n + 1$), whereas the latter category may represent several recruitments ($n + 2$, $n + 3$, $n + 4$, etc.). Once ornithopod growth curves of the type proposed for *Maiasaura* are established, there is considerable potential for estimating dinosaur age from footprints. In the meantime, however, large track samples can be analyzed for the size class information they contain. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Cretaceous; dinosaur footprints; size frequency; age class estimates

1. Introduction

Estimation of the age of dinosaurs is an intriguing but different problem. We know that age is related to size but the exact relationship is unknown. Nevertheless, abundant size-frequency data derived from footprints can be analyzed with a view to providing insights into dinosaur ontogeny and population structure.

There have been a few detailed studies of dinosaur growth rates. The best example is the ontogenetic series of *Protoceratops* specimens collected by the American Museum (Brown and Schlaikjer, 1940; Dodson, 1976), which is believed to show sexual dimorphism. However, even in this sample, estimates of age have proved speculative and controversial (Case, 1978). Growth rates have been plotted for modern vertebrates such as elephants, alligators and ostriches (Dodson, 1975; Western et al., 1983; Morell, 1987; Obata and Tomida, 1990). Kurtén (1953) showed that such growth rates can be com-

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pared with growth curves for fossil mammals. In summaries of data obtained by Jack Horner, Morell (1987) and Obata and Tomida (1990) plotted growth curves for *Maiasaura* and compared them with those obtained from ontogenetic studies of alligators and ostriches. They concluded that *Maiasaura* probably grew very rapidly like an ostrich, rather than like an alligator, reaching sexual maturity within 5–7 years. This general model is endorsed by Russell (1989). However, they did not convincingly show how age estimates and growth curves were obtained for *Maiasaura*. They inferred a rapid growth rate among nestlings, approximating an increase in length from 33 to 120 cm during the 'fledgling' season of about 2–3 months. Thus by extrapolation yearlings would have grown to be about 3 m long after 12 months (Horner and Makela, 1979; Horner, 1992). Although Lockley (1994) estimated the ages of *Caririchnium leonardii* trackmakers (Ornithopoda) from the Cretaceous of Colorado based on comparison with the *Maiasaura* growth curve, there is no evidence that growth rates of the two taxa are similar. On the other hand, it is reasonable to assume that the growth rate of large ornithopods was similar among related species. Lockley (1994) pointed out that growth rates throughout ontogeny vary with the morphologic features measured, and may be linear or curvilinear (allometric). This allows us to estimate relative age based on size, although we can not establish absolute age. Until now no studies have mentioned relative age estimates based on tracks.

In this paper, we estimate relative ages of *Caririchnium leonardii* trackmakers (Ornithopoda) from the middle Cretaceous Dakota Group in the eastern part of the Colorado Plateau, North America based on comparison of ornithopod growth curves. Our measurements are derived from 284 trackways consisting of 598 footprints. We discuss age estimation of *Caririchnium leonardii* trackmakers and the geographical distribution of age groups.

2. Geologic setting and distribution of tracksites

The Cretaceous Dakota Group (or Dakota Sandstone) is widely distributed on the Colorado Plateau. The group is Albian to Cenomanian in age in the eastern part of the basin, where the tracks discussed
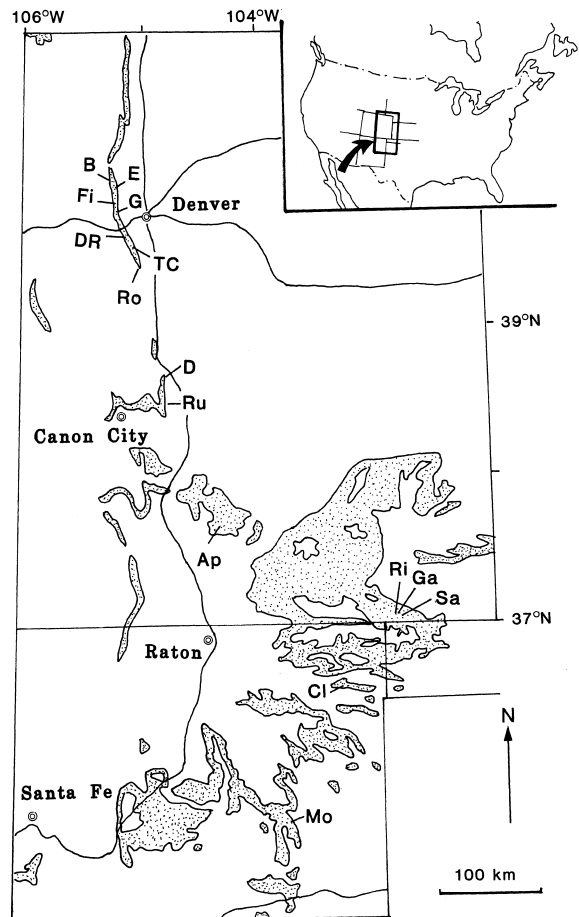

Fig. 1. The distribution of dinosaur footprint sites in the Dakota Group in Colorado, New Mexico, and Oklahoma. Stippled area represents outcrops of the Dakota Group (after Lockley et al., 1992). Letter abbreviations refer to geological names of tracksites on Table 1.

in this study were discovered. In the eastern margins of the basin (Fig. 1), the Colorado Front Range and southern High Plains of Colorado, Oklahoma and northeastern New Mexico, the group is considered to be made up of three sequences (sequence 1 to 3) based on sequence stratigraphic interpretation (Weimer, 1989; Holbrook and Dunber, 1992). There are various interpretations proposing different lithostratigraphic divisions for the group in different areas (Fig. 2; e.g. Gustason and Kauffman, 1985; Kues and Lucas, 1987; Holbrook et al., 1987).

According to Lockley et al. (1992), the dinosaur tracks in this region are restricted to a thin strati-

North-central CO South-central CO Northeastern NM East-central NM

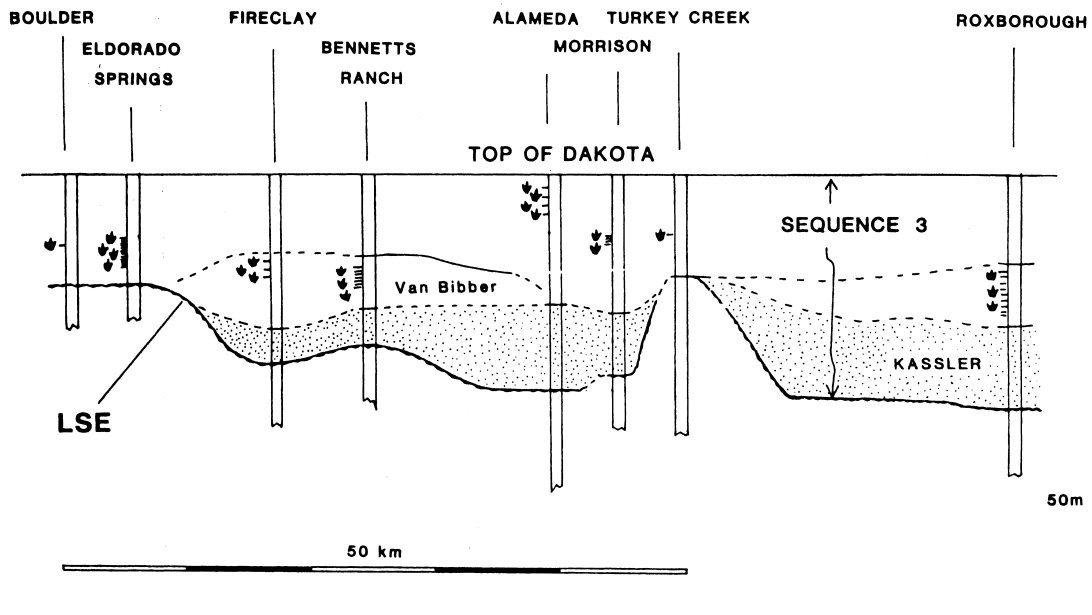|		WEIMER (1989) North-Central Colorado	Modified From GUSTASON & KAUFFMAN (1985) South-Central Colorado	KUES & LUCAS (1987) Northeastern New Mexico	KUES & LUCAS (1987) HOLBROOK, ET AL. (1987) East-Central New Mexico	
Cenomanian	Sequence 3	Graneros Shale	Graneros Shale	Graneros Shale	Graneros Shale	
Albian		Mowry Shale	Mowry Shale	Romeroville Sandstone	Romeroville Sandstone	
		Muddy (J) Formation	Upper Transitional Member	Pajarito Formation	Pajarito Formation	TRACK ZONE
			Lower Channel Sandstone Member	Mesa Rica Sandstone (channel)	Mesa Rica Sandstone (channel--marine)	
Aptian-Albian	Sequence 2	SB 3	SB3	SB3	SB3	
		Skull Creek Shale	Glencairn Formation	Glencairn Formation	Tucumcari Shale	
		Plainview Sandstone	Plainview Formation	Long Canyon Sandstone Bed	Campana Sandstone Bed	
	Seq.1	SB2	SB2	SB2	SB2	
		Lytle Formation	Lytle Sandstone	Lytle Sandstone		
		SB1	SB1	SB1		
		Jurassic Morrison Formation	Jurassic Morrison Formation	Jurassic Morrison Formation	Jurassic Morrison Formation	

Fig. 2. (Top) Relationship of track-bearing zone to Dakota sequences from north-central Colorado to east-central New Mexico (after Gustason and Kauffman, 1985; Kues and Lucas, 1987; Holbrook et al., 1987; Weimer, 1989). (Bottom) Track-bearing levels in the middle parts of the Muddy Formation (Van Bibber and Upper J Sandstone) in the Dakota group between Boulder and Roxborough, Colorado. Modified after Lockley et al. (1992).

graphic interval, locally as much as 10 m in thickness, that represents various terrestrial and marginal marine deposits preserved during lowstand and the early phase of transgression that led to the accumu-

lation of sequence 3 of the Dakota Group. A corresponding distribution can be traced from north-central Colorado to northeastern New Mexico through southeastern Colorado and the Oklahoma panhandle,

a distance of more than 700 km. In north-central Colorado, the dinosaur tracksites are all within the upper part of the Dakota Group (within the middle to upper parts of the Muddy Formation or the J Sandstone) and especially within sequence 3 (sensu Weimer, 1989; Weimer and Sonnenberg, 1989; Weimer et al., 1990). Track-bearing strata of the middle to upper part of the Muddy Formation evidently represent onlap of coastal deposits and backfilling of valleys during transgression. In theory, track-bearing sequences may be thicker and contain more levels in paleovalleys where subsidence and aggradation rates are highest. In southeastern Colorado, the Oklahoma panhandle and northeastern New Mexico, dinosaur tracks are confined to the uppermost layers of the Mesa Rica Sandstone and its equivalent strata and the Pajarito Formation which are within sequence 3. The Mesa Rica Sandstone represents a widespread, continuous sheet of channel sandstones deposited by lateral migration and avulsion of rivers (Holbrook and Dunber, 1992). Basal Pajarito strata represent floodplain deposits of contemporary Mesa Rica channels during the lowstand phase of sequence 3. This coastal plain covered most of northeastern New Mexico and probably much of southeastern Colorado as well.

3. General characteristics of the track sample

Footprints from the Dakota Group are identified as *Caririchnium leonaridii*; they have an ornithopod-like pes characterized by three broad digits and a large heel, and elliptical or subrounded manus (Fig. 3; Lockley, 1985, 1987a, 1988, 1990; Currie et al., 1991; Lockley et al., 1992). The sample consists of several hundred well-preserved single footprints and trackways (Table 1). The range of observed footprint size (pes length) is between 17.0 and 53.0 cm in mold occurrence, and between 16.5 and 55.0 cm in casts. At the Alameda Avenue locality known as Dinosaur Ridge (DR in Fig. 1) in Colorado, we counted 53 *Caririchnium leonardii* trackmakers from trackways or single footprints on a single bedding plane (Lockley, 1985, 1987a,b, 1988, 1990, 1991; Lockley and Hunt, 1994). There are at least two trackway trends, from northwest to southeast and from northeast to southwest. Similarly, at Mosquero Creek (Mo in Fig. 1) in northeastern New Mexico, 72 *Caririchnium leonardii* trackmakers, represented by trackways or single footprints, have been recorded from a single bedding plan (Lockley et al., 1993; Lockley and Hunt, 1995). More than 50 parallel trackways, oriented from southeast to northwest, represent small-sized quadrupedal track-
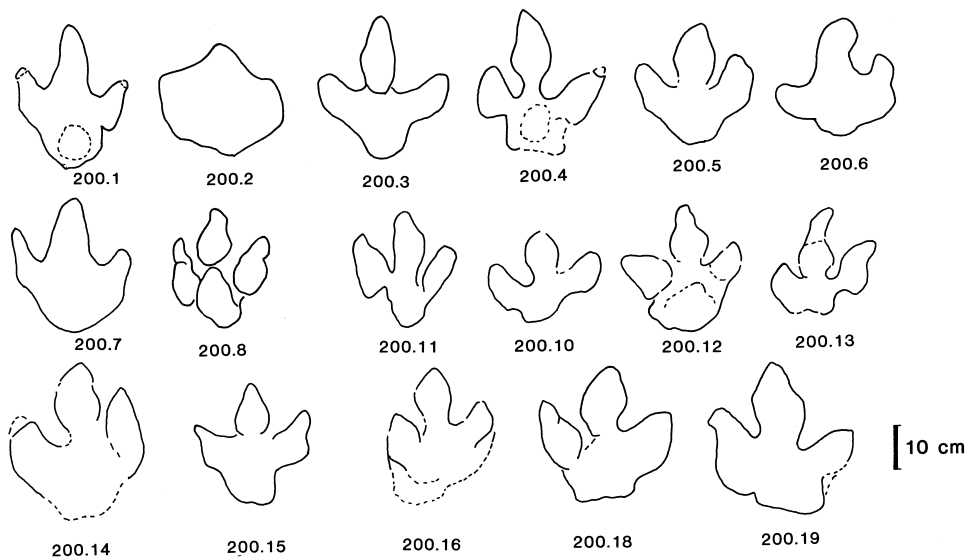

Fig. 3. Various casts of footprints identified as *Caririchnium leonardii*. Prefix CU-MWC are abbreviated for numbers. All specimens housed in the University of Colorado at Denver.

Table 1

List of locations and trackway and specimen numbers in the Dakota Group

Location		Trackway	Cast/mold	Specimen numbers
Boulder	B	1	cast	1
Eldorado Springs	E	4	mold	34
			cast	1
Fireclay	Fi	4	cast	4
Golden	G	1	cast	18
Dinosaur Ridge	DR	53	mold	91
			cast	17
Turkey Creek	TC	3	mold	8
Roxborough	Ro	2	mold	31
			cast	2
Dedman's Canyon	D	1	cast	1
Rule Canyon/ Colorado Colledge	Ru	1	mold	2
Apishapa (Tim's)	Ap	6	mold	6
Richardson Ranch	Ri	121	cast	121
Gallinas	Ga	13	cast	10
			mold	3
Sand Canyon	Sa	1	mold	1
Clanyton	Cl	1	mold	1
Mosquero	Mo	72	mold	246
Total		284		598

makers. All have a similar depth of about one centimeter. They provide strong evidence for a herd moving northwest, with all individuals in motion together. Morphological uniformity of the footprints and parallel trackways support this inference and suggest animals of the same species. Such gregarious behavior is similar to that observed in modern herd animals such wildebeest, caribou, gnu and buffalo.

4. Rationale for statistical analyses

Our large sample permits us to undertake a number of statistical analyses and to compare data derived from casts and molds, from right and left footprints and from single or multiple sites. The following questions were posed with suitable parameters measured for statistical analysis and testing.

4.1. Which morphologic features of pes or manus, are suitable for statistical analysis?

The Pearson's coefficient of variation is useful for understanding of variation and polymorphism (Imbrie, 1956; Hayami, 1969). For dinosaur footprints, eight parameters (Table 2; Fig. 4) namely right pes length, left pes length, right pes width, left pes width, right manus length, left manus length, right manus width and left manus width, were examined for this analysis.

Table 2

Data of the trackway number 28 at Mosquero

	RPL	LPL	RPW	LPW	RML	LML	RMW	LMW
1	21	17	18	20	6.5	6	5	3.5
2	21	19.5	16.5	18	5.5	5.5	4	4
3	18	22	14	18	6	5.5	3.5	4.5
4	20	19.5	19	16.5	6.5	5	4	3.5
5	20	20	18	18.5	7	6	3	4.5
6	19	19	19	16	5.5	5.5	3.5	3.5
7	21	17	18	17.5	5.5		3	
8	18	19	18	17.5				
Average	19.75	19.13	17.56	17.75	6.07	5.58	3.71	3.92
Stdev	1.282	1.620	1.635	1.225	0.608	0.376	0.699	0.492
N	8	8	8	8	7	6	7	6
Min	18	17	14	16	5.5	5	3	3.5
Max	21	22	19	20	7	6	5	4.5
V	6.49	8.47	9.31	6.90	10.02	6.74	18.84	12.55

RPL = right pes length; LPL = left pes length; RPW = right pes width; LPW = left pes width; RML = right manus length; LML = left manus length; RMW = right manus width; LMW = left manus width.

Stdev = standard deviation; N = number of individuals; Min = minimum; Max = maximum; V = Pearson's coefficients.
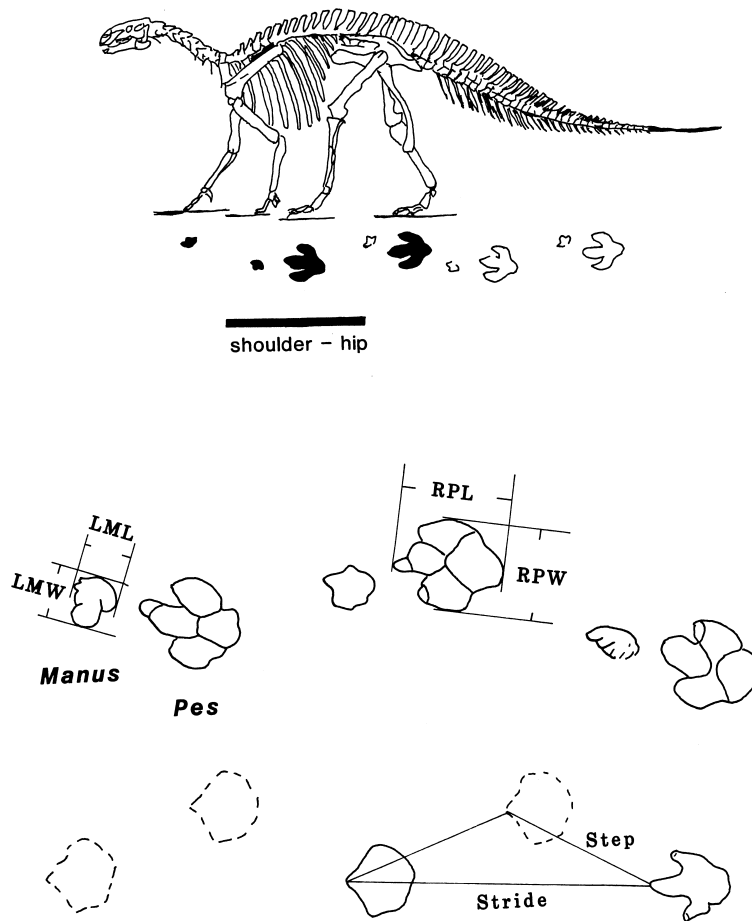
shoulder − hip

Fig. 4. Measurements used in describing footprints and trackway.

Trackway number 28 at Mosquero, which is the longest trackway in the Dakota Group, is suitable for an examination of Pearson's coefficient of variation. The trackway consists of sixteen pes prints (eight of both right and left), and seven right and six left manus prints. Pearson's coefficient variations indicate that pes morphology is less variable than manus morphology (coefficients of pes range from $V = 6.49$ to $V = 9.31$ but three manus values are over $V = 10$: Table 2). Pes length is less variable than width (coefficients of length are smaller than width: Table 2). Pes length, therefore, was selected as most suitable for statistical analyses.

4.2. Is there any statistically significant morphological variation between right and left pes footprints?

We tested our data to determine whether right and left footprint measurements should be pooled. Three tests — chi-square test, *F*-test and Student's *t*-test — are available for assessing data derived from both right and left pes prints. Table 3 shows the results of these tests on the basis of trackway number 28 at Mosquero Creek, the longest trackway studied in the Dakota Group. Chi-square analysis of the eight left and right pes prints indicate that they are correlated to the normal distribution, which means both samples are regarded as part of the same population. The *F*-test is judged to be insignificant at the 5%

Table 3
Chi-square test of right and left pes length on the basis of trackway #28 at Mosquero

	N	χ^2 0.05 ($\nu = 3$)	χ^2 value	Result	Correlation
Right pes length of 28	8	7.81	3.33	not significant	normal distribution
Left pes length of 28	8	7.81	2.47	not significant	normal distribution

Table 4
F- and Student's t-test between right and left pes

Character	Pes length	
	right	left
N	8	8
m	19.75	19.13
S	1.20	1.52
F-value	0.623	
$F7/7$ (0.05)	3.77	
Significancy	not significant	
Judgment	high probability of same population	
t-value	1.66	
t (0.05) ($\nu = 14$)	2.15	
Significancy	not significant	
Judgment	high probability of same population	

level (Table 4); this means a high probability that both populations (left and right pes lengths) are the same. The Student's t-test observed value (Table 4) also indicates that both samples of pes show high probability of the same population. This means we can combine data from right and left pes prints. Our result confirms the common sense assumption that the right and left footprints of any animal should be shown by statistical analysis to originate from the same population, barring exceptional pathological deformity to one or more feet. In other words, one would not expect intra-trackway variation to exceed inter-trackway variation, unless extra-morphological factors such as slope, substrate consistency or erosion come into play.

4.3. Are there any statistically significant differences between footprint molds and casts?

Both molds and casts are found at many sites in the Dakota Group and are available for analysis. Consequently, it is desirable to determine whether they produce significantly different results. At the Galinas site (Ga in Fig. 1), both molds and casts of footprints occur at the same level. For this test, we used three pes molds and ten pes casts. The top of the Table 5 shows the results. Both casts and molds are correlated to the normal distribution, respectively. This means both samples of pes are regarded as an individual population. The F-test observed value (Table 6) is not judged to be significant at the 5% level. This means a high probability that both pop-

Table 5
Some chi-square tests between mold and cast specimens

	N	χ^2 0.05 ($\nu = 3$)	χ^2 value	Result	Correlation
Chi-square test between mold and cast specimens at Gallinas					
Mold	3	7.81	2.72	not significant	normal distribution
Cast	10	7.81	0.70	not significant	normal distribution
Chi-square test between mold and cast specimens of small groups in all Dakota Group sites					
Mold (17.0–21.5 cm)	30	7.81	1.92	not significant	normal distribution
Cast (16.5–23.0 cm)	11	7.81	6.66	not significant	normal distribution
Chi-square test between mold and cast specimens of middle groups in all Dakota Group sites					
Mold (21.7–28.4 cm)	56	7.81	3.37	not significant	normal distribution
Cast (23.5–29.0 cm)	45	7.81	1.84	not significant	normal distribution
Chi-square test between mold and cast specimens of large groups in all Dakota Group sites					
Mold (28.5–53.0 cm)	40	7.81	4.37	not significant	normal distribution
Cast (29.3–55.0 cm)	101	7.81	5.33	not significant	normal distribution

Table 6
F- and Students *t*-test between mold and cast at Gallinas

Character	Pes length	
	mold	cast
N	3	10
m	33.77	37.06
S	7.04	10.84
F-value	0.569	
*F*2/9 (0.05)	4.26	
Significancy	not significant	
Judgment	high probability of same population	
t-value	0.487	
t (0.05) (*v* = 11)	2.201	
Significancy	not significant	
Judgment	high probability of same population	

ulations of pes molds and casts are the same. The Student's *t*-test observed value (Table 6) also indicates that both samples of pes show high probability of representing the same population.

This means we can combine data from molds and casts of pes footprints. For this test, we used 126 pes molds and 157 casts of footprints from all Dakota sites. Three size groups — small, middle and large — are recognized, based on allometric analysis discussed below. Table 7 shows the result of these tests. Both casts and molds in these three groups are statistically regarded as part of the same population. *F*-test, observed values (0.267, 1.600 and 1.116 for small, middle and large groups, respectively) are smaller than the critical values of 2.70, 1.64 and 1.50 for 29/10, 55/44 and 39/100 of freedom; The difference is, therefore, judged to be insignificant at the 5% level. This means a high probability that both populations of molds and casts are the same. Then, *t*-test observed values (1.369, 1.157 and 0.255 for small, middle and large groups, respectively) are smaller than 5% limited significance values (*t* = 2.021, 1.980, 1.960) for 39, 99 and 139 degrees of freedom. As both samples show a high probability of origination from the same population, this means we can combine data from molds and casts of pes of footprints for statistical purposes. It is worth noting that pes print casts are generally deeper than molds because they were originally made in mud rather than sand (cf. Lockley and Hunt, 1994). Our analyses, however, apply to the two-dimensional shape (outline) of tracks.

Table 7
Some *F*- and Student's *t*-tests between mold and cast

F-test and Student's *t*-test between mold and cast of small groups in all Dakota Group sites

Character	Pes length	
	mold (17.0–21.5 cm)	cast (16.5–23.0 cm)
N	30	11
m	20.15	20.8
s	1.05	1.97
F-value	0.267	
*F*29/10 (0.05)	2.70	
Significancy	not significant	
Judgment	high probability of same population	
t-value	1.369	
t (0.05) (*v* = 39)	2.021	
Significancy	not significant	
Judgment	probability of same population	

F-test and Student's *t*-test between mold and cast of middle groups in all Dakota Group sites

Character	Pes length	
	mold (21.7–28.4 cm)	cast (23.5–29.0 cm)
N	56	45
m	24.59	26.78
s	2.17	1.71
F-value	1.600	
*F*55/44 (0.05)	1.64	
Significancy	not significant	
Judgment	probability of same population	
t-value	1.157	
t (0.05) (*v* = 99)	1.980	
Significancy	not significant	
Judgment	probability of same population	

F-test and Student's *t*-test between mold and cast of large groups in all Dakota Group sites

Character	Pes length	
	mold (28.5–53.0 cm)	cast (29.3–55.0 cm)
N	40	101
m	38.53	38.5
s	6.95	6.63
F-value	1.116	
*F*39/100 (0.05)	1.50	
Significancy	not significant	
Judgment	probability of same population	
t-value	0.255	
t (0.05) (*v* = 139)	1.960	
Significancy	not significant	
Judgment	high probability of same population	

5. Discussion

5.1. Age estimation

Allometric analysis using footprints is useful for an estimation of dinosaur age, because they are much more common than body fossils. Fig. 5 is a double logarithmic scatter diagram showing the relation between foot length and foot width of all specimens (including both molds and casts) of *Caririchnium leonardii* from the Dakota Group. Relative growth is statistically regarded as isometric in the early stage, shows positive allometry in the middle stage and exhibit negative allometry in the later stage. Two critical points are identified using the formula for the analysis of relative growth (Hayami and Matsukuma, 1971); therefore we can recognize three stages of growth, corresponding to foot lengths of 16.5 to 21.7 cm, 21.7 to 29.3 cm and 29.3 to 55.0 cm. These may correspond to juvenile (yearling), subadult and adult stages. Based on comparison with Horner's growth curve (in Morell, 1987; Obata and Tomida, 1990), yearlings are a little less than half adult size (linear

Table 8
Ontogenetic development in *Caririchnium leonardii*, based on length of molds of pes

Size of length (cm)	Ratio of biped/ quadruped	Allometry	Growth stage	
55.0				
	2.36 (26/11)	negative	3rd	adult
29.3				
	1.35 (35/26)	positive	2nd	subadult
21.7				
	0.26 (6/23)	isometry	1st	juvenile
16.5				

dimension); hence the first growth stage identified herein could be correlated with yearlings.

The tracks of *Caririchnium leonardii* from the Dakota Group in the Colorado Plateau represent both bipeds and quadrupeds. The ratio of bipeds to quadrupeds gradually increases from juvenile to adult stages (Table 8), although this could be in part an artifact of preservation. At the largest single site, Mosquero Creek, the smaller individuals were quadrupedal and the larger individuals appear bipedal.

Currie and Sarjeant (1979) reported both juvenile and adult ornithopod, *Amblydactylus kortmeyeri*, footprints from the Lower Cretaceous strata in Canada, and Currie (1983) used them to analyse growth and behaviour. They did not, however, derive age estimates for *Amblydactylus kortmeyeri*.

Lim (1990) studied dinosaur tracks from the Cretaceous of Korea and identified various ornithopod trackways in the categories B1, B2, B3, etc. (B = Biped). Analysis of his data does not show the three 'growth' stages identified for the Colorado sample. As the Korean trackmakers were all bipedal — unlike the Colorado quadrupeds — a different species population structure might be inferred. Indeed, Lockley (1994) noted a very different size-frequency distribution from that recorded in the Dakota Group.

5.2. Interpretation of population structure

Since, based on foot length, three age groups (juvenile, subadult and adult) are inferred, 'generations' or recruitment structure can be inferred from selected localities in the Dakota Group (Table 9; Fig. 6). Juvenile size groups occur from the following locations
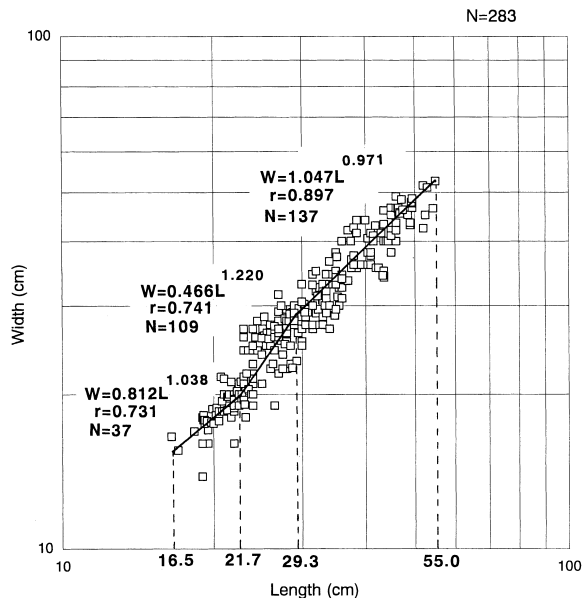

Fig. 5. Double logarithmic scatter diagram showing the relation between foot length and foot width of *Caririchnium leonardii* from the Dakota Group in the eastern part of the Colorado Plateau.

Table 9
Geographical distribution of individuals divided into three growth stages. The tracks sites refer to Table 1

Location		Trackway	Cast/mold	Juvenile	Sub-adult	Adult	Total
Boulder	B	1	cast		1		1
Eldorado Springs	E	4	mold		3		3
			cast	1			1
Fireclay	Fi	4	cast	1	3		4
Golden	G	1	cast		1		1
Dinosaur Ridge	DR	53	mold		17	19	36
			cast		5	12	17
Turkey Creek	TC	3	mold			3	3
Roxborough	Ro	2	mold		1		1
			cast	1			1
Dedman's Canyon	D	1	cast			1	1
Rule Canyon/Colorado Colledge	Ru	1	mold		1		1
Apishapa (Tim's)	Ap	6	mold		2	4	6
Richardson Ranch	Ri	121	cast	6	33	82	121
Gallinas	Ga	13	cast	1	1	8	10
			mold		1	2	3
Sand Canyon	Sa	1	mold			1	1
Clayton	Cl	1	mold			1	1
Mosquero	Mo	72	mold	31	31	10	72
Total		284		41	100	143	284

from north to south: E, Fi, Ro, Ri, Ga and Mo (see Fig. 1 for locality abbreviations). At Mosquero Creek (location Mo) in the most southern part of the area, 31 individuals appear to be juvenile; this is the highest number recorded in the Dakota Group. The second highest frequency of juveniles is recorded at Richardson Ranch (locality Ri), also in the southern part of the area. Other locations yielded only isolated juvenile individuals. There is a tendency, therefore, to find a higher frequency of juvenile individuals in the southern part of the Dakota Group outcrop.

Adult size groupings occur in the following nine locations from north to south, DR, TC, D, Ap, Ri, Ga, Sa, Cl and Mo. Among them, location Ri has 82 individuals, the highest number, and location DR has 31 individuals, the second highest number; locations Mo and Ga rank equal third, with 10 individuals. Adult size groups therefore are recognized throughout the Dakota Group.

The subadult size group appears in locations B, E, Fi, G, DR, Ro, Ru, Ap, Ri, Ga and Mo. Northern location DR and southern locations Ri and Mo reveal more than 20 individuals, showing that this size group ranged over the whole area. This distribution is as extensive as that of the adult size group.

The juvenile size group usually accompanies one or both of the adult and subadult size groups. Adult and subadult size groups, however, may occur separately. This suggests that juvenile size groups are typically accompanied by adults or subadults. Mixed size groups are also known to occur among sauropods herds, as for example at the famous Davenport Ranch site (Bird, 1941; Lockley, 1987b, 1991). In the case of ornithopods, it is well known that a social structure existed between juveniles and adults (Horner and Gorman, 1988; Horner, 1992).

5.3. Further inferences

From size-frequency distributions, some inferences of life-span are possible. Fig. 7 shows the size-frequency distribution for pes length, revealing a skewed distribution that consists of four minor right-skewed distributions or subsets. Footprints in the first subset (marked *n* in Fig. 7) are inferred to include those that are smaller than the minimum size recorded, but they are not recorded for preservational reasons (e.g. rapid early growth rates, cf. Horner, 1992, or reduced potential for imprinting due to small size, Lockley, 1991). Based on allo-
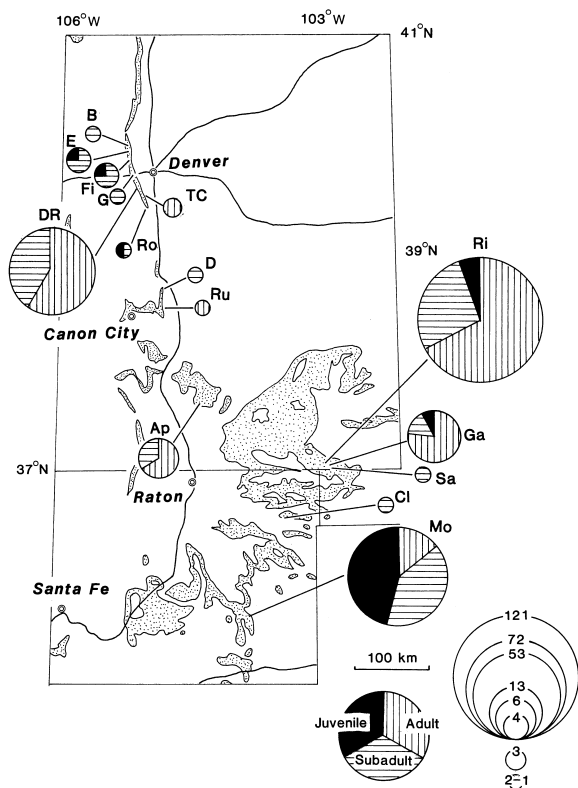
Fig. 6. Assemblage age structure of *Caririchnium leonardii* in the eastern part of the Colorado Plateau.

Fig. 7. Size-frequency distribution of pes length of molds of *Caririchnium leonardii*.

metric analyses, the juvenile size stage consists of tracks less than 21.7 cm, the subadult size is between 21.7 and 29.3 cm, and the adult size is above 29.3 cm. Four minor skewed distributions suggest that the *Caririchnium leonardii* trackmaker in the Dakota Group sample comprised four generations (size classes). We assume seasonal breeding that led to annual recruitments. It is also probable that, after individuals had reached full adult size, individual size classes corresponding to annual recruitments become hard to recognize.

6. Conclusions

Allometric analyses of dinosaur tracks are useful for estimating relative age of dinosaurs. Size classes can be compared with the growth curves of Horner (see Morell, 1987; Obata and Tomida, 1990) to suggest probable age classes (or recruitments).
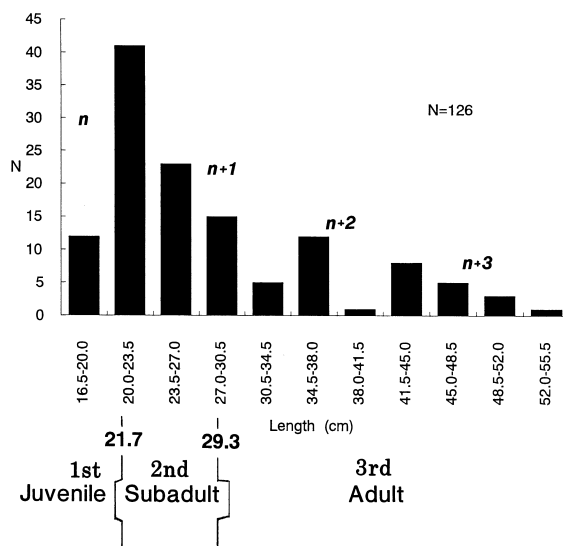
Based on allometric analyses of the footprints of *Caririchnium leonardii*, three age classes can be inferred. They correspond to juvenile, subadult and adult stages. The *Caririchnium leonardii* trackmaker may have shown an ontogenetic tendency to shift from quadrupedal to bipedal locomotion with age.

Juvenile *Caririchnium leonardii* trackmakers are usually accompanied either by adult and subadults, or by both size groups, throughout their geographical distribution.

The *Caririchnium leonardii* trackmaker may be represented by four 'size' generations and presumably reproduced by seasonal breeding animal like most comparable large terrestrial vertebrates.

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