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

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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.
track-trackmaker correlation with the possible pareiasauromorph producers, following the methodology of Voigt et al. (2007) and Marchetti et al. (2017a) 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. (2019c). The 3D models were uploaded to the digital repository MorphoSource (Marchetti et al. 2020b). 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, Musée 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-LI, Dalle Paleontologique de la Lieude, D8, Mérisons, France (45°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. 2019a). More occurrences are known from the Arenaria di Val Gardena Formation in the western Dolomites (Valentini et al. 2009; Marchetti et al. 2019a), in Veneto (Marchetti et al. 2017b) and Friuli (Dalla Vecchia et al. 2012).

Other ichnospecies. Pachypes loxodactylus (Dudgeon, 1878) after Marchetti et al. (2019b) and P. olliieri (Ellenberger, 1983a) 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), Corneckle and Locharbriggs formations of Scotland (Marchetti et al. 2019b). 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. 2019b) 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. 2020a; 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 | I L  | II L | III L | IV L  | V L  | div I–II | div II–III | div III–IV | div IV–V | div FL/FW |
|----------|----|-----|-----|-------|------|------|-------|-------|------|----------|------------|------------|----------|-----------|
| FS-LL 3  | 1.567666 | 1.02943 | 2.32225239 | 22713 | 24 | 34 | 78 |
| FS-LL 4  | 2.07868 | 1.1345 | 2.3192573547 | 48199 | 18 | 11 | 41 | 79 |
| FS-LL 9  | 2.56464 | 1.02455 | 2.71318283920 | 12199 | 9 | 24 | 64 |
| FS-LL 10 | 2.08563 | 1.33656 | 2.3212535506 | 2617 | 15 | 11 | 36 | 70 |
| FS-LL 15 | 1.56659 | 1.13138 | 2.21120273922 | 2714 | 7 | 31 | 79 |
| FS-LL 16 | 1.55649 | 1.13040 | 1.9121922313 | 1012 | 12 | 12 | 54 | 89 |
| MASR 13  | 1.56752 | 1.33244 | 2.11632 | 3821 | 17 | 12 | 22 |
| FS-SR 7  | 2.06355 | 1.12639 | 2.416202636 | 1514 | 16 | 14 | 30 | 74 |
| UD-MitG 15 | 1.54950 | 1.02033 | 2.41823 | 2730 | 21 | 16 | 16 | 24 | 86 |
| UD-MitG 20 | 1.55351 | 1.01930 | 2.81321 | 2537 | 11 | 39 | 24 |
| GRCA 3172 | 2.02726 | 1.01417 | 2.0711 | 1419 | 23 | 33 | 21 |
| FS-TB 1  | 2.09896 | 1.04565 | 2.22936 | 5060 | 32 | 22 | 14 | 19 | 44 | 99 |
| FS-MA B1 | 1.55036 | 1.42027 | 2.5118 | 2131 | 11 | 20 | 17 |
| FS-MA B2 | 2.03731 | 1.22029 | 1.86 | 1115 | 21 | 28 | 39 | 25 |
| UGKU 1973 | 2.05454 | 1.02541 | 2.21315 | 2639 | 19 | 23 | 34 | 27 | 98 |
| MF-NN 1  | 2.04741 | 1.12029 | 2.31320 | 2933 | 17 | 7 | 17 |
| UM LOD 96 | 1.55953 | 1.12541 | 2.31422 | 2937 | 17 | 33 | 10 |
| MNHN.F.LOD142 | 2.03536 | 1.01722 | 2.01116 | 1722 | 10 | 18 | 28 | 27 | 39 | 112 |
| MNHN.F.LOD143 | 2.54952 | 0.92238 | 2.21720 | 2833 | 15 | 7 | 0 | 26 | 45 | 78 |

**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  | 2.05964 | 0.93253 | 1.82026 | 3033 | 17 | 22 | 22 | 1.1 |
| FS-LL 4  | 2.06169 | 0.93256 | 1.91923 | 3131 | 18 | 15 | 22 | 14 | 51 | 102 | 1.3 |
| FS-LL 9  | 2.56365 | 1.13553 | 1.81619 | 2630 | 18 | 14 | 4 | 1.3 |
| FS-LL 10 | 2.06356 | 1.13553 | 1.81619 | 2630 | 18 | 14 | 4 | 1.3 |
| FS-LL 15 | 1.55557 | 1.03049 | 1.82324 | 2729 | 16 | 13 | 18 | 1.2 |
| FS-LL 16 | 1.54648 | 1.03040 | 1.51216 | 2139 | 21 | 18 | 31 | 100 | 1.2 |
| MASR 13  | 2.05252 | 1.03141 | 1.72324 | 2529 | 12 | 27 | 8 | 1.3 |
| FS-SR 7  | 1.04945 | 1.12939 | 1.71819 | 2024 | 21 | 27 | 8 | 1.3 |
| UD-MitG 15 | 1.53740 | 0.92331 | 1.61415 | 1719 | 13 | 14 | 30 | 1.3 |
| UD-MitG 20 | 2.04549 | 0.92537 | 1.81720 | 2221 | 27 | 12 | 25 | 1.2 |
| GRCA 3172 | 2.02228 | 0.81321 | 1.78910 | 1211 | 10 | 20 | 32 | 1.3 |
| FS-TB 1  | 1.55982 | 0.72959 | 2.02125 | 2932 | 23 | 30 | 26 | 1.7 |
| FS-MA B1 | 2.03846 | 0.82138 | 1.81317 | 2020 | 11 | 10 | 17 | 9 | 34 | 70 | 1.3 |
| FS-MA B3 | 2.05873 | 0.82852 | 2.12226 | 3330 | 14 | 26 | 18 |
| MF-NN 1  | 2.04343 | 1.02131 | 2.11620 | 2122 | 12 | 10 | 23 | 1.1 |
| UM LOD 96 | 2.04743 | 1.12143 | 2.21721 | 2730 | 5 | 18 | 12 | 1.3 |
| MNHN.F.LOD142 | 2.03535 | 1.01623 | 2.31618 | 1817 | 15 | 9 | 26 | 1.0 |
| MNHN.F.LOD143 | 2.54447 | 0.91933 | 2.32022 | 2312 | 15 | 11 | 31 | 32 | 88 | 1.1 |

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.
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 semi-plantigrade footprints of a quadrupedal, heteropod reptile, with tracks more deeply-pressed medially. It differs from temnospondyl and lepospondyl tracks such as *Batrachichnus*, *Limmopus* and *Mattheiichnus*, which have instead a tetradactyl manus. It differs from synapsid tracks such as *Brontopus*, *Capitosauroides*, *Dicynodontipus*, *Dimetropus* 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*, 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, 1983a) comb. nov.  
Figures 1–7, Tables 1–3

1983a *Paranomodontipus ollieri* Ellenberger, pp. 12–13, figs 2, 8.  
1983a *Theriopodiscus lieudensis* Ellenberger, p. 20, fig. 10.  
1983b *Eotheriopodiscus lenis* Ellenberger (*nomen nudum*), p. 557, pl. 1.13.  
1992 *Limmopus 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 olliorum* 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, 83.  
2016 undetermined tetrapod tracks; Mujal et al., fig. S4.

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

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**Table 3.** Ichnological parameters of vertebrate trackways.  

| Specimen | SLp | PLp | PAp | LPp | WPp | DIVp | SLm | 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  |
| FS-LL 4  | 601 | 403 | 96  | 291 | 273 | –10  | 615 | 418 | 97  | 304 | 282  | –1  | 85 | 362    | 7.7    | 3.5  |
| FS-LL 9  | 453 | 357 | 79  | 225 | 275 | –3   | 445 | 313 | 91  | 222 | 220  | –2  | 99 | 323    | 7.1    | 4.3  |
| FS-LL 10 | 440 | 368 | 73  | 219 | 286 | –2   | 494 | 337 | 94  | 246 | 226  | 0   | 88 | 307    | 5.2    | 3.4  |
| FS-LL 15 | 476 | 347 | 86  | 236 | 255 | –16  | 459 | 317 | 93  | 229 | 217  | 11  | 77 | 300    | 7.2    | 3.9  |
| FS-LL 16 | 578 | 384 | 97  | 288 | 253 | –3   | 593 | 354 | 113 | 296 | 195  | 2   | 60 | 343    | 10.3   | 4.5  |
| MASR 13  | 369 | 266 | 87  | 173 | 197 | –19  | 335 | 233 | 91  | 164 | 166  | 0   | 77 | 253    | 5.5    | 3.0  |
| UD-MitG  | 258 | 224 | 71  | 129 | 182 | 4    | 265 | 208 | 79  | 133 | 160  | –3  | 40 | 163    | 9.5    | 6.7  |
| MF-NN 1  | 522 | 489 | 182 | –4  | 529 | 487  | 206 | 4    | 76  | 77  | 253  | 0   | 24 | 121    | 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).
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, Lodeve Basin, Cisuralian, France: UM-

FIG. 1. *Pacificus 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.
are thick and end in rounded tips. The digit IV impressions are the longest; 19 mm long, it is about as long as wide, and clearly ectaxonic (digit IV–quadruped tetrapod). The pes imprint is about 30 mm long, and superimposed for most of their length, and they have rounded terminations. Manus impressions are slightly ectaxonic to mesaxonic with external digit impressions slightly shorter (especially digit V impression), but the lengths of digits II–IV are remarkably similar. The digit I impression 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 70–110° 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 (1983a), who introduced the ichnotaxon ‘Paranomodontipus’ olliero with a short description and drawings of five different trackways from the La Lieude site in southern France (La Lieude Formation; Ellenberger 1983a, 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 olliero-rum’ 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 paralecotypes (maximum grade 2.0 for both the pes and the manus tracks) (Figs 2, 3).
Another more digitigrade ichnotaxon, ‘Therioptodus lieudensis’, was based on a morphologically-similar trackway from the same locality (Ellenberger 1983a, fig. 10b). We consider ‘Therioptodus 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 1983a, pp. 12–13, 15, 17, 20), we think that the requirements of the ICZN (1999) were fulfilled, so these names are not nomina nudum as suggested by Gand et al. (2000). Indeed, as part of his description of P. ollieri, Ellenberger (1983a, 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, 1983a 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 Pachytes 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. 2019a). The overall morphology and proportions of ‘Paranomodontipus ollieri’ are consistent with Pachytes 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. 2019a).

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, 1983a) for the material previously assigned to ‘Paranomodontipus ollieri’ and its junior synonyms ‘Therioptodus lieudensis’ and ‘Lunaepes ollierorum’.

This ichnospecies differs also from Pachytes loxodactylus (Fig. 4C), described from the Lopingian Locharbriggs Formation of Scotland and revised by Marchetti et al. (2019b). 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. 2020a). 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
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 (1983b). 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
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*
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. 2020c) 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 *Tam- bachichnium* 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.
(1983a) hypothesized a small theropod 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 (1983b) attributed the material from 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. Amphiasaurus isp. Similarly, Demathieu et al. (1992) attributed the material from the Le Muy Formation to temnospondyl anamniotes, as indicated by the assignment to Limnonectes 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 mesaxyony. 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, Dolomites, and Karoopes) that show instead a deeper lateral part of the tracks (Marchetti et al. 2019; 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. olieri comb. nov. Therefore, an assignment to synapsid producers is excluded.

In contrast, the Lopingian material assigned to the ichnogenus Pachytypes has been consistently attributed to pareiasauran 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. 2019a, 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. Brachysaurus, Embiricosaurus, 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. olieri 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. olieri 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. olieri comb. nov. These taxa are generally known as nyceroleters and include: an indeterminate nyceroler from the Cisuralian of Texas (Chickasha Formation; Reisz & Laurin 2002; Tsuji 2006; Lucas 2018); Bashkiretether, Macroletether, Nycterolether, Rhipaeosaurus and Tokosaurus from the Guadalupian of Russia (Tsuji et al. 2012); Emerolether from the lower Lopingian of Russia (Ivakhnenko 1997); and an indeterminate nyceroler from the upper Guadalupian of South Africa (Cisneros & Tsuji 2009). For the Texas occurrence, we follow the age interpretation of Lucas & Golubev (2019).

Only Emerolether, Macroletether (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 Macroletether (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 Macroletether (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. *Macroletter 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, intermediate; mc, metacarpal; mt, metatarsal; ph, phalange; ra, radius; rl, radiale; ti, tibia; u, unguial. Roman numerals indicate the digit number or the distal centra number. All scale bars represent 1 cm.
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
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 Chashingsan *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.* 2019a). 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

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**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, Isheev 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.
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. 2019b). 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. 2019a; 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. 2019b). 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. 2019b; 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. 2020a) 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. 2019d).

**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.
records from Arizona, southern France and the Catalan
pha in the Cisuralian of Europe (Lucas 2018). The track
the track record from southern France and the Catalan
Oklahoma; Reisz & Laurin 2001). It is also remarkable that
erally-correlated formation (lower Chickasha Formation of
Golubev 2019) that matches the skeletal record from a lat-
gurian record from Texas (San Angelo Formation; Lucas &
Peranera Forma-
again of the stratigraphic and palaeogeographic distribution of
pareiasauromorphs (Fig. 9) allows a substantial extension
of the stratigraphic and palaeogeographic distribution of
pareiasauromorpha (Fig. 10). This ichnotaxon occurs
attribution of P. ollieri comb. nov. to nyciteroleter
pareiasauromorphs similar to Macrolet-
Tsuji 2009).

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 Pachy-
nes in units older than late Capitanian (Valentini et al. 2009; Voigt & Lucas 2018). We propose the new combination P. ollieri (Ellen-
berger, 1983a) for this material. A track–trackmaker corre-
looks at the east of the Americas and the west of Europe, and suggests a Late Permian
the track record. Moreover, the tetrapod footprints high-
represent the oldest worldwide evidence of Pareiasauromorpha, at least 10 myr before the earliest known skeletal record (Lucas 2018) (Fig. 10).

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