

FOOTPRINTS OF THE EARLIEST REPTILES: *NOTALACERTA MISSOURIENSIS* – ICHNOTAXONOMY, POTENTIAL TRACKMAKERS, BIOSTRATIGRAPHY, PALAEOBIOGEOGRAPHY AND PALAEOECOLOGY

Lorenzo MARCHETTI^{1*}, Sebastian VOIGT², Spencer G. LUCAS³,
Matthew R. STIMSON^{4,5}, Olivia A. KING^{4,5} & John H. CALDER^{5,6}

¹Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung,
Berlin, Germany; e-mail: lorenzo.marchetti@mfj.berlin

²Urweltmuseum GEOSKOP/Burg Lichtenberg (Pfalz), Thallichtenberg, Germany;
e-mail: s.voigt@pfalzmuseum.bv-pfalz.de

³New Mexico Museum of Natural History, Albuquerque, New Mexico, USA;
e-mail: spencer.lucas@state.nm.us

⁴Steinhammer Paleontological Laboratories, Geology/Paleontology section,
Natural History Department, New Brunswick Museum, Saint John New Brunswick, Canada;
e-mails: mstimson29@gmail.com; olivia.king@smu.ca

⁵Saint Mary's University, Halifax Nova Scotia, Canada

⁶Nova Scotia Department of Natural Resources, Halifax, Nova Scotia, Canada;
e-mail: johncalder99@gmail.com

* Corresponding author

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Abstract: The origin of reptiles in the tetrapod footprint record has always been a debated topic, despite the great potential of fossiliferous ichnosites to shed much light on reptile origins when compared to the much less extensive skeletal record. This is in part due to an unclear ichnotaxonomy of the earliest tracks attributed to reptiles that has resulted in unreliable trackmaker attributions. We comprehensively revise the earliest supposed reptile ichnotaxon, *Notalacerta missouriensis*, based on a neotype and a selection of well-preserved material from the type locality and other sites. A synapomorphy-based track-trackmaker attribution suggests eureptiles and, more specifically, 'protorothyridids' such as *Paleothyris* as the most probable trackmakers. A revision of the entire Pennsylvanian-Cisuralian record of this ichnotaxon unveils an unexpected abundance and a wide palaeogeographical distribution. The earliest unequivocal occurrence of *Notalacerta* is in the middle Bashkirian (early Langsettian) at the UNESCO World Heritage Site, Joggins Fossil Cliffs (Joggins, Nova Scotia, Canada). This occurrence also coincides with the earliest occurrence of reptile body fossils (*Hylonomus lyelli*), which are found at the same site. *Notalacerta* is abundant and widely distributed during the Bashkirian, mostly in sediments deposited in tidal palaeoenvironments, and less common in the Moscovian and Kasimovian. During the Gzhelian and Asselian, *Notalacerta* occurrences are unknown, but it occurs again during the Sakmarian and is widespread but not abundant during the Artinskian, mostly in fully continental palaeoenvironments.

Key words: Carboniferous, Permian, reptile tracks, *Notalacerta*, ichnotaxonomy, trackmaker

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INTRODUCTION

The ichnogenus *Notalacerta* Butts, 1891a is the most abundant Pennsylvanian ichnogenus that has been ascribed to reptiles (e.g., Chesnut *et al.*, 1994). Although several publications have reported *Notalacerta*, few have investigated

its ichnotaxonomy (e.g., Lucas *et al.*, 2004; Haubold *et al.*, 2005; Voigt and Lucas, 2015a; Marchetti *et al.*, 2019a). As a consequence, this ichnogenus is currently poorly defined, as are the type ichnospecies (*N. missouriensis*) and

the ichnospecies that have been associated with it (e.g., *N. jacksonensis* and *N. magna*). This is in part due to the holotype being lost (Baird, 1982) and the original description presenting only an outline drawing of the specimen (Butts, 1891a, Fig. 1A). Also, the designation of a neotype has not thus far been considered. These reasons alone would be enough to suggest a comprehensive revision of the ichnotaxon. Also, conflicting reports have generated ambiguity about the earliest known tracks attributable to reptiles (e.g., Falcon-Lang *et al.*, 2007; Keighley *et al.*, 2008; Falcon-Lang *et al.*, 2010).

Occurrences of *Notalacerta* in Permian (Cisuralian) strata are generally few, and some of them need to be re-investigated (Haubold, 1970; Baird *in* Calder *et al.*, 2004, Voigt and Lucas, 2015a). Further research is needed in this time interval, in which morphologically-similar reptile ichnogenera such as *Erpetopus*, *Hyloidichnus* and *Varanopus* are generally recognised, raising the possibility that some of the material previously assigned to these ichnotaxa may actually be *Notalacerta*.

Given that *Notalacerta* is the earliest known ichnogenus ascribed to reptiles, establishing a track-trackmaker correlation is important. However, historically, only one publication has discussed the potential trackmakers in detail (Chesnut *et al.*, 1994).

The purpose of this contribution is an ichnotaxonomic revision of the ichnogenus *Notalacerta* Butts, 1891a, including the designation of a neotype to better define the ichnogenus concept for *Notalacerta*, in terms of its diagnostic features and morphological variability. The entire Pennsylvanian-Cisuralian record of *Notalacerta* is revised in order to provide new biostratigraphic, palaeobiogeographic and palaeoecologic data. Moreover, some new considerations of the possible trackmakers are proposed.

MATERIAL AND METHODS

The studied material includes a selection of about 160 specimens from 22 Pennsylvanian-Permian units that bear *Notalacerta*-like footprints. This material was studied firsthand, whenever possible. When the specimens were not relocated, published drawings and photos were analysed. On these slabs, only the footprints that show good morphological preservation *sensu* Marchetti *et al.* (2019a) were considered for ichnotaxonomy and footprint measurements, preferably along trackways. Trackways showing morphological variability along their course were used as a reference to establish the morphological variability of the studied ichnotaxon. The preservation scale of Marchetti *et al.* (2019a) was applied to some significant examples of the illustrated

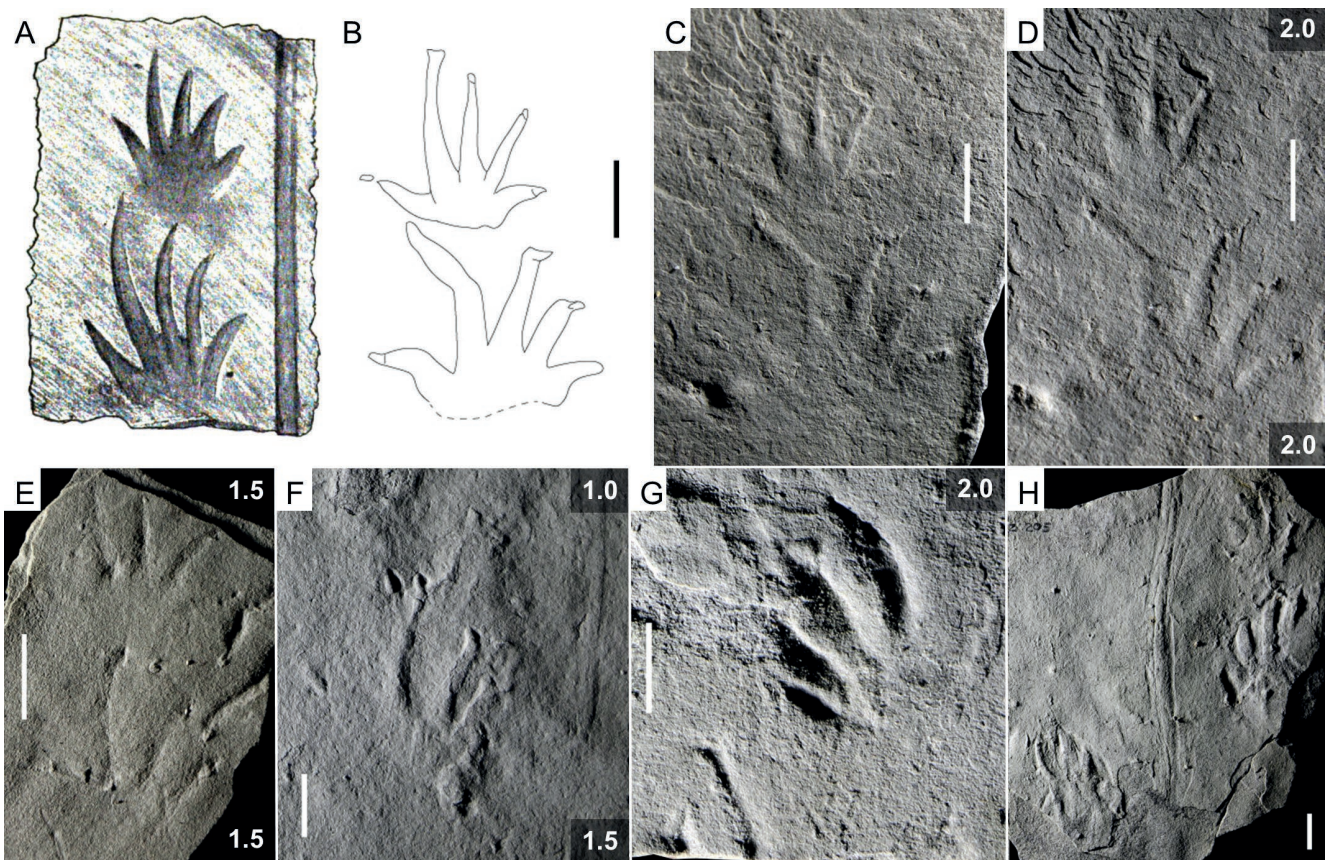


Fig. 1. Type material and topotypes of *Notalacerta missouriensis* Butts, 1891a. Cement City Limestone, Chanute Formation, Pennsylvanian, Kansas City, Missouri, USA. **A.** Pes-manus couple and straight tail impression. Drawing from Butts (1891a), modified. **B–D.** USNM 7321. Neotype of *Notalacerta missouriensis*, right pes-manus couple, convex hyporelief, interpretive drawing and photos with different light direction. **E.** MCZ 205B, left pes-manus couple, concave epirelief. **F.** FMC-P 25486, right pes-manus couple and tail impression, convex hyporelief. **G.** MCZ 204, right manus imprint, concave epirelief. **H.** MCZ 205A, incomplete step cycle and tail impression, convex hyporelief. Numbers beside tracks refer to the preservation scale. Scale bars: 1 cm.

material. The track and trackway measurements follow the conventions of Leonardi (1987). The measurements were listed in Tables 1–3. The track-trackmaker correlation follows the methodology of Voigt *et al.* (2007) and Marchetti *et al.* (2017).

Institutional abbreviations

DUE	Department of Earth Science, Chouaïb Doukkali University, El Jadida, Morocco
FMC	Field Museum of Natural History, Chicago, Illinois, USA
GHUNLPam	Paleontology Collection, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Argentina
HF	Prince Edward Island Museum and Heritage Foundation, Prince Edward Island, Canada
JL	Private collection of Jim Lacefield, Tusculumbia, Alabama, USA
KGS	Paleontological Collections of the Kentucky Geological Survey, Kentucky, USA
KU	Biodiversity Institute & Natural History Museum, Lawrence, Kansas, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MNG	Museum of Nature, Stiftung Schloss Friedenstein, Gotha, Germany
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NBMG	New Brunswick Museum, Saint John, New Brunswick, Canada
NHMMZ	Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany
NHMS	Naturhistorisches Museum Schloss Bertholdsburg Schleusingen, Germany
NMMNH	New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA
NSM	Nova Scotia Museum, Halifax, Nova Scotia, Canada
RM	Redpath Museum, McGill University, Montréal, Québec, Canada
SSM	Springfield Science Museum, Springfield, Massachusetts, USA
UD	Université de Bourgogne, Dijon, France
UGKU	Urweltmuseum GEOSKOP, Thallichtenberg, Germany
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
YPM	Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

SYSTEMATIC PALAEOONTOLOGY

Ichnogenus *Notalacerta* Butts, 1891a
Notalacerta missouriensis Butts, 1891a
 Figs 1, 2A, 3A, 4–8, Tables 1–3

- 1891a *Notalacerta missouriensis* n. isp. – Butts, p. 18, fig. 1.
- non 1891a *Notalacerta jacksonensis* n. isp. – Butts, p. 18, fig. 2.
- 1932 *Collettosaurus missouriensis* – Branson et Mehl, pp. 391–392, pl. 10.3.
- non 1971 *Notalacerta pentadactyla* – Haubold, p. 19, fig. 13.12.
- 1971 *Notalacerta missouriensis* – Haubold, p. 19, fig. 13.14.
- non 1971 *Notalacerta magna* – Haubold, p. 19.
- non 1977 *Notalacerta* isp. – Conti, Leonardi, Mariotti et Nicosia, p. 15, fig. 8.
- 1989 *Varanopus rigidus* n. isp. – Gand, pp. 280–287, figs 4f, 5b.
- Notalacerta missouriensis* – Chesnut, Baird, Smith et Lewis, pp. 154–155, figs 3, 4.
- 1994 *Notalacerta* isp. – Lucas, Lerner, Bruner et Shipman, p. 51, fig. 4a.
- 2001 aff. *Hyloidichnus* – Melchor, p. 37, pl. 1h.
- 2004 *Hyloidichnus bifurcatus* – Melchor et Sarjeant, pp. 69–70, fig. 9E.
- non 2004 *Notalacerta* isp. – Calder, Baird et Urdang, pp. 221–223, figs 3, 5b.
- 2005 *Notalacerta missouriensis* – Haubold, Allen, Atkinson, Buta, Lacefield, Minkin et Relihan, p. 96, fig. 7a–d.
- non 2006 ?*Notalacerta* isp. – Calder, Gibling, Scott, Davies et Hebert, p. 186, fig. 15d.
- 2013 *Notalacerta missouriensis* – Voigt, Lucas, Buchwitz et Celeskey, p. 449, fig. 4b.
- 2014 *Notalacerta* isp. – Lagnaoui, Voigt, Saber et Schneider, pp. 229–230, fig. 6.
- non 2014 *Notalacerta* isp. – Fichman, Crespi, Getty et Bush, p. 582, fig. 7.
- 2015 *Varanopus* cf. *hermitanus* – Voigt et Haubold, pp. 116–117, fig. 5.
- 2015 *Notalacerta missouriensis* – Voigt et Lucas, p. 160, figs 6, 10E.
- 2019a *Notalacerta missouriensis* – Marchetti, Belvedere, Voigt, Klein, Castanera, Diaz-Martinez, Marty, Xing, Feola, Melchor et Farlow, pp. 125–126, fig. 9.

Table 1

Ichnological parameters of pedal footprints. N, specimen number; FL, foot length; FW, foot width; sL, sole length; psW, sole width; L, free length of digit; div, divergence; I–V, digit numbers. Length measures in mm, angular measures in degrees, values are averages.

N	FL	FW	FL/FW	psL	psW	I L	II L	III L	IV L	V L	div I-II	div II-III	div III-IV	div IV-V	div
NMMNH P 31705	20.2	22.7	0.9	6.4	12.4	5.9	8.3	12.0	15.2	10.4	19.9	26.5	19.4	36.9	102.7
NMMNH P 31746-7	17.6	22.2	0.8	6.1	8.9	5.4	8.3	10.9	14.0	10.0	27.5	15.7	24.4	26.9	94.5
NMMNH P 31749	17.9	20.2	0.9	6.0	10.6	5.0	7.5	10.4	13.9	8.9	31.9	21.4	23.2	31.0	107.5
NMMNH P 31751	14.8	19.1	0.8			3.9	6.8	9.2	12.2	8.3	24.2	28.7	27.4	31.4	111.7
NMMNH P 31759-61	16.2	20.6	0.8	5.0	9.9	4.9	7.9	11.0	13.9	9.1	25.4	21.2	21.4	31.9	99.9
USNM 7321	24.0	30.3	0.8	10.7	14.7	7.3	10.1	14.1	18.2	10.7	35.1	14.9	19.8	40.8	110.5

Table 2

Ichnological parameters of manual footprints. N, specimen number; p, pes; m, manus; FL, foot length; FW, foot width; psL, sole length; psW, sole width; L, free length of digit; div, divergence; I–V, digit number; FLp/FLm, pes/manus foot length ratio. Length measures in mm, angular measures in degrees, values are averages.

N	FL	FW	FL/FW	psL	psW	I L	II L	III L	IV L	V L	div I-II	div II-III	div III-IV	div IV-V	div	FLp/FLm
NMMNH P 31705	15.9	15.4	1.0	5.5	7.8	4.5	6.7	10.1	11.9	6.1	22.2	20.0	23.6	39.2	104.9	1.3
NMMNH P 31746-7	13.9	15.3	0.9	5.1	8.6	3.1	6.1	9.9	10.7	4.9	19.3	26.9	17.5	47.3	111.0	1.3
NMMNH P 31749	13.9	15.3	0.9	4.4	6.0	4.1	6.6	9.1	10.2	6.5	37.2	29.8	16.2	51.0	134.2	1.3
NMMNH P 31751	11.1	14.3	0.8			4.8	5.9	6.7	6.9	3.8	27.6	23.8	30.9	45.8	128.1	1.3
NMMNH P 31759-61	12.6	14.6	0.9	3.8	7.3	3.2	5.7	8.2	9.5	4.6	46.2	25.7	17.6	52.1	141.6	1.3
USNM 7321	23.7	24.4	1.0	7.6	8.5	7.9	10.6	13.0	16.6	10.5	26.5	30.0	11.2	50.8	118.5	1.0

Table 3

Ichnological parameters of vertebrate trackways. N, specimen number; p, pes; m, manus; SL, stride length; PL, pace length; PA, pace angulation; LP, length of pace; WP, width of pace; DIV, divarication from midline (inward positive, outward negative); Dmp, distance manus-pes; BL, calculated body length; FLp, pes foot length. Length measures in mm, angular measures in degrees, values are averages.

N	SLp	PLp	PAp	LPp	WPp	DIVp	SLm	PLm	PAm	LPm	Wpm	DIVm	Dmp	BL	SLp/FLp	WPp/FLp	BL/FLp
NMMNH P 31705	74.8	51.7	92.0	36.7	37.2	1.6	74.0	53.6	84.0	35.8	39.8	3.9	18.9	55.5	3.7	1.8	2.7
NMMNH P 31746-7	69.2	42.5	107.8	34.3	24.8	7.8	74.0	46.3	104.3	36.5	28.2	11.1	20.2	56.6	3.9	1.4	3.2
NMMNH P 31749	63.4	47.3	92.6	33.3	33.2	-8.4	58.2	40.3	90.5	28.3	28.6	4.3	17.0	50.7	3.5	1.9	2.8
NMMNH P-31751	63.9	41.0	102.2	31.8	25.8	-0.7	64.0	41.6	96.8	30.9	27.8	6.4	16.3	48.0	4.3	1.7	3.2
NMMNH P-31759-61	67.1	43.2	102.6	33.7	26.8	4.2	66.1	44.3	98.1	33.7	28.7	8.0	23.4	56.7	4.1	1.7	3.5

Type material: Pennsylvanian. Chanute Formation, Missouri, USA. Given that the holotype is lost, the specimen USNM 7321 has been designated as neotype. It includes a right pes-manus couple, convex hyporelief.

Material: Pennsylvanian. Chanute Formation, Missouri, USA: MCZ 204, 205A, 205B, 206, FMC P 25486. McAlester Formation, Oklahoma, USA: NMMNH P-31705, NMMNH P-31746-7, NMMNH P-31749, NMMNH P-31751, NMMNH P-31759-61, NMMNH-NN 1, NMMNH-NN 2, NMMNH-NN 3. Potsville Formation, Alabama, USA: UGKU 1914, JL NN-1. Lee Formation, Kentucky, USA: KGS 1381. Joggins Formation, Nova Scotia, Canada: NSM008GF031.068, NSM008GF039.336, YPM-PU 16985. Lancaster Formation, New Brunswick, Canada: NBMG 21024. Galmous Formation, Morocco: CDUE 265.

Permian. Robledo Mountains Formation, New Mexico, USA: NMMNH P-62216. Carapacha Formation, Argentina: GHUNLPam 3295. Peranera Formation, Spain: UGKU 1931. Gres du Dordou Formation, France: UD CVG 1. Meisenheim Formation, Germany: NHMMZ PW 2020/2-LS. Tambach Formation, Germany: NHMS-WP 11479.

Emended diagnosis: Semiplantigrade, pentadactyl footprints of small quadrupeds that differ from anamniote footprints such as *Batrachichnus*, *Limnopus* and *Ichniotherium*, which are plantigrade and/or have a tetradactyl manus. Each footprint has very slender digit imprints that differ from *Hyloidichnus*, *Hylopus*, *Robledopus* and *Varanopus*, which have robust digit imprints. Digit terminations may be acuminate, bifurcated or pointed, with evidence of thin, sharp claw impressions (different from *Hylopus* and *Amphisauropus*, which show enlarged and/or rounded digit terminations). Manus with a different morphology compared to the pes (different from *Dromopus*, which shows the same morphology of manus and pes imprints). Pes digit IV clearly longer than pes digit III (different from *Robledopus* and *Varanopus*, which show subequal pes digits III and IV). Pes digit V imprint as long as digits II–III (different from *Hyloidichnus* and *Erpetopus*, which have a pes digit V imprint about as long as digit I). Well-spread digit imprints and digit V imprint in line with digits I–IV (different from *Dromopus*, *Erpetopus*, *Robledopus* and *Varanopus*, which show tightly-grouped digit I–IV imprints superimposed at their base, and a proximal digit V imprint). Straight pes digit V imprint, different from *Erpetopus*, which has an outward-bent pes digit V imprint. Thin and usually medially-directed pes digit I imprint (different from *Robledopus* and *Varanopus*, which show a thick, well-impressed and usually forward-directed digit I imprint). Variable orientation of digit imprints, especially digit III imprint, that can be parallel to digit IV in the manus and to digit II in the pes (different from *Hyloidichnus*, *Hylopus*, *Robledopus* and *Varanopus*, which have digit imprints with consistent orientation). Medial-lateral decrease in relief of the pes (different from *Dromopus*, which is more deeply impressed in the distal part of digits III and IV). Very short and shallow sole and palm impressions, and absence of rounded basal pads (different from *Hylopus*, which may show a rounded basal pad of digit I and broad palm and sole impressions) (modified from Butts, 1891a).

Description: Relatively small (pes length of 15–24 mm; Table 1), pentadactyl, semiplantigrade footprints of a quadrupedal tetrapod. Relatively long and very slender digit imprints, tapering from the base to the extremity and terminating in sharp or pointed claw impressions. The digit tips may be bifurcated due to digit extraction (Fig. 1G, H). Clear ectaxonic tracks, with digit imprints increasing in length from digit I to digit IV, pes digit V imprint about as long as digits II–III; manus digit V imprint about as long as digit II. Digit I–IV imprints usually distally-bent inwards, digit V imprint straight. Pes imprint longer than the manus (manus length 11–24 mm; Table 2). Manus about as long as wide, and pes about as long as wide or slightly wider than long. Pes imprints less deeply impressed than the manus and showing a marked medial-lateral decrease in relief (Fig. 1C–E), which is present but less evident in the manus imprints. The distal part of the digits and the digit tips are usually more deeply impressed than their proximal part and the palm/sole impression. High digit divergence in both the pes and the manus. Digit imprints not superimposed at their base, and the imprints of digits I and V may be perpendicular to digit III (Fig. 1B–D). Digit imprints variably oriented: digits I and II or digits II and III may be parallel in the pes (Fig. 1H), and digits III and IV may be parallel in the manus (Fig. 1B–D). Very short and shallow palm and sole impressions, with a concave proximal margin in the manus and a convex proximal margin in the pes. Simple alternating arrangement of pes-manus couples in wide trackways with relatively low pace angulation (about 80–110°; Table 3). Partial primary overstep of the pes on the manus rarely observed (Fig. 1F, H), secondary overstep never observed. Manus in front, lateral or medial compared to the pes. Pes parallel to the midline or turned outwards, manus parallel to the midline or slightly turned inwards. Common occurrence of straight and continuous tail/body impression (Fig. 1H).

Remarks: *Notalacerta missouriensis* was erected by Butts (1891a), based on material from the Cement City Limestone, Chanute Formation (late Missourian, late Kasimovian; Heckel, 1975) of Kansas City, Missouri (Fig. 1A). He provided a short description and a simple outline drawing (Fig. 1A), but no photographs were published. However, Butts (1891a) did not designate a holotype, and the original material has never been relocated (Baird, 1982; Chesnut *et al.*, 1994). Baird (1982) reported finding a photographic catalogue of the possible original material made in the 1890's by Sid J. Hare, curator of the Kansas City Academy of Science (before its closure), and deposited the original catalogue at the National Museum of Natural History, Smithsonian Institution. Baird (1982) also inferred that the original material might have been at the University of Michigan. Also, Chesnut *et al.* (1994) referred to this catalogue, but its photographs were never published. We contacted the Smithsonian, Princeton University, the Yale Peabody Museum and the University of Michigan, but there is no record or evidence of the original material and/or photographs of it. The only known specimens coming from the type locality and preserving possible *Notalacerta missouriensis* tracks are: MCZ 204–206, USNM 7321 and FMC P 25486 (Fig. 1B–H). A further specimen from the same locality was illustrated by Branson and Mehl (1932, pl. 10.3).

Accordingly, we designate as neotype of *Notalacerta missouriensis* the specimen USNM 7321 (Fig. 1B), which shows a complete and well-preserved pes-manus couple that closely resembles Butts (1891a) original illustration. The laterally-bent pes digits IV and V are not considered diagnostic but just part of the morphological variation of the ichnotaxon. We use the remaining material from the type locality and the extensive record from other Carboniferous-Permian sites to emend the diagnosis of *Notalacerta missouriensis* Butts, 1891a.

Notalacerta is clearly distinct from morphologically-similar pentadactyl and semiplantigrade ichnogenera from Pennsylvanian-Cisuralian units (Figs 2, 3); also see the dichotomous key (Fig. 4). It differs from *Hyloidichnus*

Gilmore, 1927 (Figs 2B, 3B) because of the more slender, curved and mobile digit imprints and the relatively longer pes digit V. Also, the digit imprints I–IV are more curved than in *Hyloidichnus*. It differs from *Varanopus* Moodie, 1929 (Figs 2C, 3C) and *Robledopus* Voigt et al., 2013 (Figs 2D, 3D) because of the more slender and mobile digit imprints, the less deeply-impressed pes digit I, the non-superimposed digit bases, the non-concave proximal margin of the sole, the relatively longer pes digit IV and the relatively shorter pes digit V. It differs from *Erpetopus* Moodie, 1929 (Figs 2E, 3E) because of the non-superimposed digit bases, the non-concave proximal margin of the sole and the relatively longer, non-proximal and non-distally bent pes digit V. It differs from *Dromopus* Marsh, 1894 (Figs 2F, 3F)

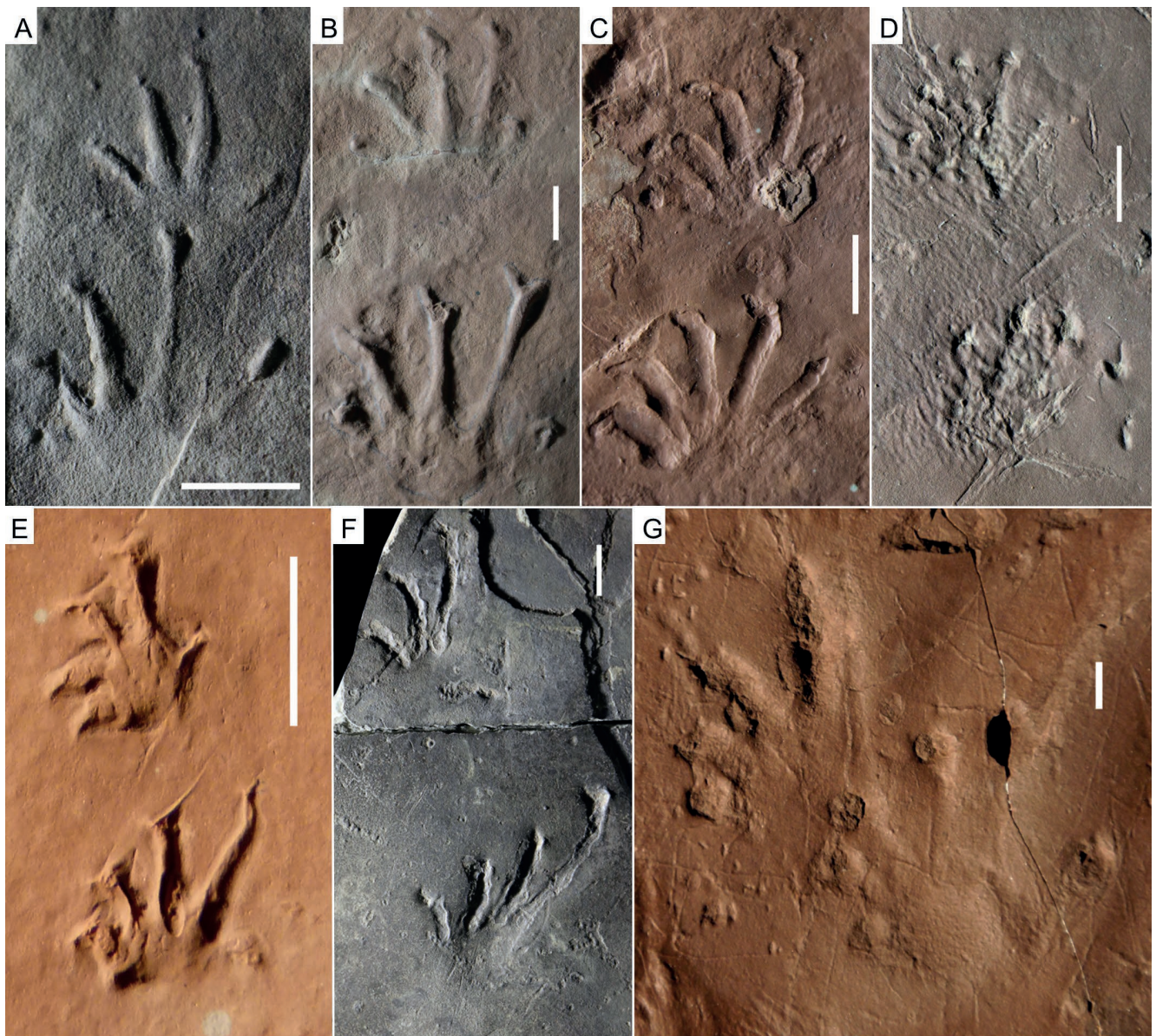


Fig. 2. *Notalacerta* and morphologically-similar ichnotaxa. **A.** NMMNH P-31746-7. *Notalacerta missouriensis*, left pes-manus couple, convex hyporelief. **B.** USNM 11518. *Hyloidichnus bifurcatus*, left pes-manus couple, convex hyporelief (holotype). **C.** NMMNH P-32391-2. *Varanopus curvidactylus*, left pes-manus couple, convex hyporelief. **D.** NMMNH P-23120. *Robledopus macdonaldi*, right pes-manus couple, concave epirelief (holotype). **E.** UGKU 1803. *Erpetopus willistoni*, right pes-manus couple, concave epirelief. **F.** MNG 13436B. *Dromopus lacertoides*, right pes-manus couple, concave epirelief. **G.** NMMNH-NN 1. *Hylopus hardingi*, right pes-manus couple, concave epirelief. Scale bars: 1 cm.

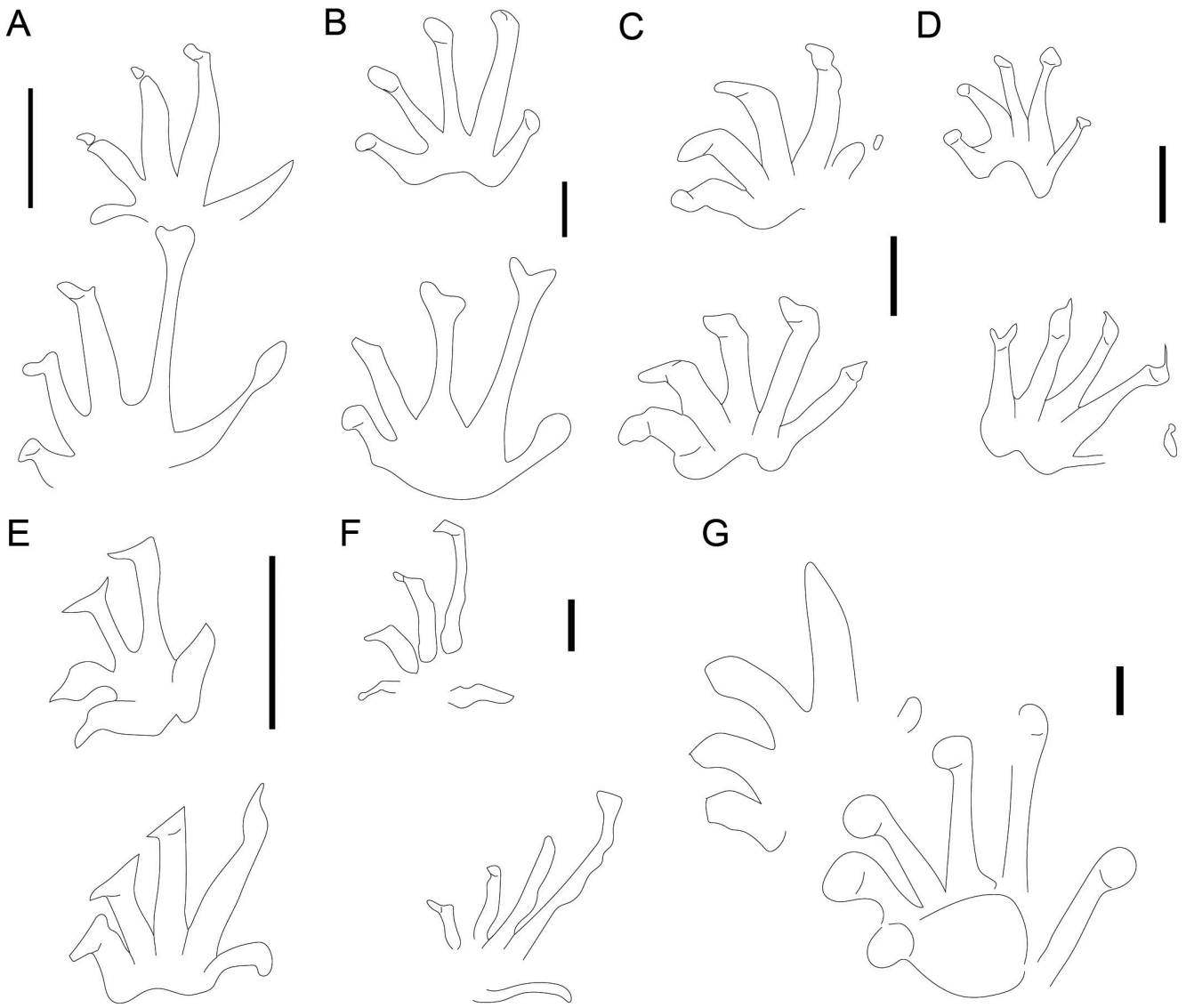


Fig. 3. *Notalacerta* and morphologically-similar ichnotaxa, interpretive drawings. A–G. See caption of Figure 2. Scale bars: 1 cm.

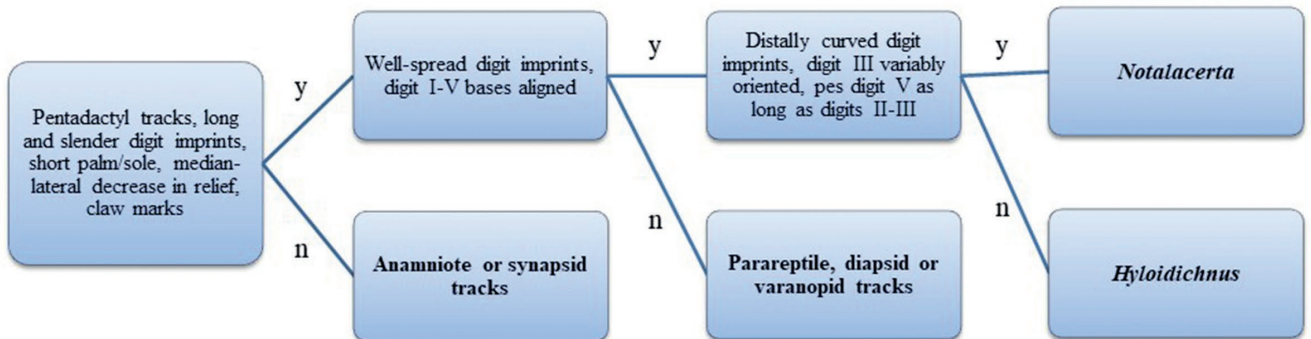


Fig. 4. Simplified dichotomous key for the assignment of footprints to *Notalacerta*. Y – yes, N – no. Notice that Y requires the presence of all the indicated features. Anamniote tracks include: *Amphisauropus*, *Batrachichnus*, *Hylopus*, *Ichniotherium*, *Limnopus* and *Matthewichnus*. Synapsid tracks include: *Brontopus*, *Capitosauroides*, *Dicynodontipus*, *Dimetropus*, *Karooopes*. Parareptile tracks include: *Erpetopus*, *Pachypes*, *Procolophonichnium* (only *P. nopcsai* and *P. tirolensis*), *Robledopus* and *Varanopus*. Diapsid tracks include: *Dromopus*, *Paradoxichnium*, *Protochirotherium* and *Rhynchosauroides*. Varanopid tracks include *Tambachichnium*.

because of the differing morphology of the manus and pes, the less pronounced ectaxy, the non-superimposition of digit bases, the non-proximal digit V, and the semiplantigrady. It differs from *Hylopus* Dawson, 1882 (Figs 2G, 3G) because *Notalacerta* has more slender digit imprints, sharp claw marks, lacks circular basal pads of digit I and has a shorter sole imprint. All the above-mentioned features are

not gait- nor substrate- dependant because they are consistently observed along trackways with different pace values in different lithofacies.

The most extensive and best-preserved collection of *Notalacerta missouriensis* is from the late Moscovian (Desmoinesian) Keota Sandstone Member of the McAlester Formation, Oklahoma. A preliminary description of these

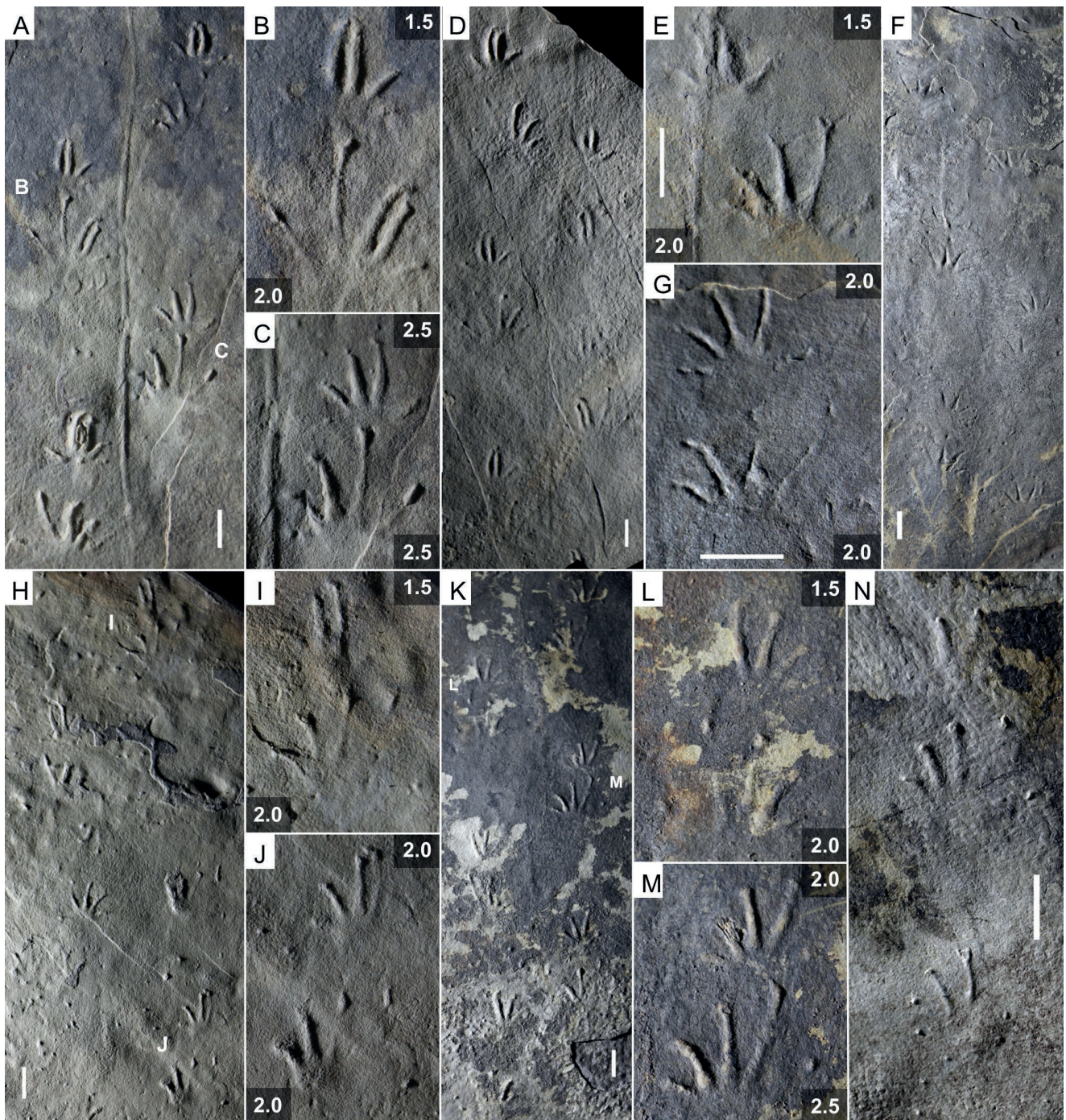


Fig. 5. Pennsylvanian occurrences of *Notalacerta missouriensis*. Keota Sandstone Member, McAlester Formation, Oklahoma. **A.** NMMNH P-31746-7, trackway with straight tail impression, convex hyporelief. **B, C.** Enlargements of **E**, pes-manus couples. **D.** NMMNH P-31759-61. Trackway, concave epirelief. **E.** NMMNH P-31749. Left pes-manus couple, convex hyporelief. **F-G.** NMMNH P-31751. **F.** Trackway, concave epirelief. **G.** Right pes-manus couple, concave epirelief. **H-J.** NMMNH-NN 1, **H** – trackway, convex hyporelief, **I-J**, – enlargements of **H**, left pes manus couples. **K-M.** NMMNH-NN 2, **K** – trackway, convex hyporelief, **L, M** – enlargements of **K**, pes-manus couples. **N.** NMMNH-NN 3. Two consecutive left pes-manus couples, convex hyporelief. Numbers beside tracks refer to the preservation scale (Marchetti *et al.*, 2019a). Scale bars: 1 cm.

specimens has been made by Lucas *et al.* (2004). This material includes long trackways encompassing a wide range of intraspecific variation (Figs 5, 6), such as: alignment of digit I–II or II–III imprints in the pes and of digit III–IV imprints in the manus (Fig. 5B, I, J); digit tip bifurcation (Fig. 5E); incomplete or missing digit impressions (Fig. 5D, F, H, K, N); and transition between thick- and thin-digit imprint morphology (Fig. 5N).

Notalacerta missouriensis has also been reported from the Rockcastle Sandstone Member, Lee Formation (late Westphalian A, Bashkirian) of Kentucky, by Chesnut *et al.* (1994). The material includes a trackway with a straight tail impression and well-preserved manus imprints (Fig. 7A, B). The pes is more incompletely impressed, but the digit morphology, arrangement and proportions are consistent with the type concept of *Notalacerta missouriensis*, so we agree with this assignment.

Notalacerta missouriensis was described from the Mary Lee Coal Zone, Pottsville Formation (early Westphalian A, Bashkirian) of Alabama by Haubold *et al.* (2005). Some specimens include trackways with complete and well-preserved pes and manus imprints (Fig. 7C, E), therefore we can confirm this assignment. *Notalacerta* from the Westphalian strata of Kentucky, Alabama, Nova Scotia and Morocco show significantly outward-rotated pes imprints. Until more complete material is found, especially material that better documents gait transitions and a complete pes digit V impression, this feature is considered part of the intraspecific variation of *Notalacerta missouriensis*.

Some undescribed material from the Lancaster Formation (late Westphalian A, Bashkirian) of New Brunswick includes complete and well-preserved pes-manus couples (Fig. 7G), which show all the diagnostic features of *Notalacerta missouriensis*, therefore we propose such an assignment.

Undescribed material from the Joggins Formation (early Westphalian A, Bashkirian) of Nova Scotia, preserves trackways and incomplete step cycles with well-preserved and complete manus imprints and more incomplete pes imprints (Fig. 7H–J). We assign this material to *Notalacerta missouriensis*.

An incomplete step cycle from the Galmous Formation (Westphalian B–C, Bashkirian–Moscovian) of Morocco has been assigned to *Notalacerta* isp. by Lagnaoui *et al.* (2014). Because of the well-preserved pes imprint and the recognisable pentadactyl manus, which are consistent with this ichnogenus (Fig. 7K), we re-assign this material to *Notalacerta missouriensis*.

The Cisuralian record of *Notalacerta* is little discussed in literature. Only recently, *Notalacerta missouriensis* footprints have been described from the Robledo Mountains Formation of New Mexico (early Artinskian; Voigt and Lucas, 2015a). This material includes a trackway with two consecutive left, well-preserved pes-manus couples (Fig. 8A).

A specimen from the Carapacha Formation of Argentina (late Cisuralian – early Guadalupian), first reported by Melchor (2001) and later assigned to *Hyloidichnus bifurcatus* by Melchor and Sarjeant (2004), includes a pes-manus

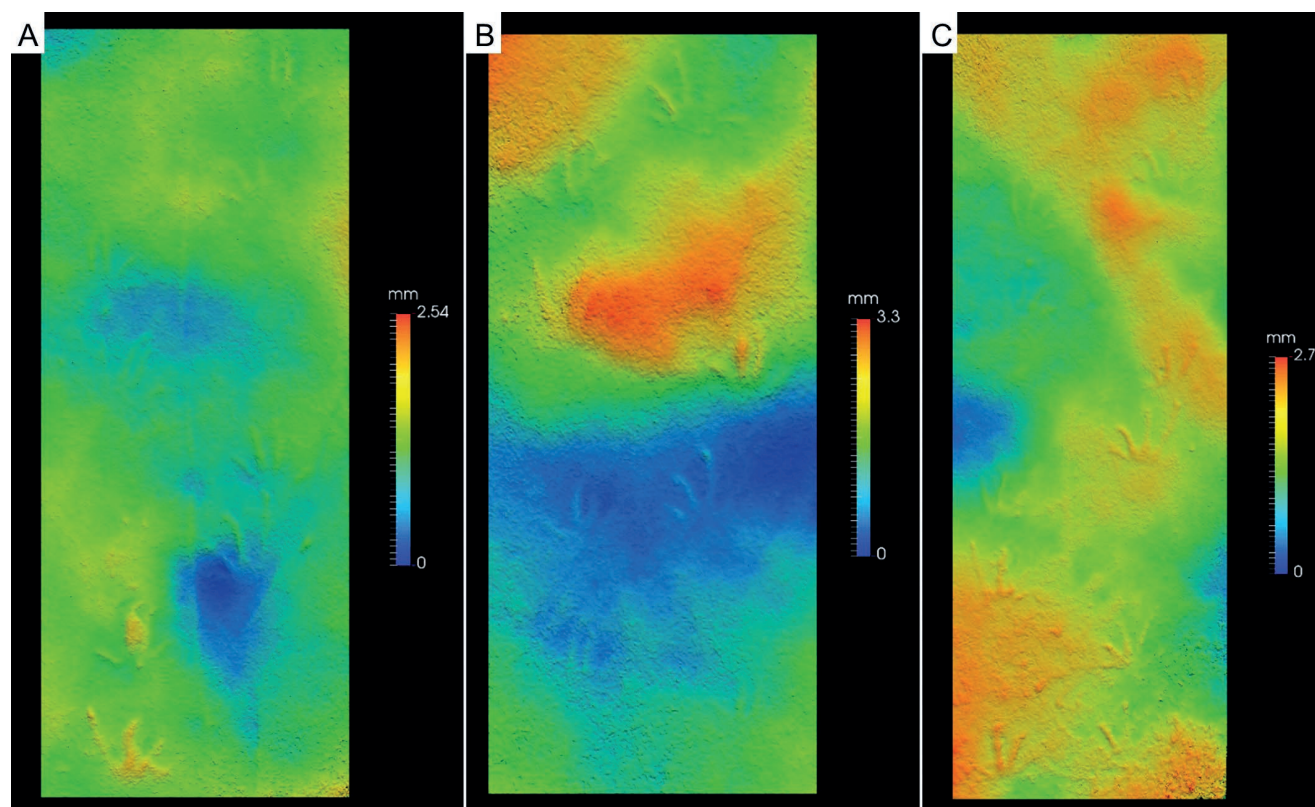


Fig. 6. Pennsylvanian occurrences of *Notalacerta missouriensis*. False-colour depth map of selected trackways. Keota Sandstone Member, McAlester Formation, Oklahoma. **A.** NMMNH P-31746-7. **B.** NMMNH P-31759-61. **C.** NMMNH-NN 2. All in convex hyporelief. Note the marked median-lateral decrease in relief of footprints, which is more evident in the pes imprints.

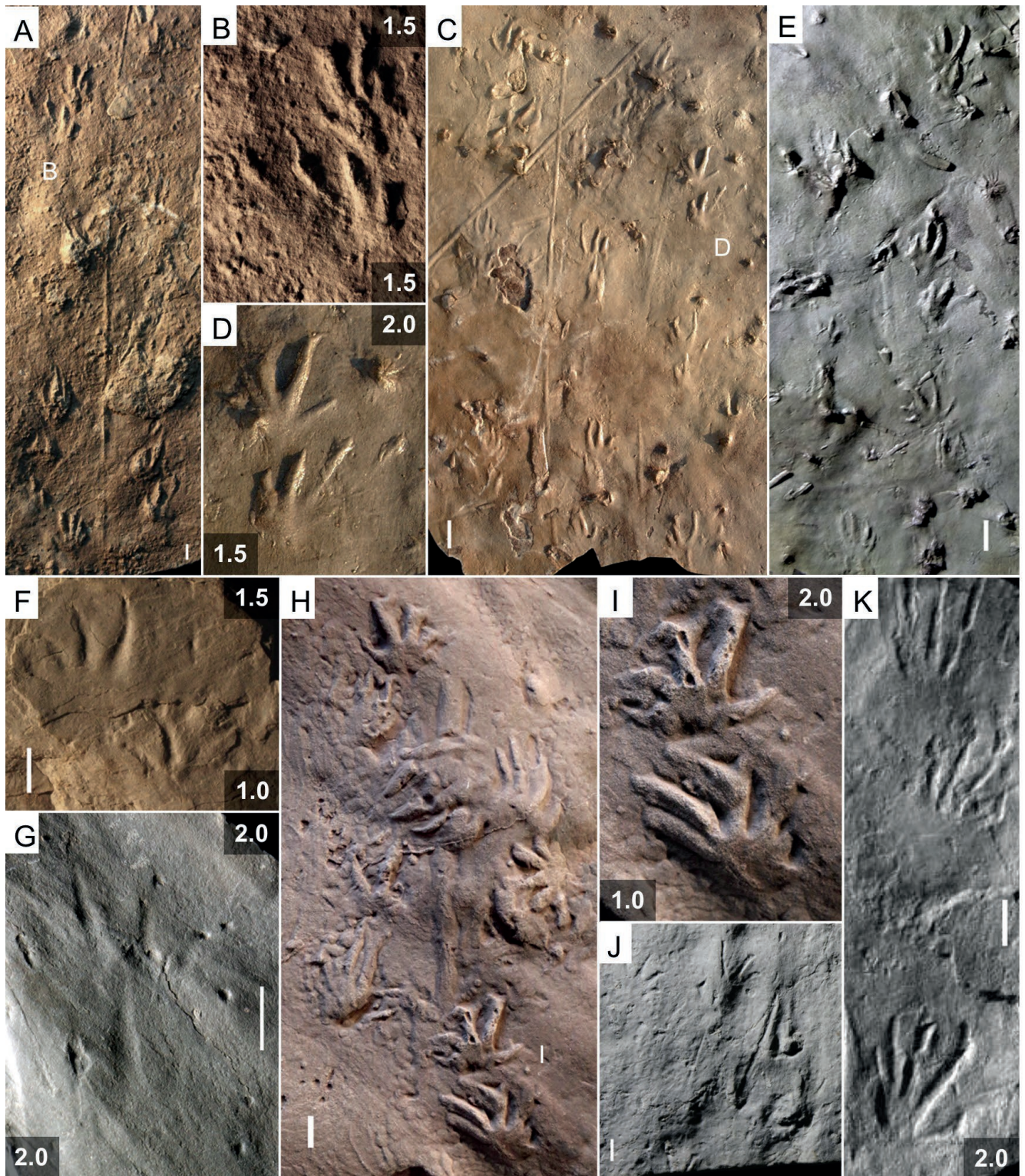


Fig. 7. Pennsylvanian occurrences of *Notalacerta missouriensis* (A–E, G–K) and cf. *Notalacerta* isp. (F). **A.** KGS 1381. Trackway, convex hyporelief. Rockcastle Sandstone Member, Lee Formation, Kentucky. **B.** Enlargement of A. Right pes-manus couple. **C–E.** Pottsville Formation, Alabama, C – JL NN-1. trackways with tail impression, convex hyporelief, D – enlargement of C. Left pes-manus couple, E – UGKU 1914. Trackway, convex hyporelief. **F.** KU 8357. Right pes-manus couple, concave epirelief. Stanton Formation, Kansas. **G.** NBMG 21024. Left pes manus-couple with claw impressions, concave epirelief. Lancaster Formation, New Brunswick. **H–J.** Joggins Formation, Nova Scotia, H – NSM 008GF031.068. Trackway with tail impression, convex hyporelief, I – Enlargement of H, left pes-manus couple, J – NSM 008GF039.336. Incomplete step cycle and manus imprint, concave epirelief. **K.** CDUE 265. Two consecutive left pes-manus couples. Galmous Formation, Morocco. Numbers beside tracks refer to the preservation scale. Scale bars: 1 cm.

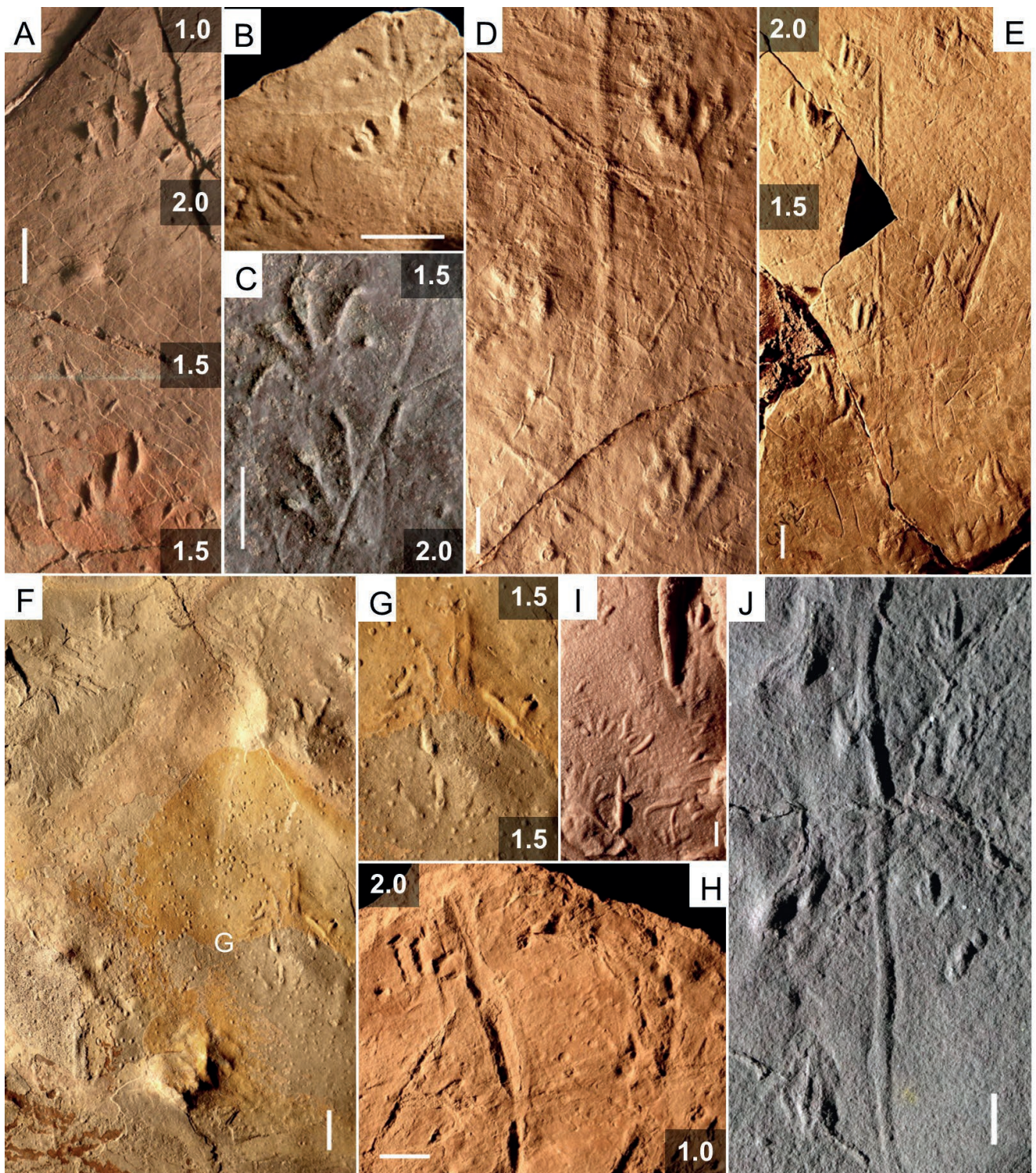


Fig. 8. Permian occurrences of *Notalacerta missouriensis* (A–C, E–G, J) and cf. *Notalacerta* isp. (D, H, I). **A.** NMMNH P-62216. Two consecutive left pes-manus couples, convex hyporelief. Robledo Mountains Formation, New Mexico. **B.** GHUNLPam 3295. Right pes-manus couple and isolated left manus, concave epirelief. Carapacha Formation, Argentina. **C.** UGKU 1931. Left pes-manus couple, convex hyporelief. Peranera Formation, Spain. **D.** MNHN LOD 4. Trackway and straight tail impression, convex hyporelief. Rabejac Formation, France. **E.** UD CVG 1. Trackway with straight tail impression. Paratype of *Varanopus rigidus* Gand 1989. Gres du Dourdou Formation, France. **F.** NHMMZ PW 2020/2-LS. Incomplete step cycle, convex hyporelief. Meisenheim Formation, Germany. **G.** Enlargement of F, left pes-manus couple. **H.** NHMMZ PW 2016/2000 a+b-LS. Incomplete step cycle, concave epirelief. Standenbühl Formation, Germany. **I.** **J.** Tambach Formation, Germany. **I.** MNG 13490. Incomplete step cycle, convex hyporelief, artificial cast. **J.** NHMS-WP 11479. Trackway with straight tail impression, convex hyporelief. Numbers beside tracks refer to the preservation scale. Scale bars: 1 cm.

couple and an isolated manus with parallel digit III and IV imprints and a pes digit V relatively longer than that of *Hyloidichnus* (Fig. 8B). Because of these features, we re-assign this material to *Notalacerta missouriensis*.

An incomplete step cycle from the Peranera Formation of Spain (Artinskian) was assigned to *Varanopus* cf. *hermitanus* by Voigt and Haubold (2015). However, the best-preserved pes-manus couple (Fig. 8C) shows a thin pes digit I imprint, a wide digit divarication of the pes and a convex proximal margin of the sole imprint. These features are not consistent with *Varanopus* (e.g., Haubold and Lucas, 2003). We re-assign this specimen to *Notalacerta missouriensis*.

A pes-manus couple from the Viala Formation of France (early Artinskian) has been assigned to *Varanopus rigidus* by Gand (1989; fig. 5b). Although no photographs of this specimen are available, and the specimen itself could not be relocated, the digit I imprint morphology and orientation observed in the outline drawing is not consistent with *Varanopus*. We conditionally re-assign this specimen to *Notalacerta missouriensis*.

A trackway from the Gres du Dourdou Formation of France (early Artinskian) is a paratype of the ichnotaxon *Varanopus rigidus* Gand, 1989 (Fig. 8E). However, the thin and inward-oriented pes digit I imprint, the convex proximal margin of the sole impression and the relatively short imprint of pes digit V are not in agreement with the ichnogenus concept of *Varanopus*. We re-assign this material to *Notalacerta missouriensis*.

An unpublished incomplete step cycle from the Meisenheim Formation of Germany (Sakmarian) shows very thin and well-diverging digit imprints in the pes and parallel digit III–IV imprints in the manus (Fig. 8F, G). We assign this material to *Notalacerta missouriensis*.

An undescribed trackway from the Tambach Formation of Germany (early Artinskian) shows very thin manus digit imprints, a relatively small pes digit V imprint, a pes digit tip impression at the same level of the proximal margin of the sole imprint, and a continuous tail/body trace (Fig. 8J). All these features are consistent with *Notalacerta missouriensis*, so we propose such an assignment.

Similar material: Some small footprints interpreted as reptile footprints from the Rock Lake Member, Stanton Formation (Kasimovian) of Garnett, Kansas, have been reported by Reisz *et al.* (1982) and assigned to *Notalacerta* isp. by Reisz (1990), based on a personal communication from D. Baird. The specimen KU 8357 (Fig. 7F) can be assigned to cf. *Notalacerta* isp. because of the well-spread, curved and thin digit imprints ending in sharp claw marks.

The holotype of the ichnotaxon *Colletosaurus indianaensis* Cox, 1874 from the Lower Coal Measures (Westphalian A?) of Indiana includes a step cycle that can be tentatively attributed to cf. *Notalacerta* isp. The incompleteness and poor preservation of the material, which apparently has been lost, and lack of additional specimens from the type locality do not allow a certain attribution, so we consider *Colletosaurus indianaensis* a *nomen dubium* and reject the synonymy of *Colletosaurus* and *Notalacerta* proposed by Gilmore (1927) and used by Branson and Mehl (1932).

The ichnotaxon *Cincosaurus cobbi* Aldrich, 1930 (in Aldrich and Jones, 1930) is a locally-used ichnotaxon for

the Alabama ichnoassociation from the Mary Lee Coal Zone of Pottsville Formation of Alabama. The holotype shows a trackway with slow gait and deformed pes impressions. We consider *Cincosaurus cobbi* a *nomen dubium* because of the relatively poor preservation of the holotype. The morphological similarity with *Notalacerta* is evident, so we re-assign this material to cf. *Notalacerta* isp. This material is generally characterised by an outward-rotated and incompletely-impressed pes imprint. Thousands of “*Cincosaurus*” tracks were described and reported from Alabama, but due to the poor preservation, it is presently difficult to distinguish them from *Hylopus hardingi*: the two ichnotaxa co-occur at that site, so all the “*Cincosaurus*” from this site were probably either *Notalacerta* or *Hylopus*, although the first was likely much more abundant.

Keighley *et al.* (2008) suggested a possible oldest occurrence of reptile tracks from the Port Hood Formation (Namurian C, Bashkirian) of Nova Scotia, first described by Keighley and Pickerill (1998). Only an uncollected specimen of their morphotype D (fig. 8) may be consistent with the diagnostic features of *Notalacerta*. Because of its incompleteness and poor preservation, we re-assign this trackway to cf. *Notalacerta* isp.

The ichnotaxa *Cursipes dawsoni* Matthew, 1903 and *Cursipes levis* Matthew 1905, known from the Joggins Formation of Nova Scotia, were illustrated by Matthew (1905). The holotypes (RM 2.1145 and RM 2.1147, respectively) show a pentadactyl manus with a morphology consistent with *Notalacerta*. Nevertheless, the pes is incomplete. Therefore, we consider these ichnotaxa to be *nomina dubia* and assign this material to cf. *Notalacerta* isp.

An incomplete step cycle from the Kenilworth Sandstone (Cisuralian) of England was assigned to cf. *Notalacerta* isp. by Haubold and Sarjeant (1973). The relative length of the pes digit V imprint is consistent with *Notalacerta* rather than with *Varanopus*. Therefore, we agree with the assignment of this material to cf. *Notalacerta* isp.

A trackway from the Sangre de Cristo Formation (early Artinskian, Cisuralian) of New Mexico has been assigned to cf. *Notalacerta* isp. by Voigt and Lucas (2015b, fig. 10b). The digit proportions and morphology are consistent with *Notalacerta*, but the small digit divergence of the pes and the concave proximal margin of the sole are instead consistent with ichnotaxa such as *Robledopus* or *Varanopus*. Pending a comprehensive revision of the latter ichnogenera, we rely on the assignment by Voigt and Lucas (2015b).

A specimen from the Arroyo de Alamillo Formation (early Kungurian, Cisuralian) of New Mexico has been assigned to undetermined reptile tracks and compared with *Notalacerta* (Voigt and Lucas, 2017: fig. 13B). A revision of the reptile track record of this formation is necessary to eventually confirm this assignment.

A trackway (MNHN LOD 4) from the Rabejac Formation of France (late Artinskian, Cisuralian), formerly considered an atypical *Hyloidichnus* by Heyler and Gand (2001), shows a pes digit V imprint clearly longer than that observed in *Hyloidichnus* (Fig. 8D). We re-assign this material to cf. *Notalacerta* isp.

An incomplete step cycle from the basal Standenbühl Formation (early Artinskian, Cisuralian) of Germany

(NHMMZ PW 2016/2000 a+b-LS), previously assigned to *Varanopus microdactylus* by Fichter (1979), is here re-assigned to cf. *Notalacerta* isp. (Fig. 8H) because of the different morphology of the pes. A specimen from the Tambach Formation (MNG 13490) of Germany, previously assigned to *Varanopus microdactylus* by Voigt (2005), is here re-assigned to cf. *Notalacerta* isp. (Fig. 8I) because of the more slender and well-spread digit imprints compared to *Varanopus*.

Material not assignable to *Notalacerta*: The ichnospecies *Notalacerta jacksonensis* Butts, 1891a, from the type locality of *N. missouriensis*, shows a possible tetradactyl manus with thick digit imprints and rounded digit terminations. These features would be consistent with anamniote tracks such as *Batrachichnus*. Consequently, we consider *N. jacksonensis* as belonging to a different ichnogenus. The ichnotaxon *Notamphibia magna* Butts, 1891b, from the type locality of *Notalacerta missouriensis*, was synonymised in the new combination *Collettosaurus magna* by Gilmore (1927) and *Notalacerta magna* by Haubold (1971). The illustrated holotype is an isolated pentadactyl imprint with long and parallel digits of similar length and a proximal digit V. This is clearly not consistent with *Notalacerta* as revised above, so we disagree with the synonymy proposed by Haubold (1971). Because both *N. jacksonensis* and *N. magna* are here considered to not be part of *Notalacerta*, we regard the ichnogenus *Notalacerta* to be monospecific, the only valid ichnospecies being *N. missouriensis*.

An isolated manus track from the Rhode Island Formation (Westphalian C, Moscovian) of Massachusetts (specimen SSM 2014/4-2) was assigned to *Notalacerta* isp. by Fichman *et al.* (2015). The digit terminations are rounded and a small rounded pad is impressed at the base of digit I. These features are rather in agreement with *Hylopus* (e.g., Marchetti *et al.*, 2019a). Additional undescribed material from this locality including trackways confirms this hypothesis.

The occurrence of small reptile tracks from the Pennsylvanian of Canada is a long-debated topic. Small reptile-like traces have been described from the Grande Anse Formation (Bashkirian) of New Brunswick by Falcon-Lang *et al.* (2007) as *Pseudobradypus* and considered the earliest record of reptiles. This hypothesis was later rejected by Keighley *et al.* (2008), Fillmore *et al.* (2012), Marchetti *et al.* (2019a) and Lucas (2019), considering the reptile appearance of these tracks due to the extensive extramorphological distortion on these specimens. Marchetti *et al.* (2019a) considered *Pseudobradypus* to be a *nomen dubium*. In the same paper, the material from the Grande Anse Formation was clearly distinguished from *Notalacerta* and re-assigned to the ichnogenus *Hylopus*, which is interpreted as footprints made by anthracosaurids (e.g., Fillmore *et al.*, 2012).

Falcon-Lang *et al.* (2010) claimed the occurrence of amniote tracks from the Tynemouth Creek Formation of New Brunswick. Nevertheless, the material attributed to the supposed amniote ichnotaxon *Pseudobradypus* (figs 8–10) shows rather diagnostic features of the amniote ichnotaxon *Hylopus*, such as the rounded digit terminations and the thick digit imprints. This and the broad sole impression differ from supposed reptile tracks such as *Notalacerta*.

Calder *et al.* (2006, fig.15d) assigned a specimen from the Joggins Formation of Nova Scotia to ?*Notalacerta* isp., however, the small tetradactyl manus and the secondary overstep of the pes on the manus are consistent with the anamniote ichnotaxon *Matthewichnus caudifer* Kohl and Bryan, 1994, rather than *Notalacerta*.

Despite the extensive Pennsylvanian tetrapod footprint record of Canada, which includes the famous locality of Joggins, *Notalacerta* was only reported from earliest Permian red beds of Prince Edward Island of eastern Canada early in the 21st century (Calder *et al.*, 2004). An incomplete step cycle from the Hillsborough River Formation (Carboniferous-Permian transition) of Prince Edward Island was assigned to *Notalacerta* isp. by Donald Baird in Calder *et al.* (2004). Nevertheless, the best-preserved pes-manus couple (HF-NN 1) (figs 3, 5b) shows a pes with closely-grouped digits I–V at their base, a pes digit I thicker than other digits and pes digits III and IV of subequal length. These features are rather in agreement with *Varanopus* (e.g., Voigt, 2005). However, the poor preservation of the manus and the non-impression of pes digit V hamper a definitive assignment. Until additional specimens are discovered on Prince Edward Island, the assignment of this material to *Notalacerta* is equivocal.

The ichnotaxon *Collettosaurus pentadactylus* Gilmore, 1927 from the Cisuralian Hermit Formation of Arizona was synonymised with *Notalacerta* in the new combination *Notalacerta pentadactyla* by Haubold (1971). Marchetti *et al.* (2019a) considered this ichnotaxon to be a *nomen dubium*, Marchetti *et al.* (2020) re-assigned this material to cf. *Dimetropus* isp.

Notalacerta isp. (Haubold, 1970, fig. 6h) from Cisuralian deposits of the Thuringian Forest, Germany, is an isolated pes-manus couple with extramorphologically-extended digit imprints of the pes and a poorly-preserved manus imprint, possibly assignable to *Amphisauropus* (Voigt, 2005) or *Varanopus*.

Conti *et al.* (1977, fig. 8) assigned a pentadactyl lacer-toid track from the Lopingian Arenaria di Val Gardena Formation (Italy) to *Notalacerta* isp. This specimen has been re-assigned to *Rhynchosauroides* isp. by Conti *et al.* (2000).

TRACKMAKER ATTRIBUTION

The ichnotaxon *Notalacerta missouriensis* has been attributed to reptiles since Butts (1891a); in fact, the Latin translation of the ichnogenus epithet means “lizard mark.” Nevertheless, no detailed discussion of the possible trackmaker was included in Butts’ (1891a) original discussion beyond the ichnotaxon name. A new trackmaker attribution was proposed by Haubold (1971), who proposed amphibians of the family Dissorophidae as possible producers of *N. missouriensis*. Of note, specimens here assigned to cf. *Notalacerta* isp., including the type material of *Collettosaurus indianensis*, *Cursipes dawsoni* and *Cincosaurus cobbi*, were also attributed to Dissorophidae by Haubold (1971), in agreement with an amniote attribution previously hypothesised by Cox (1874) and Matthew (1903).

The most detailed track-trackmaker attribution of *N. missouriensis* is by Chesnut *et al.* (1994), based on their material from the Langsettian of Kentucky. These authors rejected the possibility that temnospondyl anamniotes were the trackmakers, because of the clear reptiliomorph morphology of these tracks. Also, Chesnut *et al.* (1994) considered seymouriamorph and anthracosaurid anamniotes to not be consistent with the morphology of *N. missouriensis*, because of their short and thick pes and manus digits. Among Carboniferous amniotes, these authors discarded as possible trackmakers the synapsids because of their thick digits, and the diapsids because they have been considered the trackmakers of *Dromopus* Marsh, 1894. The only Carboniferous forms with pes and manus of similar morphology to *N. missouriensis* were considered by Chesnut *et al.* (1994) to be forms generally attributed to “Protorothyrididae” (i.e., non-diapsid reptiles), such as *Paleothyris* and *Anthracodromeus*, of which a reconstruction of the pes and manus skeleton is available (Carroll, 1969; Carroll and Baird, 1972). Moreover, the relatively short trunk length of these forms was considered by Chesnut *et al.* (1994) to be consistent with the trackway pattern of *N. missouriensis*. Subsequent interpretations generally use this trackmaker attribution (e.g., Lucas *et al.*, 2004; Haubold *et al.*, 2005; Voigt *et al.*, 2013; Lagnaoui *et al.*, 2014; Voigt and Lucas, 2015a). The material here assigned to *N. missouriensis*, previously assigned to *Varanopus rigidus* by Gand (1989), was originally attributed to captorhinomorphs such as *Captorhinus*, *Captorhinikos* and *Labidosaurus* or parareptiles such as *Rhipaeosaurus* and *Procolophon*.

We herein discard the following as potential trackmakers of *N. missouriensis*, due to fundamental differences between the track morphology and potential trackmaker. Temnospondyl and lepospondyl anamniotes are discarded because these forms have a tetradactyl manus (e.g., Dilkes, 2014), whereas *Notalacerta* is pentadactyl in both manus and pes. Diadectomorph anamniotes such as *Diadectes* and *Orobates* and seymouriamorph anamniotes such as *Seymouria* are here discarded as potential trackmakers due to the thick digits of these forms and their broad and complex tarsus, which is instead in agreement with the broad sole impressions and/or rounded basal pad imprints at the base of the medial digits observed in *Amphisauropus* and *Ichnoterium*. Also, the size range is different (e.g., Voigt *et al.*, 2007; Marchetti *et al.*, 2017). Anthracosaurid anamniotes such as *Proterogyrinus* are also excluded as the trackmakers of *Notalacerta* because these forms also show thick digits and a complex tarsus with a small tibiale, a small first centrale, and the first distal tarsal supporting most of the weight of the tibia and part of the weight of the fibula through the intermedium (Holmes, 1984). This anatomy would have likely generated a very deep impression of this part of the sole, such as a basal pad, which is not observed in *N. missouriensis* but is recognised instead in *Hylopus*. Therefore, anthracosaurid anamniotes such as *Proterogyrinus* were more likely the trackmakers of *Hylopus* rather than of *N. missouriensis*.

Synapsids can also be ruled out as the possible trackmakers of *N. missouriensis* because, with the exception of varanopids, they had a very broad and compact tarsus and

metatarsus compared to the phalanges, thus resulting in a broad sole, as is observed in *Dimetropus* (e.g., Voigt, 2005). Further features include a semi-circular arrangement of distal tarsals and carpals, thick lateral elements of the manus/pes and a digital arcade, resulting in a concave proximal margin of the palm/sole, a median-lateral increase in relief and paw-like impressions (Marchetti *et al.*, 2019b). All these features differ from *Notalacerta*.

Some small diapsid eureptiles and parareptiles have feet that would match the morphology and proportions of *N. missouriensis* but, as observed by Lee (1997), these tetrapods are also characterised by overlapping metatarsals, thus resulting in parallel and superimposed digit impressions at their base, as observed, for instance, in the ichnotaxa *Dromopus*, *Erpetopus*, *Procolophonichnium nopcsai*, *Robledopus* and *Varanopus* (e.g., Marchetti *et al.*, 2019c). This feature is clearly different from *N. missouriensis*, which shows well-splayed and non-overlapping pes digits. Also, varanopid synapsids show this feature, so they could not have been the producers of *N. missouriensis*.

As correctly highlighted by Chesnut *et al.* (1994), the digit morphology and proportions of ‘protorothyridids’ such as *Paleothyris* and *Anthracodromeus* (Carroll, 1969; Carroll and Baird, 1972) are consistent with *N. missouriensis*. Although this group was indicated among those with overlapping metatarsals by Lee (1997), the articulated pes skeletons of the protorothyridid-like forms *Hylonomus*, *Paleothyris* and *Thuringothyris* do not show this feature, because the metatarsals are not overlapping at their base (Carroll, 1964, 1969; Müller *et al.*, 2006). They are instead separated, as in the more derived captorhinid eureptiles (Fig. 9C, D). Moreover, the simple and relatively small tarsal structure of these forms is in agreement with the very short sole impression of *N. missouriensis* (Fig. 9B). The relatively longer pes digit V compared to that of the manus observed in *Notalacerta* is also observed in the reconstruction of *Paleothyris* (Fig. 9B). The more marked medial-lateral decrease in relief observed in the *Notalacerta* pes imprints compared to the manus imprints is also consistent with the carpal and tarsal structure of *Paleothyris* (Fig. 9A, B), in which the distal tarsals I–III were subject to more compression than the distal carpals I–III, where the weight was more evenly distributed. Also, the glenoacetabular length/pes length ratio of *Anthracodromeus*, *Paleothyris* and *Thuringothyris* (2.1–3.0) is similar to the same ratio measured from the trackways of *N. missouriensis* (2.7–3.5; Table 3). Therefore, we identify the trackmaker of *N. missouriensis* as basal non-diapsid eureptiles such as *Anthracodromeus*, *Hylonomus*, *Paleothyris* and *Thuringothyris*.

BIOSTRATIGRAPHY, PALAEOBIOGEOGRAPHY, PALAEOECOLOGY

Notalacerta is the oldest ichnogenus attributed to reptiles and the most abundant reptile track in terms of both number of specimens and number of occurrences during the Pennsylvanian period (e.g., Schneider *et al.*, 2020),

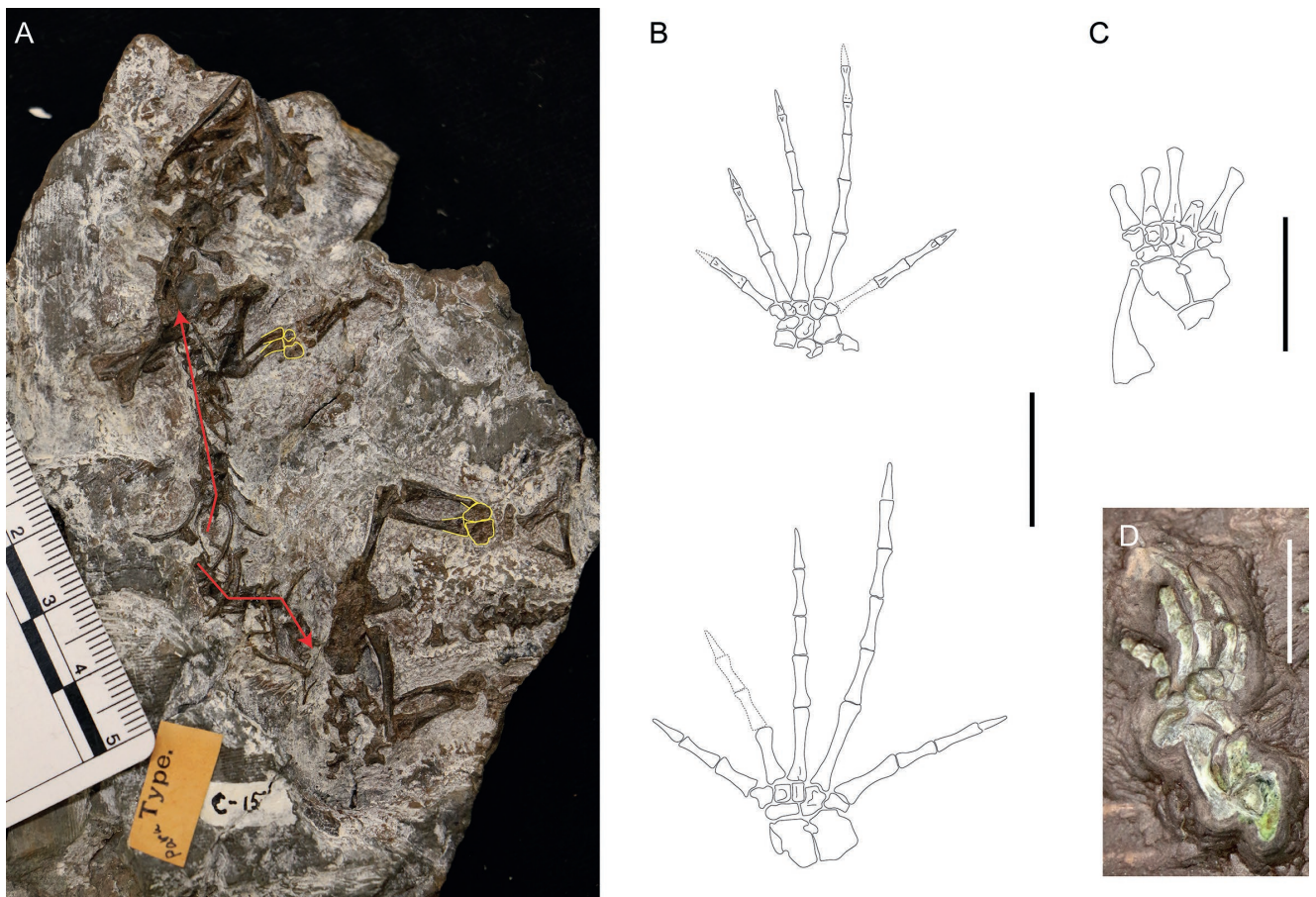


Fig. 9. Possible trackmakers of *Notalacerta missouriensis*. **A.** MCZ 3482. Paratype of *Paleothyris acadiana*, ventral view. The red arrows indicate the glenoacetabular length. The yellow lines highlight the limb elements contacting with the carpus and tarsus. Morien Group, Pennsylvanian, Nova Scotia. **B.** Reconstruction of the pes and manus of *Paleothyris acadiana*, redrawn from Carroll (1969). **C.** MCZ 3481. Holotype of *Paleothyris acadiana*. Articulated tarsus, dorsal view, redrawn from Carroll (1969). Note the non-overlapping metatarsals. Morien Group, Pennsylvanian, Nova Scotia. **D.** MNG 10183 V. *Thuringothyris mahlendorffae*. Articulated left tarsus, dorsal view. Note the non-overlapping metatarsals. Tambach Formation, Cisuralian, Germany. Scale bars: 1 cm.

therefore an in-depth understanding of its stratigraphic and palaeobiogeographic distribution is central for the understanding of Pennsylvanian tetrapod faunas and to build a meaningful tetrapod footprint biostratigraphy. Due to its notable abundance (it has been recorded in 10 different units/formations, Fig. 10), this ichnotaxon is the reference ichnogenus for the *Notalacerta* biochron of Fillmore *et al.* (2012), with the earliest occurrence of the ichnogenus from the early Langsettian site of Joggins, Canada (Joggins Formation; Davies *et al.*, 2005; Utting *et al.*, 2010; Lucas, 2019; this work; Fig. 10). This coincides with the earliest skeletal record of reptiles (*Hylonomus lyelli*), occurring at the same site (Dawson, 1895; Carroll, 1964, 1970, 1988, 2009; Reisz, 1972; Clack, 2002; Calder *et al.*, 2006).

It is also time-equivalent to the first occurrence of *Notalacerta* from Alabama (Mary Lee Coal Zone, lower Pottsville Formation, early Langsettian; e.g., Haubold *et al.*, 2005; Fig. 10). Earlier occurrences of tracks interpreted to be made by reptiles were identified by Falcon-Lang *et al.* (2007) from the Grande Anse Formation of New Brunswick, by Falcon-Lang *et al.*, 2010 from the Tynemouth Creek Formation of New Brunswick, and by Keighley *et al.* (2008)

from the Port Hood Formation of Nova Scotia (Fig. 10), all date to the late Namurian-early Langsettian, with an ambiguous age for the Grande Anse Formation (Keighley *et al.*, 2008). Nevertheless, the material from the Grande Anse Formation was re-assigned to the ichnotaxon *Hylopus* and interpreted to be made by anthracosaurids by Marchetti *et al.* (2019a), and the material from the Tynemouth Creek Formation is here re-assigned to *Hylopus*. A single uncollected specimen from the Port Hood Formation (Namurian C) illustrated in Keighley and Pickerill (1998) is here assigned to cf. *Notalacerta* isp. Consequently, further research is needed in order to provide clear *Notalacerta* specimens from stratigraphic intervals older than the Joggins Formation and the Mary Lee Coal Zone of the Pottsville Formation. Thus, the lower boundary of the *Notalacerta* biochron is currently still within the early Langsettian (Bashkirian).

The ichnogenus *Notalacerta* shows a highly variable distribution in the Pennsylvanian through to the Carboniferous-Permian boundary. It was common and widespread in central Euramerica during the Bashkirian (Westphalian A), when it is found in an area encompassing Alabama, Kentucky, New Brunswick and Nova Scotia (Fig. 10). The *Notalacerta*

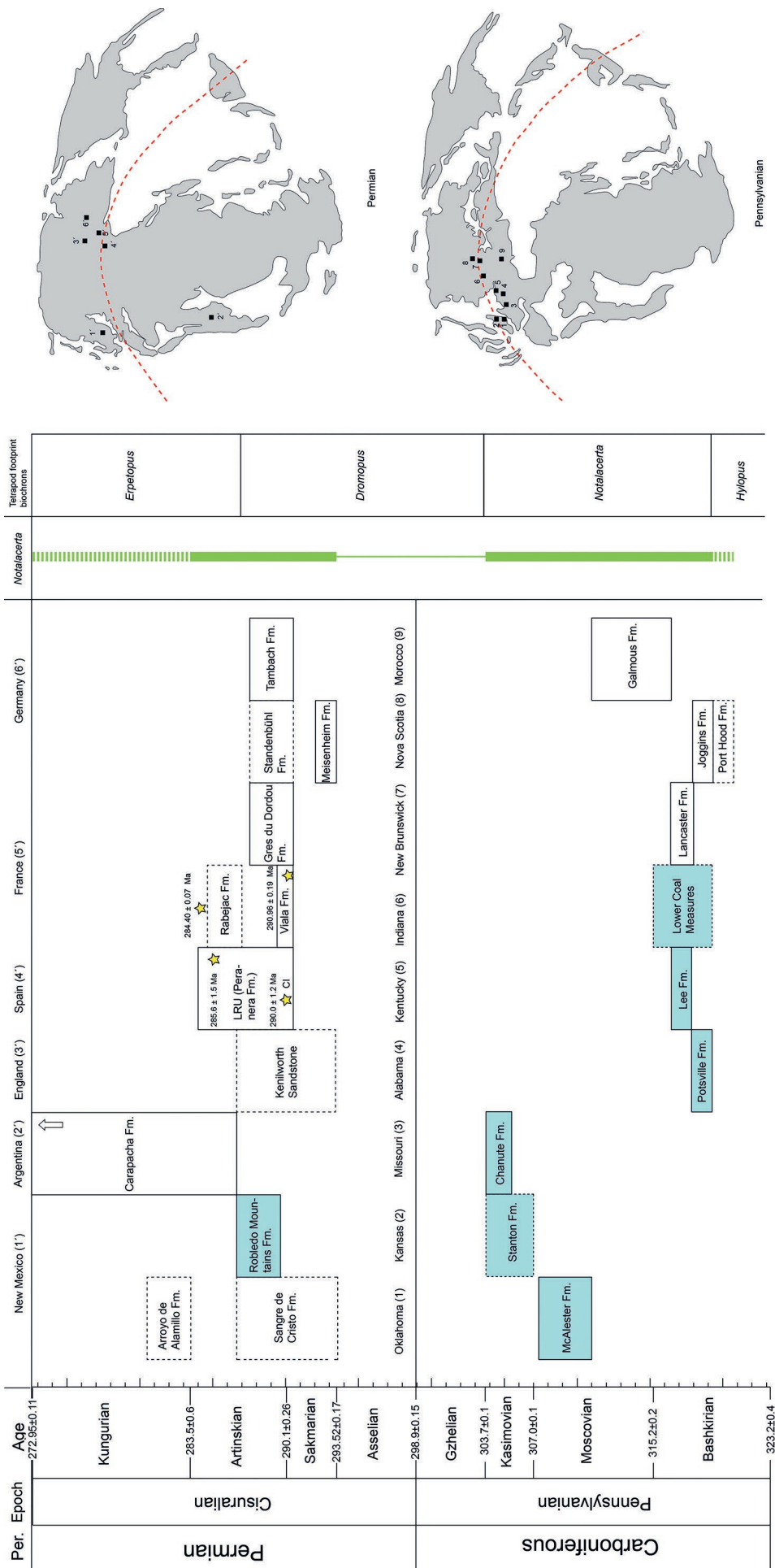


Fig. 10. Stratigraphic and palaeogeographic distribution of *Notalacerta missouriensis*. Dashed box lines mean uncertain occurrence. Stars indicate the radioisotopic ages. Marginal marine units are in light blue. The arrow at the top of Carapacha Formation indicates that this unit may be younger. Dashed green line means uncertain unit age or uncertain occurrence of *Notalacerta*. Palaeogeographic maps redrawn from Blakey (2008). Dashed red lines indicate the equator. Tetrapod footprint biostratigraphic locations after Schneider *et al.* (2020).

specimens from the Rockcastle Sandstone Member, Lee Formation, Kentucky (Chesnut *et al.*, 1994) and from the Lancaster Formation, New Brunswick are of late Bashkirian (late Langsettian) age. During the Bashkirian, *Notalacerta* occurrences are also known from the lower Coal Measures of Indiana (cf. *Notalacerta* isp., Cox, 1874). This seems to suggest a possible early diversification of reptiles during the Bashkirian, soon after the origin of reptiles.

Notalacerta occurrences in the Moscovian (Westphalian B–D; Fig. 10) are known from the Keota Sandstone Member of the McAlester Formation, Oklahoma, within the *Notalacerta* tetrapod footprint biochron (Lucas, 2001, 2019; Fillmore *et al.*, 2012), however younger occurrences are herein identified (Lucas *et al.*, 2004; Marchetti *et al.*, 2019a; this work). The Galmous Formation of Morocco is considered Westphalian B–C in age (Lagnaoui *et al.*, 2014), therefore this *Notalacerta* occurrence is constrained between the late Bashkirian to the middle Moscovian.

Younger occurrences of *Notalacerta* in the Carboniferous are known from the Kasimovian (Fig. 10) from the Cement City Limestone of the Chanute Formation, Missouri, the type locality (Butts, 1891a; this work) and possibly the Rock Lake Member of the Stanton Formation, Garnett, Kansas (Reisz, 1990). Nevertheless, the ichnogenus almost disappeared around the C–P transition, as no reliable examples are known from the Gzhelian and Asselian (Fig. 10)

During the Cisuralian, after the Asselian, *Notalacerta* was again widespread, although numerically rare, during the Sakmarian–early Artinskian (Fig. 10), at the end of the *Dromopus* biochron. Occurrences of this time period are known from the Robledo Mountains Formation of New Mexico (Voigt and Lucas, 2015a), the Viala and Gres du Dourdou formations of France (e.g., Gand, 1989, this work) and the Meisenheim, Standenbühl and Tambach formations of Germany (this work). The possible occurrence from the Kenilworth Sandstone of England (Haubold and Sarjeant, 1973) is probably within this time interval.

The subsequent decline and disappearance of *Notalacerta* during the late Artinskian (France, Spain) or possibly early Kungurian (New Mexico) or late Cisuralian–early Guadalupian (Argentina), seems to be confined to the early *Erpetopus* biochron. This happened just after the reptile radiation described by Marchetti *et al.* (2019d; Fig. 10), matching the stratigraphic distribution of non-diapsid eu-reptiles more basal than captorhinids (e.g., Modesto *et al.*, 2014). Some of the youngest occurrences of *Notalacerta* are Artinskian in age, from the Peranera Formation of Spain (Voigt and Haubold, 2015; Mujal *et al.*, 2016), and possibly the Rabejac Formation of France (this work). The possible early Kungurian occurrence from the Arroyo de Alamillo Formation of New Mexico is still a tentative assignment (Voigt and Lucas, 2017). The occurrence from the Carapacha Formation of Argentina (Melchor and Sarjeant, 2004) may be even younger, but its age is poorly constrained (late Cisuralian – early Guadalupian).

Some further considerations can be made based on palaeoecology. During the Pennsylvanian, *Notalacerta* is more common in tidal flat and marginal marine units (e.g., McAlester, Stanton, Chanute, Potsville, Lee formations and Lower Coal Measures of Indiana) than in continental

alluvial and wetland units (e.g., Lancaster, Joggins, Port Hood, Galmous formations; Fig. 10). During the Permian, *Notalacerta* is instead more common in continental alluvial and marginal lacustrine units (e.g., Arroyo de Alamillo, Sangre de Cristo, Carapacha, Kenilworth, Peranera, Viala, Rabejac, Gres du Dourdou, Meisenheim, Standenbühl, Tambach formations) than in tidal flat and marginal marine units (e.g., Robledo Mountains Formation; Fig. 10). Therefore, the apparent disappearance of this ichnogenus around the C–P boundary may be due to the scarcity of marginal marine tracksites described from this time interval (research and/or preservation bias), while the subsequent late Cisuralian radiation, mostly observed in strictly continental units, may be due to the colonization of more inland environments by the trackmakers because of more favourable conditions, possibly linked to the increased seasonality and aridity observed during the late Cisuralian (e.g., DiMichele *et al.*, 2006).

CONCLUSIONS

The first comprehensive ichnotaxonomic revision of *Notalacerta missouriensis* reveals an unexpected abundance of this ichnotaxon in Pennsylvanian–Cisuralian units. A neotype was provided and the diagnosis emended, with the study of additional well-preserved material and a detailed comparison with morphologically-similar ichnotaxa such as *Hyloidichnus*, *Varanopus*, *Robledopus*, *Erpetopus*, *Dromopus* and *Hylopus*. *Notalacerta* is considered monospecific. A synapomorphy-based track-trackmaker correlation is based on: 1) digit and digit imprint proportions, 2) metatarsal and pes digit imprint arrangement, 3) carpus/tarsus structure and palm/sole impression morphology; and 4) gleno-acetabular length/pes length ratios inferred from skeletons and trackways. These features suggest the “protorothyridid” eureptiles such as *Hylonomus*, *Paleothyris* and *Thuringothyris* as the most probable producers of *Notalacerta*.

A review of the Pennsylvanian–Cisuralian record of *Notalacerta* reveals: 1) the FAD (First Appearance Datum) of *Notalacerta* currently coincides with the occurrence of the earliest reptile, *Hylonomus lyelli*. Also, they are found at the same site (UNESCO World Heritage Site, Joggins Fossil Cliffs, Joggins, Nova Scotia, Canada). Possible older occurrences, such as some tracks from the Port Hood Formation (Nova Scotia, Canada), need to be verified. 2) *Notalacerta* is abundant and widespread during the Bashkirian (in a large part of the North American continent), possibly suggesting a reptile radiation immediately after reptile origins. 3) *Notalacerta* is more common in marginal marine than in continental palaeoenvironments during the Pennsylvanian. 4) *Notalacerta* is not recorded around the CP transition (Gzhelian–Asselian), possibly because of research or preservation bias. 5) *Notalacerta* is again widely-distributed although numerically non-abundant during the Sakmarian–Artinskian (North America, South America, Europe). In this time interval, it is more common in continental than marginal marine palaeoenvironments. 6) The *Notalacerta* LAD (Last Appearance Datum) is in the late Artinskian; younger occurrences (Arroyo de Alamillo

Formation, New Mexico, USA) need to be verified or better constrained (Carapacha Formation, Argentina).

This revision highlights *Notalacerta missouriensis* as a fundamental ichnotaxon of the Pennsylvanian–Cisuralian, that is important for tetrapod footprint biostratigraphy, palaeobiogeography, palaeoecology and may shed light on the controversial topic of the origin of reptiles.

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