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Bird footprints from the Anacleto Formation (Late Cretaceous) in Neuquén Province, Argentina

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Abstract. Bird footprints recovered from the Anacleto Formation (Campanian, Upper Cretaceous) at Sierra Barrosa, northeast of Plaza Huincul, Neuquén Province represent the earliest records of bird traces from Patagonia. All of the specimens were recovered from two sites at the same stratigraphic level separated by less than a hundred meters. They are tridactylous, clawed prints with divarications greater than 90° between digits II and IV, and seem to represent three different ichnotaxa. The most common avian footprint lacks hallux traces and can be referred to *Aquatilavipes.* A smaller number of the footprints includes distinct hallux impressions, and are similar to *Ignotornis* and *Jindongornipes.* The third type represents a new ichnotaxon, *Barrosopus slobodai* ichnogen. et ichnosp. nov. characterized by smaller size and a Digit II impression that is separate from the conjoined third and fourth ones. These fossilized bird tracks are the first reported from the Neuquén Basin, and double the number of Cretaceous occurrences of avian footprints in Argentina.

Resumen. Huellas de aves de la Formación Anacleto (Cretácico Superior), Neuquen, Argentina. Se coleccionaron huellas de aves en depósitos campanianos de la Sierra Barrosa, noreste de Plaza Huincul, Provincia del Neuquén, las que representan el registro de trazas de aves más antiguo de Patagonia. Todos los ejemplares fueron colectados del mismo nivel estratigráfico en dos sitios distanciados por menos de 100 metros. Las huellas son tridáctilas, con marcas de garras y ángulos de divergencia entre dígitos II y IV mayores de 90°, y parecen representar tres icnotaxones diferentes. La huella de ave más frecuentemente registrada carece de marca de espolón y puede ser referida a *Aquatilavipes.* Un número menor de huellas posee marcas de espolón y son similares a *Ignotornis* y *Jindongornipes*. El tercer tipo representa un nuevo icnotaxón, *Barrosopus slobodai* ichnogen. et ichnosp. nov. caracterizado por ser de pequeño tamaño y poseer la impresión del dígito II separada de la marca impresa por los dígitos III y IV. Estas huellas fósiles de aves son las primeras dadas a conocer para la Cuenca Neuquina, y duplican el registro Cretácico de huellas de aves en Argentina.

Key words. Key words. Footprints. Birds. Cretaceous. Patagonia.

Palabras clave. Huellas. Aves. Cretácico. Patagonia.

Introduction

In February 2001, a joint paleontological expedition conducted by the Museo Carmen Funes (Plaza Huincul, Neuquen, Argentina) and the Royal Tyrrell Museum of Palaeontology (Drumheller, Alberta, Canada) discovered numerous bird footprints in the Anacleto Formation (Campanian, Upper Cretaceous; Dingus et al., 2000) of Sierra Barrosa (figure 1), northeast of Plaza Huincul, Neuquén Province (Coria *et al.*, 2001). The footprints are well preserved and some of them are arranged in trackways, and, apparently represent several avian taxa.

Worldwide, ichnological evidence suggests that Cretaceous birds were highly diverse (Lockley *et al.*, 1992; McCrea *et al.*, 2001), and supplements an increasing number of avian taxa based on skeletal fossils (Hou, 1998; Chiappe *et al.*, 1999; Sanz, 1999). Fossilized bird footprints have been recovered from the uppermost Cretaceous of northern Argentina (Alonso and Marquillas, 1986). *Yacoraitichnus avis*, a tridactylous, relatively large clawed footprint with phalangeal pad impressions on the third digit, was the first record of Cretaceous bird footprints from Argentina. Casamiquela (1987) briefly mentioned some charadriform-like bird footprints from Rio Negro Province that he named *Patagonichnornis venetiorum*. Unfortunately, he did not provide drawings, photographs, a diagnosis, specimen numbers or locality information, and the name must be regarded as *nomen nudum*. Other tridactylous avian ichnites, possibly the same ones that were mentioned by Casamiquela (1987), have been illustrated from the

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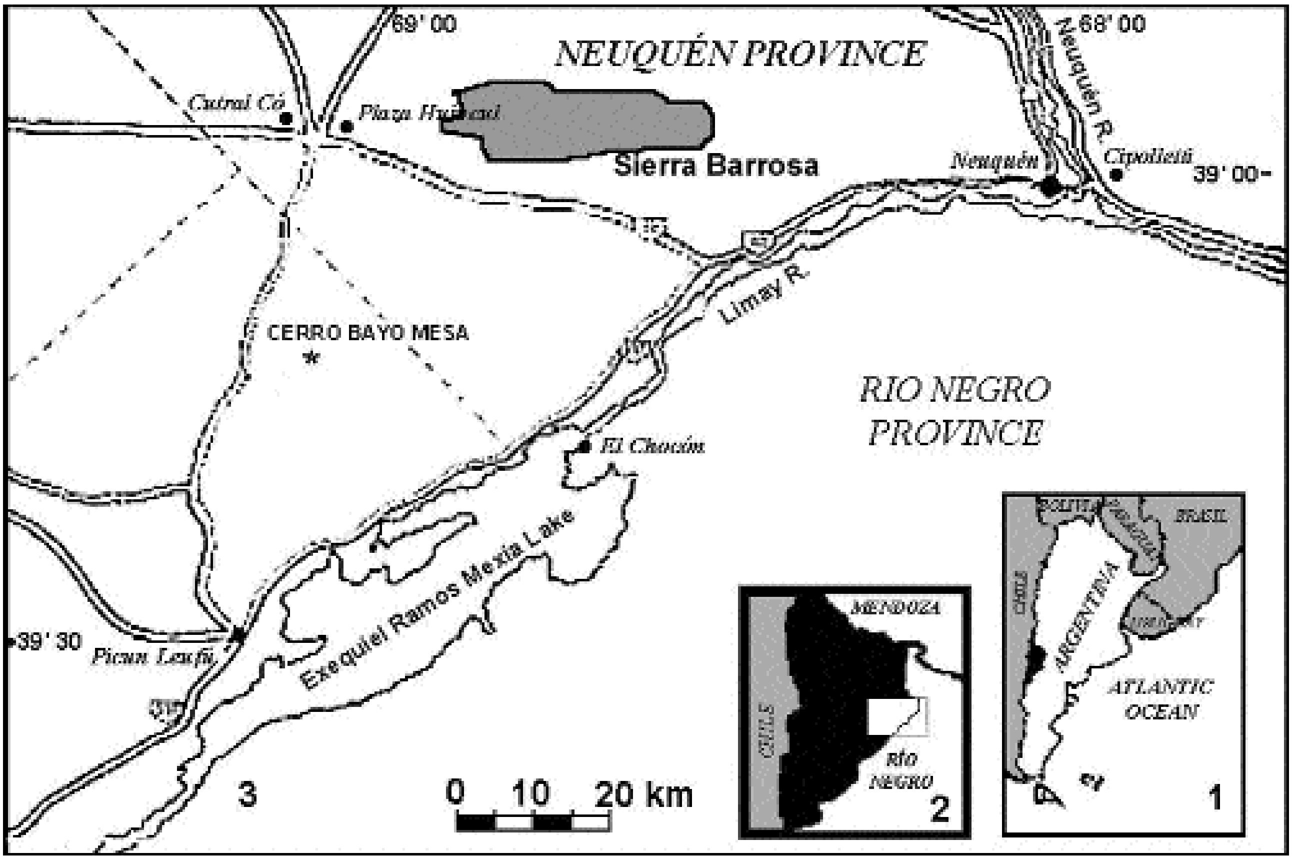


Figure 1. Locality map of the bird footprint site on Sierra Barrosa / *Mapa del sitio con huellas de aves en la localidad de Sierra Barrosa.*

Upper Cretaceous of Patagonia (Leonardi, 1987, Plate 18c; Lockley *et al.*, 1992), but still have not been described. Very recently, Triassic bird-like fossil footprints were described from northeastern Argentina, although their assignation to birds remains unclear (Melchor *et al.*, 2002). Here we present descriptions of three different ichnotaxa, which include *Barrosopus slobodai*, ichnogen. et ichnosp. nov., that altogether represent the first ichnological avian record from the Neuquén Basin.

Material

Many of the footprints found on Sierra Barrosa were collected, but most of them remain still *in situ*. The better preserved footprints were photographed, measured (table 1), and mapped by tracing their outlines onto clear polyethylene film. The resultant map is on file at Museo Municipal "Carmen Funes" (catalogued as MCF-PVPH-SB 337), and includes most of the footprints exposed at the main site. A second locality (97 meters northwest of the first) was not excavated, although one sample (MCF-PVPH-SB 415-18) was collected for reference.

All specimens are catalogued under the accession number Museo Municipal "Carmen Funes" MCF-PVPH-SB 415. MCF-PVPH-SB 415.1 to MCF-PVPH-SB 415.9, MCF-PVPH-SB 415.11 to MCF-PVPH-SB 415.17 (figures 2, 3, 4) are from Locality A, which is on Sierra Barrosa, 30 km NE Plaza Huincul. The position description is 38o51.168' South, 68o48.656' West. MCF-PVPH-SB 415.18 was collected from Locality B, which is also on Sierra Barrosa, at 38o51.131' South, 68o48.698' West (positions taken by GPS on February 8, 2001).

Horizon. Anacleto Formation (Campanian, Dingus *et al.*, 2000), Rio Colorado Subgroup, Neuquén Group, Neuquén Basin.

Abbreviations. MCF-PVPH-SB, Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huincul, Sierra Barrosa collection; MUCPv, Museo Universidad Nacional del Comahue, Paleontología de Vertebrados, Neuquén.

Stratigraphy and descriptive sedimentology

The track locality occurs in the lower portion of the Anacleto Formation, 18-19 meters above the contact with the underlying Bajo de la Carpa Formation (figure 2A). In this area, the preserved Anacleto Formation is 50 m thick and incomplete, truncated at the top by modern erosion. In general, the Anacleto Formation is characterized by the presence of stacked, massive, medium-to-coarse-grained, sand-

Table 1. Measurements of bird footprints from the Anacleto Formation taken directly from specimens and measured to nearest 0.5 mm. Abbreviations: Cat. #, catalogue number from Museo Municipal "Carmen Funes"; Div, divarication between toes II and IV; L, length; Lay, layer; P, pace; S, stride; W, width; W/L, width to length ratio. Measurements were taken in millimeters to the nearest 0.5mm, except for divarication, which is in degrees. / *Medidas de las huellas de aves de la Formación Anacleto tomadas directamente de los especímenes y medidos con redondeo de 0.5 mm. Abreviaciones: Cat. #, número de catálogo del Museo Municipal "Carmen Funes"; Div, divergencia entre dígitos II y IV; L, largo; Lay, nivel; P, paso; S, zancada; W, ancho; W/L, razón entre ancho y largo. Medidas tomadas en milimetros con redondeo el los 0.5 mm, excepto para la divergencia que es en ángulos.*

#	Cat. #	Lay	L	W	W/L	Div	P	S	Hallux
a	415.14	1	54	56	1.04	94	-	-	no
b	415.14	1	49	56	1.14	106	89	-	no
c	415.14	1	50	50	1	92	72	159	no
d	415.14	1	54	55	1.02	104	-	-	no
e	415.14	1	54	61	1.13	116	59	-	no
f	415.14	1	58	57	0.98	88	70	127	no
g	415.14	1	51	58	1.14	117	-	-	no
h	415.14	1	51	58	1.14	95	-	-	no
I	415.14	1	55	66	1.2	107	-	-	no
j	415.14	1	-	61	-	102	-	-	no
k	415.14	1	48	56	1.17	112	-	-	no
l	415.15	2	35	41	1.17	118	-	-	no
m	415.15	2	47	61	1.3	106	-	-	no
n	415.15	2	46	59	1.28	122	-	-	no
o	415.15	2	47	53	1.13	105	-	-	no
p	415.15	2	47	56	1.19	112	-	-	no
q	415.15	2	48	62	1.29	119	-	-	no
r	415.15	2	52	55	1.06	103	-	-	no
s	415.15	2	52	57	1.1	107	-	-	no
t	415.15	2	-	43	-	108	-	-	no
u	415.15	2	46	56	1.22	123	-	-	no
v	415.15	2	45	-	-	104	-	-	no
1	In situ	3	57	66	1.16	150	-	-	no
2	In situ	3	53	60	1.13	150	-	-	no
3	In situ	3	45	60	1.33	155	-	-	yes
4	In situ	3	49	64	1.31	135	-	-	no
5	In situ	3	57	65	1.14	135	-	-	yes
6	In situ	3	-	-	-	-	-	-	no
7	In situ	3	50	60	1.2	135	-	-	yes?
8	In situ	3	53	-	-	135	-	-	no
9	In situ	3	49	64	1.31	125	-	-	no
10	In situ	3	43	58	1.35	150	-	-	yes
11	In situ	3	50.5	60	1.19	135	-	-	yes
12	In situ	3	49	48	0.98	108	-	-	yes?
13	In situ	3	51	47.5	0.93	170	-	-	yes
14	In situ	3	52.5	56	1.07	120	-	-	yes
15	In situ	3	50	54.5	1.09	140	-	-	yes
16	In situ	3	54.5	57	1.05	135	-	-	yes
17	In situ	2	37.5	47.5	1.27	125	-	-	no
18	In situ	1	42.5	-	-	-	-	-	yes
19	In situ	1	52	-	-	110	-	-	no
20	In situ	3	42.5	50	1.18	180	-	-	yes
21	In situ	3	58	62	1.07	150	90	270	yes
22	In situ	3	53	50	0.94	150	117	330	yes
23	In situ	3	-	-	-	-	170	330	yes?
24	In situ	3	52	58.5	1.13	130	-	-	yes
25	In situ	3	53	52.5	0.99	130	170	325	yes
26	In situ	3	57.5	56	0.97	125	170	240	yes?
27	In situ	3	49	51.5	1.05	140	175	-	yes?
28	In situ	3	50.5	62.5	1.24	110	-	-	yes?
29	In situ	3	32.5	27.5	0.85	130	-	-	no
30	In situ	3	44	59	1.34	150	-	-	yes
31	In situ	3	57.5	56	0.97	120	-	-	yes
32	In situ	3	-	55.5	-	110	-	-	yes
33	In situ	3	-	62	-	150	-	-	no
34	In situ	3	53.5	63	1.18	130	-	-	yes
35	In situ	3	49	57	1.16	100	-	-	yes
36a	In situ	3	29.5	38	1.29	180	-	-	no
36b	In situ	3	30	38	1.27	105	-	-	no
37	In situ	3	43	60	1.4	135	-	-	no
38	In situ	3	48	54.5	1.14	155	-	-	no
39	In situ	3	36	-	-	150	-	-	no
40	In situ	3	52	-	-	165	-	-	no
41	In situ	3	59.5	58	0.97	140	-	-	yes
42	In situ	3	39	43	1.1	120	-	-	no
43	In situ	3	30	39	1.3	120	-	-	yes
44	In situ	3	59	54	0.92	140	-	-	yes
45	In situ	3	55.5	-	-	140	-	-	yes
46	In situ	3	48.5	37	0.76	110	-	-	no
47	In situ	3	47.5	68	1.43	135	-	-	no
48	In situ	3	38	57.5	1.51	135	-	-	no
49	In situ	3	50	65.5	1.31	140	-	-	no
50	In situ	3	55	60	1.09	110	-	-	yes
51	In situ	3	58	68.5	1.18	110	-	-	yes
52	In situ	3	44.5	-	-	155	-	-	yes
53	In situ	3	50.5	70	1.39	125	-	-	no
54	In situ	3	58.5	56	0.96	120	-	-	yes
55	In situ	3	50	60	1.2	125	-	-	yes
56	In situ	3	46	60	1.3	120	-	-	yes
57	In situ	3	42.5	58	1.36	110	-	-	no
58	In situ	3	40	63.5	1.59	170	-	-	no
59	In situ	3	56.5	57.5	1.02	115	-	-	no
60	In situ	3	51	67.5	1.32	135	-	-	yes?
61	In situ	3	-	-	-	-	-	-	no?
62	In situ	3	44	55	1.25	145	-	-	no
63	In situ	3	-	55	-	105	-	-	yes
64	In situ	3	57.5	-	-	120	-	-	yes
65	In situ	3	21	-	-	120	-	-	no
66	In situ	3	52	-	-	-	-	-	no
67	In situ	3	41.5	-	-	-	-	-	no
68	In situ	3	35.5	62	1.75	150	-	-	yes
69	In situ	3	32.5	-	-	-	-	-	no
70	In situ	3	39	46.5	1.19	180	-	-	no
71	In situ	3	45	60.5	1.34	150	-	-	yes
72	In situ	3	55	52	0.95	115	-	-	yes
73	In situ	3	43	57	1.33	135	-	-	yes
74	In situ	3	47.5	60	1.26	135	-	-	no
75	In situ	3	45	60.5	1.34	165	-	-	yes
76	In situ	3	37.5	45	1.2	135	-	-	yes
77	In situ	3	34.5	50	1.45	155	-	-	no
78	415.17d,f	3	40	58	1.45	150	-	-	no
79	415.17d	3	51	-	-	-	-	-	no
80	415.17d	3	54.5	67	1.23	135	-	-	no
81	415.17d	3	50.5	58.5	1.16	138	-	-	no
82	In situ	3	59.5	58	0.97	120	140	-	no
83	In situ	3	52	48	0.92	90	-	-	no
84	415.17e	3	55.5	42	0.76	125	-	-	no
85	415.17e,f	3	51.5	68.5	1.33	135	-	-	no
86	415.17a,b	3	-	-	-	120	120	230	no
87	415.17c	3	29	35	1.21	115	110	210	no
88	415.17c,k	3	29	31	1.07	120	100	235	no
89	415.17c,k	3	34.5	37	1.07	110	135	225	no
90	415.17e	3	30	-	-	-	90	165	no
91	415.17e	3	40	40	1	100	110	185	no
92	415.17g,h	3	30	36	1.2	140	30	135	no
93	415.17g,h	3	35.5	44	1.24	120	-	-	no
94	In situ	3	28	37.5	1.34	120	-	-	no
95	415.17d	3	51	-	-	90	190	380	no
96	415.17c,k	3	53.5	56	1.05	105	200	-	no
97	415.17c	3	47.5	50	1.05	90	-	-	no
98	415.17g	3	37.5	53	1.41	155	-	-	no
99	In situ	3	28	29.5	1.05	105	-	-	no
100	In situ	3	27	27	1	100	-	-	no

101	In situ	3	48.5	53	1.09	105	-	-	no
102	In situ	3	55	74	1.35	120	-	-	yes
103	In situ	3	48	69	1.44	130	-	-	yes
104	In situ	3	46.5	34	0.73	-	-	-	no
105	In situ	3	55	62.5	1.14	105	-	-	no
106	In situ	3	53	55.5	1.05	170	-	-	no
107	In situ	3	52	69	1.33	120	-	-	no
108	In situ	3	61	71	1.16	125	-	-	no
109	In situ	3	52.5	57	1.09	100	-	-	yes
110	In situ	3	21.5	-	-	-	-	-	no
111	In situ	3	37	48	1.3	170	-	-	no
112	In situ	3	53	55	1.04	120	-	-	no
113	In situ	3	50	-	-	-	-	-	no
114	In situ	3	47	-	-	-	-	-	no
115	In situ	2	44	63	1.43	120	-	-	no
116	In situ	2	46	51	1.11	100	-	-	no
117	In situ	2	48	57.5	1.2	100	-	-	no
118	In situ	2	52	56	1.08	100	-	-	no
119	In situ	2	49	72	1.47	135	-	-	no
120	In situ	1	53	48	0.91	90	-	-	no
121	In situ	1	46	46	1	135	-	-	no
122	In situ	1	55.5	62	1.12	105	-	-	no
123	In situ	1	57	61	1.07	105	-	-	no
124	In situ	1	41	44	1.07	130	-	-	no
125	In situ	3	55	51	0.93	120	-	-	no
126	In situ	3	42	51	1.21	150	-	-	yes
127	In situ	3	27.5	48.5	1.76	150	-	-	yes
128	In situ	3	41.5	61	1.47	150	-	-	no
129	In situ	3	51	73.5	1.44	150	-	-	yes
130	In situ	3	52.5	69	1.31	150	-	-	yes
131	In situ	3	45	-	-	-	-	-	no
132	In situ	3	46	45	0.98	105	-	-	no
133	In situ	3	37	32	0.86	90	-	-	no
134	In situ	3	52	53	1.02	105	155	-	yes
135	In situ	3	44.5	57.5	1.29	105	-	-	yes
Averages				47	55	1.17	126	-	-

stone bodies with locally occurring extraformational granules, pebbles and cobbles. Sandstone bodies are typically sheet-shaped, but lenticular bodies occur locally. Sediments are almost uniformly red in color (5R4/2, 10R5/4, 10R4/6, 10R4/2), but some gray to yellow sandstones occur also. Sandstones are heavily bioturbated with localized occurrences of decimeter-scale, "lumpy" to vertically oriented calcareous concretions that preferentially cement planolites burrow-fills, and a variety of more complex burrow/dwelling structures of unknown origin. The uppermost horizons in this area exhibit massive sandy siltstones with decimeter-thick zones of in-situ calcareous glaebules and nodules typical of modern caliches. The track locality is in the lowest 20 m of the formation, which is dominated by darker red colors (e.g., 5R4/2). This part of the formation has subequally interbedded meter-scale sandstones; sandy, planar-bedded siltstones; and massive, locally-variegated mudstones. Reworked fossil bones, including the remains of sauropods and turtles, are common in the fine-grained facies of this lower interval.

The bird tracks of locality A occur on three separate bedding surfaces within a 2.5 cm thick interval in an overall, 53 cm thick, tabular, sandstone bed (figures 2.B and 2.C). The bed consists of a crudely upward-fining, medium-to-coarse grained, massive sandstone. The lowermost 33 cm of the sandstone succession is well indurated and is capped by the track horizons, whereas the uppermost 20 cm (above the track horizons) is poorly consolidated and consists of centimeter-scale beds of variegated, medium-to-coarse grained sandstone. The track-bearing unit is capped by an interbedded succession of medium-grained sandstone and sandy siltstone layers with locally developed planar, wavy and current-ripple laminations.

The lowest track surface, designated layer 1 (figure 2B), consists of a dense and heavily packed track assemblage preserved in a medium grained sandstone. Intense overprinting of tracks appears to have disrupted and reworked an original lamina of sandy siltstone that draped the sandstone. Trackways are indiscernible. Although individual tracks are abundant, they are not clear because of overprinting and track-maker bioturbation. No tracks were used from layer 1 in the following descriptions.

The middle surface, layer 2, consists of a lamina of sandy siltstone overlying a centimeter thick coarse-grained, massive sandstone (figure 2.B). The surface has a lower density of tracks than Layer 1. Most tracks are 2-3 mm deep, and are well-preserved.

Layer 3, the uppermost surface, is similar to layer 2 in that it consists of a sandy siltstone lamina that drapes a 1.5 cm-thick bed of coarse-grained, massive sandstone (figure 2.B). The shallowly imprinted, low-density track assemblage includes three trackways in an area of approximately 5 m2.

Layers 2 and 3 have shallow, wavy relief, and local circular depressions that are 35-40 cm in diameter and 2-3 cm deep. Symmetrical, parallel-crested ripples were noted extending radially from the center of one depression on layer 3.

Trace fossils of fodinichnia (*Planolites* and *Taenidium*), ?domichnia (unnamed vertical burrow-fills the size of *Planolites*), and repichnia (furrowed, bedding-plane crawler/grazer trails, cf. *Scolicia)* occur in association with all three surfaces. The vertical burrow-fills comprise coarse-grained sandstone derived from the overlying variegated sandstones. The abundance of invertebrate trace fossils is notably less than in beds 10 m higher in the Anacleto Fm.

Paleoenvironmental interpretation

Intense bioturbation makes it difficult to interpret some features. Nevertheless, sandbody thickness and geometry are the same as those in clearly alluvial units below the Anacleto Formation, and trace and skeletal fossil assemblages also support an overall alluvial interpretation. Intense bioturbation in the upper beds of the Anacleto Formation reflects the prolonged mainte-

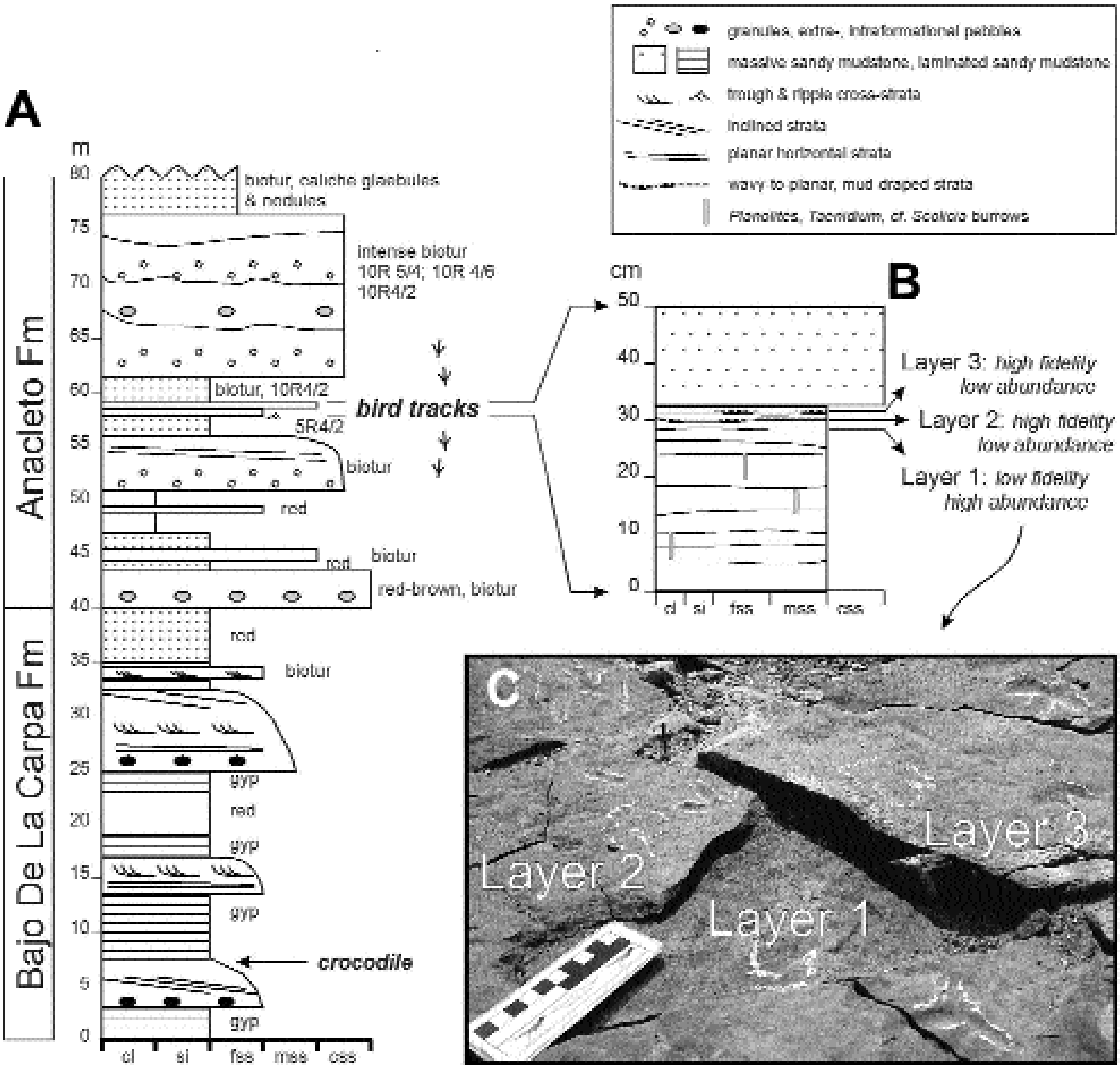


Figure 2. Geological section the Anacleto Formation showing the footprint bearing horizon / *Perfil geológico de la sección de la Formación Anacleto indicando el horizonte portador de huellas.*

nance of wet substrates and non-deposition. Caliche horizons in the highest sections indicate evaporative-transpirative processes and non-deposition within the seasonally dry, interchannel environments that were eventually established in this area.

In an alluvial paleoenvironment, stacked massive-to-planar bedded and wavy-to-ripple-laminated sandstones with bird tracks and invertebrate trace fossils reflect a succession of upper-flow-regime to waning-flow, sheet-flood-events (cf. Eberth et al., 2000). In addition, these features suggest the subsequent establishment of shallowly submerged substrates on which silts were quickly deposited from suspension. In modern alluvial plains that experience seasonal to periodic overbank floods, this is typical of distal levee, splay, and marginal lacustrine-to-paludal settings. The absence of shrinkage cracks in these and other horizons of the Anacleto Formation suggests long-term and frequent saturation by water. The abundance of tracks on Layer 1 might indicate, for example, either longer exposure, different depositional conditions, or better food resources. The sparse assemblages of invertebrate traces throughout these beds, and the existence of only a single, thin lamina of siltstone on each track surface, indicates short time intervals between successive flood / depositional events. Eberth et al. (2000) describe a similar stacked succession of fossiliferous sheetflood deposits of Permian age.

The circular depressions were shallowly submerged, as indicated by the presence of wind-generated, oscillation/symmetrical ripples. The co-occurrence of bird tracks and invertebrate trace fossils, which probably included arthropods and/or crustaceans, and gastropods (e.g., Bromley, 1990; Chamberlain, 1975), may indicate some interaction within their ecosystem. The variegated sandstones overlying the track horizon suggest a shallow and fluctuating water table was established after each subsequent flooding event.

Systematic paleontology

A total of 157 footprints from the three layers were mapped and measured (table 1). Many more ichnites are present but they are not well enough preserved to provide useful, unambiguous information. The footprints (figures 3, 4, 5 and 6) range in length between 21.5 and 61 mm, although most are between 45 and 55 mm. Among the well-preserved footprints, there are three distinct types.

Aves
Ichnogenus** cf.* ***Aquatilavipes Currie 1981
Figures 3.A-B, 4, 5, 6

Description. The most common (77 ichnites) come from all three layers and are comparable with the ichnogenera *Yacoraitichnus* (Alonso and Marquillas, 1986) and *Aquatilavipes* (Currie, 1981, Lockley *et al.*, 1992, McCrea and Sarjeant, 2001) in having separate narrow digital outlines (often with claw marks); proximal union of pedal digits II, III and IV; footprint width greater than length; interdigital span in excess of 95o; distinct depression for the metatarsal pad; and no hallux (digit I) impression (figures 3.A-B). Their average length is 47 mm, the average width is 55 mm (17% greater than length), and the average divarication is 123 degrees (table 1). These footprints tend to be arranged in dense clusters and often overlap each other (figures 4-5), which makes it difficult to associate individual footprints into trackways. Nevertheless, several narrow trackways (figures 4.A, 6) show that the feet turned slightly anteromedially towards the track midline as in most theropods. The pace ranges from 59 mm in a slow walking bird, to 200 mm in a fast moving individual (table 1).

Discussion. Footprints lacking hallux impressions can come from a taxonomically diverse range of birds. In this respect, the Anacleto tracks resemble *Aquatilavipes* from the lower Cretaceous of Canada (Currie, 1981; McCrea and Sarjeant, 2001) and possibly Japan (Lockley *et al.*, 1992), *Yacoraitichnus* (Alonso and Marquillas, 1986) from the Late Cretaceous of Salta, Argentina, *Koreanaornis* (Kim, 1969) from the lower Cretaceous of Korea (Lockley *et al.*, 1992), and the footprints of modern shorebirds. *Yacoraitichnus* tracks are substantially bigger than any of the tracks found on Sierra Barrosa, and furthermore have not been adequately diagnosed to distinguish them from *Aquatilavipes*. Consequently, we tentatively refer these tracks to *Aquatilavipes* on the basis of similar divarication, size, absence of hallux, and other morphological characters.

Dinosauria
Theropoda
Aves
***Ichnogenus** cf. Ignotornis* Mehl, 1931
Figures 3.C-D

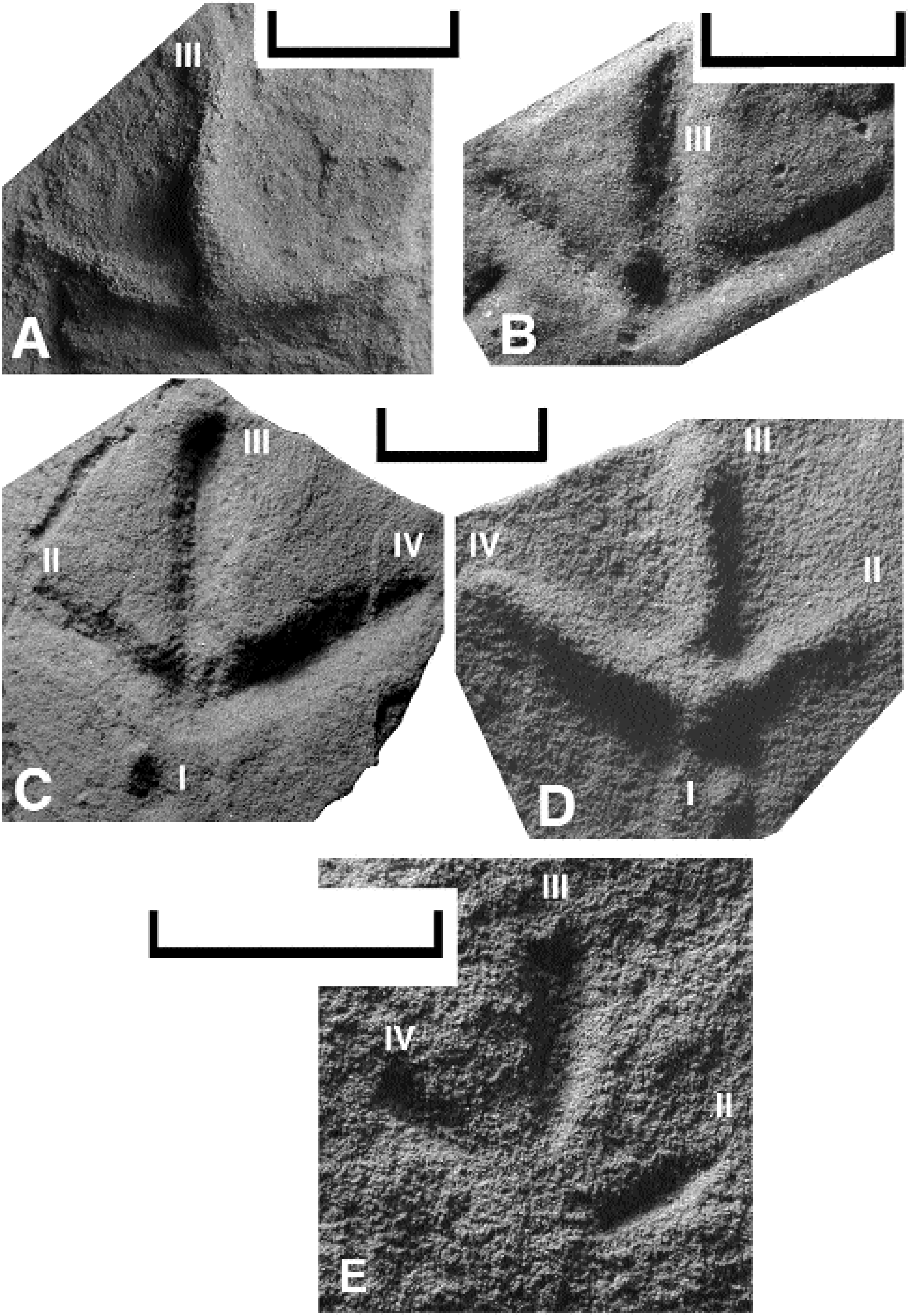
Description. This type of bird ichnites is similar in shape and size to *cf. Aquatilavipes*, but has a distinct hallux impressions (figures 3.C-D)and it is comparable to the ichnogenera *Ignotornis* (Mehl, 1931), and *Jindongornipes* (Lockley *et al.*, 1992). The 52 footprints with hallux impressions (table 1), found on layers 1 and 3, have an average length of 50 mm (excluding the hallux), an average width 58 mm, and an average divarication between digits II and IV of 132 degrees. Although the measurements broadly overlap with those of *cf. Aquatilavipes*, the averages suggest this bird was slightly larger with more widespread second and fourth toes. The second digit seems to be much thinner than the third and fourth digits in the majority of specimens (figures 3.C-D). Amongst the three identified trackways of *cf. Ignotornis*, pace ranges from 90 to 170 mm, and stride from 270 to 330 mm.

Discussion. These footprints, whith hallux impressions, resemble *Ignotornis* (Mehl, 1931; Currie, 1981). No Mesozoic avian footprints have been described so far from South America with hallux impressions. In addition, these footprints can be distinguished from *cf. Aquatilavipes* by the relative thicknesses of the second to fourth digits, by the slightly larger average size, and by the greater divarication angle.

Dinosauria
Theropoda
cf. Aves
Barrosopus slobodai ichnog., ichnosp. nov.
Figure 3.E

Holotype. MCF-PVPH-SB 415-17c, footprint #87 (Fig. 3E)

Figure 3. Photographs of bird footprints collected from the Anacleto Formation of Sierra Barrosa / *Fotografías de las huellas de aves coleccionadas de la Formación Anacleto de Sierra Barrosa.* **A. *cf. Aquatilavipes***, MCF-PVPH-SB 415.20. **B. *cf. Aquatilavipes***, MCF-PVPH-SB 415.14. **C. *cf. Ignotornis*** footprint part / *huella positiva* (MCF-PVPH-SB 415.16b). **D. *cf. Ignotornis***, counterpart / *huella negativa* (MCF-PVPH-SB 415.16a). **E. *Barrosopus slobodai*** footprint, #87 on slab MCF-PVPH-SB 415.17c. Abbreviations: I, II, III, IV; digits / *dígitos* I, II, III, IV. Scale bar / *Escala*: 3 cm.


III
A
III
B
III
II
IV
I
C
III
IV
II
I
D
III
IV
II
E

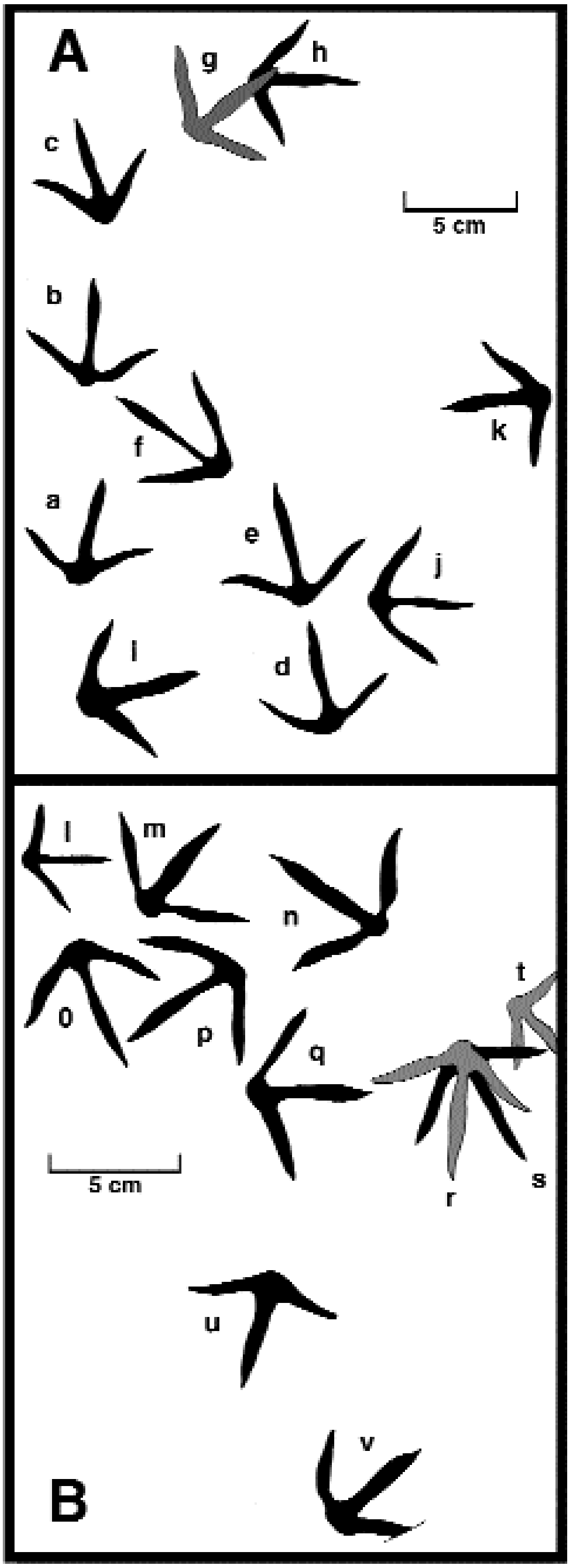


Figure 4. Outline drawings of the better-preserved footprints (*cf.* ***Aquatilavipes***) from bird footprint Locality **A,** Sierra Barrosa / *Dibujo esquemático de las huellas mejor preservadas (cf.* ***Aquatilavipes****) de la localidad A en Sierra Barrosa.* A) MCF-PVPH-SB 415.15 from layer 1. B) MCF-PVPH-SB 415.14 from layer 3.

Specimens. MCF-PVPH-SB 415-2, 415-17 (footprints #86 to 94).

Diagnosis. Tridactylous footprint of a small-sized avian theropod characterized by having conspicuous separation of digit II impression from the other two digits. Divarication between digits II and IV ranges between 100o and 120o. Trackways show a long stride, suggesting the trackmaker was long-legged.

Etymology. "*Barrosopus*" after Sierra Barrosa, the locality where the holotype was found. "Barrosa" is Spanish for "muddy", "pous" is Greek for "foot", and *Barrosopus* can be translated as "muddy foot". "*slobodai*" in honor of Wendy Sloboda, who discovered the footprints.

Description. *Barrosopus slobodai* ichnites are small with an average length of 31 mm, and an average width of 36 mm. None of the footprints has either a hallux or metatarsal pad impressions, and the divarication angle between the second and fourth toes is 118o. The second digit impression is consistently separated from the others (figure 3.E). The narrow toes all end in claw impressions. A single trackway from Layer 3 includes nine footprints of this type of the total of ten present in the surface(#86 to #94, plus MCF-PVPH-SB 415-2, see table 1), and has an average pace of 99 mm and an average stride of 198 mm.

Discussion: *Barrosopus slobodai* ichnites are smaller (average length is 31 mm, average width is 36 mm) than *cf. Aquatilavipes* and *cf. Ignotornis* tracks from the same locality. They are not only different in size, but also have a smaller average divarication (by at least 5o) between the second and fourth digits, and show a consistent separation of the second digit from the rest of the footprint. Despite having a narrower divarication than the other two types, the digits still have the wide divarication (greater than 90o) expected from avians. The average stride of the single known trackway (MCF PVPH-SB 415.17, footprints #86 to #94, figure 6) is 6.4 times longer than average footprint length, compared with 5.0 times in cf. *Aquatilavipes* (MCF PVPH-SB 415.14, footprints a to c, d to f, figure 4.A; MCF PVPH-SB 415.17, footprints #95 to #97, figure 6) and 5.4 times in cf. Ignotornis (MCF PVPH-SB 337 field map, footprints #19 to #23, #25 to #28).

The avian trackmakers at Sierra Barrosa

Bird footprints are easily distinguished from those of small, non-avian theropods, mainly because of the relatively wide divarication of digits (almost always greater than 90° between digits II and IV), and the distinctive "heel" impression made by the metatarsal pad (Currie, 1981; Lockley *et al.*, 1992; McCrea, 2000). The wide divarication and presence of a common point of digit divergence probably re-

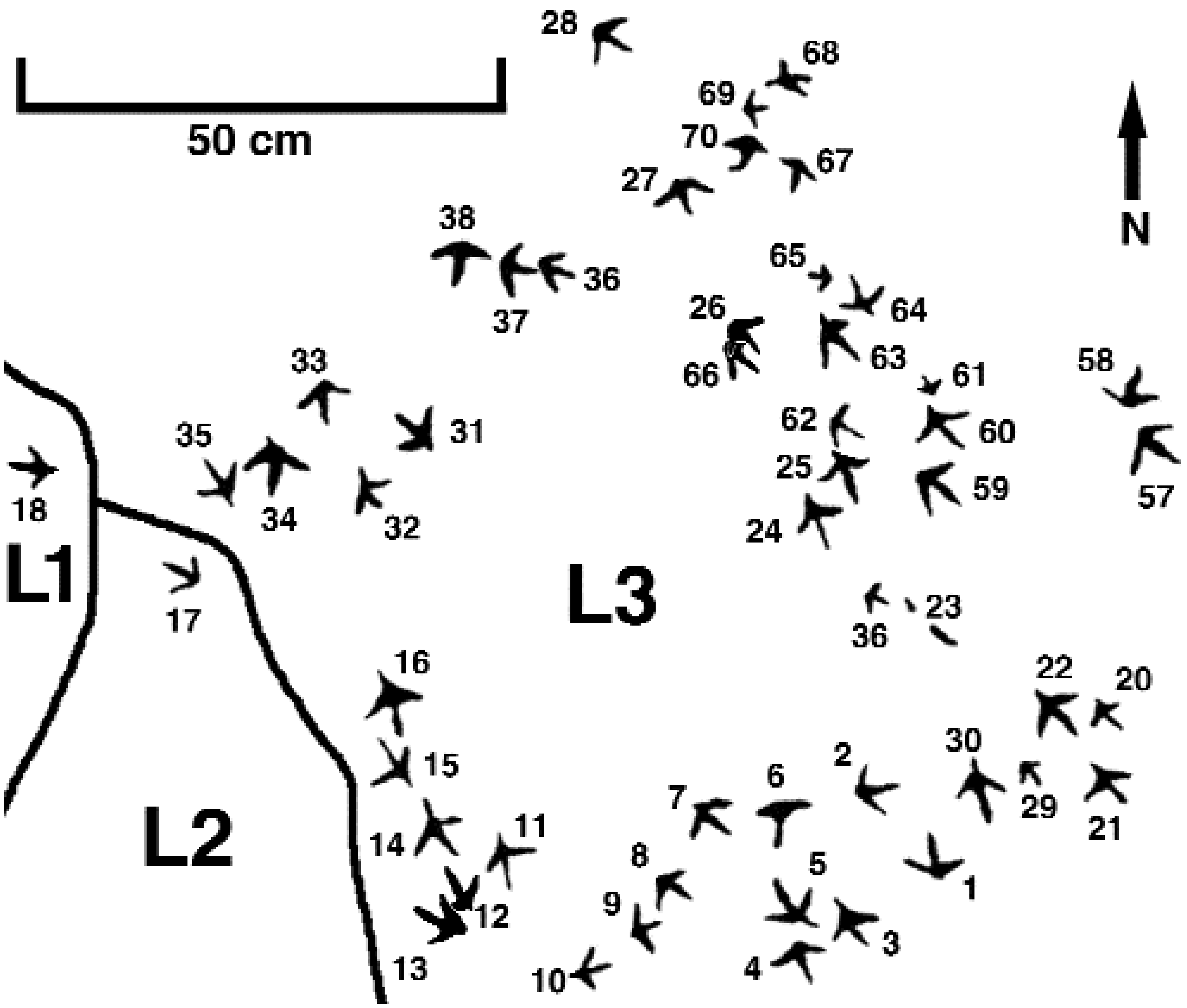


Figure 5. Part (about 20%) of the map (MCF PHPV-SB 337) of locality A, Sierra Barrosa showing footprints of *cf.* ***Aquatilavipes*** and *cf.* ***Ignotornis***. Abbreviations: L1, L2, L3; layers 1, 2, 3. Numbers correlate with footprint numbers in table 1 / *Parte de aproximadamente 20% del mapa (MCF PHPV-SB 337)de la localidad A en Sierra Barrosa mostrando las huellas de cf.* ***Aquatilavipes*** *y cf.* ***Ignotornis****. Abreviaciones: L1, L2, L3; niveles 1, 2, 3.*

lates to the restructuring of the foot, including the fusion of the metatarsals, for perching (Currie, 1981). This character is visible in all the specimens reported here. When such a footprint also includes a hallux impression, the identification is unequivocal, as no other vertebrate is known with a relatively long, posteriorly directed first digit. In most bird footprints, the impressions of the hallux and metatarsal pad ("heel") are continuous, and only a small percentage of unequivocal bird footprints from any age lack them (Lockley *et al.*, 1992). In non-avian dinosaur footprints, the hallux impression is more medial than posterior in position and is oriented anteriorly, and unless the animal stepped into deep mud, only the tip of the claw leaves a trace.

The *cf. Aquatilavipes, cf. Ignotornis* and Barrosopus footprints from Sierra Barrosa were unquestionably made by birds. However, the taxa responsible for their creation cannot be determined because no fossilized avian bones have been recovered from the Anacleto Formation. Furthermore, avian foot structure is conservative and it is almost impossible to correlate footprints with fossil species based on skeletons.

Nevertheless, the underlying Bajo de la Carpa Formation has produced avian fossils (Alvarenga and Bonaparte, 1992; Chiappe and Calvo, 1994) that may provide clues to identify the trackmakers. Two avian species have been described from the Bajo de la Carpa Formation — the basal paleognathe *Patagopterix deferrarisi* (Alvarenga and Bonaparte, 1992; Chiappe, 1996) and the enantionithine Neuquenornis volans (Chiappe and Calvo, 1994). *Patagopterix* has been proposed as a cursorial bird. Its fossils, known from almost complete skeletons, show that the hallux was positioned too high on the fused metatarsus to

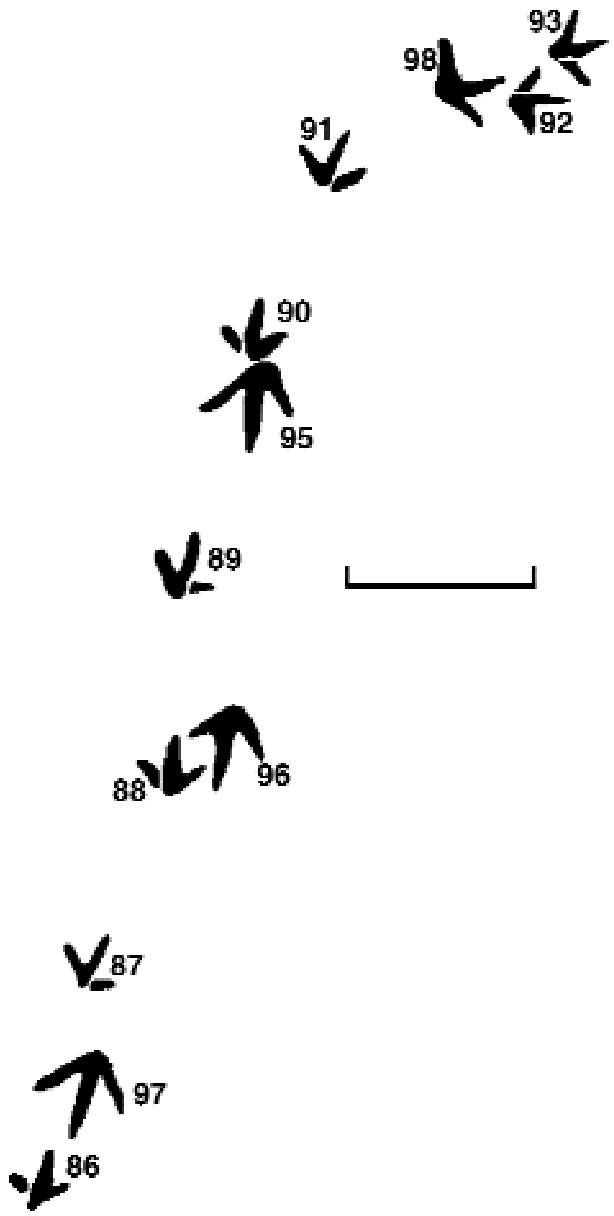


Figure 6. Part of the map (MCF PHPV-SB 337) of locality **A,** Sierra Barrosa showing trackways of *cf.* ***Aquatilavipes*** (footprints #95 to #97) and ***Barrosopus slobodai*** (footprints #86 to #93). Numbers correlate with footprint numbers in table 1. Scale bar: 10 cm / *Parte del mapa MCF PHPV-SB 337 de la localidad A, Sierra Barrosa mostrando rastrilladas de cf.* ***Aquatilavipes*** *(huellas #95 to #97) y* ***Barrosopus slobodai*** *(huellas #86 to #93). Los números se correlacionan con aquellos de las huellas de la tabla 1.*

have left significant impressions in the substrate. It is therefore unlikely to be related to the trackmaker of *Ignotornis.* The 5 cm length of the third toe suggests that it may have been responsible for producing *Aquatilavipes*-like tracks.

Neuquenornis from the Bajo de la Carpa formation seems to have been an active flier, and also has a well-developed, reversed hallux (Chiappe, 1996). Interestingly, the second digit is gracile in *Neuquenornis*, just as the second digital impression of the *cf. Ignotornis* footprints is narrow. Although the foot of *Neuquenornis* is incomplete, the second digit of the holotype is 30.6 mm long (MUCPv-142), which falls within the range of second digit length in the Anacleto footprints (for example, digit II impression of footprint #102 is 34 mm long). It is therefore possible that the *cf. Ignotornis* footprints at Sierra Barrosa were made by an animal similar to *Neuquenornis.*

Barrosopus slobodai has the widely spread second and fourth toes expected in an avian track, but otherwise seems similar to a non-avian theropod. It is therefore worthwhile to also consider theropods distinct from birds as the possible trackmakers of these footprints. Unfortunately, there are no published records of theropods from the Anacleto Formation in this part of the Neuquén Basin. Farther north, the formation has produced an abelisaur theropod (Coria *et al.*, 2002 and in press b), but it is far too big to have produced the *Barrosopus* footprints. The underlying Bajo de la Carpa Formation has yielded small theropods, such as the enigmatic *Alvarezsaurus* and *Velocisaurus* (Bonaparte 1991). The former would have had an estimated footprint length of 4.5 cm, and the latter 7 cm (Bonaparte 1991)suggesting that both taxa are too large to have made the *Barrosopus* ichnites. In *Velocisaurus*, the third metatarsal protruded far beyond the ends of the other metatarsals. Therefore, the digital impressions of its footprint would have been separated as in the *Barrosopus* footprints. However, both *Alvarezsaurus* and *Velocisaurus* have unfused metatarsals, and probably would not have produced footprints with divarications of more than 90 degrees, making these animals questionable sources for *Barrosopus* footprints.

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References

Alonso, R.N. and Marquillas, R.A. 1986. Nueva localidad con huellas de dinosaurios y primer hallazgo de huellas de aves en la Formación Yacoraite (Maastrichtiano) del norte argentino. *4° Congreso Argentino de Paleontología y Bioestratigrafía, Actas* 2, pp. 33-42.

Alvarenga, H.M.F. and Bonaparte, J.F. 1992. A new flightless land bird from the Cretaceous of Patagonia. *Proceedings of the Second International Symposium on Avian Paleontology* (Los Angeles, 1988): 51-64.

Bonaparte, J.F. 1991. Los vertebrados fósiles de la Formación Rio Colorado, de la Ciudad de Neuquén y cercanías, Cretácico Superior, Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales* 4: 17-123.
Bromley, R.G. 1990. Trace Fossils: Biology and Taphonomy. *Special Topics in Palaeontology*. Unwin Hyman Ltd., London. 280 p.
Casamiquela, R.M. 1987. Novedades en ichnología de vertebrados en la Argentina. *Anais do 10o Congresso Brasileiro de Paleontologia*, Rio de Janeiro, pp. 445-456.
Chamberlain, C.K. 1975. Recent lebensspuren in nonmarine aquatic environments. In: R.W. Frey (ed.), *The Study of Trace Fossils,* Springer, New York, 576 p.
Chiappe, L.M. 1993. Enantiornithine (Aves) tarsometatarsi from the Cretaceous Lecho Formation of northwestern Argentina. *American Museum of Natural History, Novitates* 3083: 1-27.
Chiappe, L.M. 1996. Late Cretaceous birds of southern South America: anatomy and systematics of Enantiornithes and *Patagopteryx deferrariisi. Münchener Geowissenshaftlichen Abhandlungen* A 30: 203-244.
Chiappe, L.M. and Calvo, J.O. 1994. *Neuquenornis volans*, a new Upper Cretaceous bird (Enantiornithes: Avisauridae) from Patagonia, Argentina. *Journal of Vertebrate Paleontology* 14: 230-246.
Chiappe, L.M., Coria, R.A., Dingus, L. and Fox, M. 1998. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature* 396: 258-261.
Chiappe, L.M., Ji, S.A., Ji, Q. and Norell, M.A. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. *American Museum of Natural History, Bulletin* 242: 1-89.
Coria, R.A., Currie, P.J., Eberth, D., Garrido, A. and Koppelhus, E. 2001. Nuevos vertebrados fósiles del Cretácico Superior de Neuquén. Resúmenes 17o Jornadas Argentinas de Paleontología de Vertebrados. *Ameghiniana* 38 Suplemento Resúmenes: 6R.
Coria, R.A., Chiappe, L.M. and Dingus, L. 2002. A new close relative of Carnotaurus sastrei (Abelisauridae, Theropoda) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* 22: 460-465.
Currie, P.J. 1981. Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of northeastern British Columbia, Canada. *Journal of Vertebrate Paleontology* 1: 257-264.
Dingus, L., Clarke, J., Scott, G.R., Swisher, C.C. III, Chiappe, L.M., and Coria, R.A. 2000. Stratigraphy and magnetostratigraphic/faunal constraints for the age of sauropod embryo-bearing rocks in the Neuquén Group (Late Cretaceous, Neuquén Province, Argentina). *American Museum Novitates* 3290: 1-11.
Eberth, D.A., Berman, D.S, Sumida, S.S., and Hoff, H. 2000. Lower Permian terrestrial paleoenvironments and vertebrate paleoecology of the Tambach Basin (Thuringia, Central Germany): The upland holy grail. *Palaios* 15: 293-313.
Hou, L.H. 1998. *Mesozoic Birds of China.* Phoenix Valley Bird Park, Lugu Hsiang, Taiwan. 228 pp.
Leonardi, G. (ed.) 1987. *Glossary and manual of tetrapod footprint palaeoichnology*. República Federativa do Brasil, Ministério das Minas e Energia, Departamento Nacional da Producion mineral, 72 pp.
Lockley, M.G., Yang, S.Y., Matsukawa, M., Fleming, F. and Lim, S.K. 1992. The track record of Mesozoic birds: evidence and implications. *Philosophical Transactions of the Royal Society*, London 336: 113-134.
Lockley, M.G., Janke, P. and Theisen, L. 2001. First reports of bird and ornithopod tracks from the Lakota Formation (Early Cretaceous), Black Hills, South Dakota. In: D.H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*, Indiana University Press, Indianapolis, pp. 443-452.
McCrea, R.T. 2000. [*Vertebrate palaeoichnology of the Lower Cretaceous (lower Albian) Gates Formation of Alberta*. University of Saskatchewan, Department of Geological Sciences. MSc thesis, 133 pages. Unpublished].
McCrea, R.T. and Sarjeant, W.A.S. 2001. New ichnotaxa of bird and mammal footprints from the Lower Cretaceous (Albian) Gates formation of Alberta. In: D.H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*, Indiana University Press, Indianapolis, pp. 453-478.
Mehl, M.G. 1931. Additions to the vertebrate record of the Dakota sandstone. *American Journal of Science* 21: 441-452.
Melchor, R.N., de Valais, S. and Genise, J.F. Bird-like fossil footprints from the Late Triassic. *Nature* 417: 936-938.
Sanz, J.L. 1999. *Los Dinosaurios voladores, Historia evolutiva de las Aves primitivas.* Mundo Vivo Liberarias, Spain, 239 pp.

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