[Papers in Palaeontology, Vol. 7, Part 3, 2021, pp. 1297–1319]

EXTENDING THE FOOTPRINT RECORD OF PAREIASAUROMORPHA TO THE CISURALIAN: EARLIER APPEARANCE AND WIDER PALAEOBIOGEOGRAPHY OF THE GROUP

by LORENZO MARCHETTI[1], SEBASTIAN VOIGT[2], EUDALD MUJAL[3,4], SPENCER G. LUCAS[5], HEITOR FRANCISCHINI[6], JOSEP FORTUNY[4] *and* VINCENT L. SANTUCCI[7]

[1]Museum für Naturkunde, Leibniz-Institut für Evolutions-und Biodiversitätsforschung, Invalidenstrasse 43, 10115 Berlin, Germany; lorenzo.marchetti@mfn.berlin
[2]Urweltmuseum Geoskop, Burgstraße 19, 66871 Thallichtenberg, Germany
[3]Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany
[4]Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain
[5]New Mexico Museum of Natural History & Science, 1801 Mountain Road NW, Albuquerque, NM 87104, USA
[6]Laboratório de Paleontologia de Vertebrados, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS Brazil
[7]Geologic Resources Division, National Park Service, 1849 C Street, NW, Room 2644, Washington, DC 20240, USA

Typescript received 5 April 2020; accepted in revised form 18 August 2020

Abstract: Pareiasauromorpha is one of the most important tetrapod groups of the Permian. Skeletal evidence suggests a late Kungurian origin in North America, whereas the majority of occurrences come from the Guadalupian and Lopingian of South Africa and Russia. However, Pareiasauromorpha footprints include the ichnogenus *Pachypes*, which is unknown from strata older than late Guadalupian. A revision of several *Pachypes*-like footprints from the Cisuralian–Guadalupian of Europe and North America confirm the occurrence of this ichnogenus and of the ichnospecies *Pachypes ollieri* comb. nov. beginning in the Artinskian. This is the earliest known occurrence of *Pachypes* and it coincides with the Artinskian reptile radiation. Based on a synapomorphy-based track–trackmaker correlation, *P. ollieri* can be attributed to nycteroleter pareiasauromorphs such as *Macroleter*. Therefore, the earliest occurrences of pareiasauromorph footprints precede by at least 10 myr the earliest occurrence of this group in the skeletal record. Moreover, the palaeobiogeography of the group is extended to the Cisuralian and Guadalupian of western Europe.

Key words: Pareiasauromorpha, *Pachypes*, Cisuralian–Guadalupian, tetrapod footprint, reptile radiation.

PAREIASAUROMORPHA is the most abundant, diverse and widespread parareptile group of the Permian and is composed of the nycteroleters (*sensu* Tsuji *et al.* 2012 and Tsuji 2013) and the Pareiasauria (Lucas 2006, 2018; Tsuji & Müller 2009; Tsuji *et al.* 2012). However, few occurrences of this group are known from low Pangaean palaeolatitudes (i.e. western Europe, North Africa and the USA), and only a single occurrence is known from Cisuralian strata (Lucas 2002, 2006), although different interpretations of the age of these strata exist (Reisz & Laurin 2001). Also, the origin of the group is poorly understood and constrained (Tsuji & Müller 2009). An independent source of information about this group may come from the study of Pareiasauromorpha tracks. The only ichnogenus with a reliable attribution to Pareiasauromorpha is *Pachypes* Leonardi *et al.*, 1975 (Conti *et al.* 1977; Valentini *et al.* 2008, 2009; Marchetti *et al.* 2019*a*, *b*). However, all the records of *Pachypes* thus far known are of late Guadalupian or Lopingian age (Voigt & Lucas 2018).

Nevertheless, some ichnogenera from the Guadalupian of France such as '*Paranomodontipus*' Ellenberger, 1983*a* and '*Lunaepes*' Gand *et al.*, 1995 and some tetrapod footprints from the Cisuralian and Guadalupian of Texas (USA; Lucas & Hunt 2005), Arizona (Marchetti *et al.* 2020*a*), southern France (Demathieu *et al.* 1992; Gand *et al.* 2000; Heyler & Gand 2000) and the Catalan Pyrenees (Spain; Mujal *et al.* 2016) show noteworthy similarities to *Pachypes*, although these footprints are generally smaller. All of this material needs an ichnotaxonomic revision based on well-preserved tracks (*sensu* Marchetti *et al.* 2019*c*), as well as a detailed

doi: 10.1002/spp2.1342

track–trackmaker correlation with the possible pareiasauromorph producers, following the methodology of Voigt *et al.* (2007) and Marchetti *et al.* (2017*a*) for a synapomorphy-based trackmaker attribution. The aim of this study is to provide an anatomy-consistent ichnotaxonomic revision of this material with the evaluation of previously undescribed specimens from Arizona, Texas, Spain and France. This includes a detailed track–trackmaker correlation and the discussion of the implications for the evolution and palaeobiogeography of Pareiasauromorpha.

MATERIAL AND METHOD

The material includes both tetrapod footprints currently in museum collections and *in situ* specimens in the field. All the specimens were studied first-hand and photographed perpendicular to the trampled surface and with adequate light conditions (oblique light, artificial or natural) and a metric scale. The photographs included trackway sections, manus–pes couples and single imprints. Outline drawings on transparent films were also obtained for some specimens. The best-preserved footprints were also photographed to obtain 3D models by using the photogrammetry technique. The 3D models were built using the software Agisoft Photoscan Professional (v.1.4.0); meshes were edited with the software MeshLab (v.2016.12), and contour lines and colour depth maps were obtained using the software Cloud Compare (v.2.8 beta) and ParaView (v.5.0.1). 3D models were also obtained using a Next Engine 3D Scanner. Specimens were selected based on the quality of morphological preservation and the preservation scale *sensu* Marchetti *et al.* (2019*c*). The 3D models were uploaded to the digital repository MorphoSource (Marchetti *et al.* 2020*b*). The selected material was digitally measured with Gimp (v.2.8.16), and the measurements are reported in Tables 1–3.

Institutional abbreviations. DUMFM, Dumfries Museum and Camera Obscura, Dumfries, Scotland; GRCA, Grand Canyon National Park, Yavapai Geological Museum, Grand Canyon Village, Arizona, USA; IPS, Institut Català de Paleontologia Miquel Crusafont (formerly Institut de Paleontologia de Sabadell), Sabadell, Catalonia, Spain; MASR, Musée Archéologique de Saint-Raphaël, Saint-Raphaël, France; MF, Musée Fleury, Lodève, France; MNHN.F.LOD, Lodève collection, Muséum National d'Histoire Naturelle, Paris, France; PIN, Paleontological Institute, Moscow, Russia; UD-MitG, Université de Dijon, Dijon, France; UGKU, Urweltmuseum Geoskop, Thallichtenberg, Germany; UM-LOD, Lodève collection, Université de Montpellier, Montpellier, France; UR, Palaeontological Museum of the University 'La Sapienza', Rome, Italy; UTM, University of Toronto at Mississauga, Mississauga, Ontario, Canada.

Field specimens. FS-LL, Dalle Paléontologique de la Lieude, D8, Mérifons, France (43°37′54.3″N 3°16′08.4″E); FS-MA-B, Section MA-B of Mujal *et al.* (2016, 2018), about 600 m north of La Mola d'Amunt, Lleida, Catalonia, Spain (42°23′56.3″N 0°52′17.9″E); FS-SR, Avenue Ronsard, Saint Raphaël, France (43°25′28.8″N 6°47′00.9″E); FS-TB, 'The Bluffs' housing subdivision, Georgetown, Texas, USA (30°35′13.7″N 97°38′26.8″W).

Anatomical abbreviations. FL, foot (pes) length; m, manus; SL, stride length; p, pes; PA, pace angulation; psL, sole length; WP, width of pace.

SYSTEMATIC PALAEONTOLOGY

Ichnogenus PACHYPES Leonardi *et al.*, 1975

Type ichnospecies. Pachypes dolomiticus Leonardi *et al.*, 1975

Type strata and locality. Arenaria di Val Gardena Formation (Lopingian); Bletterbach Gorge, Redagno, Bolzano/Alto Adige Province, western Dolomites, Italy (Valentini *et al.* 2009; Marchetti *et al.* 2019*a*). More occurrences are known from the Arenaria di Val Gardena Formation in the western Dolomites (Valentini *et al.* 2009; Marchetti *et al.* 2019*a*), in Veneto (Marchetti *et al.* 2017*b*) and Friuli (Dalla Vecchia *et al.* 2012).

Other ichnospecies. Pachypes loxodactylus (Dudgeon, 1878) after Marchetti *et al.* (2019*b*) and *P. ollieri* (Ellenberger, 1983*a*) comb. nov. We do not consider *P.* '*primus*' (Gubin *et al.* 2003) *sensu* Valentini *et al.* (2009) to be a valid ichnospecies because of the poor preservation of the type material.

Other occurrences. **Lopingian**: Ikakern Formation of Morocco (Voigt *et al.* 2010), Moradi Formation of Niger (Smith *et al.* 2015), Cornockle and Locharbriggs formations of Scotland (Marchetti *et al.* 2019*b*). Possible further occurrences are from the Poldarsa Formation and the Vyatkian horizon of Russia (Gubin *et al.* 2003; Surkov *et al.* 2007; Valentini *et al.* 2009), the Cornberg Formation and the Mammendorf horizon of Germany (Buchwitz *et al.* 2017; Marchetti *et al.* 2019*b*) and the Upper Red Unit (*sensu* Gisbert 1981, Cadí sub-basin, Pyrenean Basin) of the Catalan Pyrenees, Spain (Mujal *et al.* 2017). The above-mentioned units from Morocco, Niger, Germany (Mammendorf horizon) and Spain may also be uppermost Guadalupian.

Guadalupian: La Lieude, Pradineaux and Le Muy formations of southern France (Gand & Durand 2006; this work).

Cisuralian: Hermit Formation of Arizona (Marchetti *et al.* 2020*a*; this work); San Angelo Formation of Texas (Lucas & Hunt 2005; this work); Peranera Formation (Lower Red Unit *sensu* Gisbert 1981, Erillcastell-Estac

TABLE 1. Ichnological parameters of pedal footprints.

Specimen	MP	FL	FW	FL/FW	psL	psW	FL/psL	I L	II L	III L	IV L	V L	div I–II	div II–III	div III–IV	div IV–V	div
FS-LL 3	1.5	67	66	1.0	29	43	2.3	22	25	32	39	22	7	13	24	34	78
FS-LL 4	2.0	78	68	1.1	34	52	2.3	19	25	37	48	19	9	18	11	41	79
FS-LL 9	2.5	64	64	1.0	24	55	2.7	13	18	28	39	20	12	19	9	24	64
FS-LL 10	2.0	85	63	1.3	36	56	2.3	21	25	35	50	26	7	15	11	36	70
FS-LL 15	1.5	66	59	1.1	31	38	2.2	11	20	27	39	22	27	14	7	31	79
FS-LL 16	1.5	56	49	1.1	30	40	1.9	12	19	22	31	13	10	12	12	54	89
MASR 13	1.5	67	52	1.3	32	44	2.1		16	32	38	21		17	12	22	
FS-SR 7	2.0	63	55	1.1	26	39	2.4	16	20	26	36	15	14	16	14	30	74
UD-MitG 15	1.5	49	50	1.0	20	33	2.4	18	23	27	30	21	30	16	16	24	86
UD-MitG 20	1.5	53	51	1.0	19	30	2.8	13	21	25	37		11	39	24		
GRCA 3172	2.0	27	26	1.0	14	17	2.0	7	11	14	19		23	33	21		
FS-TB 1	2.0	98	96	1.0	45	65	2.2	29	36	50	60	32	22	14	19	44	99
FS-MA B1	1.5	50	36	1.4	20	27	2.5	11	18	21	31		11	20	17		
FS-MA B2	2.0	37	31	1.2	20	29	1.8	6	11	15	21		28	39	25		
UGKU 1973	2.0	54	54	1.0	25	41	2.2	13	15	26	30	19	23	34	14	27	98
MF-NN 1	2.0	47	41	1.1	20	29	2.3	13	20	29	33		17	7	17		
UM LOD 96	1.5	59	53	1.1	25	41	2.3	14	22	29	37		17	33	10		
MNHN.F.LOD142	2.0	35	36	1.0	17	22	2.0	11	16	17	22	10	18	28	27	39	112
MNHN.F.LOD143	2.5	49	52	0.9	22	38	2.2	17	20	28	33	15	7	0	26	45	78

div, digit divergence; FL, foot length; FW, foot width; I–V, digit number; L, free length of digit; MP, morphological preservation grade; psL, sole length; psW, sole width. Length measurements in mm; angular measurements in degrees; values are averages (mean) except for MP, which shows the maximum value.

TABLE 2. Ichnological parameters of manual footprints.

Specimen	MP	FL	FW	FL/FW	psL	psW	FL/psL	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
FS-LL 3	2.0	59	64	0.9	32	53	1.8	20	26	30	33		17	22	22			1.1
FS-LL 4	2.0	61	69	0.9	32	56	1.9	19	23	31	31	18	15	22	14	51	102	1.3
FS-LL 9	2.5	56	60	0.9	31	47	1.8	17	22	29	27	15	14	23	25	41	103	1.1
FS-LL 10	2.0	63	56	1.1	35	53	1.8	16	19	26	30		18	14	4			1.3
FS-LL 15	1.5	55	57	1.0	30	49	1.8	23	24	27	29		16	13	18			1.2
FS-LL 16	1.5	46	48	1.0	30	40	1.5	12	16	21	23	9	21	18	31	31	100	1.2
MASR 13	2.0	52	52	1.0	31	41	1.7	23	24	24	25		12	27	8			1.3
FS-SR 7	1.0	49	45	1.1	29	39	1.7	18	19	20	24		21	27	8			1.3
UD-MitG 15	1.5	37	40	0.9	23	31	1.6	14	15	17	19		13	14	30			1.3
UD-MitG 20	2.0	45	49	0.9	25	37	1.8	17	20	22	21		27	12	25			1.2
GRCA 3172	2.0	22	28	0.8	13	21	1.7	8	9	10	12		11	20	32			1.3
FS-TB 1	1.5	59	82	0.7	29	59	2.0	21	25	29	32		23	30	26			1.7
FS-MA B1	2.0	38	46	0.8	21	38	1.8	13	17	20	20	11	10	17	9	34	70	1.3
FS-MA B3	2.0	58	73	0.8	28	52	2.1	22	26	33	30		14	26	18			
MF-NN 1	2.0	43	43	1.0	21	31	2.1	16	20	21	22		12	10	23			1.1
UM LOD 96	2.0	47	43	1.1	21	43	2.2	17	21	27	30		5	18	12			1.3
MNHN.F.LOD142	2.0	35	35	1.0	16	23	2.3	16	18	18	17		15	9	26			1.0
MNHN.F.LOD143	2.5	44	47	0.9	19	33	2.3	20	22	23	25	12	15	11	31	32	88	1.1

div, digit divergence; FL, foot length; FLp/FLm, foot length pes/foot length manus ratio; FW, foot width; I-V, digit number; L, free length of digit; MP, morphological preservation grade; psL, sole length; psW, sole width. Length measurements in mm; angular measurements in degrees; values are averages (mean) except for MP, which shows the maximum value.

TABLE 3. Ichnological parameters of vertebrate trackways.

Specimen	SLp	PLp	PAp	LPp	WPp	DIVp	SLm	PLm	PAm	LPm	WPm	DIVm	Dmp	BL	SLp/FL	WPp/FL	BL/FL
FS-LL 3	525	380	87	262	274	−1	547	366	97	273	242	6	83	350	7.8	4.1	5.2
FS-LL 4	601	403	96	291	273	−10	615	418	97	304	282	−1	85	362	7.7	3.5	4.6
FS-LL 9	453	357	79	225	275	−3	445	313	91	222	220	−2	99	323	7.1	4.3	5.1
FS-LL 10	440	368	73	219	286	−2	494	337	94	246	226	0	88	307	5.2	3.4	3.6
FS-LL 15	476	347	86	236	255	−16	459	317	93	229	217	11	77	300	7.2	3.9	4.6
FS-LL 16	578	384	97	288	253	−3	593	354	113	296	195	2	60	343	10.3	4.5	6.1
MASR 13	369	266	87	173	197	−19	335	233	91	164	166	0	77	253	5.5	3.0	3.8
UD-MitG 15						−11		155		62	141	0	46				
GRCA 3172	258	224	71	129	182	4	265	208	79	133	160	−3	40	163	9.5	6.7	6.0
FS-TB 1		522		489	182	−4		529		487	206	4	76			1.9	
MF-NN 1		300		140	265	11	342	271	78	171	208	0	24			5.6	

BL, calculated body (glenoacetabular) length; DIV, divarication from midline (inward positive, outward negative); Dmp, distance manus–pes (negative with pedal overstepping); FL, foot length of the pes; LP, length of pace; m, manus; p, pes; PA, pace angulation; PL, pace length; SL, stride length; WP, width of pace. Length measurements in mm, angular measurements in degrees, values are averages (mean).

sub-basin, Pyrenean Basin) of Catalan Pyrenees, Spain (Mujal *et al.* 2016; this work); Rabejac Formation of southern France (Gand & Durand 2006; this work).

Diagnosis. (Emended after Valentini *et al.* 2009.) Pentadactyl and semiplantigrade footprints of a quadrupedal, heteropod reptile, with tracks more deeply-impressed medially. It differs from temnospondyl and lepospondyl tracks such as *Batrachichnus*, *Limnopus* and *Matthewichnus*, which have instead a tetradactyl manus. It differs from synapsid tracks such as *Brontopus*, *Capitosauroides*, *Dicynodontipus*, *Dimetropus*, *Dolomitipes* and *Karoopes*, which have instead plantigrade footprints and/or tracks more deeply-impressed laterally. Sturdy, short digits with rounded or flat terminations not separated from the palm/sole impression. This is generally different from reptile tracks such as *Dromopus*, *Erpetopus*, *Rhynchosauroides* and *Varanopus*, which have instead long and slender digits and sharp claw impressions and from synapsid tracks such as *Brontopus*, *Dicynodontipus*, *Dimetropus* and *Dolomitipes*, which have digit imprints separated from the palm and sole impressions. Digits I–IV closely-grouped and proximally superimposed. This differs from anamniote tracks such as *Amphisauropus*, *Ichniotherium* and *Limnopus*, and captorhinid tracks such as *Hyloidichnus* and *Notalacerta*, which show instead well-spread digit imprints. Pes digit imprints increase in length from I to IV; shorter digit V. More symmetrical manus, imprints of digits II–IV being sub-equal in length; shorter external digits. Manus smaller in size with respect to the pes and slightly turned inward with respect to the pes. Pes subparallel with respect to the trackway midline; this differs from *Amphisauropus*, which shows instead a markedly inward-turned manus and outward-turned pes. Well-developed and deep sole and palm impressions. No tail-drag traces.

Pachypes ollieri (Ellenberger, 1983*a*) comb. nov.
Figures 1–7, Tables 1–3

1983*a* *Paranomodontipus ollieri* Ellenberger, pp. 12–13, figs 2, 8.
1983*a* *Theriopodiscus lieudensis* Ellenberger, p. 20, fig. 10.
1983*b* *Eotheriopodiscus lenis* Ellenberger (*nomen nudum*), p. 557, pl. 1.13.
1992 *Limnopus zeilleri* Delage, 1912; Demathieu *et al.*, pp. 26, 29, figs 3.2–4.
1995 *Lunaepes fragilis* Gand *et al.*, pp. 114–116, figs 8–9, pl. 3b–d.
2000 *Lunaepes ollierorum* Gand *et al.*, pp. 12–23, figs 6–9, pls 2, 3.1–3, 6.
2000 Tetrapod tracks indet. Heyler & Gand, p. 20, fig. 30.
2005 cf. *Amphisauropus* Haubold, 1970; Lucas & Hunt, p. 205, fig. 8e–f.
2016 cf. *Amphisauropus* Haubold, 1970; Mujal *et al.*, pp. 585–586, figs 5, S2d–l, S3.
2016 undetermined tetrapod tracks; Mujal *et al.*, fig. S4.

Material. (Marchetti *et al.* 2020*c*) **La Lieude Formation, Lodève Basin, Guadalupian, France**: FS-LL 9, lectotype trackway, including tracks belonging to 40 pes–manus

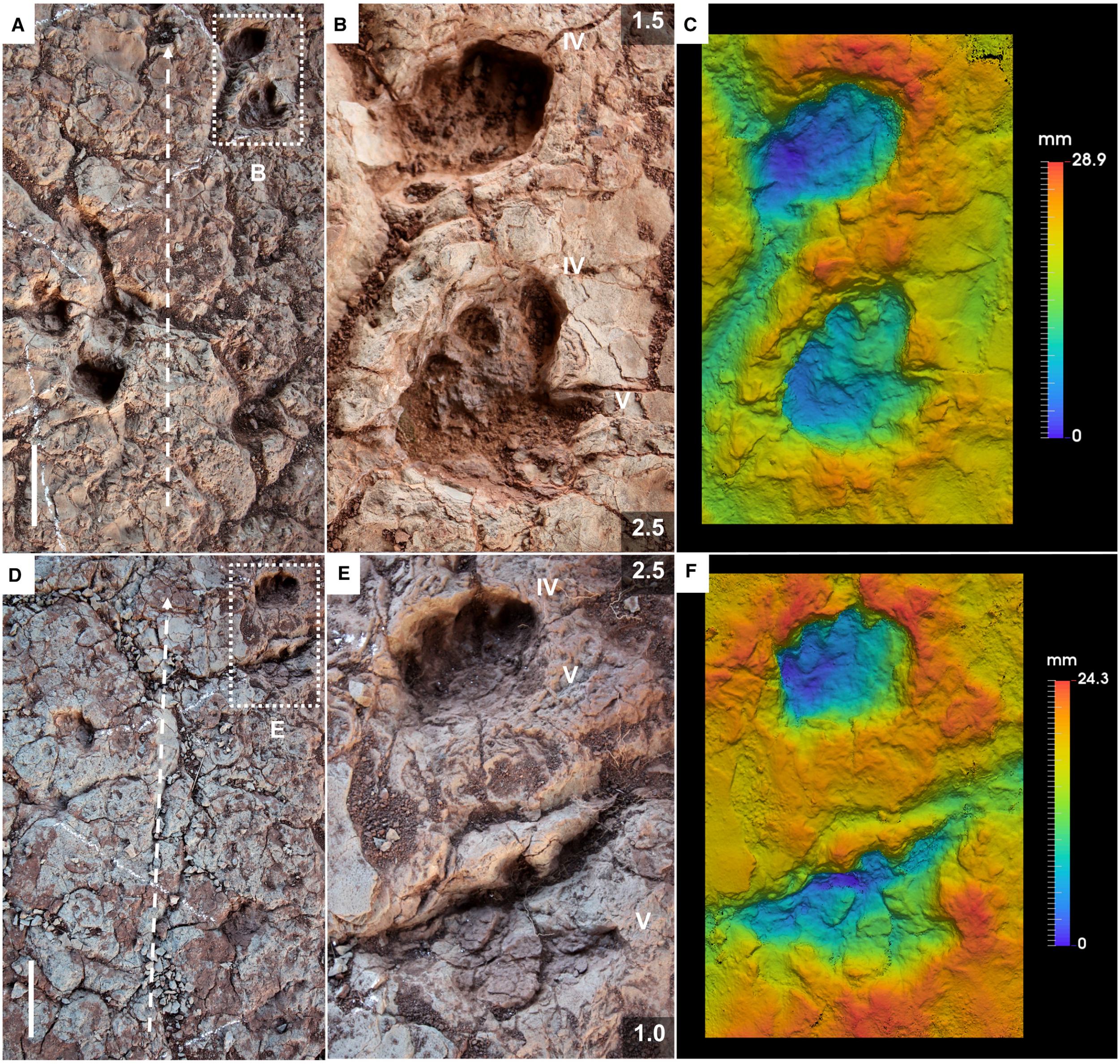

FIG. 1. *Pachypes ollieri* comb. nov., Guadalupian, La Lieude Formation, southern France. Lectotype, FS-LL 9, concave epirelief. A, trackway section. B, enlargement of A, right pes–manus couple. C, false-colour depth map of B. D, trackway section. E, enlargement of D, right pes–manus couple. F, false-colour depth map of E. The dashed arrows represent the trackway midline and direction of progression. Roman numerals indicate the digit imprint number. Values in the dark boxes (B, E) refer to the preservation scale. Both scale bars represent 10 cm.

couples, in concave epirelief. UM-LOD 16, plaster cast of a left pes–manus couple of the lectotype trackway, convex hyporelief. FS-LL 3, paralectotype trackway, including tracks belonging to 26 pes–manus couples, concave epirelief. FS-LL 4, paralectotype trackway, including tracks belonging to 16 pes–manus couples, concave epirelief. FS-LL 10, paralectotype trackway, including tracks belonging to 27 pes–manus couples, concave epirelief. FS-LL 11, paralectotype trackway, including tracks belonging to 37 pes–manus couples, concave epirelief. FS-LL 14, 15, 16, 17, more incomplete and poorly-preserved trackways, concave epirelief. **Le Muy Formation, Bas-Argens Basin, Guadalupian, France**: UD-MitG 15, incomplete step cycle with a right manus and a left pes–manus couple, convex hyporelief. UD-MitG 18, several isolated tracks, convex hyporelief. UD-MitG 20, incomplete step cycle with a right manus and a left pes–manus couple, convex hyporelief. **Rabejac Formation, Lodève Basin, Cisuralian, France**: UM-

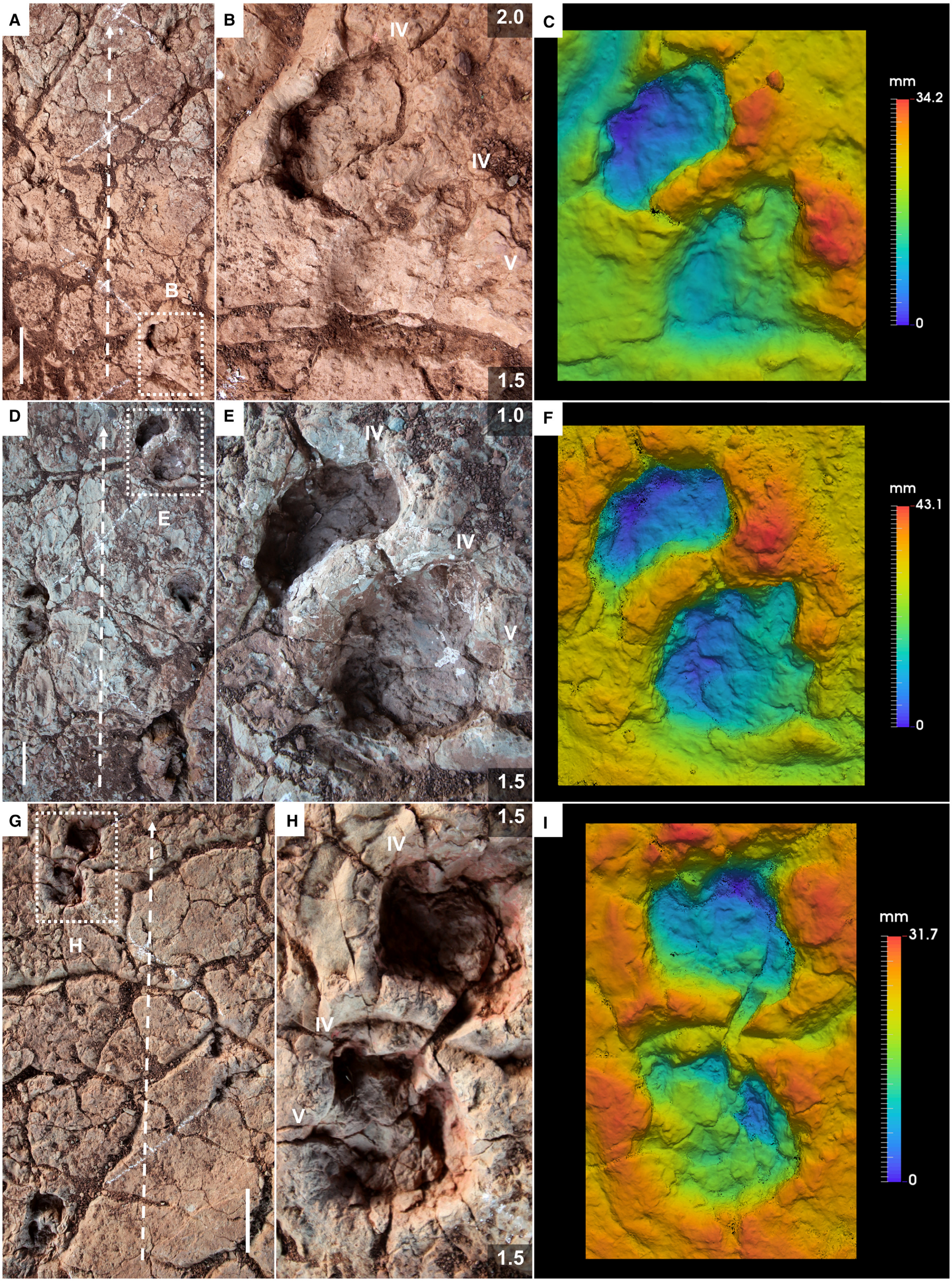
A
B
B
IV
IV
V
2.0
1.5
C
mm
34.2
0
D
E
E
IV
IV
V
1.0
1.5
F
mm
43.1
0
G
H
H
IV
IV
V
1.5
1.5
I
mm
31.7
0

FIG. 2. *Pachypes ollieri* comb. nov., Guadalupian, La Lieude Formation, southern France. Paralectotype, FS-LL 3, concave epirelief. A, trackway section. B, enlargement of A, right pes–manus couple. C, false-colour depth map of B. D, trackway section. E, enlargement of D, right pes–manus couple. F, false-colour depth map of E. G, trackway section. H, enlargement of G, left pes–manus couple. I, false-colour depth map of H. The dashed arrows represent the trackway midline and direction of progression. Roman numerals indicate the digit imprint number. Values in the black boxes (B, E, H) refer to the preservation scale. All scale bars represent 10 cm.

LOD 96, left pes–manus couple, convex hyporelief. MNHN.F.LOD142, left pes–manus couple, concave epirelief. MNHN.F.LOD143, left pes–manus couple, concave epirelief, plaster cast. MNHN.F.LOD144, left pes–manus couple, convex hyporelief, plaster cast. MNHN.F.LOD.145, isolated track, convex hyporelief, plaster cast. MF-NN 1, incomplete step cycle with two consecutive pes–manus couples, convex hyporelief. A *Tamabachichnium* pes–manus couple on the same slab. **Peranera Formation (Lower Red Unit), Erillcastell-Estac sub-basin (Pyrenean Basin), Cisuralian, Spain**: FS-MA-B 1, right pes–manus couple, convex hyporelief. FS-MA-B 2, left pes–manus couple, convex hyporelief. FS-MA-B 3, isolated manus and three partial pes tracks, convex hyporelief. IPS73723, right manus track, convex hyporelief. IPS82605, several tracks including step cycles and pes–manus couples, convex hyporelief, silicone mould and synthetic resin cast. UGKU 1973, incomplete right pes imprint, convex hyporelief. **Hermit Formation, Hermit Basin, Cisuralian, Arizona, USA**: GRCA 3172, trackway with three consecutive pes–manus couples, concave epirelief. GRCA 3173, counterpart of GRCA 3172, incomplete step cycle with two consecutive pes–manus couples, convex hyporelief. **San Angelo Formation, Permian Basin, Cisuralian, Texas, USA**: USA.FS-TB 1, incomplete step cycle with two consecutive pes–manus couples, concave epirelief.

Diagnosis. Pachypes ollieri comb. nov. differs from *P. dolomiticus* Leonardi *et al.*, 1975 and *P. loxodactylus* (Dudgeon, 1878) in the detectably higher values of WP/FL, SL/FL, PA and its smaller maximum size (Tables 1, 2). All of the *Pachypes* ichnospecies show parallel, stout digit imprints superimposed at their base. Nevertheless, the degree of digit thickness, grouping and superimposition differs among the three ichnospecies. *Pachypes ollieri* comb. nov. shows an intermediate condition: it differs from *P. dolomiticus* in the less closely grouped and superimposed digit impressions (higher FL/psL; Tables 1, 2); it differs from *P. loxodactylus* in its thicker, shorter, closely-grouped and superimposed digit impressions (lower FL/psL; Tables 1, 2).

Description. Semiplantigrade and pentadactyl footprints of a quadrupedal tetrapod. The pes imprint is about 30–100 mm long, it is about as long as wide, and clearly ectaxonic (digit IV impression is the longest; 19–60 mm long). Digit impressions are thick and end in rounded tips. The digit I–IV impressions are closely-grouped, superimposed at their bases and may be distally bent inwards (medially-oriented). The digit V impression is relatively short (10–22 mm long, about as long as I, 6–29 mm long), thin, in a proximal position and may be distally bent outwards (laterally oriented). The sole impression is elliptical and wider than long. Digit terminations and the medial (inner) side of the footprint are more deeply impressed than the digit III–V bases, sometimes resulting in a crescent-moon shape in incompletely impressed tracks. The manus imprint, wider than long, is slightly smaller and more deeply impressed than the pes imprint. The manus footprint depth is more equally distributed than in the pes imprints. Digit impressions are extremely short and tightly-grouped and superimposed for most of their length, and they have rounded terminations. Manus imprints are slightly ectaxonic to mesaxonic with external digit imprints slightly shorter (especially digit V impression), but the lengths of digits II–IV are remarkably similar. The digit I imprint may show a rounded basal pad. The digit V imprint is in a proximal position. The palm impression is elliptical and wider than long. The trackway pattern is characterized by a simple alternating arrangement of manus–pes couples with a short manus–pes distance and long stride length and width of pace compared to the pes length (SLp/FL and WPp/FL ratios of 7.5 and 4.1 on average, respectively). Despite the long stride, the pace angulation is relatively low (about 70–100° for the pes and 80–110° for the manus). The pes imprint is aligned with the midline, and the manus imprint is in front of the pes imprint, slightly medially positioned and slightly rotated inward respect to the pes. No tail/body impressions have been reported for this ichnogenus, and digit drag traces are rarely observed.

Remarks. The first ichnotaxonomic description of this material was by Ellenberger (1983*a*), who introduced the ichnotaxon '*Paranomodontipus*' *ollieri* with a short description and drawings of five different trackways from the La Lieude site in southern France (La Lieude Formation; Ellenberger 1983*a*, fig. 2). These trackways were later indicated with trackway numbers 3, 4, 9, 10 and 11 by Gand *et al.* (2000). A holotype was not designated, so these five trackways are syntypes, according to the ICZN (1999). Trackway 9 is relatively better-preserved (maximum grade 2.5 for both the pes and the manus tracks), it is also the holotype of the ichnospecies '*Lunaepes ollierorum*' Gand *et al.*, 2000 and a plaster cast of the best-preserved pes–manus couple (Fig. 1B) is stored in a repository (UM-LOD 16). We consider trackway 9 as the lectotype (Fig. 1) and trackways 3, 4, 10 and 11 as paralectotypes (maximum grade 2.0 for both the pes and the manus tracks) (Figs 2, 3).

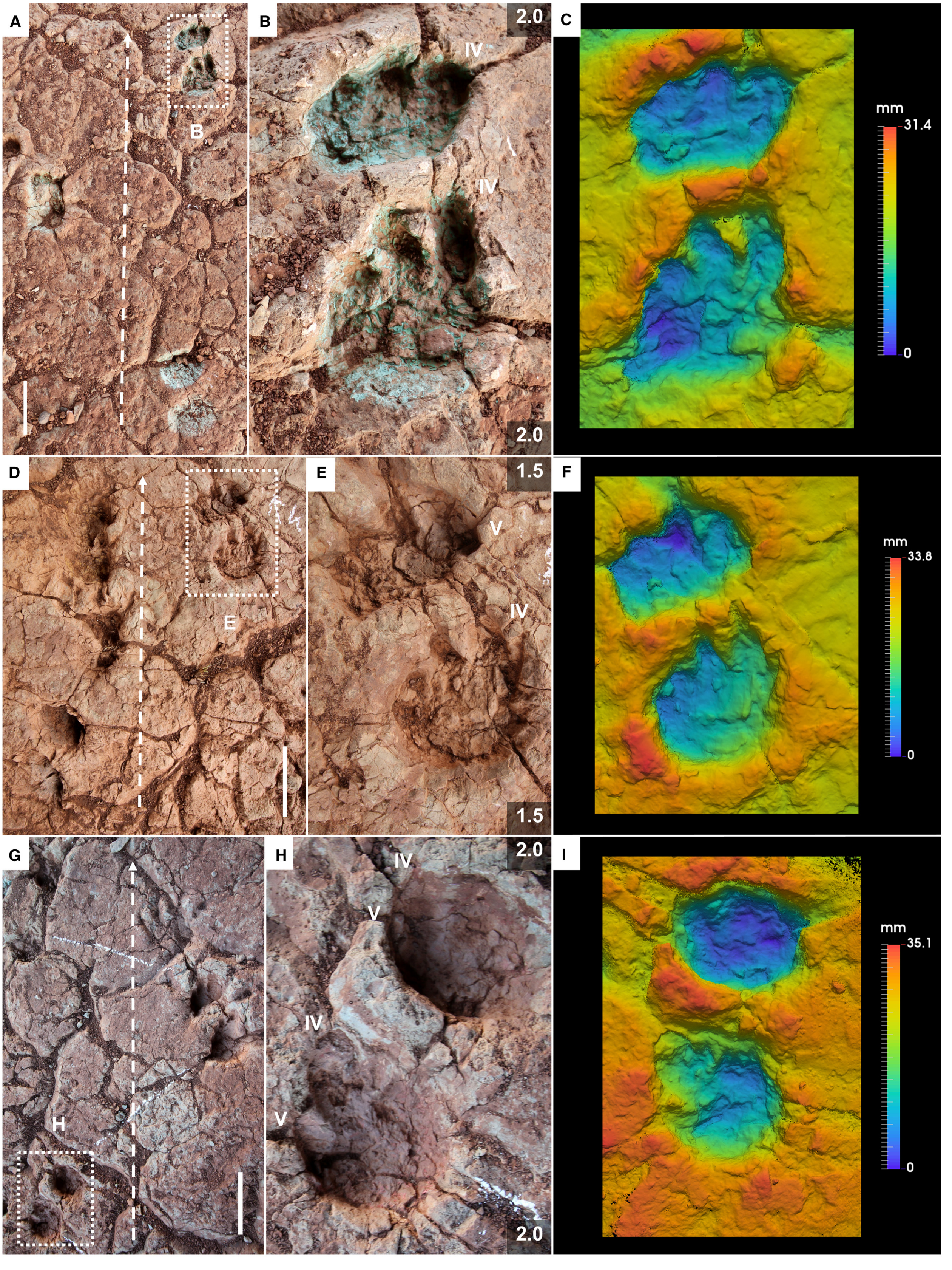
A
B
2.0
C
IV
IV
B
2.0
mm
31.4
0
D
E
1.5
F
V
IV
E
1.5
mm
33.8
0
G
H
2.0
I
IV
V
IV
V
H
2.0
mm
35.1
0

FIG. 3. *Pachypes ollieri* comb. nov., Guadalupian, La Lieude Formation, southern France. A–F, paralectotype, FS-LL 4, concave epirelief: A, trackway section; B, enlargement of A, right pes–manus couple; C, false-colour depth map of B; D, trackway section; E, enlargement of D, right pes–manus couple; F, false-colour depth map of E. G–I, paralectotype, FS-LL 10, concave epirelief: G, trackway section; H, enlargement of G, left pes–manus couple; I, false-colour depth map of H. The dashed arrows represent the trackway midline and direction of progression. Roman numerals indicate the digit imprint number. Values in the dark boxes (B, E, H) refer to the preservation scale. All scale bars represent 10 cm.

Another more digitigrade ichnotaxon, '*Theriopodiscus lieudensis*', was based on a morphologically-similar trackway from the same locality (Ellenberger 1983*a*, fig. 10b). We consider '*Theriopodiscus lieudensis*' to be a junior synonym of '*Paranomodontipus*' *ollieri* because the overall morphology and trackway pattern are identical in these two ichnotaxa, whereas the digitigrade impressions are a common feature in the type material of both ichnotaxa. In fact, transitions between these two differently impressed morphologies were observed along the same individual trackway (Fig. 2G).

Because these two ichnotaxa were clearly described and illustrated (Ellenberger 1983*a*, pp. 12–13, 15, 17, 20), we think that the requirements of the ICZN (1999) were fulfilled, so these names are not *nomina nuda* as suggested by Gand *et al.* (2000). Indeed, as part of his description of *P. ollieri*, Ellenberger (1983*a*, pp. 13–14) provided statements that compare and contrast the ichnotaxon that we take to state 'characters that are purported to differentiate the taxon'; thus, *P. ollieri* is available according to the mandates of ICZN Article 13.1.1.

Considering *P. ollieri* to be a *nomen nudum*, Gand *et al.* (2000) used one of the syntypes of *P. ollieri* as the holotype of their new ichnospecies '*Lunaepes ollierorum*'. However, given that *P. ollieri* Ellenberger, 1983*a* was not a *nomen nudum*, but an available name, the ichnospecies '*Lunaepes ollierorum*' is simply an objective junior synonym of *P. ollieri*.

The ichnotaxon '*Paranomodontipus*' *ollieri* shares numerous features (such as the thick parallel digits and the short digit V impression) with the ichnotaxon *Pachypes dolomiticus* Leonardi *et al.*, 1975 (Fig. 4A), introduced for an isolated but complete and well-preserved pes imprint from the Lopingian Arenaria di Val Gardena Formation of the Dolomites (Southern Alps, Italy). Subsequent studies refined the diagnosis of this ichnotaxon, based on a large number of additional specimens from the type locality, including well-preserved pes–manus couples, isolated footprints, a few incomplete step cycles and a trackway (Conti *et al.* 1977; Valentini *et al.* 2008, 2009; Marchetti *et al.* 2019*a*). The overall morphology and proportions of '*Paranomodontipus*' *ollieri* are consistent with *Pachypes dolomiticus* (Fig. 4A) with the exception of the digit thickness and superimposition, the trackway pattern and the maximum footprint size (Tables 1–3; Valentini *et al.* 2009; Marchetti *et al.* 2019*a*). We consider these differences adequate for a differentiation at the ichnospecies level, but not sufficient to distinguish two ichnogenera (note also that size is not a valid ichnotaxobase). Therefore, we synonymize the two ichnogenera and propose the new combination *P. ollieri* (Ellenberger, 1983*a*) for the material previously assigned to '*Paranomodontipus*' *ollieri* and its junior synonyms '*Theriopodiscus lieudensis*' and '*Lunaepes ollierorum*'.

This ichnospecies differs also from *Pachypes loxodactylus* (Fig. 4C), described from the Lopingian Locharbriggs Formation of Scotland and revised by Marchetti *et al.* (2019*b*). In fact, *P. ollieri* comb. nov. is characterized by relatively shorter and thicker digit impressions of the pes and a different trackway pattern compared to *P. loxodactylus*.

Some specimens from the Cisuralian of the USA (Hermit and San Angelo formations) and Europe (Rabejac Formation, southern France and Peranera Formation, Lower Red Unit, Catalan Pyrenees, Spain) and the Guadalupian of France (Le Muy Formation) show features similar to *P. ollieri* comb. nov.

The specimen GRCA 3172-3173, from the Hermit Formation of Grand Canyon National Park (Arizona, USA), includes a trackway with three consecutive pes–manus couples (Fig. 5A–E; Marchetti *et al.* 2020*a*). The morphology of the pes is similar to *Amphisauropus* because of the medial–lateral decrease in relief and the thick and straight digit impressions with rounded terminations, but the manual tracks are evidently different, because the digit impressions are extremely short, and the central digit impressions show a very similar length. The morphology of the manus imprint is similar to incompletely-impressed *Dimetropus* tracks (Voigt 2005), because the semi-circular arrangement of digits resembles the semi-circular arrangement of basal pads of *Dimetropus*. However, no claw or digit-tip impressions were registered, so they probably represent complete digits, not just basal digital pad impressions. Moreover, the pes impression is completely different from *Dimetropus* (Voigt 2005; Lucas *et al.* 2016). In fact, it does not show a medio-laterally expanded sole impression, the digit impressions have rounded terminations without claw traces and the medial side of the footprint is more impressed than the lateral side. This latter feature is the opposite in *Dimetropus* (see also discussion in Mujal *et al.* 2020). Also, the trackway pattern is different from both *Dimetropus* and *Amphisauropus*. All the morphological traits, including the

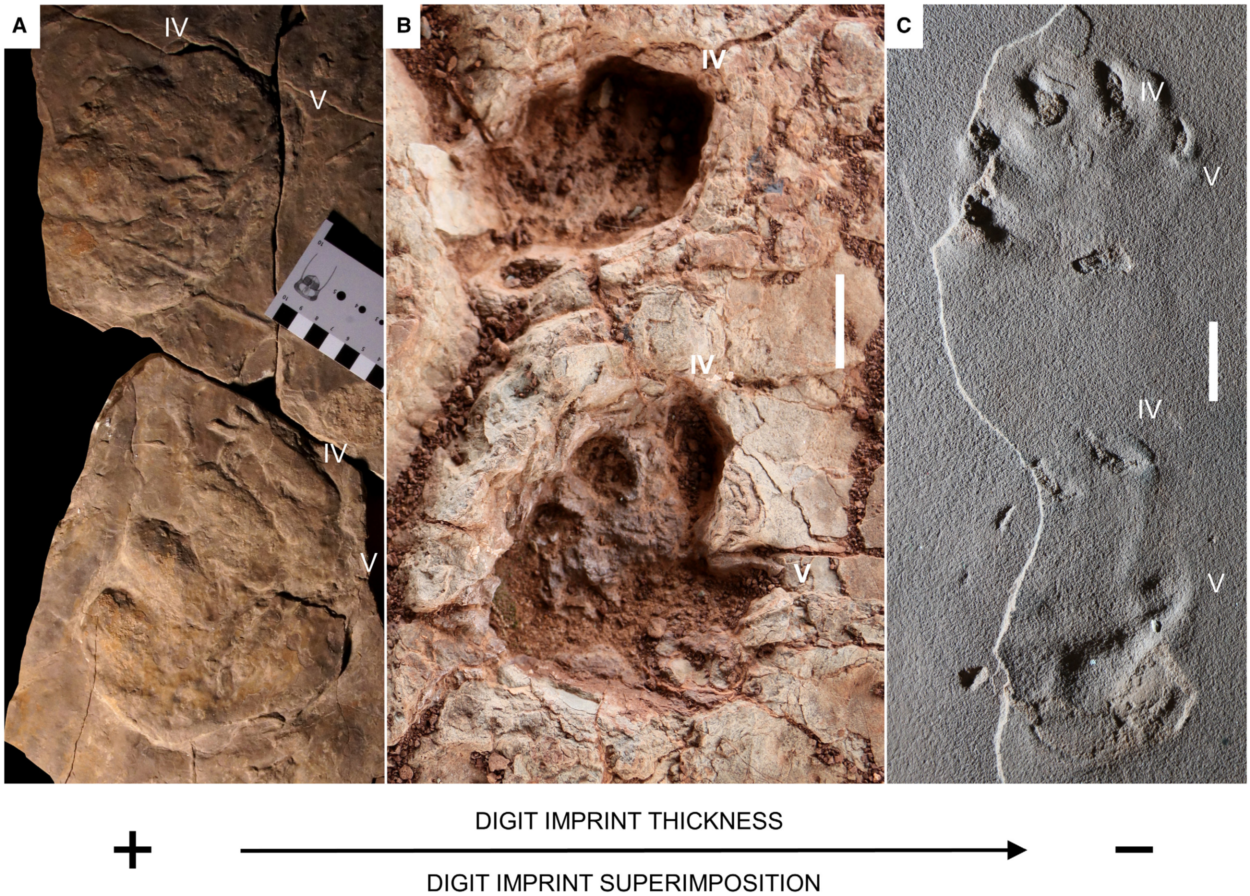

FIG. 4. Comparison of valid *Pachypes* ichnospecies. A, UR-NS 34-28, *Pachypes dolomiticus* Leonardi *et al.*, 1975, left pes–manus couple, convex hyporelief. B, FS-LL 9, *Pachypes ollieri* (Ellenberger, 1983*a*), right pes–manus couple, concave epirelief. C, DUMFM-NN 2, *Pachypes loxodactylus* (Dudgeon, 1878), right pes–manus couple, concave epirelief. Roman numerals indicate the digit imprint number. Both scale bars represent 2 cm.

stout, short and superimposed digits and the trackway pattern are instead consistent with *P. ollieri* comb. nov.

An incomplete step cycle, including two consecutive pes–manus couples from the San Angelo Formation of Texas (Lucas & Hunt 2005, fig. 8e–f), was tentatively assigned to cf. *Amphisauropus* isp. (Fig. 5F, G). However, the digit impressions of the manus are very short, and the pes digit impressions are thick, closely-grouped and distally bent inward (medially). Also, the typical marked impression of the digit I base of *Amphisauropus* (Voigt 2005) is absent, and the trackway pattern is different, because the pes imprints are not markedly rotated outwards. Therefore, this specimen is not assignable to *Amphisauropus*. All the morphological traits and the trackway pattern are instead consistent with *P. ollieri* comb. nov.

Specimens from the Peranera Formation (Lower Red Unit) of the Catalan Pyrenees (north-eastern Iberian Peninsula) (Fig. 6) previously referred to cf. *Amphisauropus* (including IPS73723, the mould and replica IPS82605 and other *in situ* tracks) and others identified as indeterminate tracks (Mujal *et al.* 2016, figs 5, S2d–l, S3, S4) also resemble *P. ollieri* comb. nov. These tracks are generally wider than long, and display very short and round digit impressions (increasing in length from I to IV, with a shorter digit V, though not always impressed), which are often deeper than the sole/palm impressions, different from *Amphisauropus*. We re-assign all these footprints to *P. ollieri* comb. nov.

The specimen UM-LOD 96 from the Rabejac Formation (Lodève Basin) of southern France (Fig. 7A, B), including an isolated left pes–manus couple, was assigned to the supposed therapsid track '*Eotheriopodiscus lenis*' by Ellenberger (1983*b*). Because this ichnotaxon was not described but only illustrated and listed, we consider it to be *nomen nudum* in agreement with the ICZN (1999). Some similar material from the same formation (MNHN.F.LOD142–145) was later listed and illustrated (Heyler & Gand 2000, fig. 30), but not assigned to an ichnotaxon. These specimens include a left pes–manus couple (MNHN.F.LOD142) (Fig. 7C, D) and some plaster

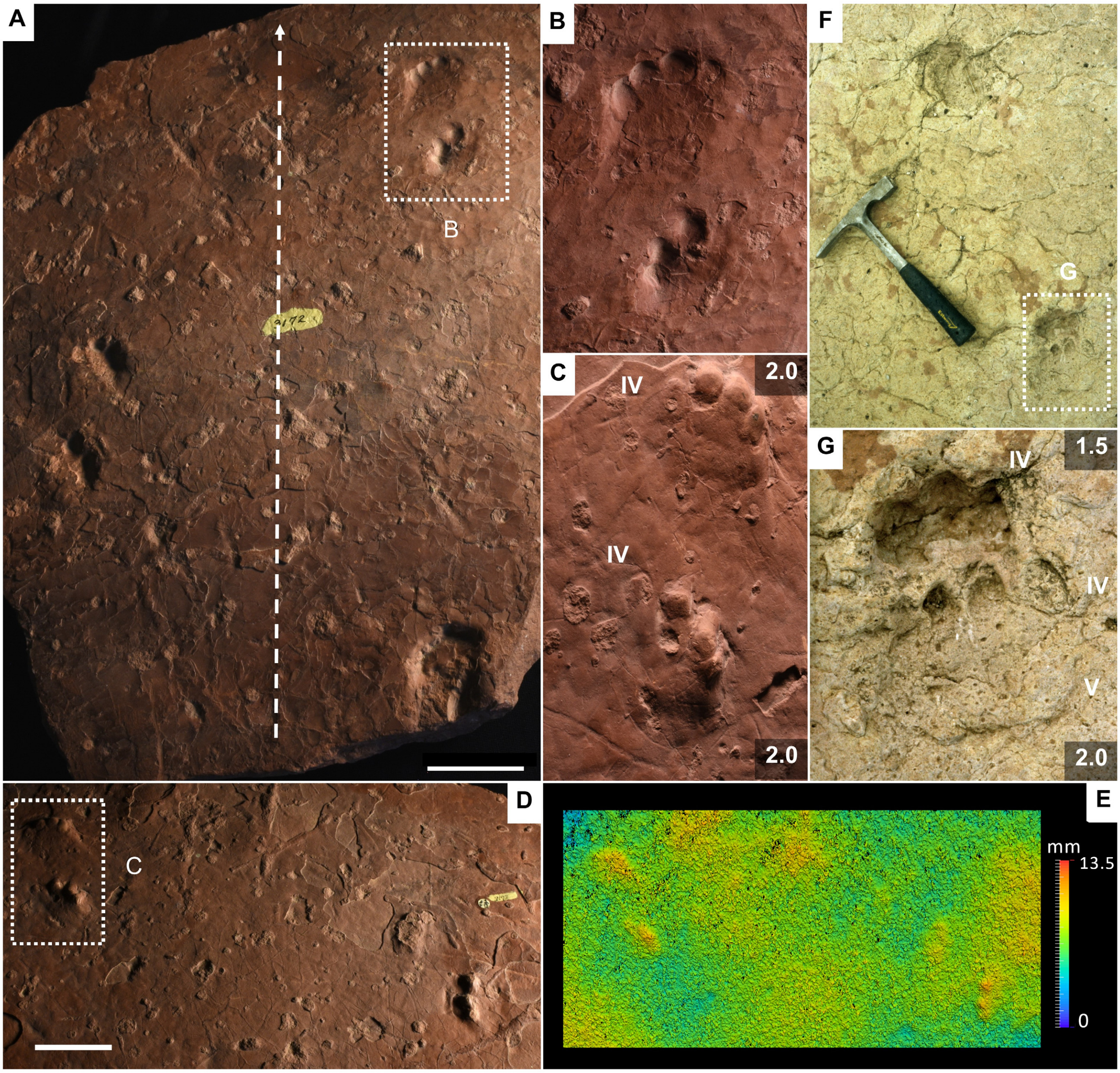

FIG. 5. *Pachypes ollieri* comb. nov., upper Cisuralian, USA. A–E, Hermit Formation, Arizona: A, GRCA 3172, trackway, concave epirelief; B, enlargement of A, right pes–manus couple; C–E, GRCA 3173, counterpart of B, convex hyporelief; C, right pes–manus couple; D, two consecutive pes–manus couples; E, false-colour depth map of D. F–G, FS-TB 1, incomplete step cycle, San Angelo Formation, Texas: F, two consecutive pes–manus couples, concave epirelief; G, enlargement of F, right pes–manus couple. The dashed arrow represents the trackway midline and direction of progression. Roman numerals indicate the digit imprint number. Values in the dark boxes (C, G) refer to the preservation scale. Both scale bars represent 5 cm.

casts of pes–manus couples (MNHN.F.LOD143–145; Fig. 7E). A further undescribed specimen (MF-NN 1; Fig. 7F, G) includes an incomplete step cycle with a manus and two consecutive pes–manus couples, and a larger pes–manus couple assignable to *Tambachichnium* isp. The incomplete step cycle on MF-NN 1 and the pes–manus couples of the specimens UM-LOD 96 and MNHN.F.LOD142–145 show morphological traits consistent with *P. ollieri* comb. nov., including stout, short and superimposed digit imprints and the trackway pattern.

Some specimens found in the Le Muy Formation (Fig. 7H), close to the transition between the Le Mitan and Le Muy formations, initially assigned to *Limnopus* (Demathieu *et al.* 1992), are also assignable to *P. ollieri*

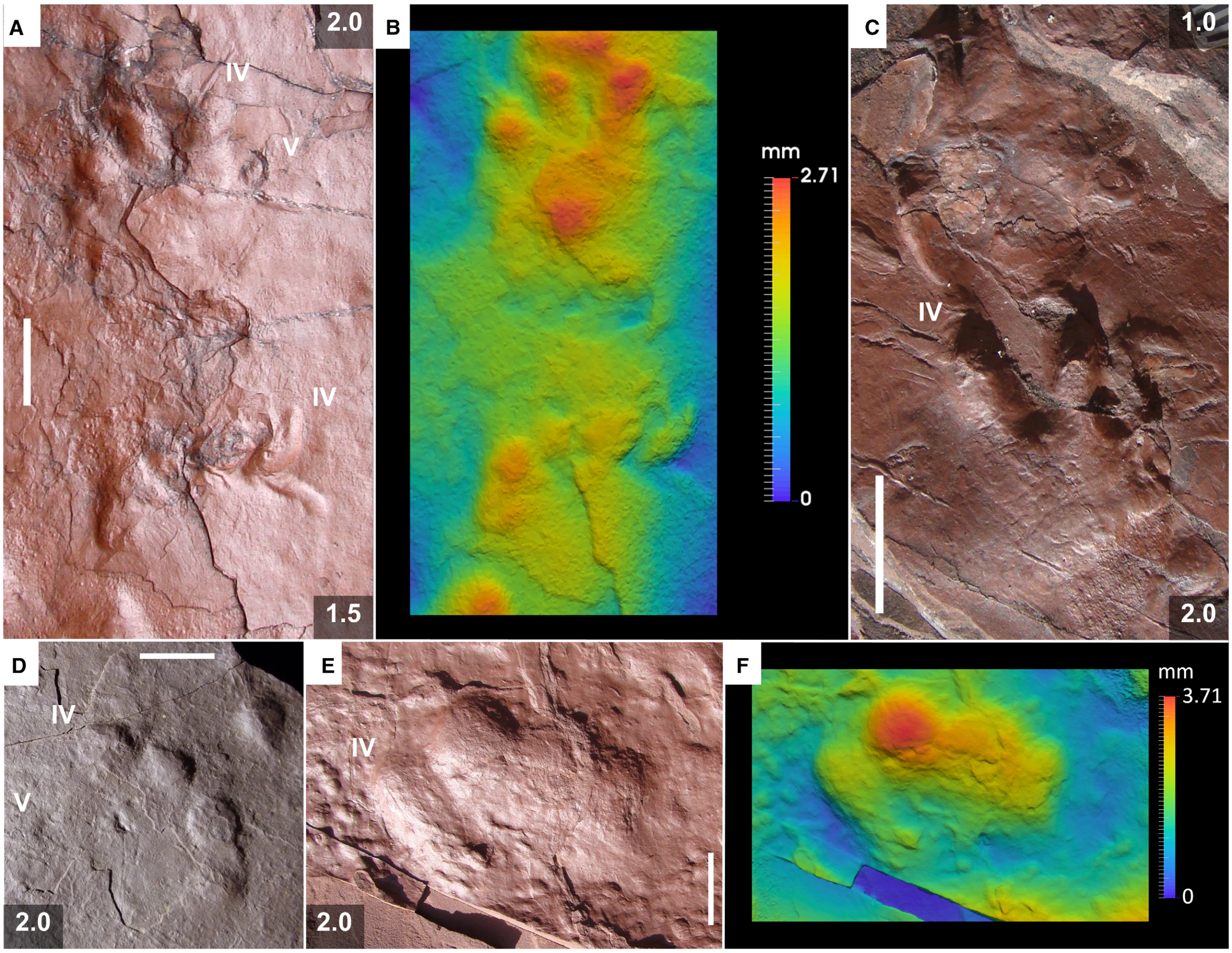

FIG. 6. *Pachypes ollieri* comb. nov., upper Cisuralian, Peranera Formation (Lower Red Unit), Catalan Pyrenees, Spain. A, FS-MA-B1, left pes–manus couple, convex hyporelief. B, false-colour depth map of A. C, FS-MA-B 2, right pes–manus couple, convex hyporelief. D, UGKU 1973, incomplete right pes, convex hyporelief. E, FS-MA-B3, right manus imprint, convex hyporelief. F, false-colour depth map of E. Roman numerals indicate the digit imprint number. Values in the dark boxes (A, C, D, E) refer to the preservation scale. All scale bars represent 2 cm.

comb. nov., because of the closely-grouped pes digit imprints and the morphology of manus digit imprints, which are very short and subequal in length (Fig. 7H).

Similar material. **Pradineaux Formation, Estérel Basin, Guadalupian, France**: FS-SR 7. Holotype trackway of '*Lunaepes fragilis*', including tracks belonging to 24 pes–manus couples, concave epirelief. MASR 13. Plaster cast of FS-SR 7 including five consecutive pes–manus couples, concave epirelief.

Remarks. The ichnotaxon '*Lunaepes fragilis*' Gand *et al.*, 1995, based on a trackway from the Guadalupian Pradineaux Formation in the Provence basins, is characterized by a peculiar pes imprint morphology resembling a crescent moon. Although the holotype is poorly-preserved (the digit impressions are mostly not visible, and the footprints are not completely impressed) a few couples (Marchetti *et al.* 2020*c*) show the typical morphological traits and trackway pattern of *P. ollieri* comb. nov., such as the thick, parallel and superimposed digits (more than *P. loxodactylus* and less than *P. dolomiticus*) and the wide trackways with well-spaced pes–manus couples. Due to the poor preservation of the holotype, we consider '*Lunaepes fragilis*' a *nomen dubium* and assign this material to cf. *Pachypes* isp.

TRACKMAKER ATTRIBUTION

The material herein assigned to *P. ollieri* comb. nov. has received different trackmaker attributions. Ellenberger

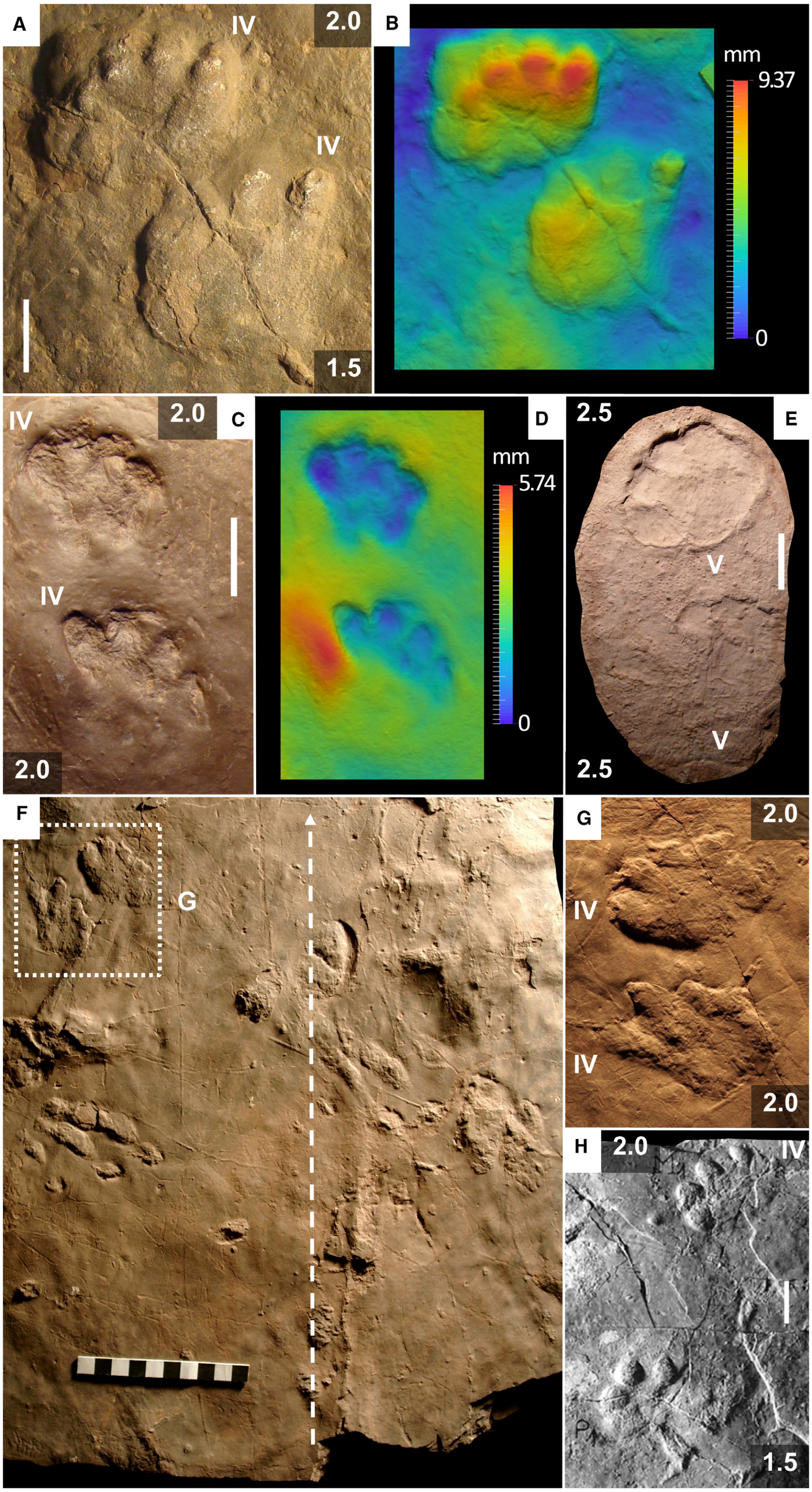

FIG. 7. *Pachypes ollieri* comb. nov., upper Cisuralian, Rabejac Formation (A–G) and Guadalupian Le Muy Formation (H), southern France. A, UM LOD 96, left pes–manus couple, convex hyporelief. B, false-colour depth map of A. C, MNHN.F.LOD142, left pes–manus couple, concave epirelief. D, false-colour depth map of C. E, MNHN.F.LOD143, plaster cast, left pes–manus couple, concave epirelief. F, MF-NN 1, incomplete step cycle assigned to *P. ollieri* comb. nov. and pes–manus couple assigned to *Tambachichnium* isp., convex hyporelief. G, enlargement of F, right pes–manus couple. H, UD-MitG 20, left pes–manus couple, convex hyporelief, from Demathieu *et al.* (1992), modified. The dashed arrow represents the trackway midline and direction of progression. Roman numerals indicate the digit imprint number. Values in the dark boxes (A, C, E, G, H) refer to the preservation scale. All scale bars represent 2 cm.

(1983*a*) hypothesized a small therocephalian or dicynodontid therapsid producer for the material from La Lieude Formation, although he noted the primitive foot structure indicated by the footprints. Gand (in Gand *et al.* 2000) hypothesized a small gorgonopsid therapsid producer for the same material, because it would fit better the pedal proportions. Gand *et al.* (1995) attributed the material from the Pradineaux Formation to small therapsids, noticing the absence of a primitive feature such as the tail impression. Ellenberger (1983*b*) attributed the material from the Cisuralian Rabejac Formation to small therapsids, probably because of the similarity with the Guadalupian material from La Lieude Formation. Lucas & Hunt (2005) and Mujal *et al.* (2016), respectively, attributed the incomplete step cycle from the San Angelo Formation and the manus–pes couples and isolated tracks of the Peranera Formation (Lower Red Unit) to seymouriamorph anamniotes, as indicated by the assignment to cf. *Amphisauropus* isp. Similarly, Demathieu *et al.* (1992) attributed the material from the Le Muy Formation to temnospondyl anamniotes, as indicated by the assignment to *Limnopus zeilleri*.

The markedly ectaxonic pes of these specimens with a relatively short sole is not consistent with a dicynodont therapsid producer, because they are characterized by a broad tarsus and mesaxony. Moreover, the deeper medial part of the pes impression is clearly inconsistent with all the widely-recognized synapsid tracks of the Permian (*Brontopus*, *Capitosauroides*, *Dicynodontipus*, *Dimetropus*, *Dolomitipes* and *Karoopes*) that show instead a deeper lateral part of the tracks (Marchetti *et al.* 2019*e*; Mujal *et al.* 2020). Also, the characteristic semi-circular basal pad arrangement of digits well-separated from the digit tips and forming paw-like impressions observed in therapsid tracks does not occur in material here assigned to *P. ollieri* comb. nov. Therefore, an assignment to synapsid producers is excluded.

In contrast, the Lopingian material assigned to the ichnogenus *Pachypes* has been consistently attributed to pareiasaurian producers, because of the parallel/superimposed digit impressions and the marked reduction of external digits (Leonardi *et al.* 1975; Conti *et al.* 1977; Valentini *et al.* 2008, 2009; Marchetti *et al.* 2019*a*, *b*). However, no pareiasaurs are known from Laurasia during the late Cisuralian to Guadalupian interval. Guadalupian pareiasaurs are known only from South Africa (e.g. *Bradysaurus*, *Embrithosaurus*, *Nochelosaurus*; Day *et al.* 2015) and Brazil (e.g. *Provelosaurus*; Araújo, 1985) but, with the exception of *Provelosaurus* (body length of 1.0 m), their size is too large (body length of 2.5–3.0 m) to have been the producers of *P. ollieri* comb. nov. Also, the phalangeal formula of pareiasaurs is very reduced (manus 2-3-3-3-2; pes 2-3-3-4-3; e.g. Turner *et al.* 2015) and this is inconsistent with the material assigned to *P. ollieri* comb. nov.

Nevertheless, several small-sized non-pareiasaur pareiasauromorphs are known from the upper Cisuralian to lower Lopingian of Laurasia (Sennikov & Golubev 2017; Lucas 2018) matching relatively well the stratigraphic distribution and size of *P. ollieri* comb. nov. These taxa are generally known as nycteroleters and include: an indeterminate nycteroleter from the Cisuralian of Texas (Chickasha Formation; Reisz & Laurin 2002; Tsuji 2006; Lucas 2018); *Bashkyroleter*, *Macroleter*, *Nycteroleter*, *Rhipaeosaurus* and *Tokosaurus* from the Guadalupian of Russia (Tsuji *et al.* 2012); *Emeroleter* from the lower Lopingian of Russia (Ivakhnenko 1997); and an indeterminate nycteroleter from the upper Guadalupian of South Africa (Cisneros & Tsuji 2009). For the Texas occurrence, we follow the age interpretation of Lucas & Golubev (2019).

Only *Emeroleter*, *Macroleter* (Figs 8, 9) and *Rhipaeosaurus* have well-preserved and relatively complete appendicular skeletons. The pes of *Rhipaeosaurus* is relatively similar to the pareiasaur pes because of the robust digits and the ectaxony (Efremov 1940), although the phalanges are more elongated, and the phalangeal formula is more primitive: 2-3-4-5-4. The ectaxonic condition is marked, and digit V is shorter than digit III, and in a proximal position. Digits I–IV are closely-packed, and the metatarsals are overlapped. The metatarsals decrease in thickness from digit I to digit V. The distal tarsals are robust and angular, especially distal tarsals I–IV. The astragalus and calcaneum are compact but not fused in a single element (the astragalocalcaneum), as in pareiasaurs (Tsuji *et al.* 2012). The pes is about 100 mm long. The limb bones are robust but slenderer and more elongate than in pareiasaurs. In a similar way, the vertebral column is also relatively longer. The tail is very thin and short, the manus is not known (Efremov 1940).

The pes of *Macroleter* (Figs 8A–D, 9B) is similar to the pes of *Rhipaeosaurus*. The ectaxony is marked, and the digit V is very short and in a proximal position. Digits I–IV are closely-packed, and the metatarsals are overlapped. The metatarsals decrease in thickness from digit I to digit V and increase in length between digits I–IV. The phalangeal formula is 2-3-4-4-2 (Fig. 9B). The distal tarsals are robust and angular, especially distal tarsals I–IV. There is also a fused astragalocalcaneum, as in pareiasaurs. The pes is about 60 mm long.

The manus of *Macroleter* (Figs 8E–H, 9B) is relatively smaller than the pes (about 40 mm long). The metacarpals are thick and increase in length between metacarpals I and IV and show a marked overlap. Digits II–IV are larger and more robust than digit I; digit V was not observed. The phalangeal formula is probably similar to

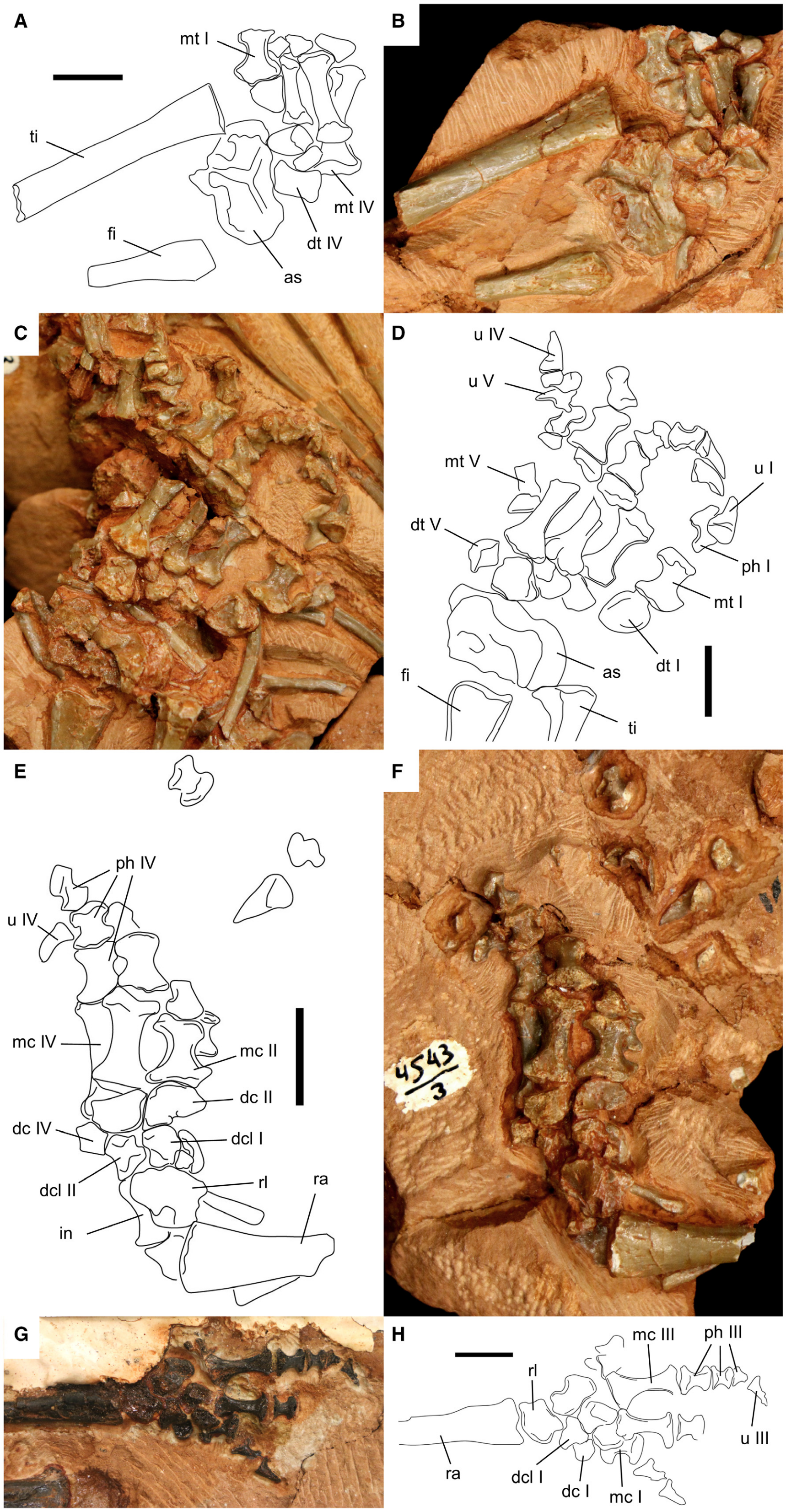

FIG. 8. Postcranial material (photos and interpretative drawings) of nycteroleter Pareiasauromorpha. *Macroleter poezicus* from the Mezen Assemblage, Guadalupian, Russia. A–F, PIN 4543/3: A–B, left pes, ventral view; C–D, right pes, ventral view; E–F, left manus, ventral view; G–H, UTM/Mezen/2001/3, left manus, dorsal view. *Abbreviations:* as, astragalocalcaneum; dc, distal carpal; dcl, distal centrale; dt, distal tarsal; fi, fibula; in, intermedium; mc, metacarpal; mt, metatarsal; ph, phalange; ra, radius; rl, radiale; ti, tibia; u, ungual. Roman numerals indicate the digit number or the distal centralia number. All scale bars represent 1 cm.

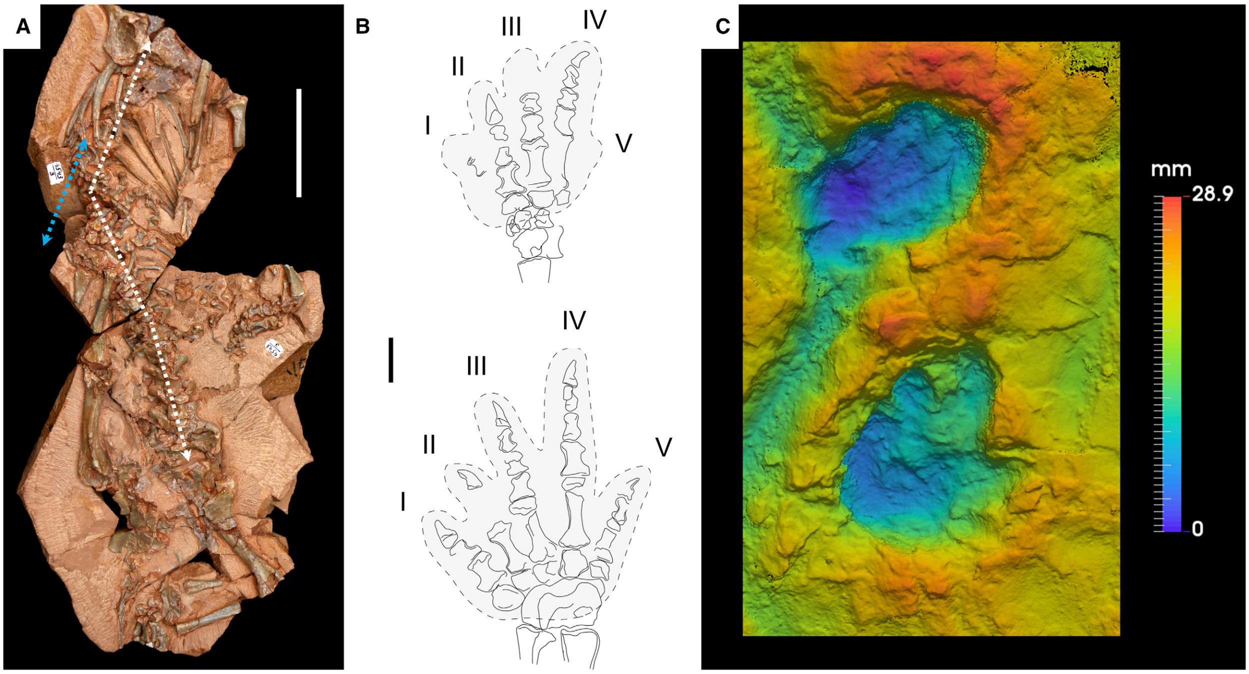

FIG. 9. Track–trackmaker correlation. A, PIN 4543/3, complete skeleton of *Macroleter poezicus*, dorsal view; white dashed line = glenoacetabular distance; blue dashed line = pes length. B, reconstruction of a right pes–manus couple (ventral side) of *Macroleter poezicus*, based on PIN 4543/3, reflected and superimposed on a right pes–manus couple of *Pachypes ollieri* comb. nov. (in grey) to facilitate comparison. C, false-colour depth map of a right pes–manus couple of *P. ollieri* comb. nov. Roman numerals indicate the digit number for both tracks and skeletons. Scale bars represent: 5 cm (A); 1 cm (B).

that of the pes: 2-3-4-4-?2 (Fig. 9B). The distal carpals are robust and angular, so that the carpus structure is compact.

Emeroleter presents a pedal phalangeal formula of 2-3-4-5-3. As in pareiasaurs and *Macroleter*, the astragalus and the calcaneum are fused in adults and the pes is considerably larger than the manus (Tsuji *et al.* 2012). The metapodium and acropodium elements are slenderer than in *Macroleter* and therefore differ from those observed in pareiasaurs. Metapodial elements are longer and slenderer than the phalanges. The manus probably has the same number of phalanges as the pes (Tsuji *et al.* 2012).

The hind limb bones of *Emeroleter* and *Macroleter* are slenderer and more elongate than in *Rhipaeosaurus*, while the front limbs of *Macroleter* are quite robust (Fig. 9A). Also, the vertebral column of *Emeroleter* and *Macroleter* (Fig. 9A) is longer than in *Rhipaeosaurus*, compared to the total body length. The glenoacetabular length/pes length ratio of *Macroleter* is 4.6 (Fig. 9A), which is close to the average value of 4.9 for calculated body length/foot length ratio measured from the trackways of *P. ollieri* comb. nov. (Table 3), whereas *Emeroleter* and *Rhipaeosaurus* have lower ratios (3.54 and 3.65, respectively). The ectaxonic pes of *Rhipaeosaurus*, *Macroleter* and *Emeroleter* is consistent with *P. ollieri* comb. nov. The phalangeal formula of *Macroleter* (2-3-4-4-2) is more consistent with the manus digit imprint proportions of *P. ollieri* comb. nov. than that of *Emeroleter* (Fig. 9B). The thick, overlapping metatarsals and metacarpals, increasing in length and decreasing in thickness between digits I–IV, and the compact structure of the tarsus and carpus observed in *Rhipaeosaurus* and *Macroleter* are consistent with *P. ollieri* comb. nov., because the digit imprints are separated only distally, and the medial part of the footprints is the most deeply impressed (Fig. 9C). The pes size, the relative length of pes digit V, the more robust fore limb and the elongated limbs of *Macroleter* are also consistent with *P. ollieri* comb. nov., because of the digit proportions of the pes imprints, the very high SLp/FL and WPp/FL ratios and the more deeply impressed manus imprints (Fig. 9; Tables 1, 3). Also, the stratigraphic distribution of *Macroleter* (Roadian–Wordian; e.g. Sennikov & Golubev 2017) and *Rhipaeosaurus* (Roadian; e.g. Sennikov & Golubev 2017) matches better the stratigraphic distribution of *P. ollieri* comb. nov. (Artinskian–Capitanian; e.g. Gand & Durand 2006; Michel *et al.* 2015) than that of *Emeroleter* (early Wuchiapingian) (Tsuji *et al.* 2012; Sennikov & Golubev 2017). In addition, *P. ollieri* comb. nov. and the earliest known nycteroleter are known from laterally-correlated units (San Angelo Formation, Texas, USA; and

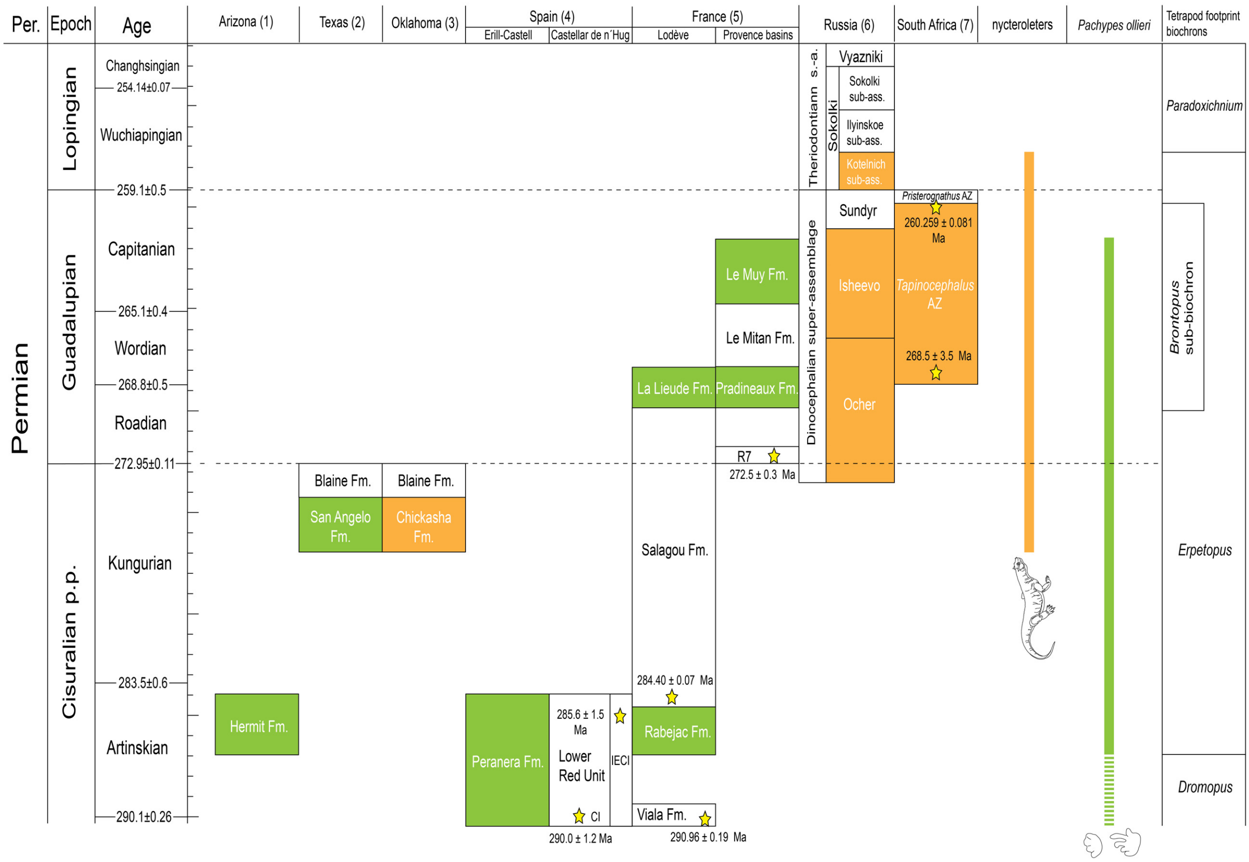

FIG. 10. Chronostratigraphic scheme showing the occurrences of nycteroleter pareiasauromorph tracks (*Pachypes ollieri* comb. nov., in green) and skeletons (in orange). The chronostratigraphic chart is based on the International Chronostratigraphic Chart v 2018/8 (Cohen *et al.* 2013). Stars refer to the radiometric ages. (1) Arizona, Hermit Formation (Haubold *et al.* 1995). (2) Texas, San Angelo Formation (Lucas & Hunt 2005). (3) Oklahoma, Chickasha Formation (Reisz & Laurin 2001; Lucas 2002). (4) Spain, Catalan Pyrenees, Peranera Formation (Voigt & Haubold 2015; Mujal *et al.* 2016, 2018); radiometric ages from Pereira *et al.* 2014 and stratigraphy of the volcanic units from Gisbert (1981); CI, Castellar de n'Hug Ignimbrite; IECI, Ignimbrite Enclave of Castellar de n'Hug. (5) France, Rabejac Formation (Heyler & Gand 2000) and Pradineaux and Le Muy formations (Demathieu *et al.* 1992; Gand *et al.* 1995); radiometric ages from Zheng *et al.* 1992 and Michel *et al.* 2015; R7, Rhyolite 7. (6) Russia, Orcher, Isheevo and Sokolki assemblages (Tsuji *et al.* 2012; Sennikov & Golubev 2017). (7) South Africa, *Tapinocephalus* AZ (Cisneros & Tsuji 2009); radiometric ages from Lanci *et al.* 2013 and Day *et al.* 2015. Tetrapod footprint biochrons based on Schneider *et al.* 2020. Fm., formation; Ma, million years ago; AZ, assemblage zone.

lower part of the Chickasha Formation, Oklahoma, USA; Lucas & Hunt 2005; Lucas 2018). Therefore, we attribute *P. ollieri* comb. nov. to nycteroleter pareiasauromorphs such as *Macroleter*, although presently we cannot exclude forms such as *Rhipaeosaurus* as producers of some of the analysed tetrapod footprint material. Because of the slender and elongated pes structure and the same stratigraphic distribution (lower Wuchiapingian), *Emeroleter* is instead a possible producer of *Pachypes loxodactylus*.

TRACK BIOSTRATIGRAPHY

The ichnotaxonomic revision of tracks here assigned to *P. ollieri* comb. nov. substantially extends the stratigraphic record of the ichnogenus, previously known exclusively from units of Guadalupian or Lopingian age. In fact, *P. dolomiticus* and *Pachypes* isp. are currently known from the upper Wuchiapingian and lower Changhsingian Arenaria di Val Gardena Formation of Italy, the Ikakern Formation of Morocco and the Moradi Formation of Niger (Valentini *et al.* 2009; Voigt *et al.* 2010; Smith *et al.* 2015; Bernardi *et al.* 2017; Marchetti *et al.* 2019*a*). The T2 member of the Ikakern Formation of Morocco and the Moradi Formation of Niger are considered to be either Guadalupian or Lopingian because of the tetrapod fauna (Olroyd & Sidor 2017). Nevertheless, the occurrence of gorgonopsid remains in the Moradi Formation and the occurrence of therocephalian tracks in the T2 member may be in agreement with a post-dinocephalian extinction

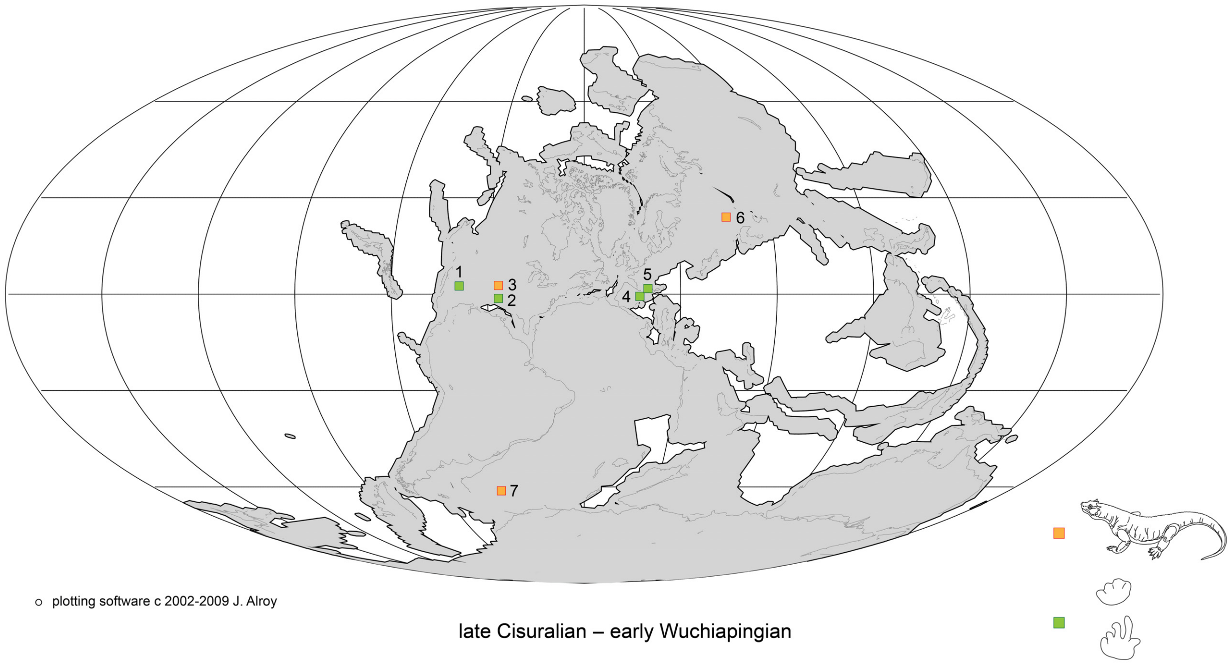

FIG. 11. Palaeogeographical scheme showing the occurrences of nycteroleter pareiasauromorph tracks (*Pachypes ollieri* comb. nov., in green) and skeletons (in orange). The numbers are the fossil localities of Fig. 10. Map from Alroy (2013), modified.

age (i.e. late Capitanian to Lopingian) for these two units (Schneider *et al.* 2020). *Pachypes loxodactylus* is known from the Cornockle and Locharbriggs formations of Scotland, considered to be upper Capitanian to Lopingian from tetrapod track biostratigraphy (Marchetti *et al.* 2019*b*). Other possible records of *Pachypes* are from the Cornberg Formation and the Mammendorf locality of Germany (upper Capitanian to lower Wuchiapingian), the Poldarsa Formation (lower Lopingian) and the Vyatkian horizon (upper Changhsingian) of Russia and the Upper Red Unit (Unidad Roja Superior; Guadalupian–Lopingian) of the Catalan Pyrenees (Gubin *et al.* 2003; Surkov *et al.* 2007; Buchwitz *et al.* 2017; Marchetti *et al.* 2019*a*; Mujal *et al.* 2017). All these units are considered to be Guadalupian or Lopingian in age (Schneider *et al.* 2020). Therefore, these occurrences belong to the late *Erpetopus* biochron (mostly or entirely post-*Brontopus* sub-biochron) and to the *Paradoxichnium* biochron (Voigt & Lucas 2018; Marchetti *et al.* 2019*b*). Conversely, the stratigraphic range of *P. ollieri* comb. nov. is from the Artinskian (represented by the Hermit Formation, Arizona; the Rabejac Formation, France; and the Peranera Formation, Spain) to the lower Capitanian (Le Muy Formation; France), therefore it belongs to the older part of the *Erpetopus* biochron and to the *Brontopus* sub-biochron (Voigt & Lucas 2018; Marchetti *et al.* 2019*b*; Schneider *et al.* 2020) (Fig. 10). The FAD (first appearance datum) of *P. ollieri* comb. nov. is in the upper Artinskian of the Rabejac Formation of France, age constrained by radiometric ages (Schneider *et al.* 2006; Michel *et al.* 2015). This is in agreement with the late Artinskian age of the Hermit Formation of Arizona inferred from marine biostratigraphy of laterally-correlated and bracketing units (lower Leonardian; Blakey 1990; Marchetti *et al.* 2020*a*) and the Artinskian age of the Peranera Formation of Spain inferred from radiometric ages from the laterally-correlated Lower Red Unit and Ignimbrite Enclave of Castellar de n'Hug (Gisbert 1981; Pereira *et al.* 2014; Mujal *et al.* 2018). Further age constraints on the Peranera Formation are provided by Voigt & Haubold (2015), Mujal *et al.* (2016) and Mujal *et al.* (2018) through biostratigraphy and lithostratigraphic correlation.

Importantly, the first occurrence of *Pachypes* coincides with (or even slightly precedes) the beginning of the *Erpetopus* biochron, in agreement with the reptile radiation of parareptile and eureptile captorhinomorph tracks that began during the Artinskian (Marchetti *et al.* 2019*d*).

PAREIASAUROMORPHA OCCURRENCES

The Pareiasauromorpha is the most diverse and abundant parareptile group of the Guadalupian and Lopingian. The majority of the Guadalupian occurrences are from South Africa and Russia, and a form is also known from Brazil

(Lucas 2006, 2018). The South African taxa are large pareiasaurs (e.g. *Bradysaurus*, *Embrithosaurus*, *Nochelosaurus*; Day *et al.* 2015; with the exception of the indeterminate nycteroleter described by Cisneros & Tsuji 2009). *Provelosaurus americanus* from Brazil is considered a dwarf form (Araújo 1985; Cisneros *et al.* 2005) closely related to the Lopingian pumiliopareiasaurs *Anthodon*, *Nanoparia* and *Pumiliopareia* (Lee 1997). Otherwise, the eastern European forms comprise only smaller nycteroleters (*Bashkyroleter*, *Macroleter*, *Nycteroleter*, *Rhipaeosaurus* and *Tokosaurus*; Tsuji *et al.* 2012; Sennikov & Golubev 2017). Conversely, a single occurrence is known from the Cisuralian, represented by an indeterminate nycteroleter from the Chickasha Formation of Oklahoma (Reisz & Laurin 2001), initially considered to be Guadalupian in age (Reisz & Laurin 2002; Benton 2012) but later constrained by marine biostratigraphy to the Kungurian (Lucas 2002, 2006, 2018; Lucas & Golubev 2019). The Guadalupian (Roadian) age for the Chickasha Formation was based on the correlation with the Russian Mezen tetrapod fauna (Benton 2012; Olroyd & Sidor 2017). However, the only taxon in common, *Macroleter*, is now considered to be an indeterminate nycteroleter (Tsuji 2006). Also, the Chickasha Formation does not include therapsid forms, while they are abundant in the Mezen fauna (Sennikov & Golubev 2017). Moreover, the tetrapod remains come from the lower part of the Chickasha Formation, which is laterally-correlated with the San Angelo Formation, constrained by marine biostratigraphy to the upper Leonardian (=Kungurian; e.g. Lucas & Golubev 2019). So, a Kungurian age for the lower Chickasha and San Angelo formations is the best supported age assignment, and is followed here.

The ichnotaxonomic revision and anatomy-consistent attribution of *P. ollieri* comb. nov. to nycteroleter pareiasauromorphs (Fig. 9) allows a substantial extension of the stratigraphic and palaeogeographic distribution of Pareiasauromorpha (Figs 10, 11). This ichnotaxon occurs in the Cisuralian of North America and Europe (Hermit and San Angelo formations of the USA, Peranera Formation of Spain and Rabejac Formation of France) and in the Guadalupian of Europe, from the Pradineaux, Le Muy and La Lieude formations of France. Therefore, this is the first Guadalupian evidence of Pareiasauromopha in the low palaeolatitudes of Pangaea (western Europe). Notably, the Cisuralian record of *P. ollieri* comb. nov. includes a Kungurian record from Texas (San Angelo Formation; Lucas & Golubev 2019) that matches the skeletal record from a laterally-correlated formation (lower Chickasha Formation of Oklahoma; Reisz & Laurin 2001). It is also remarkable that the track record from southern France and the Catalan Pyrenees constitutes the only evidence of Pareiasauromorpha in the Cisuralian of Europe (Lucas 2018). The track records from Arizona, southern France and the Catalan Pyrenees, of Artinskian age (Pereira *et al.* 2014; Michel *et al.* 2015; Mujal *et al.* 2018; Schneider *et al.* 2020) represent the oldest worldwide evidence of Pareiasauromorpha, at least 10 myr before the earliest known skeletal record (Lucas 2018) (Fig. 10).

CONCLUSION

The revision of several potential pareiasauromorph tracks from the Cisuralian and Lopingian of USA and western Europe allows, for the first time, the recognition of the pareiasauromorph ichnogenus *Pachypes* in units older than late Capitanian (Valentini *et al.* 2009; Voigt & Lucas 2018). We propose the new combination *P. ollieri* (Ellenberger, 1983*a*) for this material. A track–trackmaker correlation, based on synapomorphy and stratigraphy, suggests nycteroleter pareiasauromorphs similar to *Macroleter* as the most likely producers of this ichnotaxon (Tsuji *et al.* 2012). We recognize the earliest known occurrence of *Pachype*s in Artinskian units of Arizona (Hermit Formation), Spain (Peranera Formation, Lower Red Unit) and France (Rabejac Formation). This suggests a fast and palaeobiogeographically-extensive radiation of the trackmakers, which coincides with the late Artinkian reptile radiation known from both the track and the skeletal records (Marchetti *et al.* 2019*d*; and references within). The skeletal evidence of Pareiasauromorpha suggests a late Kungurian origin of the group in North America (Reisz & Laurin 2001, 2002; Lucas 2002), whereas the largest part of the skeletal occurrences comes from the Guadalupian and Lopingian of South Africa and Russia (Lee 1997; Tsuji *et al.* 2012; Sennikov & Golubev 2017). Therefore, the earliest occurrences of Pareiasauromorpha footprints precede by at least 10 myr the earliest known occurrence from the skeletal record. Moreover, the tetrapod footprints highlight for the first time Cisuralian and Guadalupian occurrences of Pareiasauromorpha in western Europe, currently unknown from the skeletal record (Lucas 2018).

Acknowledgements. For access to collections/sites and other assistance during the study we warmly thank: Bernard Mourgues of the Société de Protection de la Nature Languedoc Roussillon, Stéphane Fouché of the Musée Fleury, Laurent Marivaux, Pierre-Olivier Antoine, Maeva Orliac, Monique Vianey-Liaud and Suzanne Jiquel of the Institut des Sciences de l'Évolution de Montpellier, University of Montpellier, Nour-Eddine Jalil of the Muséum National d'Histoire Naturelle, Anne Joncheray of the Musée Archéologique de Saint-Raphaël, Emmanuel Fara and Jerome Thomas of the University of Dijon, Joanne Turner and Fiona Wilson from the Dumfries Museum and Camera Obscura, Maria Rita Palombo and Linda Riti of the Palaeontological Museum of the 'La Sapienza' University of Rome, Robert Reisz of the University of Toronto at Mississauga and Valeriy V. Bulanov, Valeriy K. Golubev, and Yuri M. Gubin of the Paleontological Institute of

Moscow. We extend our thanks to Colleen Hyde, Kim Besom and Klara Widrig, Grand Canyon National Park, for their assistance obtaining photographs of the track specimen from the Hermit Shale in the park collection. We acknowledge Sergio Llàcer, Institut Català de Paleontologia (ICP), for his assistance in the creation of several 3D photogrammetric models. We would like to thank Lara Sciscio, Massimo Bernardi, Marc J. Van den Brandt and an anonymous reviewer for useful suggestions, as well as the editors of the journal. LM was supported by the Alexander von Humboldt Foundation for his postdoc at the Urweltmuseum Geoskop of Thallichtenberg. LM is funded by the Bundesministerium für Bildung und Forschung (BMBF) for the BROMACKER project 2020. EM received funding for collection visits from: the SYNTHESYS Project (FR-TAF-3621, FR-TAF-4808; http://www.synthesys.info) which is financed by European Community Research Infrastructure Action under the FP7 'Capacities' Program, Secretaria d'Universitats i de Recerca (Departament d'Economia i Coneixement, Generalitat de Catalunya; exp. num. 2013 CTP 00013) and the Erasmus+ program (2016) of the Universitat Autònoma de Barcelona. JF is supported by the Spanish Agencia Estatal de Investigación and the European Regional Development Fund of the European Union (AEI/FEDER EU, project CGL2017-82654-P). JF is member of the consolidated research group 2017 SGR 86 GRC of the Generalitat de Catalunya. We acknowledge support from the CERCA programme (ICP) from the Generalitat de Catalunya, and the project 'Evolució dels ecosistemes durant la transició Paleozoic–Mesozoic a Catalunya' (ref. CLT009/18/00066), financially supported by the Departament de Cultura (Generalitat de Catalunya).

DATA ARCHIVING STATEMENT

Data (including DOIs for image data) for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.h9w0vt4g3

Editor. Kenneth Angielczyk

REFERENCES

ALROY, J. 2013. Online paleogeographic map generator. http://paleodb.org/?a=mapForm

ARAÚJO, D. C. F. 1985. Sobre *Pareiasaurus americanus* sp. nov., do Permiano Superior do Rio Grande do Sul, Brasil. I – Diagnose específica. *Anais da Academia Brasileira de Ciências*, **57**, 63–66.

BENTON, M. J. 2012. No gap in the Middle Permian record of terrestrial vertebrates. *Geology*, **40** (4), 339–342.

BERNARDI, M., PETTI, F. M., KUSTATSCHER, E., FRANZ, M., HARTKOPF-FRÖDER, C., LABANDEIRA, C. C., WAPPLER, T., VAN KONIJNENBURG-VAN CITTERT, J. H. A., PEECOCK, B. R. and ANGIELCZYK, K. D. 2017. Late Permian (Lopingian) terrestrial ecosystems: a global comparison with new data from the low-latitude Bletterbach Biota. *Earth-Science Reviews*, **175**, 18–43.

BLAKEY, R. C. 1990. Stratigraphy and geologic history of Pennsylvanian and Permian rocks, Mogollon Rim region, central Arizona and vicinity. *Geological Society of America Bulletin*, **102** (9), 1189–1217.

BUCHWITZ, M., LUTHARDT, L., MARCHETTI, L., TROSTHEIDE, F., VOIGT, S. and SCHNEIDER, J. W. 2017. A Middle to Late Permian tetrapod tracksite from northern Germany. *In* BORDY, E. (ed.) *2nd conference of continental ichnology, Nuy Valley, Western Cape, South Africa, 1st–4th October 2017*. Abstract Book, 15 pp.

CISNEROS, J. C. and TSUJI, L. A. 2009. Nycteroleter affinities of a Permian parareptile from the South African Karoo Basin. *Acta Palaeontologica Polonica*, **54** (1), 165–169.

—— ABDALA, F. and MALABARBA, M. C. 2005. Pareiasaurids from the Rio do Rasto Formation, southern Brazil: biostratigraphic implications for Permian faunas of the Paraná Basin. *Revista Brasiliera de Paleontologia*, **8**, 13–24.

COHEN, K. M., FINNEY, S. C., GIBBARD, P. L. and FAN, J.-X. 2013. Updated. The ICS International Chronostratigraphic Chart. *Episodes*, **36**, 199–204.

CONTI, M. A., LEONARDI, G., MARIOTTI, N. and NICOSIA, U. 1977. Tetrapod footprints of the Val Gardena Sandstone (North Italy). Their paleontological, stratigraphic and paleoenvironmental meaning. *Palaeontographia Italica*, **70**, 1–91.

DALLA VECCHIA, F. M., PONTON, M. and MUSCIO, G. 2012. Two new ichnosites from the Permo-Triassic of Carnic Alps (Friuli Venezia Giulia, NE Italy). *Gortania*, **34**, 41–50.

DAY, M. O., RAMEZANI, J., BOWRING, S. A., SADLER, P. M., ERWIN, D. H., ABDALA, F. and RUBIDGE, B. S. 2015. When and how did the terrestrial mid-Permian mass extinction occur? Evidence from the tetrapod record of the Karoo Basin, South Africa. *Proceedings of the Royal Society B*, **282**, 1–8.

DELAGE, A. 1912. *Empreintes de grands pieds de quadrupèdes de l'Hérault*. Mémoire de l'Académie des Sciences & Lettres, Montpellier.

DEMATHIEU, G., GAND, G. and TOUTIN-MORIN, N. 1992. La palichnofaune des bassins permiens provençaux. *Geobios*, **25**, 19–54.

DUDGEON, P. 1878. Note on a new fossil footprint from the Permian sandstone of Dumfriesshire. *Proceedings of the Royal Society of Edinburgh*, **9**, 154–155.

EFREMOV, J. A. 1940. New discoveries of Permian terrestrial vertebrates in Bashkiria and the Tchkalov Province. *Comptes Rendus (Doklady)*, **27**, 412–415.

ELLENBERGER, P. 1983*a*. Sur l'intérêt paléontologique de la dalle à pistes de la Lieude (commune de Mérifons, Hérault, France). *Société de la Protection de la Nature du Languedoc Roussillon*, **1**, 11–20.

—— 1983*b*. Sur la zonation ichnologique du Permien moyen (Saxonien) du bassin de Lodève (Hérault). *Comptes-Rendus des Séances de L'Académie des Sciences. Série 2, Mécanique-Physique, Chimie, Sciences de L'Univers, Sciences de la Terre*, **297**, 553–558.

GAND, G. and DURAND, M. 2006. Tetrapod footprint ichno-associations from French Permian basins. Comparisons with other Euramerican ichnofaunas. *Geological Society, London, Special Publications*, **265**, 157–177.

—— DEMATHIEU, G. and BALLESTRA, F. 1995. La palichnofaune de vertébrés tétrapodes du Permien supérieur de l'Esterel (Provence, France). *Palaeontographica Abteilung A*, **235**, 97–139.

—— GARRIC, J., DEMATHIEU, G. and ELLENBERGER, P. 2000. La palichnofaune de vertébrés tétrapodes du Permien supérieur du bassin de Lodève (Languedoc-France). *Palaeovertebrata*, **29**, 1–82.

GISBERT, J. 1981. Estudio geológico-petrológico del Estefaniense-Pérmico de la Sierra del Cadí (Pirineo de Lérida): Diagénesis y sedimentología. PhD thesis, Universidad de Zaragoza, Zaragoza, Spain.

GUBIN, Y. M., GOLUBEV, V. K., BULANOV, V. V. and PETUCHOV, S. V. 2003. Pareiasaurian tracks from the Upper Permian of Eastern Europe. *Paleontological Journal*, **37**, 514–523.

HAUBOLD, H. 1970. Versuch einer Revision der Amphibien-Fährten des Karbon und Perm. *Freiberger Forschungshefte, Hefte C*, **260**, 83–109.

—— HUNT, A. P., LUCAS, S. G. and LOCKLEY, M. G. 1995. Wolfcampian (Early Permian) vertebrate tracks from Arizona and New Mexico. *New Mexico Museum of Natural History & Science Bulletin*, **6**, 135–165.

HEYLER, D. and GAND, G. 2000. Pistes et traces du Permien du sud de la France dans les collections du Muséum National d'Historie Naturelle (Paris). *Bulletin de la Société d'Histoire Naturelle de Autun*, **176**, 7–50.

ICZN. 1999. *International code of zoological nomenclature*. 4th edn. International Trust for Zoological Nomenclature.

IVAKHNENKO, M. F. 1997. New Late Permian nycteroleterids from Eastern Europe. *Paleontological Journal*, **31**, 552–558.

LANCI, L., TOHYERR, E., WILSON, A. and FLINT, S. 2013. Upper Permian magnetic stratigraphy of the lower Beaufort group, Karoo basin. *Earth & Planetary Science Letters*, **375**, 123–134.

LEE, M. S. 1997. Pareiasaur phylogeny and the origin of turtles. *Zoological Journal of the Linnean Society*, **120**, 197–280.

LEONARDI, P., CONTI, M. A., LEONARDI, G., MARIOTTI, N. and NICOSIA, U. 1975. *Pachypes dolomiticus* n. gen. n.sp.; Pareiasaur footprint from the 'Val Gardena Sandstone'(Middle Permian) in the western Dolomites (N. Italy). *Atti Della Academia Nazionale dei Lincei*, **57**, 221–232.

LUCAS, S. G. 2002. Discussion and reply: The reptile *Macroleter*: first vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia – Discussion. *Geological Society of America Bulletin*, **114**, 1174–1175.

—— 2006. Global Permian tetrapod biostratigraphy and biochronology. 65–93. *In* LUCAS, S. G., CASSINIS, G. and SCHNEIDER, J. W. (eds). *Non-marine Permian biostratigraphy and biochronology*. Geological Society of London, Special Publications, **265**.

—— 2018. Permian tetrapod biochronology, correlation and evolutionary events. 405–444. *In* LUCAS, S. G. and SHEN, S. Z. (eds). *The Permian timescale*. Geological Society of London, Special Publications, **450**.

—— and GOLUBEV, V. K. 2019. Age and duration of Olson's gap, a global hiatus in the Permian tetrapod fossil record. *Permophiles*, **67**, 20–23.

—— and HUNT, A. P. 2005. Permian tetrapod tracks from Texas. *New Mexico Museum of Natural History & Science Bulletin*, **30**, 202–206.

—— KOLLAR, A. D., BERMAN, D. S. and HENRICI, A. C. 2016. Pelycosaurian grade (Amniota: Synapsida) footprints from the lower Permian Dunkard Group of Pennsylvania and West Virginia. *Annals of Carnegie Museum*, **83**, 287–294.

MARCHETTI, L., MUJAL, E. and BERNARDI, M. 2017*a*. An unusual *Amphisauropus* trackway and its implication for understanding seymouriamorph locomotion. *Lethaia*, **50**, 162–174.

—— BELVEDERE, M. and MIETTO, P. 2017*b*. Lopingian tetrapod footprints in the Venetian Prealps (Italy): new discoveries in a largely incomplete panorama. *Acta Palaeontologica Polonica*, **62**, 801–817.

—— VOIGT, S. and KLEIN, H. 2019*a*. Revision of Late Permian tetrapod tracks from the Dolomites (Trentino-Alto Adige, Italy). *Historical Biology*, **31**, 748–783.

—— —— and LUCAS S. G. 2019*b*. An anatomy-based study of the Lopingian eolian tracks of Germany and Scotland reveals the first evidence of the end-Guadalupian mass extinction at low paleolatitudes of Pangea. *Gondwana Research*, **73**, 32–53.

—— BELVEDERE, M., VOIGT, S., KLEIN, H., CASTANERA, D., DÍAZ-MARTÍNEZ, I., MARTY, D., XING, L., FEOLA, S., MELCHOR, R. N. and FARLOW, J. O. 2019*c*. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. *Earth-Science Reviews*, **193**, 109–145.

—— VOIGT, S., LUCAS, S. G., FRANCISCHINI, H., DENTZIEN-DIAS, P., SACCHI, R., MANGIACOTTI, M., SCALI, S., GAZZOLA, A., RONCHI, A. and MILLHOUSE, A. 2019*d*. Tetrapod ichnotaxonomy in eolian paleoenvironments (Coconino and De Chelly formations, Arizona) and late Cisuralian (Permian) sauropsid radiation. *Earth-Science Reviews*, **190**, 148–170.

—— KLEIN, H., BUCHWITZ, M., RONCHI, A., SMITH, R. M., DE KLERK, W. J., SCISCIO, L. and GROENEWALD, G. H. 2019e. Permian-Triassic vertebrate footprints from South Africa: Ichnotaxonomy, producers and biostratigraphy through two major faunal crises. *Gondwana Research*, **72**, 139–168.

—— FRANCISCHINI, H., LUCAS, S. G., VOIGT, S., HUNT, A. P. and SANTUCCI, V. L. 2020*a*. Paleozoic vertebrate ichnology of Grand Canyon National Park. 333–379. *In* SANTUCCI, V. L. and TWEET, J. S. (eds). *Grand Canyon National Park: Centennial paleontological resource inventory (non-sensitive version)*. Natural Resource Report NPS/GRCA/NRR—2020/2103. National Park Service, Fort Collins, CO.

—— VOIGT, S., MUJAL, E., LUCAS, S. G., FRANCISCHINI, H., FORTUNY, J. and SANTUCCI, V. L. 2020*b*. Project: Extending the footprint record of Pareiasauromorpha to the Cisuralian: earlier appearance and wider palaeobiogeography of the group. *MorphoSource*. https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/1085

—— —— —— —— —— —— —— 2020*c*. Data from: Extending the footprint record of Pareiasauromorpha to the Cisuralian: earlier appearance and wider palaeobiogeography of the group. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.h9w0vt4g3

MICHEL, L. A., TABOR, N. J., MONTAÑEZ, I. P., SCHMITZ, M. and DAVYDOV, V. I. 2015. Chronostratigraphy and paleoclimatology of the Lodève Basin, France: evidence for a Pan-Tropical aridification event across the Carboniferous-Permian Boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **430**, 118–131.

MUJAL, E., FORTUNY, J., OMS, O., BOLET, A., GALOBART, À. and ANADÓN, P. 2016. Palaeoenvironmental reconstruction and early Permian ichnoassemblage from the NE Iberian Peninsula (Pyrenean Basin). *Geological Magazine*, **153**, 578–600.

—— —— PÉREZ-CANO, J., DINARÈS-TURELL, J., IBÁÑEZ-INSA, J., OMS, O., VILA, I., BOLET, A. and ANADÓN, P. 2017. Integrated multi-stratigraphic study of the Coll de Terrers late Permian-Early Triassic continental succession from the Catalan Pyrenees (NE Iberian Peninsula): a geologic reference record for equatorial Pangaea. *Global & Planetary Change*, **159**, 46–60.

—— —— MARMI, J., DINARÈS-TURELL, J., BOLET, A. and OMS, O. 2018. Aridification across the Carboniferous-Permian transition in central equatorial Pangea: the Catalan Pyrenean succession (NE Iberian Peninsula). *Sedimentary Geology*, **363**, 48–68.

—— MARCHETTI, L., SCHOCH, R. R. and FORTUNY, J. 2020. Upper Paleozoic to Lower Mesozoic tetrapod ichnology revisited: photogrammetry and relative depth pattern inferences on functional prevalence of autopodia. *Frontiers in Earth Science*, **8**, 248.

OLROYD, S. L. and SIDOR, C. A. 2017. A review of the Guadalupian (middle Permian) global tetrapod fossil record. *Earth-Science Reviews*, **171**, 583–597.

PEREIRA, M. F., CASTRO, A., CHICHORRO, M., FERNÁNDEZ, C., DÍAZ-ALVARADO, J., MARTÍ, J. and RODRÍGUEZ, C. 2014. Chronological link between deep-seated processes in magma chambers and eruptions: Permo-Carboniferous magmatism in the core of Pangaea (Southern Pyrenees). *Gondwana Research*, **25**, 290–308.

REISZ, R. R. and LAURIN, M. 2001. The reptile *Macroleter*: first vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia. *Geological Society of America Bulletin*, **113**, 1229–1233.

—— —— 2002. Discussion and reply: The reptile *Macroleter*: first vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia – Reply. *Geological Society of America Bulletin*, **114**, 1176–1177.

SCHNEIDER, J. W., KÖRNER, F., ROSCHER, M. and KRONER, U. 2006. Permian climate development in the northern peri-Tethys area—the Lodève basin, French Massif Central, compared in a European and global context. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **240** (1–2), 161–183.

—— LUCAS, S. G., SCHOLZE, F., VOIGT, S., MARCHETTI, L., KLEIN, H., OPLUŠTIL, S., WERNEBURG, R., GOLUBEV, V. K., BARRICK, J. E., NEMYROVSKA, T., RONCHI, A., DAY, M. O., SILANTIEV, V. V., RÖSSLER, R., SABER, H., LINNEMANN, U., ZHARINOVA, V. and SHEN, S. 2020. Late Paleozoic–early Mesozoic continental biostratigraphy — links to the Standard Global Chronostratigraphic Scale. *Palaeoworld*, **29**, 186–238.

SENNIKOV, A. G. and GOLUBEV, V. K. 2017. Sequence of Permian tetrapod faunas of Eastern Europe and the Permian-Triassic ecological crisis. *Paleontological Journal*, **51**, 600–611.

SMITH, R. M. H., SIDOR, C. A., TABOR, N. J. and STEYER, J. S. 2015. Sedimentology and vertebrate taphonomy of the Moradi Formation of northern Niger: a Permian wet desert in the tropics of Pangaea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **440**, 128–141.

SURKOV, M. V., BENTON, M. J., TWITCHETT, R. J., TVERDOKHLEBOV, V. P. and NEWELL, A. J. 2007. First occurrence of footprints of large therapsids from the Upper Permian of European Russia. *Palaeontology*, **50**, 641–652.

TSUJI, L. A. 2006. Cranial anatomy and phylogenetic affinities of the Permian parareptile *Macroleter poezicus*. *Journal of Vertebrate Paleontology*, **26** (4), 849–865.

—— 2013. Anatomy, cranial ontogeny, and phylogenetic relationships of the pareiasaur *Deltavjatia rossicus* from the Late Permian of central Russia. *Earth & Environmental Science Transactions of the Royal Society of Edinburgh*, **104**, 1–42.

—— and MÜLLER, J. 2009. Assembling the history of the Parareptilia: phylogeny, diversification, and a new definition of the clade. *Fossil Record*, **12**, 71–81.

—— —— and REISZ R. R. 2012. Anatomy of *Emeroleter levis* and the phylogeny of the nycteroleter parareptiles. *Journal of Vertebrate Paleontology*, **32**, 45–67.

TURNER, M. L., TSUJI, L. A., IDE, O. and SIDOR, C. A. 2015. The vertebrate fauna of the upper Permian of Niger—IX. The appendicular skeleton of *Bunostegos akokanensis* (Parareptilia: Pareiasauria). *Journal of Vertebrate Paleontology*, **35** (6), e994746.

VALENTINI, M., CONTI, M. A. and NICOSIA, U. 2008. Linking tetrapod tracks to the biodynamics, paleobiogeography, and paleobiology of their trackmakers: *Pachypes dolomiticus* Leonardi et al., 1975, a case study. *Acta Geologica*, **83**, 237–246.

—— NICOSIA, U. and CONTI, M. A. 2009. A re-evaluation of *Pachypes*, a pareiasaurian track from the Late Permian. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **251**, 71–94.

VOIGT, S. 2005. Die tetrapodenichnofauna des kontinentalen Oberkarbon und Perm im Thüringer Wald: Ichnotaxonomie, paläoökologie und biostratigraphie. PhD thesis, Cuvillier Verlag, Göttingen, Germany.

—— and HAUBOLD, H. 2015. Permian tetrapod footprints from the Spanish Pyrenees. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **417**, 112–120.

—— and LUCAS, S. G. 2018. Outline of a Permian tetrapod footprint ichnostratigraphy. 387–404. *In* LUCAS, S. G. and SHEN, S. Z. (eds). *The Permian timescale*. Geological Society of London, Special Publications, **450**.

—— BERMAN, D. S. and HENRICI, A. C. 2007. First well-established track-trackmaker association of Paleozoic tetrapods based on *Ichniotherium* trackways and diadectid skeletons from the Lower Permian of Germany. *Journal of Vertebrate Paleontology*, **27**, 553–570.

—— HMINNA, A., SABER, H., SCHNEIDER, J. W. and KLEIN, H. 2010. Tetrapod footprints from the uppermost level of the Permian Ikakern Formation (Argana basin, western High Atlas, Morocco). *Journal of African Earth Sciences*, **57**, 470–478.

ZHENG, J. S., MERMET, J.-F., TOUTIN-MORIN, N., HANES, J., GONDOLO, A., MORIN, R. and FÉRAUD, G. 1992. Datation ^{40}Ar-^{39}Ar du magmatisme et de filons minéralisés permiens en Provence orientale France. *Geodinamica Acta*, **5**, 203–215.