OCCURRENCE OF A SAUROPOD DINOSAUR IN THE UPPER JURASSIC OF CHILE (REIDENTIFICATION OF *IGUANODONICHNUS FRENKI*)

KAREN MORENO [1]*, MICHAEL J. BENTON [1], DAVID RUBILAR [2], ALEXANDER VARGAS [2]. [1] University of Bristol, Earth Sciences Department, Bristol, BS8 1RJ, United Kingdom; [2] Museo Nacional de Historia Natural, Interior Quinta Normal, S/N, Casilla 787, Santiago, Chile.

Abstract

New observations from the only studied Upper Jurassic dinosaur unit in South America, the Baños del Flaco Formation, Chile, are presented here. We found that the trackways formerly assigned to the ornithopod ichnogenus *Iguanodonichnus* are incorrect and should be referred to the sauropod ichnospecies *Parabrontopodus frenki* on the basis of: (1) step-angles average less than 110º; (2) pes prints intersecting trackway midline; (3) pes print longer than wide with long axis rotated outward; (4) claw impression of digit I is prominent and directed forward. Claws on digits II and III reduced. These morphological characteristics give a clue about pes morphology of the South American Jurassic sauropods, which foot bones remains are scarce.

Keywords

Parabrontopodus, dinosaur footprints, Chile, Upper Jurassic, sauropod.

* Tel: +44 (0)117 954 5246; Fax: +44 (0)117 925 3385; e-mail: k.moreno@bris.ac.uk

Resúmen

En el presente trabajo se realizan nuevas observaciones acerca de la única unidad geológica del Jurásico Superior con registro de dinosaurios en América del Sur. Las pistas anteriormente asignadas al icnogénero *Iguanodonichnus,* atribuido a ornotópodos, son re-clasificadas como pertenecientes a *Parabrontopodus frenki* en base a: (1) promedio de ángulo de paso menor a 110º; (2) huellas pedales intersectan el eje de la pista; (3) huella pedal más larga que ancha, eje longitudinal dirigido hacia afuera; (4) impresión de garra correspondiente al dígito I es prominente y se dirige hacia adelante. Garras reducidas en dígitos II y III. Estas característica morfológicas posiblemente proveen pistas acerca de la morfología pedal de los saurópodos Jurásicos de América del Sur, cuyos restos oseos de piés son escasos.

Palabras clave

Parabrontopodus, huellas de dinosaurios, Chile, Jurásico Superior, saurópodo.

1. Introduction

The Jurassic-Cretaceous boundary marks a major transition in dinosaurian evolution, with a switch from sauropods to ornithopods as the dominant herbivores (Bakker, 1971; Weishampel and Norman, 1989). The skeletal records show major changes from classic Late Jurassic dinosaurian faunas, such as those of the Morrison Formation, containing abundant remains of 6-7 genera of sauropods, to the Early Cretaceous Wealden of Europe with rare sauropods, but abundant *Iguanodon*. Hitherto, the story of this transition in South America has been unclear, largely because of the rarity of Jurassic dinosaur finds. Middle Jurassic dinosaur remains from Chubut Province, Argentina, include the cetiosaurids *Amygdalodon patagonicus*, *Patagosaurus fariasi*, *Volkheimeria chubutensis* and *Tehuelchesaurus benitezii* and the allosaurid *Piatnitzkysaurus floresi* (e.g. Bonaparte, 1979; Rich et al., 1999). Two Early-Middle Jurassic trackbeds, from the Botucatu Formation of Brazil, and the La Matilde Formation of Argentina (Leonardi, 1989), both contain a small theropod and ornithopod ichnofauna.

Dinosaur footprints are known from seven localities in Chile (Salinas et al., 1991). The best known is Termas del Flaco, approximately 100 km south east of the city of San Fernando, VI Region (Fig. 1). This tracksite represent the only studied Upper Jurassic dinosaur unit in South America. Casamiquela and Fasola (1968) described two ichnospecies of dinosaurs from this locality; *Iguanodonichnus frenki* and *Camptosaurichnus fasolae*, as well as three trackways of large-sized footprints (trackways 3, 5 and 8) and four smaller trackways (trackways 1, 2, 6A, and 7A), both also identified as ornithopod tracks.

Casamiquela and Fasola (1968) based their diagnosis of *Iguanodonichnus frenki* on the following: (1) apparently bipedal posture; (2) large size; (3) the then current belief that

ornithopods displayed an external rotation of the sagittal axis of the feet; (4) step angle of less than 110° was identified as characteristic of the Ornithopoda; (5) dating available at the time indicated an Early Cretaceous age (Klohn, 1960), a time in which large ornithopods such as *Iguanodon* were present.

In later works, several authors (Dos Santos et al., 1992; Farlow, 1992; Lockley et al. 1994a; Sarjeant et al., 1998) dismissed the ichnospecies *I. frenki* as a nomen dubium, suggesting instead a sauropod affinity for this ichnite, based on the evidence that a step angle less than 110° is a character of Sauropoda and definitely not of Ornithopoda (Dos Santos et al., 1992), and further argued that the apparent bipedalism resulted from an overlap of manus and pes prints (Lockley et al., 1986). These authors based their discussion entirely on the description by Casamiquela and Fasola (1968).

The second ichnospecies from this locality, *Camptosaurichnus fasolae*, is characterized by three pedal digits and half-moon-shaped footprints of the forelimbs. Sarjeant et al. (1998) attributed this ichnospecies to a theropod, because Casamiquela and Fasola (1968) presented low-quality pictures, no captions, and their description contained errors. Moreno and Rubilar (1997) presented a redescription (unknown to Sarjeant et al., 1998) of the original trackways and descriptions of the newly discovered trackways from the same outcrop. The new trackways belong to two different species of ornithopods, *C. fasolae* and a more rounded pedal morphology (40% wider), and two species of theropods, a medium-sized footprint ranging from 22.5 to 26.5 cm long and 25 cm wide, and a small-sized footprint measuring 16-20 cm long, 16-18 cm wide and with the middle digit (number III) much larger than the functional laterals (digits II and IV).

Part of the redescription by Moreno and Rubilar (1997) and Rubilar et al. (1998) is extended here, including some observations made by Moreno (2000) and Moreno and Pino (2002).

2. Systematic paleontology

Ichnogenus *Parabrontopodus* Lockley et al., 1994a

Type ichnospecies: *Parabrontopodus macintoshi* Lockley et al., 1994a, Late jurassic, Morrison Formation

Parabrontopodus frenki sp. nov. *(=Iguanodonichnus frenki* Casamiquela in Casamiquela and Fasola, 1968) (see Figs. 2-6)

Etymology: In honor to Dr. Samy Frenk (Casamiquela and Fasola, 1968)

Material: Trackways 3, 5 and 8 *in situ.*

Holotype: Trackway 3 (Figs. 2, 4), cast SGPV1151.

Repository: Museo Nacional de Historia Natural, Santiago, Chile.

Locality: 100 m northeast of Termas del Flaco, northern side of Tinguiririca River, Chile (Fig. 1).

Stratigraphic position: Late Jurassic, Tithonian (Biró-Bagózcky, 1984), Baños del Flaco Formation (Klohn, 1960). Carbonate platform environment.

Diagnosis of the ichnogenus: Narrow sauropod trackway of medium to large size (footprint length approximately 50-90 cm), characterized by no space between trackway midline and inside margin of pes tracks. Pes footprint longer than wide with long axis rotated outward. Pes claw impressions, corresponding to digits I, II, and III show a

strong outward rotation. Manus tracks semicircular and small in comparison with pes tracks (i.e. pronounced heteropody).

Description: Only pedal impressions are preserved, averaging 0.62 m in length (range: 0.55-0.72 m) and 0.35 m in width (range: 0.25-0.45 m). The sagittal axis of the elongated pedal footprint is externally rotated. Step-angles average 98º, as in sauropods, less than 110º, Dos Santos et al., 1992. Claw impressions belonging to digit I are approximately 11 cm long and 5 cm wide and tend to follow a straight line parallel to the footprint axis. Claws on digits II and III are not prominent. Impressions of pedal claws corresponding to digit I are clearly visible on footprints 2, 3, 5, 6, 7 and 9 of trackway 3 (Figs. 2, 4) and footprints 1, 3, 4, 5, and 9 of trackway 8 (Fig. 3).

Trackway 5 is conserved as a convex hyporelief with no claw detail, it describe an open curve with minimal breadth between tracks (Fig. 5). The footprint shape is rather more rounded than in the other trackways. At mid-trackway (highest point of the curve) the footprints are more eroded. This trackway shows an alternation of large (averaging 0.55 m long, 0.45 m wide) and small-sized impressions (averaging 0.24 m long and 0.35 m wide) with a manus/pes heteropody ratio of about 0.5, which may be evidence of quadrupedalism. Nevertheless, weathering does not allow a better morphological description. The only diagnostic feature is a step-angle of less than 110º, allowing only tentative assignment to *P. frenki*.

Assuming a foot/hip height ratio in the range of 4-5.9 for sauropods (Alexander, 1976; Thulborn, 1989), the trackmaker hip would be about 3.1 ± 0.6 m high. This leads to a stride length/hip height ratio of 0.5-0.7 which indicate a walking gait (Thulborn and

Wade, 1984) at a speed of 0.3-0.4 m/s as estimated using the equation provided by Alexander (1976).

3. Discussion

I. frenki is reinterpreted as *Parabrontopodus*, an ichnogenus that is attributed to either basal sauropods, diplodocoids or basal macronarians, which are all narrow-hipped sauropods (Day et al., 2002). The diagnosis of Casamiquela and Fasola (1968), mentioned in the introduction is incorrect in several points:

1) Footprint size is not considered diagnostic since it varies with growth.
2) Apparently bipedal posture is observed in sauropod trackways where sections of quadrupedal walking and sections of apparently bipedal walking can be seen in a single trackway (e.g. Lockley et al., 1986). This apparent bipedalism in quadrupedal sauropods is caused by overlapping of the small forelimb footprints by the considerably larger hindlimb footprints; accordingly, some footprints of *P. frenki* show an elongate shape reflecting such footprint overlap (i.e. fig. 4), producing the wide range of "foot-lengths" registered for these trackways.
3) The external rotation of the footprint axis was formerly identified with the ornithopod *Iguanodon*, as a consequence of erroneous early skeletal mounts featuring tail-dragging and artificially outward-spread legs.
4) Finally, the alleged Early Cretaceous age was reinterpreted (Biro-Bagóczky, 1984) as Tithonian (Late Jurassic), a time in which evidence (footprints or bones) of large ornithopods such as *Iguanodon* is rare worldwide, whereas *Parabrontopodus* was made by a mainly Jurassic sauropod (Lockley et al., 1994b).

To conclude, the diagnosis of these trackways as belonging to an iguanodontid is discarded, and the genus *Iguanodonichnus* is a nomen dubium as many authors have already indicated (Dos Santos et al., 1992; Farlow, 1992; Lockley et al., 1994a; Moreno and Rubilar, 1997; Sarjeant et al., 1998).

Pedal morphology of *P. frenki* is consistent with the diagnosis of the genus, in spite of showing no clear impressions of the manus. Furthermore, the impression of digit I tending to follow a straight line parallel to the footprint axis and the absence of prominent claw impressions in digits II and III are morphological differences from *P. macintoshi* (Lockley et al., 1994a), *Brontopodus* from Eastern Utah and *Brontopodus* from Portugal (Meyer et al., 1994) (Fig. 6).

The worldwide fossil record of sauropods shows that the three pedal digits bore claws of decreasing size, and consequently the absence of those claws has been attributed to the loss of material. As we present here for *P. frenki*, the notorious difference in claw morphology from a well developed and nearly symmetric first pedal ungual impression, through rudimentary II and III to the absence of IV, could explain some apparently incomplete fossil pes remains such as *Patagosaurus fariasi*, for which only one ungual has been recognized in the only two specimens with preserved foot bones (Bonaparte, 1986). Our data suggest that this lack of the digit II-IV unguals could be a morphological consequence, and not a problem of preservation.

The *Brontopodus* ichnofacies dominated by sauropod ichnites of the *Brontopodus* type and by large theropods (Lockley et al., 1994b, c, Lockley and Conrad, 1989) has been recognized worldwide, mainly in Laurasia. This contribution confirms its presence on the South American continent. It must be mentioned, however, that the Baños del Flaco

Formation presents an Ornithopod-Theropod-Sauropod ichnocoenosis which differs slightly from the classic *Brontopodus* ichnofacies, because it contains small ornithopod footprints (less than 30 cm long), relatively small theropods, and sauropod footprints belonging to the ichnogenus *Parabrontopodus*. Note, however, that the ichnofauna is in a carbonate platform environment, which is typical of the *Brontopodus* ichnofacies (Lockley et al., 1994b, c; Lockley and Conrad, 1989).

The ichnocoenosis of the Baños del Flaco Formation agrees with the Early-Middle Jurassic fauna described in Argentina and Brazil, which is composed of a reduced variety of sauropods (only cetiosaurids), small theropods and small ornithopods. This contrasts with the abundance and diversity of large sauropods and theropods found in Laurasia and suggests that such a diversity may have appeared later on the South American continent, possibly from the late Early Cretaceous in which the first diplodocids and titanosaurids are recorded (e.g. Calvo and Salgado, 1995; Salgado and Azpilicueta, 2000).

Acknowledgements

We thank the Jurassic Foundation for funding, members of the Sociedad Paleontologica de Chile (SPACH) and the Instituto de Geociencias of the Universidad Austral de Chile for their valuable support during fieldwork, Alexandre Corgne for his help the during manuscript preparation and all people who collaborated disinterestedly with this work.

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Figure captions

Figure 1. Location map showing Chile and part of Region VI. The arrow shows the Termas del Flaco locality.

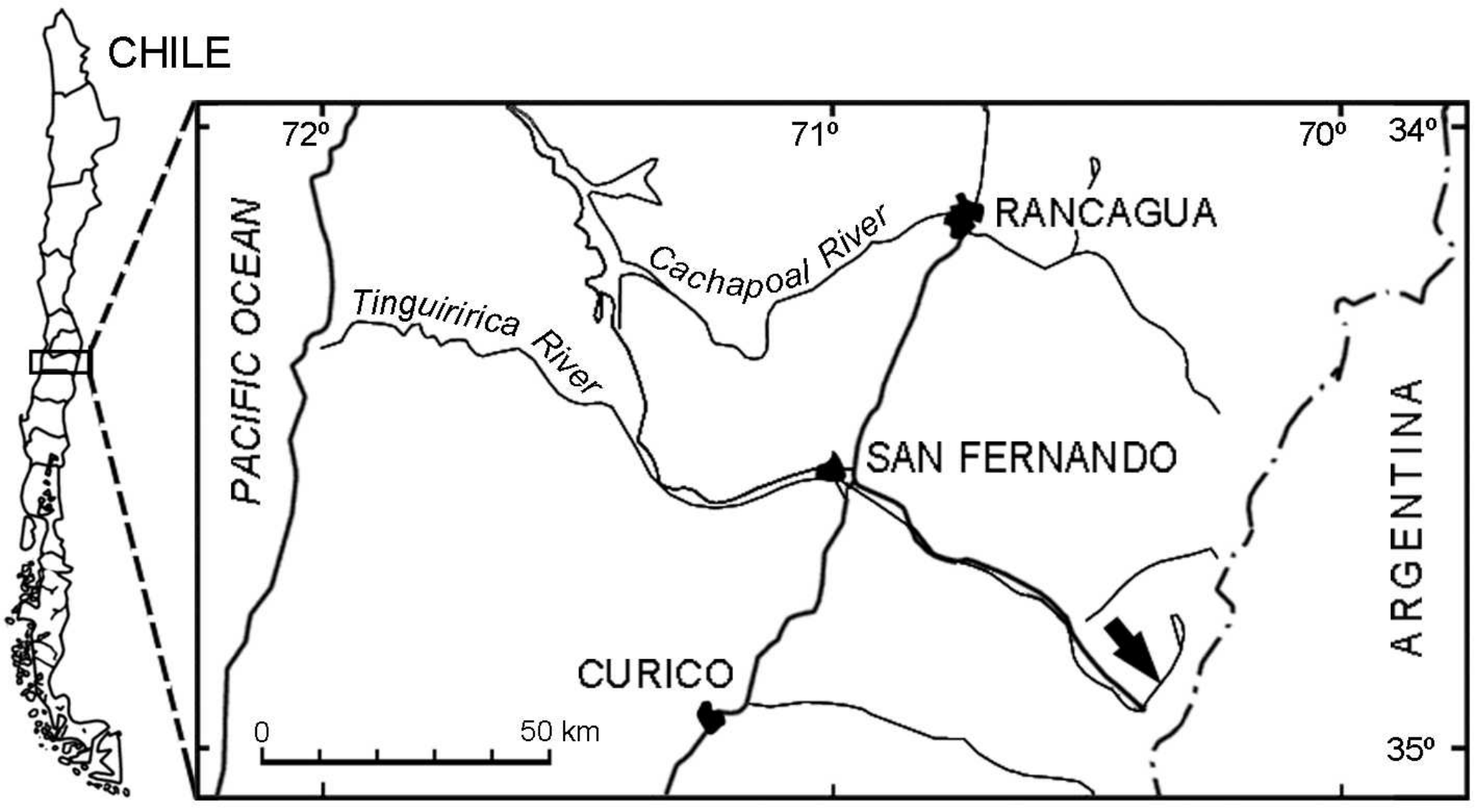
Figure 2. *Parabrontopodus frenki* Casamiquela, 1968, photograph and interpretive sketch of trackway number 3. Triangular diagram shows mean distances between prints, and the step angle. Scale, 50 cm.

Figure 3. *Parabrontopodus frenki* Casamiquela, 1968, photograph and interpretive sketch of trackway number 8. Manus and pes print outlines and mean dimensions are shown at top left. Triangular diagram shows mean distances between prints, and the step angle. Scale, 50 cm.

Figure 4. *Parabrontopodus frenki* Casamiquela, 1968, photograph and interpretive sketch of footprint number 6 of trackway number 3.

Figure 5. *Parabrontopodus frenki* Casamiquela, 1968, photograph and interpretive sketch of trackway number 5. Arrows show manus prints (see detailed sketch of trackset 18). Triangular diagram shows mean distances between prints, and the step angle.

Figure 6. Differences between *Brontopodus* from Eastern Utah, *Brontopodus* from Portugal, *P. macintoshi*, and *P. frenki* modified from Lockley et al. (1994a).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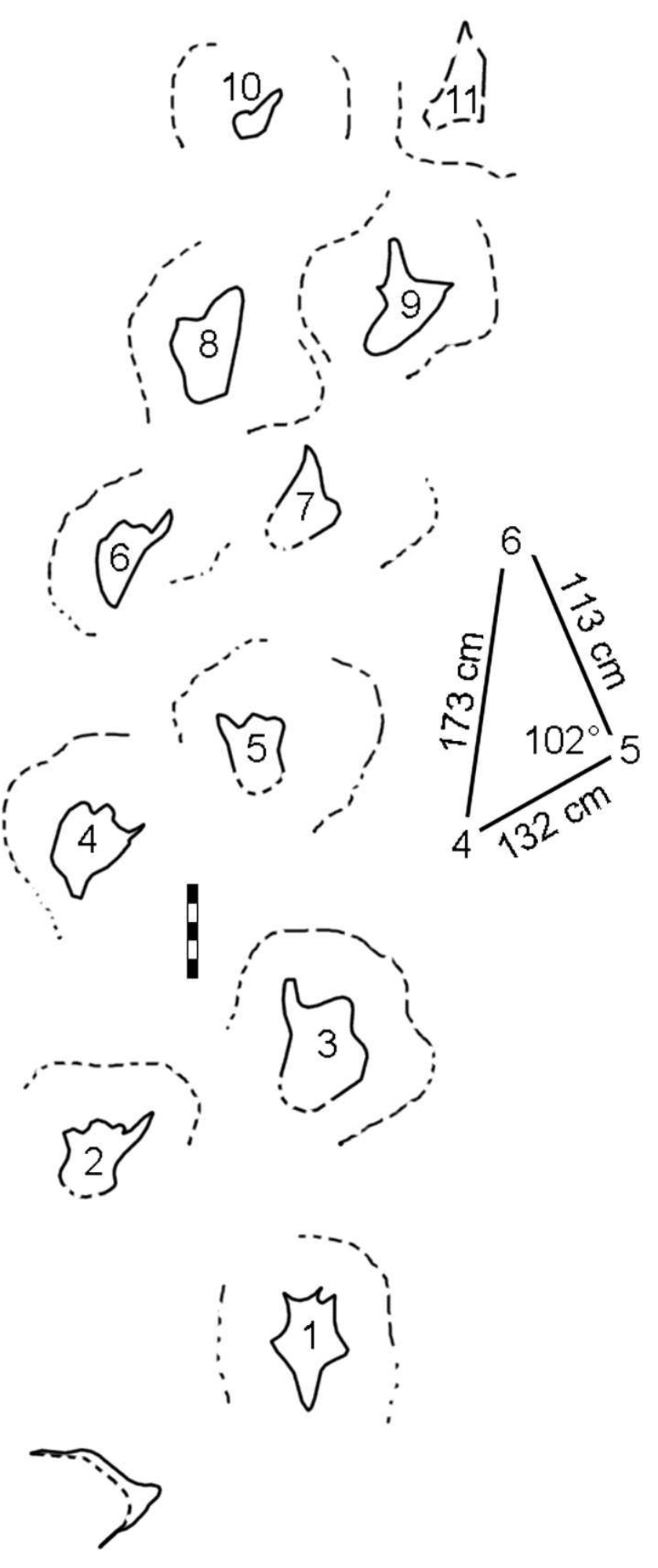
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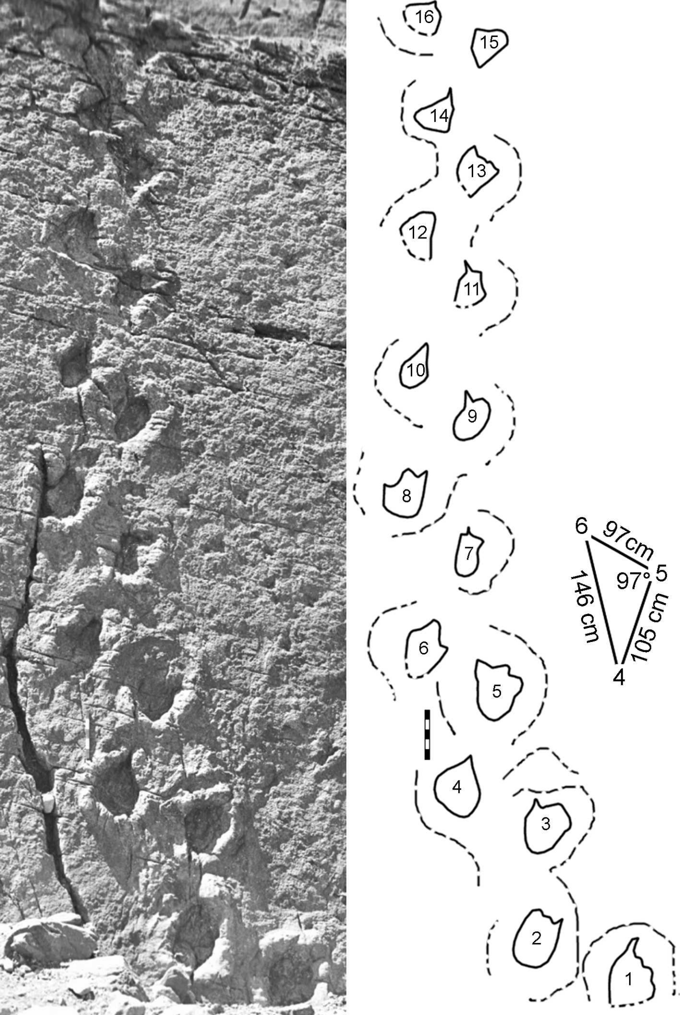
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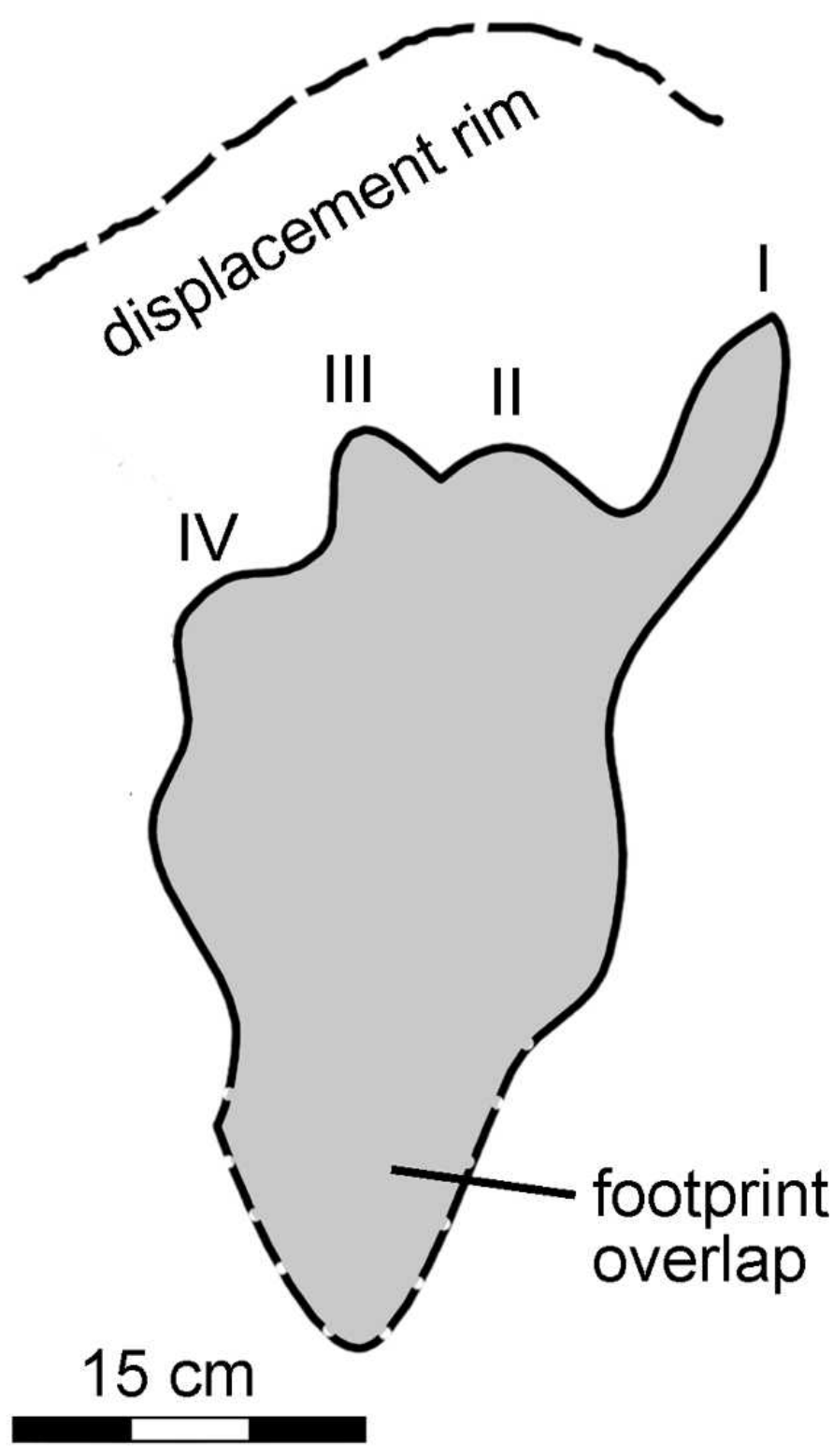
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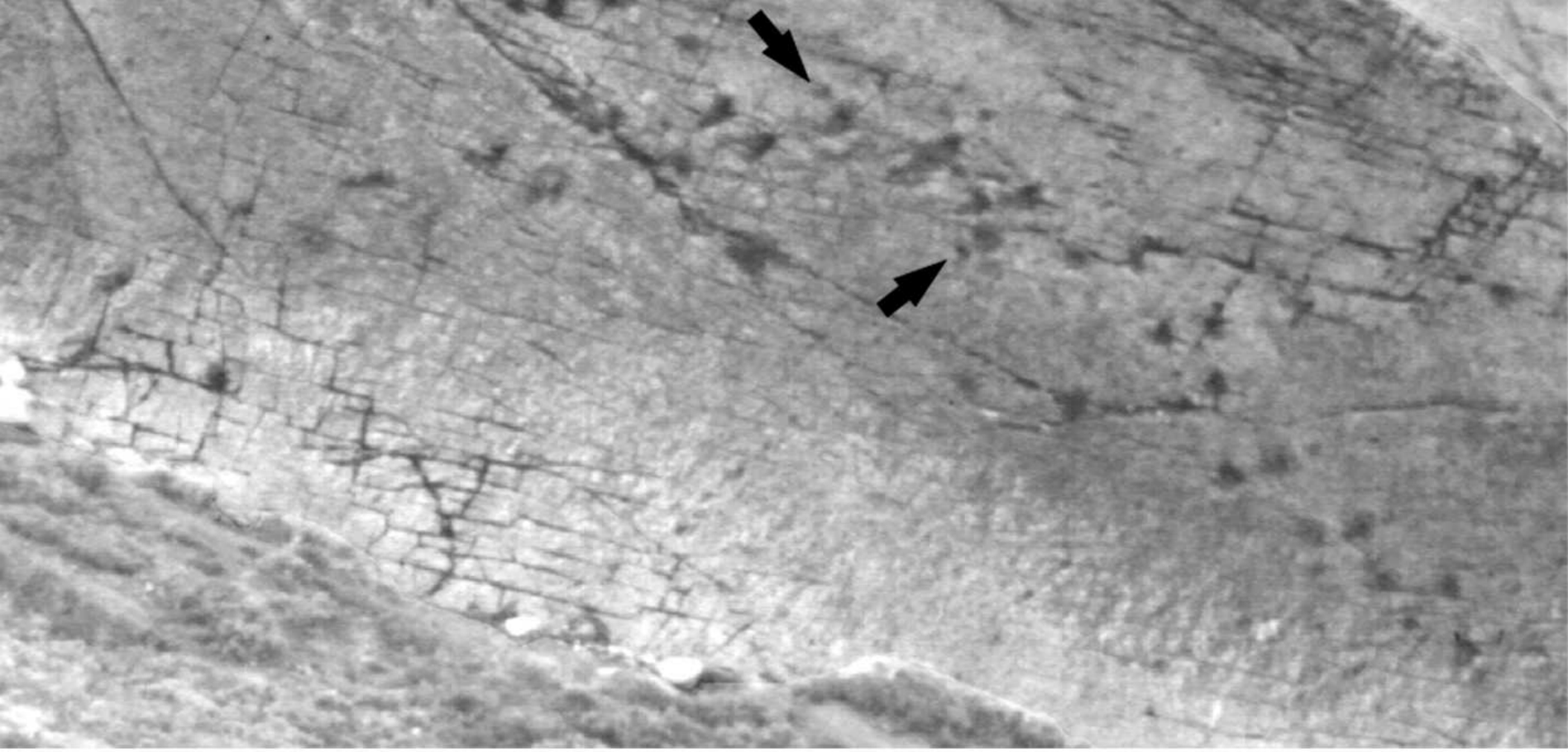

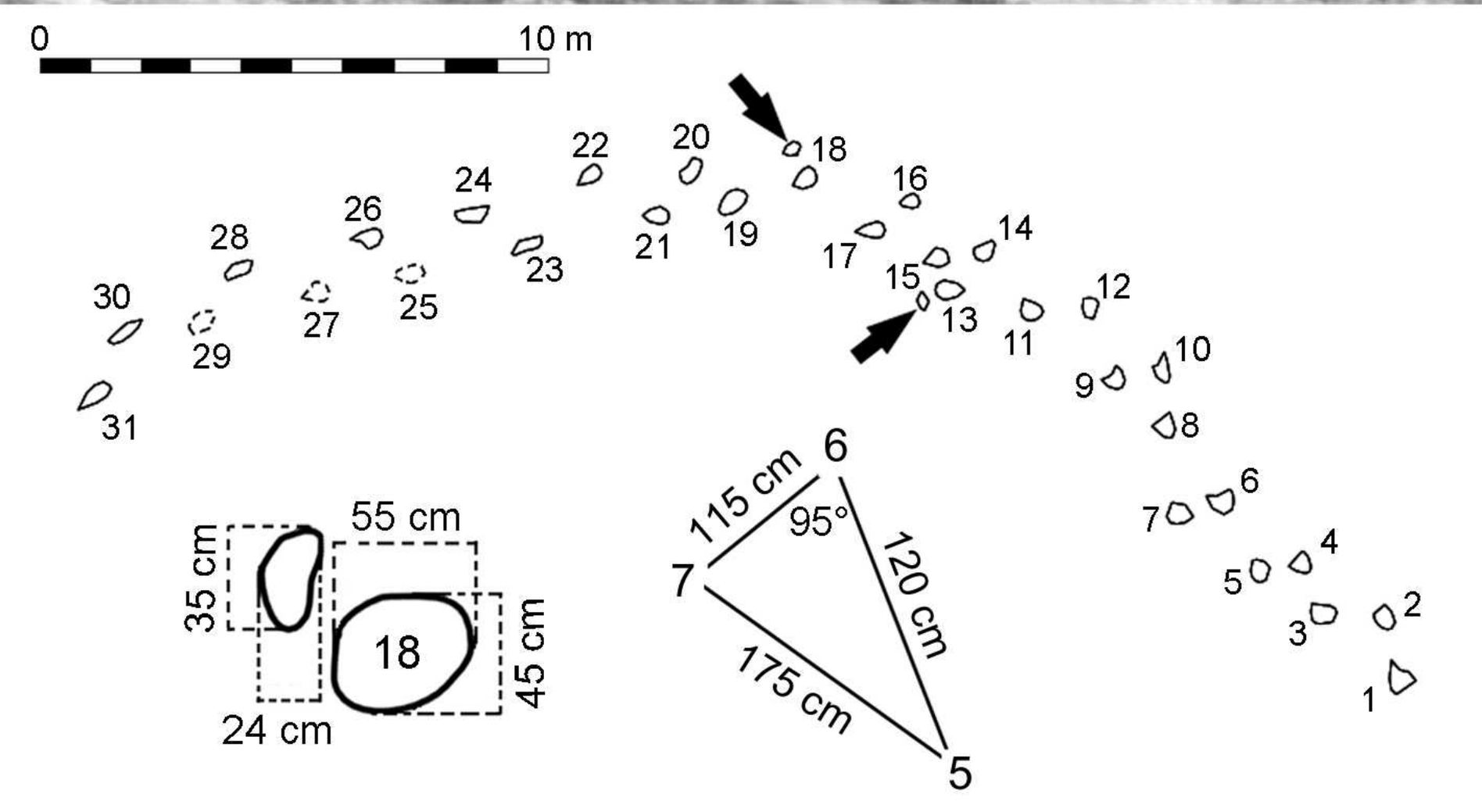
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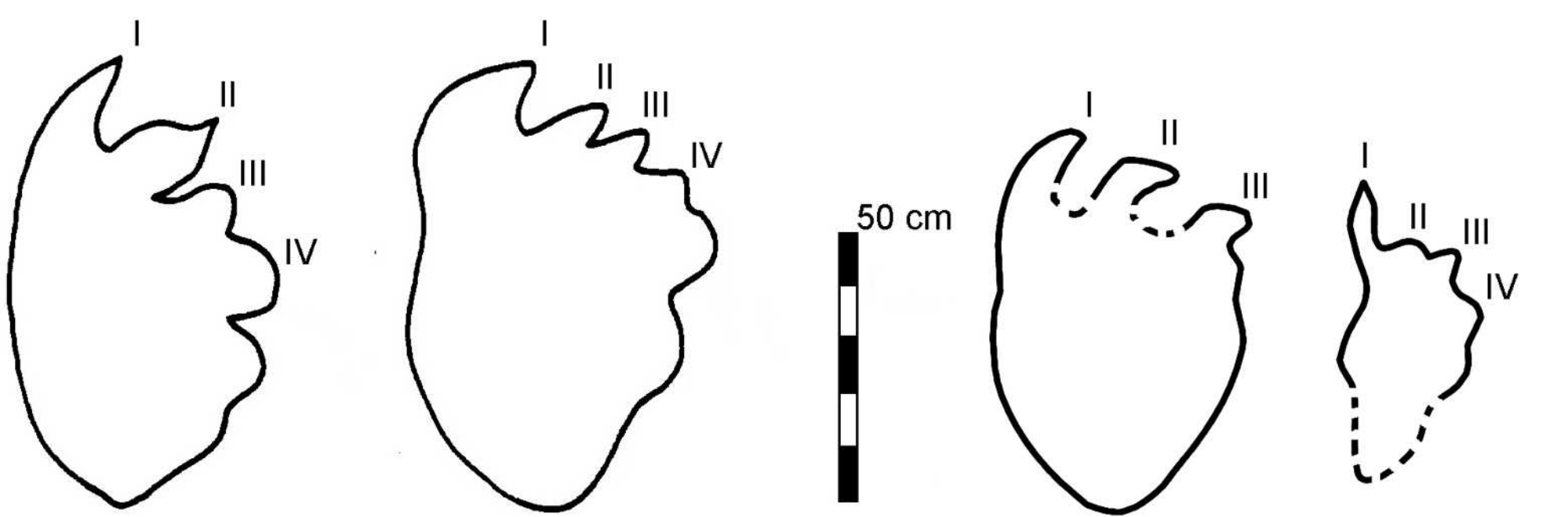

Utah

Brontopodus sp. Portugal

P. macintoshi

P. frenki