Palaeogeography, Palaeoclimatology, Palaeoecology 677 (2025) 113174

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Track-trackmaker correlation of co-occurring gorgonopsian bones and footprints from the early–?middle Permian of equatorial Pangaea

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ARTICLE INFO

Editor: Howard Falcon-Lang

Keywords:
western Mediterranean
Mallorca
Therapsida
Gorgonopsia
ichnology
locomotion
functional prevalence

ABSTRACT

Therapsids are a group of terrestrial tetrapods that gave rise to mammals during the Triassic. The oldest confirmed record of this group dates to the Permian, showing the acquisition of a new suite of morphological traits, drifting away from the 'reptilian' body plan. One of these modifications affected the girdle and limb joint anatomy and had a profound impact on posture and, by extension, locomotion. Therefore, trackways can be used as a fairly reliable proxy to track down the mode and tempo of those changes. However, references to tracks (and skeletal remains) attributed to therapsids from deposits encompassing the lower–middle Permian boundary are still scarce in the literature. Here we describe a new ichnotaxon, *Algarpes ferus* igen. *et* isp. nov., from the palaeoequatorial lower/?middle Permian of Mallorca (western Mediterranean), correlating it to gorgonopsian trackmakers. This is because the pes tracks match, in terms of proportions and size, with the gorgonopsian body fossils found in the same sedimentological succession, in the Port des Canonge Formation. The narrow gauge and the wide values of pace angulation of the studied trackways suggest a primitive upright posture with a para-sagittal mode of locomotion. These results shed light on the palaeoequatorial tetrapod communities and their importance in the diversification of early therapsids, as well as on the evolution of locomotion in this group, showing that modifications that would result in the 'mammalian' gait were already underway by the early/?middle Permian.

1. Introduction

Gorgonopsians were a group of sabre-toothed, predatory therapsids that became key components of the Lopingian terrestrial ecosystems, replacing dinocephalian and large therocephalian therapsids as top predators after the Guadalupian (Sigogneau-Russell, 1989; Day et al., 2015; Kammerer, 2016; Day and Rubidge, 2021; Kammerer and Rubidge, 2022). The origin of the group dates back to the late Cisuralian (Kammerer and Rubidge, 2022; Matamales-Andreu et al., 2024), disappearing at the end of the Permian (Ward et al., 2005). Their fossil record presents a mostly disjunct distribution across Pangaea, occurring in high palaeolatitudes of the northern (*e.g.*, Tatarinov, 1974; Ivakhnenko, 2003; Liu and Yang, 2022) and southern (*e.g.*, Sigogneau, 1970; Smith et al., 2020) hemispheres. In lower palaeolatitudes, gorgonopsian and, more broadly, therapsid remains are typically fragmentary, hindering confident taxonomic identification (*e.g.*, Smiley et al., 2008; Smith et al., 2015). Only the palaeoequatorial floodplains of Mallorca (western Mediterranean; Matamales-Andreu et al., 2022) have produced unequivocal remains of low-latitude gorgonopsians, demonstrating a trans-Pangaean distribution for this group (Matamales-Andreu et al., 2024). Still, separation of most gorgonopsians into two greater monophyletic clades ('Russian clade' and 'African clade': Kammerer and Masyutin, 2018) may suggest their dispersion potential decreased after their initial dispersal event.

So far, footprints purportedly attributed to gorgonopsians have been reported from South Africa (Marchetti et al., 2019a) and possibly from Uruguay (Piñeiro et al., 2022). In South Africa, tracks attributed to gorgonopsians were found in the uppermost *Tapinocephalus* to

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https://doi.org/10.1016/j.palaeo.2025.113174
Received 5 May 2025; Received in revised form 30 July 2025; Accepted 30 July 2025

uppermost *Pristerognathus* assemblage zones (uppermost Guadalupian), and were assigned to *Karoopes gansfonteinensis* (Marchetti et al., 2019a). This ichnotaxon corresponds to medium to large, pentadactyl, weakly ectaxonic, semiplantigrade/digitigrade tracks with curved digits and with the lateral side relatively deeper, indicating a lateral functional prevalence of autopodia (*sensu* Mujal et al., 2020). The trackways show homopody and very high pace angulation values (110–170°; Marchetti et al., 2019a, 2025). The track material from the Guadalupian–Lopingian of Uruguay is, at present, much scarcer, corresponding to large, pentadactyl, ectaxonic tracks with curved digits that have been doubtfully identified as cf. *Karoopes* by Piñeiro et al. (2022). Ichnites correlated to gorgonopsians represent a small fraction of the relatively diverse record of therapsid (and more generally synapsid) tracks and trackways (Marchetti et al., 2019a, 2025). However, they are relevant to understand the evolution of the locomotion of therapsids, because their trackways are usually narrow, with long strides and high pace angulations, differing from trackways attributed to other Permian synapsids (Marchetti et al., 2019a, 2025; Matamales-Andreu et al., 2021).

Recent fieldwork on Mallorca (Balearic Islands, western Mediterranean) has revealed rich Permian tetrapod assemblages consisting of both tracks and bone remains (Matamales-Andreu et al., 2021, 2022, 2023, 2024). Among those, the discovery of body fossils belonging to the first unequivocal gorgonopsian from equatorial Pangaea stands out, possibly representing the oldest of its clade worldwide (Matamales-Andreu et al., 2024). Some tetrapod tracks and trackways (identified as "indeterminate synapsid tracks" by Matamales-Andreu et al., 2022) were found 46 m stratigraphically above the bones, still in the same unit as the gorgonopsian body fossils, the Port des Canonge Formation (Fig. 1). The present contribution describes those footprints, erecting a new ichnotaxon and, by means of an analysis of their morphology and trackway pattern, attributes them to the clade Gorgonopsia. In the light of the track-trackmaker correlation, this work aims to contribute to the understanding of the locomotion of early therapsids.

2. Geographical and geological context

2.1. General context

Mallorca is the largest of the Balearic Islands, an archipelago located at the western Mediterranean. Permian outcrops appear in the lowermost tectonic unit of the Serra de Tramuntana, the main mountain range of the island (Fig. 1A). Permian sedimentary deposits have been recently divided into three formal lithostratigraphic units (Matamales-Andreu et al., 2022), from lower to upper: Bec de s'Àguila Formation,

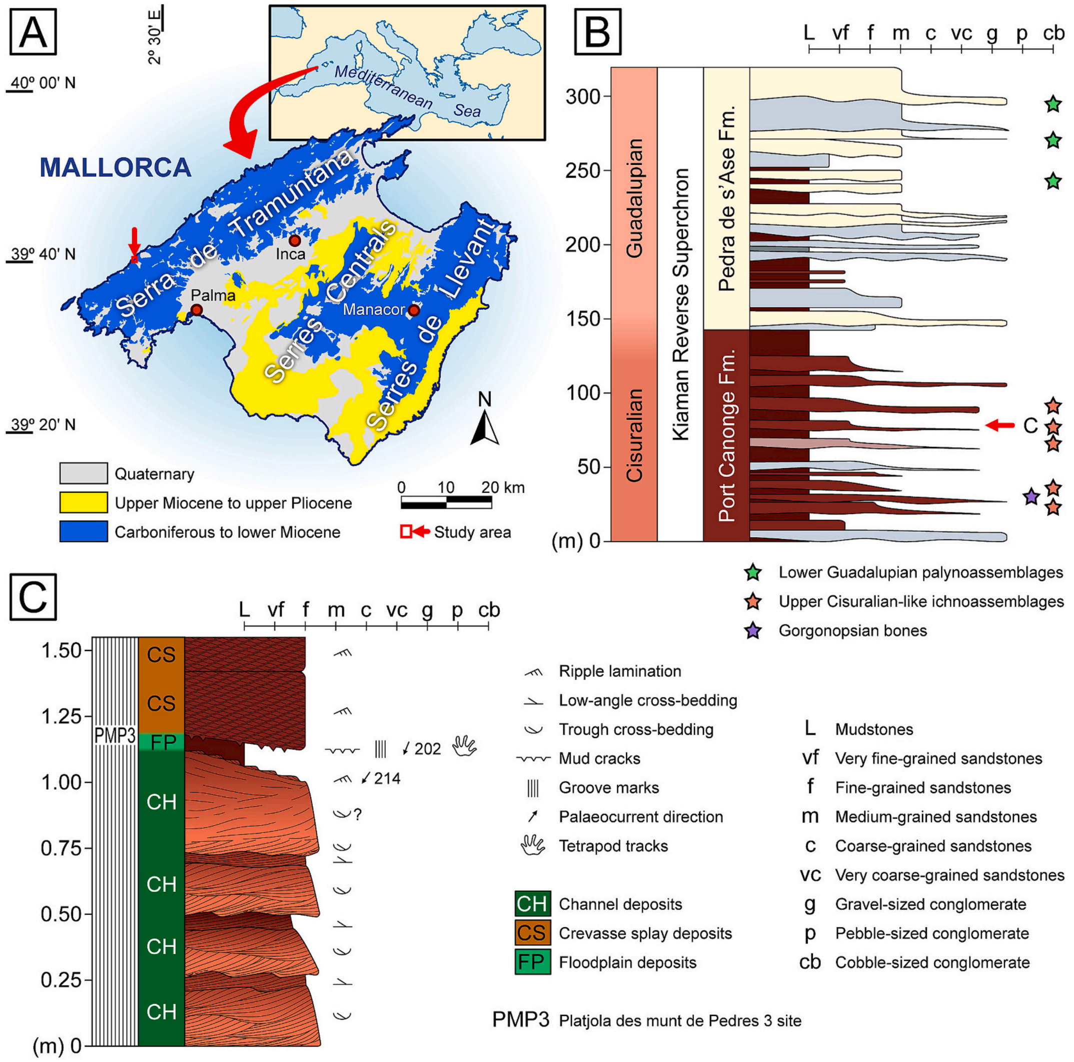

Fig. 1. Geographical and geological context for the studied samples. A: Simplified geological map of Mallorca, showing the location of the studied section. B: Simplified stratigraphic log of the Racó de s'Algar-Pedra de s'Ase section, with magneto- and biostratigraphic information, and the position of the detailed log in C. Simplified after Matamales-Andreu et al. (2022, 2024). C: Detailed stratigraphic log of the Platjola des munt de Pedres 3 tracksite (PMP3), indicating the track-bearing surface.

corresponding to alluvial fans and high-energy meandering river deposits; Port des Canonge Formation, interpreted as the deposits of low-energy meandering rivers and floodplains; and Pedra de s'Ase Formation, representing high-energy meandering river, sheetflood and floodplain deposits (Matamales-Andreu et al., 2022). Among those, the most fossiliferous is the Port des Canonge Formation, has been dated in a possible range between the upper Cisuralian (Artinskian/Kungurian) to perhaps (although unlikely) the lowermost Guadalupian (Roadian?) (Matamales-Andreu et al., 2022, 2024). It contains macroplant remains (conifers ?*Feysia* and *Hermitia*), invertebrate trace fossils indicative of freshwater settings with several degrees of transience (*Arenicolites*, *Cochlichnus*, *Cruziana*, *Palaeophycus*, *Planolites* and *Taenidium*), and tetrapod tracks and skeletons (Matamales-Andreu et al., 2021, 2022, 2023, 2024). Tetrapod footprints are represented by the ichnogenera *Hyloidichnus* (two morphotypes attributed to medium-sized and large moradisaurine captorhinid amniotes, respectively), *Dromopus* (attributed to araeoscelidian diapsid reptiles or non-varanodontine varanopids), cf. *Pachypes* (attributed to nycteroletid non-pareiasaur pareiasauromorphs), *Dimetropus* (attributed to indeterminate 'pelycosaur'-grade synapsids), cf. *Dimetropus* (tentatively attributed to caseasaurian 'pelycosaurs'), *Characichnos* (indeterminate tetrapod swimming traces) and the new tracks herein studied (Matamales-Andreu et al., 2021, 2022, 2023). Among bone remains, there is record of an indeterminate large moradisaurine captorhinid (Liebrecht et al., 2017), the medium-sized moradisaurine captorhinid *Tramuntanasaurus tiai* (Matamales-Andreu et al., 2023), and a medium-sized gorgonopsian therapsid (Matamales-Andreu et al., 2024).

2.2. Stratigraphy and sedimentology of the tracksite

The footprints studied herein were found in a single stratigraphic surface corresponding to the base of a very-fine grained sandstone bed in the upper part of the Port des Canonge Formation, designated as "Platjola des munt de Pedres 3" (PMP3; for its position in the detailed stratigraphic log of the section, see Matamales-Andreu et al., 2022) (Fig. 1B). Therefore, they are all preserved as convex hyporeliefs infilling the original tracks that were imprinted on the underlying mudstones, now eroded (the mudstones are only visible in cross section within the rock wall). The same surface contains *Hyloidichnus*, *Dromopus*, *Dimetropus*, mud cracks and abundant groove casts.

The detailed stratigraphic log (Fig. 1C) shows that, below the tracksite, there is a sandstone unit corresponding to, at least, seven cycles of infill of a fluvial channel. After an initial bed of intrabasinal breccias made up of carbonate nodules, soft pebbles and rare tetrapod bones, there is an alternation of fine- to medium-grained sandstone beds with trough cross-bedding and internal reactivation surfaces, and beds of mudstones to very fine-grained sandstones with low-angle cross-bedding, separated by erosive surfaces with occasional soft pebbles (mud chips and rip-up clasts). These deposits represent the infilling of a channel subjected to currents of varying energy and periods of still waters. Since all the cycles follow the same dynamics, each of them could correspond to a full seasonal, yearly cycle with two different rainy periods, as in modern Serengeti (*e.g.*, Yang et al., 2015; Mahony et al., 2020). The lack of palaeosols of this interval of the succession would also agree with this interpretation, since it indicates a rapid and essentially continuous deposition of the sediments. In any case, the last cycle is topped by a linguoid climbing-ripple carpet overlain by a thick bed of mudstones, which wedges laterally. The presence of mud cracks in those mudstones indicate that the channel may have, at that time, acted as a waterhole that ended up drying. It is in this surface that the tetrapod footprints were imprinted and, interestingly, they are more abundant and better preserved in what appears to be the deepest zone of the waterhole (*i.e.*, the one that dried up the last). The mud cracks on the trampled surface are relatively thin (~1.6–5.0 mm wide) and with T-junctions (*i.e.*, the intersection between two cracks is at about 90°), which is suggestive of a low number of cycles of desiccation-hydration of the substrate (Goehring et al., 2010). Therefore, it is likely that the surface was not exposed for a long time.

Above these mudstones, the dynamics of the system changed completely, with tabular, fine-grained sandstone beds with climbing-ripple lamination, probably corresponding to crevasse splay deposits of another nearby channel. The lowermost bed of those sandstones is the one that produced the natural casts of the tracks.

3. Material and methods

3.1. Collected specimens

Two specimens (DA21/15-12-02, and RA-22-20) were collected directly from the *in situ* layer using chisels, hammers and buzzsaws, with permission of the Comissió Insular de Patrimoni Històric of the Consell Insular de Mallorca (excavations/prospections with file numbers 75/2021 and 259/2022). The original material is housed at the Museu de Mallorca (Palma, Spain), acronym: DA21. The rest of the specimens remain in the field.

3.2. Three-dimensional models and silicone moulds

Digital three-dimensional (3D) models of the studied specimens were produced using photogrammetry, following the exact same methodology as in Matamales-Andreu et al. (2022) and references therein. It consists in taking a set of pictures (between 50 and 200, depending on the size of the area to modelise), capturing all the elements in different (and overlapping) perspectives, and then processing it with the software Agisoft Metashape (professional license, educational version, v.1.8.3 and v.2.1.0.), MeshLab (v.2020.07) and ParaView (v.4.1.0). The result is a false-coloured height map that may include contours (when necessary) and facilitates the interpretation of the reliefs (*e.g.*, Mujal et al., 2016, 2020). The camera used was a Panasonic Lumix DMC-TZ27, and 3D models were made of the complete trackway, specific tracks separately, and the whole slab containing multiple tracks (among others, including a trackway with poorly preserved tracks), allowing for attaining different levels of detail for the whole track sample. 3D models are available on Figshare: https://doi.org/10.6084/m9.figshare.28919465.v2.

Apart from the 3D models, six silicone moulds were made (MBCN29918, MBCN29919, MBCN29920, MBCN27438, MBCN27441, MBCN27442), comprising all the tracks herein studied that remain *in situ*. Note that, since all tracks come from the same surface, the same mould may contain different tracks herein analysed (*e.g.*, the surface containing the holotypic trackway also contains one of the paratypes and other referred manus-pes sets); otherwise, for some tracks multiple moulds were made, thus the same specimen may have different numbers.

To make the moulds, the surface was first covered in petroleum jelly. In the case of individual footprints, the polyaddition silicone paste ClayGum was applied and left to dry for about 10 min. For larger surfaces such as the trackway surface, the silicone with a thixotroping agent Silicast Tixo was used instead. First, a thin layer of about 1–3 mm thick was applied on the surface and left to dry. Once it had dried, another silicone layer, slightly thicker (5 mm), was applied over it. After drying for one night, a jacket was made using Triaxial D-5 glass fibre and Plasticrete acrylic resin in order to maintain the shape of the silicone mould. After a few hours, the silicone was peeled off the track-bearing surface, obtaining the mould. Once in the lab, casts of the moulds were produced by using Acrylic One resin, obtaining a high-fidelity copy of the original surface and allowing for a further detailed first-hand study of tetrapod ichnites. All the moulds and casts are housed at the Museu Balear de Ciències Naturals (Sóller, Spain), acronym: MBCN.

Moulds and casts of the holotype plus paratype and additional tracks (from MBCN27438: IPS-M.143600 [mould], IPS-R.127745 [cast]), paratype (from cast MBCN27440: IPS-M.131566 [mould], IPS-R.131580

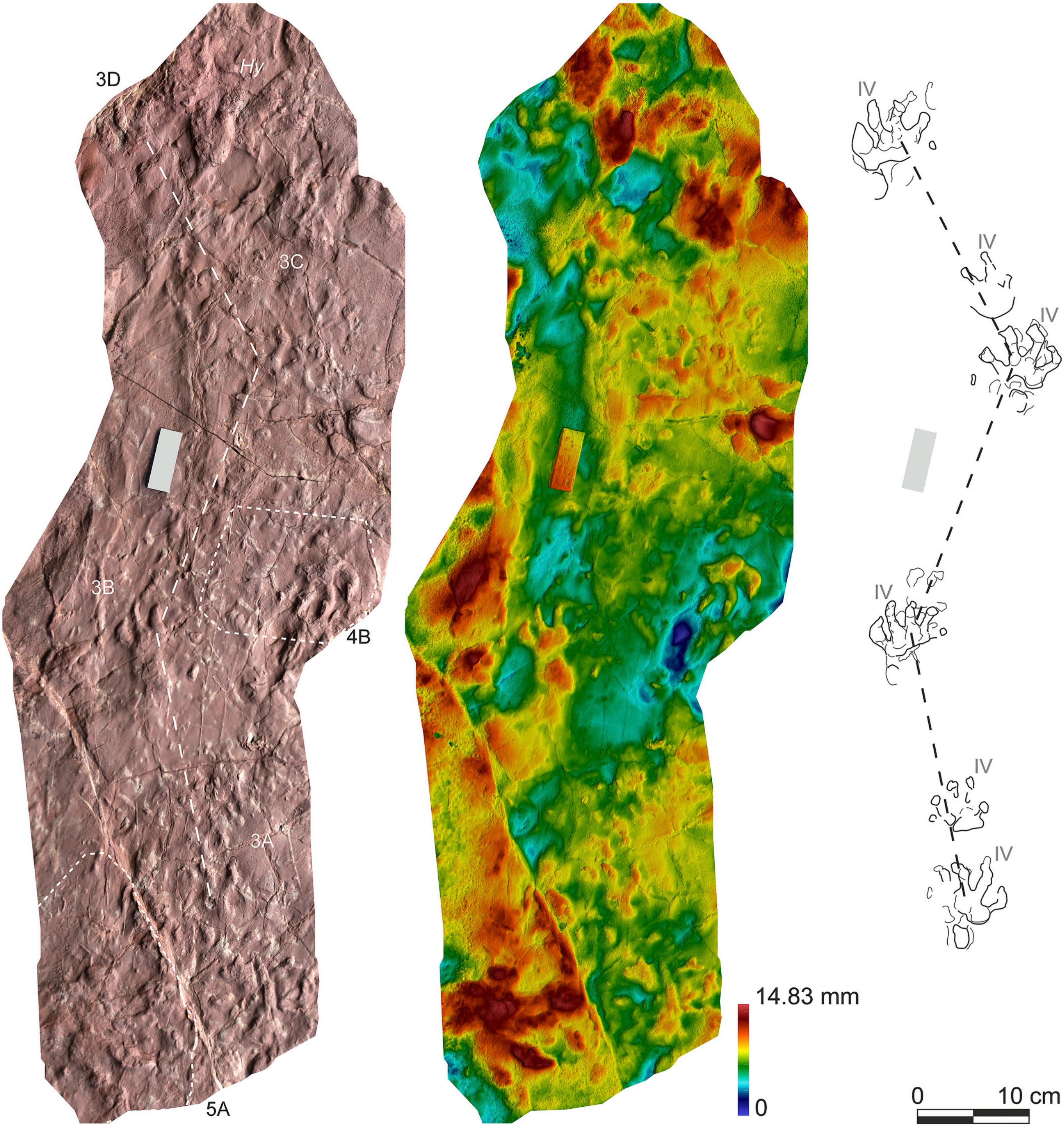

Fig. 2. Holotype of *Algarpes ferus* igen. *et* isp. nov. (mould and cast MBCN27438; field identifying number of track surface NA-77.5-01), including orthophoto (left) and false colour depth map with contours (middle) of the 3D photogrammetric model, and interpretative outline (right). The surface also preserves tracks from other ichnotaxa, not represented in the interpretative outline. Dashed lines: paces of the pes tracks. Abbreviations: *Hy*, large *Hyloidichnus* track; m, manus; p, pes; IV, digit IV. Labels 3A, 3B, 3C, 3D, 4B and 5A correspond to subsequent figures.

[cast]), and additional material (from MBCN27442: IPS-M.128183 [mould], IPS-R.139922 [cast]; from MBCN27442: IPS-M.128184 [mould], IPS-R.139923 [cast]) are also stored at the Institut Català de Paleontologia Miquel Crusafont. Acronym: IPS, Institut Català de Paleontologia Miquel Crusafont (formerly Institut de Paleontologia de Sabadell), Sabadell, Catalonia, Spain.

3.3. *Ichnological study*

Tetrapod tracks and trackways were described and measured following the conventions of Leonardi et al. (1987) (see also Lallensack et al., 2025). The relative depth pattern of the footprints (*sensu* Mujal et al., 2020) was also assessed, since it appears to be a consistent ichnotaxobase. Specimens were first studied in the field, and further observations were made in the lab from the recovered specimens, resin casts, and 3D photogrammetric models. The morphological preservation of the tracks *sensu* Marchetti et al. (2019b) ranges from 0.5 to 3, with most of the footprints scoring around 2–2.5. This, together with the presence of a trackway composed of four manus-pes sets, a trackway composed of three consecutive (yet poorly preserved) pes tracks, as well as at least two incomplete step cycles, allows for a confident ichnotaxonomic identification (following recommendations of Marchetti et al., 2019b; Lallensack et al., 2025).

4. Systematic palaeoichnology

Ichnogenus *Algarpes* igen. nov.

Life Science Identifier (LSID) in ZooBank: urn:lsid:zoobank.org:act:A56D3516-B5EB-4E7D-98A0-4B4066B2575B.

Type ichnospecies. *Algarpes ferus* igen. *et* isp. nov.

Origin of the name. *Algarpes* stems from the term *algar* (Catalan word meaning “place where seaweed accumulates”, referring to the name of the area, Racó de s’Algar) and *pes* (Latin for foot). Gender: masculine.

Diagnosis. Tetrapod pentadactyl ichnites of a remarkably heteropodic trackmaker, with manus tracks (48–64 mm long) smaller than pes tracks (67–106 mm long). Pes track semiplantigrade to plantigrade, weakly ectaxonic (digit IV the longest) with digit V longer than digit III. Pes digit imprints relatively long, thick, all of them inwardly curved and displaying large, oval-shaped claw traces. Sole imprint composed of the metatarsal-phalangeal joint mainly of digits II to V, and an oval-shaped anteroposteriorly elongated imprint located posterolaterally (calcaneum area), at the height of the digit V metatarsal-phalangeal joint, and separated from the rest of the pes imprint. Pes track more deeply impressed laterally (digit IV and corresponding metatarsal-phalangeal joint usually the deepest). Manus track plantigrade, weakly ectaxonic (digit IV only slightly longer than digit III), and more deeply impressed median-laterally (digit III and outer half of the palm more deeply impressed). Proximal margin of the palm strongly convex. Narrow trackway with regular alternating manus-pes sets; long pace and stride (pes length/stride ratio: 0.156–0.185), and very high pace angulation (pes: 132–148°; manus: 151–159°); manus tracks immediately in front of the pes tracks and slightly closer to the midline; partial overstepping of the manus by the pes tracks observed in some cases; manus tracks rotated inwards, pes tracks rotated inwards or subparallel to the trackway midline.

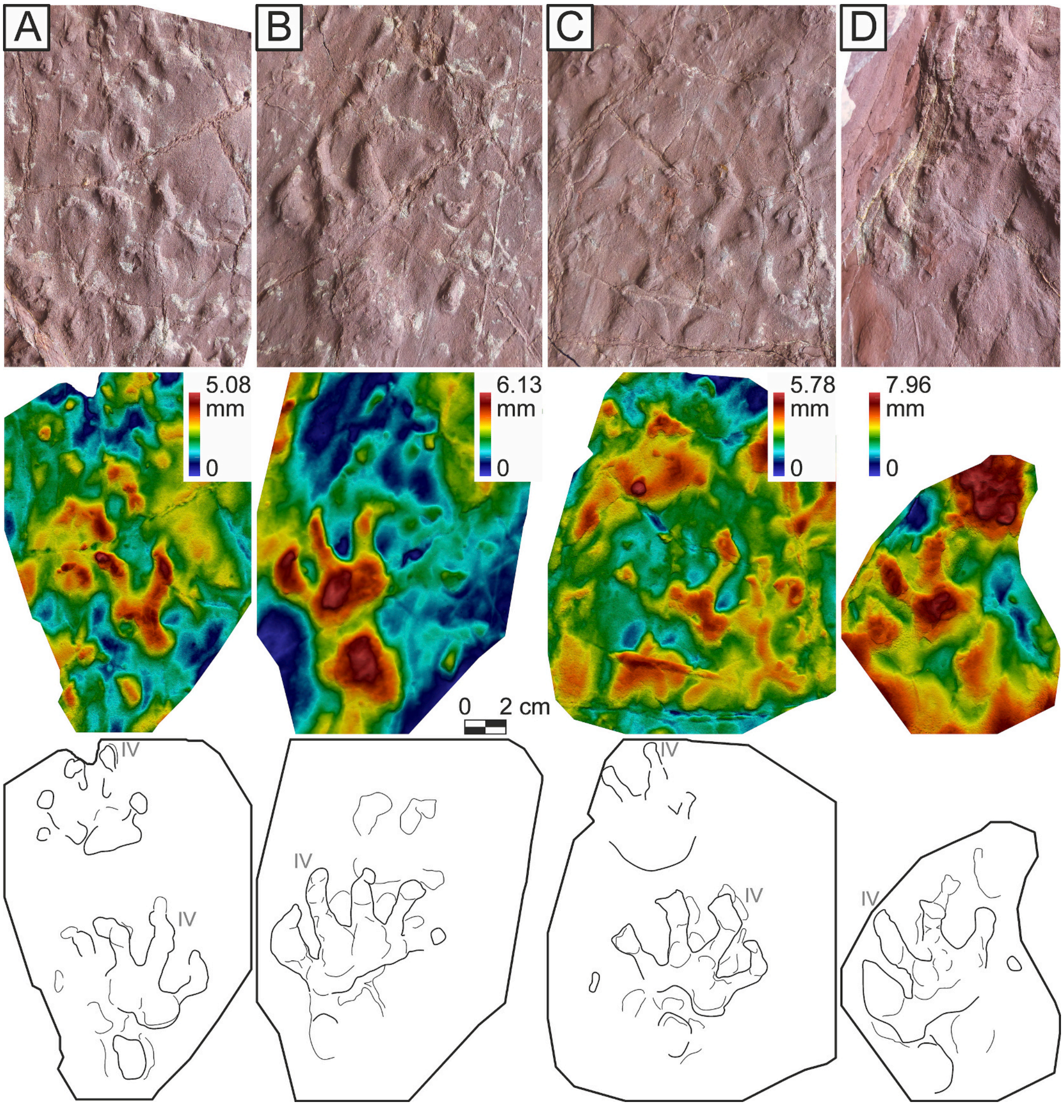

Fig. 3. Detail of the tracks composing the trackway of the holotype of *Algarpes ferus* igen. *et* isp. nov. (mould and cast MBCN27438; field identifying number of track surface NA-77.5-01). The top row includes photographs of the footprints; the middle row, false-colour depth maps with contours; the bottom row, interpretative outlines. All footprints at the same scale. A and C correspond to left side tracks; B and D correspond to right side tracks.

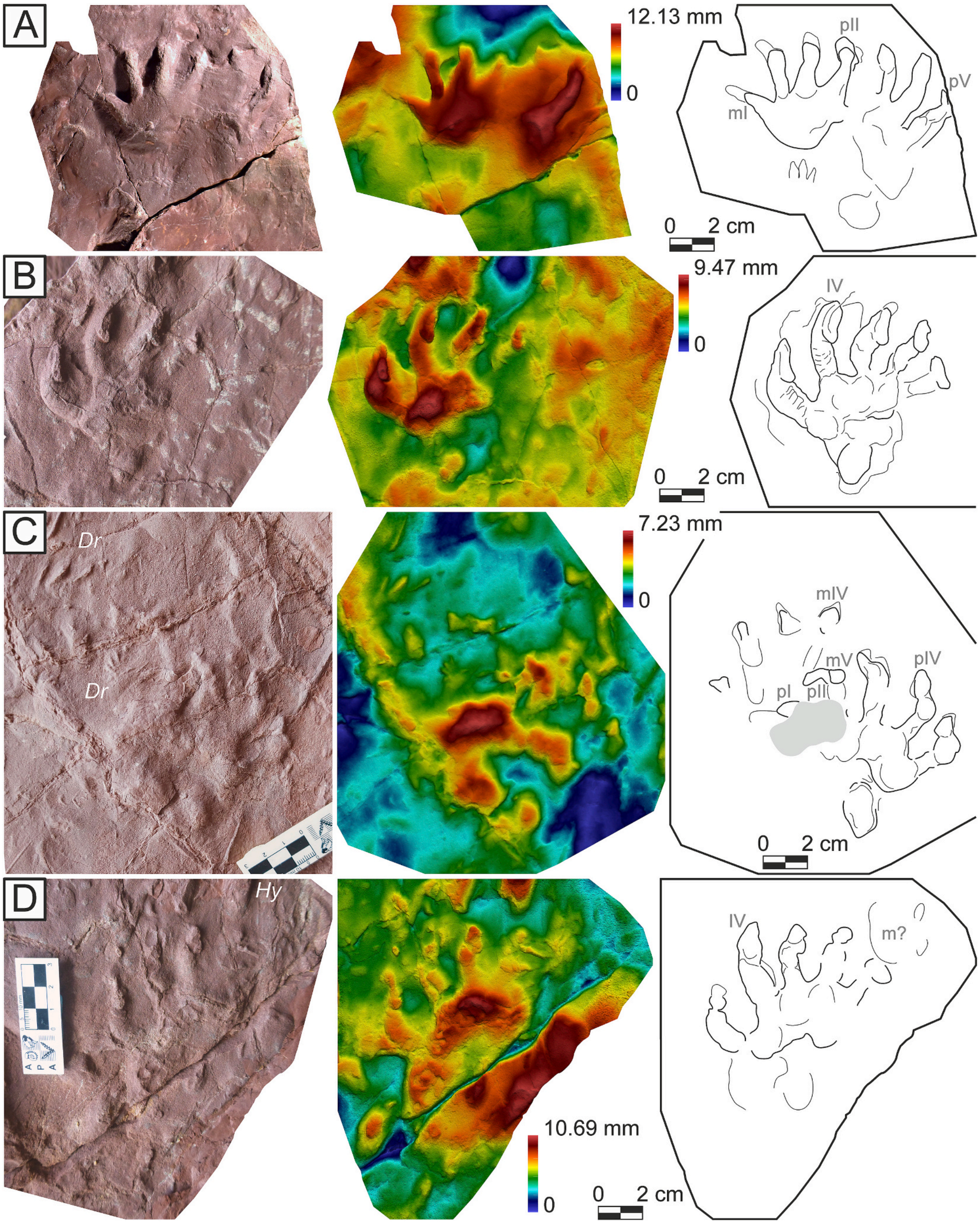

Fig. 4. Paratypes (A, B) and referred tracks (C, D) of *Algarpes ferus* igen. *et* isp. nov. A: Left couple with well-preserved manus track (field number of collected specimen RA-22-20; cast MBCN27440; field identifying number of track surface NA-77.5-05). B: Very well-preserved right pes track (collected specimen DA21/15-12-02; moulds MBCN29918, MBCN29919, MBCN27438 [also cast for the latter]; field identifying number of track surface NA-77.5-01). C: Left couple (field identifying number of track surface NA-77.5-04, not collected nor moulded). D: Right couple (mould and cast MBCN27438; field identifying number of track surface NA-77.5-01). For each specimen, from left to right: photograph; false-colour depth map with contours from the 3D photogrammetric model; interpretative outline of the tracks. Abbreviations: *Dr*, *Dromopus*; *Hy*, large *Hyloidichnus*; m, manus; p, pes; roman numbers refer to digit numbers.

Algarpes ferus igen. *et* isp. nov.

Life Science Identifier (LSID) in ZooBank: urn:lsid:zoobank.org:act:22B9023A-05A1-4B21-957D-7B849E891D13.

Figs. 2–5, Tables 1, 2

2022 "indeterminate synapsid tracks"; Matamales-Andreu *et al.*, p. 9.

Type specimens. Holotype: trackway (mould and cast MBCN27438; field identifying number of track surface NA-77.5-01) (Figs. 2, 3). Paratypes: left manus-pes set (field number of collected specimen RA-22-20; cast MBCN27440; field identifying number of track surface NA-77.5-05) (Fig. 4A); right pes track (collected specimen DA21/15-12-02; moulds MBCN29918, MBCN29919, MBCN27438 [also cast for the latter]; field identifying number of track surface NA-77.5-01) (Fig. 4B). All tracks in convex hyporelief.

Additional material. Isolated manus-pes sets: left couple (field identifying number of track surface NA-77.5-04, not collected nor moulded) (Fig. 4C); right couple (mould and cast MBCN27438; field identifying number of track surface NA-77.5-01) (Fig. 4D); isolated manus-pes set of large size (mould and cast MBCN27438; field identifying number of track surface NA-77.5-01) (Fig. 5A); trackway composed of three poorly preserved pes tracks, other incomplete step

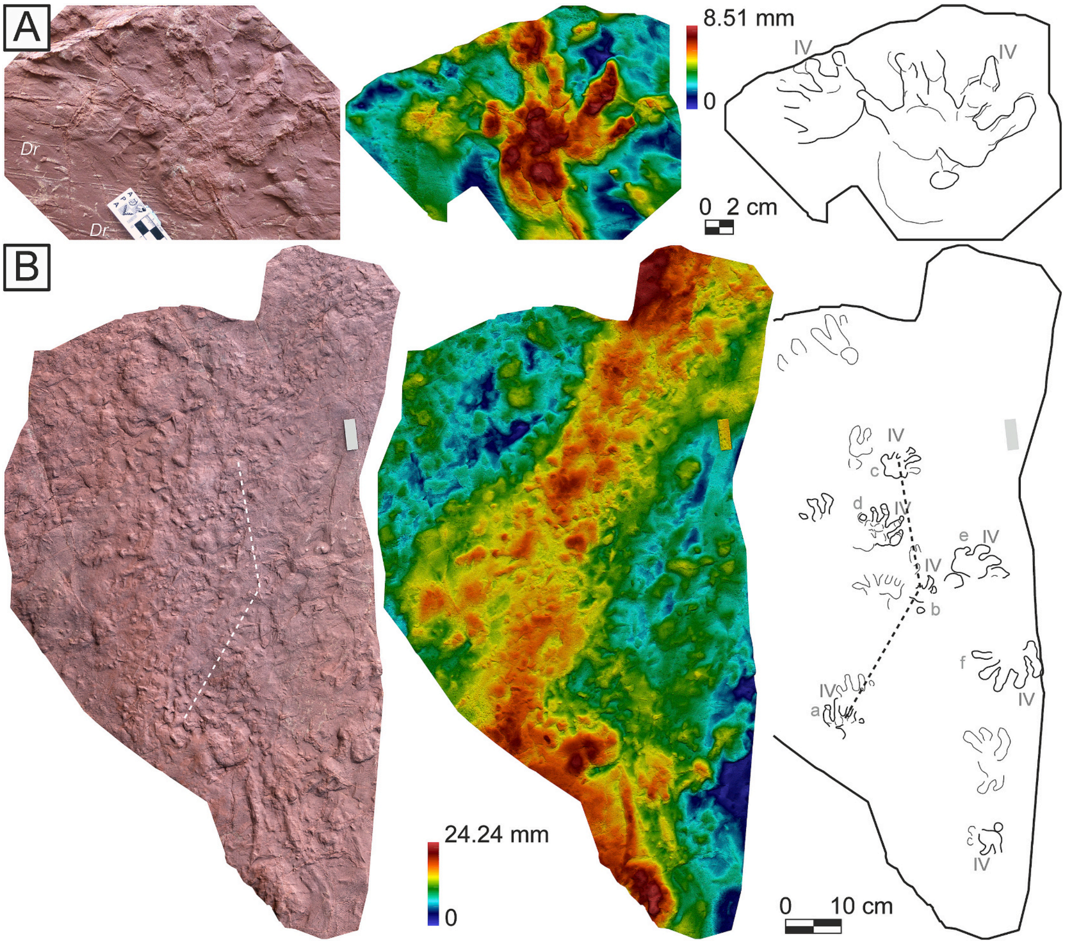

Fig. 5. Large-sized tracks and additional tracks and trackway referred to *Algarpes ferus* igen. *et* isp. nov. A: Isolated left couple (mould and cast MBCN27438; field identifying number of track surface NA-77.5-01); *Dr*, *Dromopus*. B: Densely trampled surface including several track morphotypes (mould and cast MBCN27442; field identifying number of track surface NA-77.5-02); dashed line corresponds to pes paces; grey letters (a–f) indicate tracks for which parameters were measured, and are referenced in Table 1. For each specimen, from left to right, photograph (A) and orthophoto from the 3D photogrammetric model with original texture (B); false-colour depth map with contours; interpretative outline of the studied tracks (the other track morphotypes are not represented). IV, digit number IV.

cycles, and other isolated tracks (moulds and casts MBCN27441 and MBCN27442; field identifying number of track surface NA-77.5-02) (Fig. 5B). All tracks in convex hyporelief.

Origin of the name. *ferus* stems from the Latin term *ferus* (wild, fierce), because gorgonopsians were probably the top predators in the Permian ecosystem of Mallorca (Matamales-Andreu et al., 2024).

Type level, locality and age. Platjola des munt de Pedres 3 fossil site (PMP3), Port des Canonge Formation, Racó de s'Algar–Pedra de s'Ase section (Matamales-Andreu et al., 2022); Banyalbufar, Mallorca, Balearic Islands; upper Cisuralian–?lowermost Guadalupain, Permian.

Diagnosis. As for the ichnogenus (monospecific ichnotaxon).

Description. Remarkably heteropodic ichnites (differing in both size and shape) arranged in very high pace angulation trackways produced by a quadrupedal tetrapod (Figs. 2, 3).

Manus: Ichnites produced by the manus are generally poorly preserved, mostly represented by circular to oval-shaped impressions of the palm and/or smaller somewhat elongated ovoid impressions corresponding to digit imprints. The manus track with a best-defined outline (especially regarding the proximal and mid part of the digits) corresponds to a plantigrade footprint coupled with a pes track (Fig. 4A). This manus track, however, preserves only four digit imprints. Other manus tracks associated to pes tracks show the presence of a fifth digit (Figs. 3D, 4C, 5A), confirming the pentadactyly of the manus tracks of this morphotype. This description is thus based on the features of the best defined manus track plus additional features observed on those preserving five digits. The manus tracks are plantigrade, slightly wider than long (Table 1). Digits increase in length from I to IV. Digit I is substantially shorter than digits II, III and IV. Digit IV is only slightly longer than digit III. Digit V is slightly shorter than digit I (Figs. 3D, 4C, 5A). The digit tip imprints are generally round, only slightly angular, denoting the presence of relatively wide claws in the autopodium. Digit tips are usually more deeply impressed than the other parts of the digits (Figs. 3D, 4C, 5A), with the only exception being in the best defined manus track (Fig. 4A). The digit imprints are generally straight, with the tips of digits I to IV being slightly curved inwards. All digit imprints are radially distributed from the palm impression, with the angulation of digits I–II higher than II–III and III–IV. The proximal part of the digit I to IV imprints is defined by a faint, convex (proximally curved) relief, better observed in the false-colour depth map of the 3D model and in the imprints of digits II and III (Fig. 4A). In front of the tips of each of the four digit imprints in the best defined manus track, there are shallow and short, inwardly oriented drag traces (Fig. 4A). The palm impression is wider than long, with a marked proximally convex margin. The lateral (outer) half of the palm is the most deeply impressed part of the footprint, followed by the digit III. As stated above, the poorly preserved manus tracks are mostly represented by the palm and/or the tips of the digits, denoting the strong plantigrady of these ichnites. The lateral half of the best defined manus track is more deeply impressed (Fig. 4A), indicative of a median-lateral functional prevalence of the manus autopodium, this trend is also observed in the other manus tracks

Table 1
Track parameters of *Algarpes ferus* igen. *et* isp. nov. Abbreviations: div, divarication; L, track length; Lp/s, Length of palm/sole; I L to V L, length of digits I to V; W, track width; Wp/s, Width of palm/sole; MP, morphological preservation (*sensu* Marchetti et al., 2019b). Numbers with question mark (?) indicate uncertainty in the measurement.

Museum collection number	Field number	Anatomy	L	W	Lp/s	Wp/s	I L	II L	III L	IV L	V L	div I–II	div II–III	div III–IV	div IV–V	div I–V	div I–IV	div II–V	div II–IV	MP
MBCN27438 (mould and cast). Holotype	NA-77.5-01 (field identificator of track surface)	Left manus (Fig. 3A)	49	55	19	27	18	23	27	31	15	34	35	15	25	109	84	74	49	2.5
		Left pes (Fig. 3A)	80	74	46	31	24	33	37	39	38	32	16	28	35	113	77	80	46	2.5
		Right manus (Fig. 3B)	49?	57?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.0
		Right pes (Fig. 3B)	92	84	59	42	24	31	33	41	40	47	27	20	22	116	94	68	46	2.5
		Left manus (Fig. 3C)	59	–	25	33	–	–	33	36	15?	–	–	30	27	–	–	–	–	1.0
		Left pes (Fig. 3C)	80	86	45	35	24	27	34	41	39	31	37	34	28	130	102	99	72	2.5
		Right manus (Fig. 3D)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.0
		Right pes (Fig. 3D)	91	76	59	36	21	27	31	40	38	47	31	41	10	127	118	82	72	2.5
MBCN27440 (cast). Paratype	RA-22-20 (field number of collected specimen, NA-77.5-05 (field identificator of track surface)	Left manus (Fig. 4A)	48	47?	23	26	17	22	25	27	–	36	15	26	–	–	78	–	42	2.5
		Left pes (Fig. 4A)	84	–	51	–	–	33	34	37	34	–	27	32	5	–	–	63	59	1.5
DA21/15-12-02 (collected specimen), MBCN29918, MBCN29919, MBCN27438 (moulds, also cast for the latter). Paratype	RA-21-58 (field number of collected specimen), NA-77.5-01 (field identificator of track surface)	Right pes (Fig. 4B)	83	82	44	31	28	37	38	47	45	40	27	18	35	119	85	80	45	3.0
Specimen left *in situ*	NA-77.5-04 (field identificator of track surface)	Left manus (Fig. 4C)	62	61	21	28	22	38	38	44	20	31	14	19	22	87	65	55	34	2.0
		Left pes (Fig. 4C)	80	84	46	31	28	30	33	42	42	41	20	37	22	121	99	79	57	2.0
MBCN27438 (mould and cast)	NA-77.5-01 (field identificator of track surface)	Right pes (Fig. 4D)	85	86	45	37	29	38	38	46	43	26	24	18	40	108	68	83	42	2.5
MBCN27438 (mould and cast)	NA-77.5-01 (field identificator of track surface)	Left manus (Fig. 5A)	64	72?	31	40	15?	25?	32	32	24	25	12	20	26	83	57	57	31	2.0
		Left pes (Fig. 5A)	100	121	54	55	31	43	45	56	53	43	7	34	20	103	84	60	40	2.5
MBCN27441, MBCN27442 (moulds and casts)	NA-77.5-02 (field identificator of track surface)	Right pes - a (Fig. 5B)	70	73	39	35	20	–	–	41	38	50	9	30	21	109	90	61	38	1.5
		Left pes - b (Fig. 5B)	82	–	45	32	–	–	–	31	25	–	–	37	18	–	–	–	–	1.0
		Right pes - c (Fig. 5B)	67	65	33	28	29	34	35	36?	19?	25	14	28	45	110	67	85	41	2.0
		Left pes - d (Fig. 5B)	92	83	50	37	22	32	46	52	46	42	26	25	35	130	93	89	51	2.5
		Right pes - e (Fig. 5B)	106	–	61	42	–	46?	48	49	33	–	21	38	30	–	–	92	59	1.5
		Right pes - f (Fig. 5B)	106?	130	46?	40	39	53	58	63	63	39	29	59	13	138	126	100	89	2.0

Table 2
Trackway parameters of *Algarpes ferus* igen. *et* isp. nov. Numbers with question mark (?) indicate uncertainty in the measurement. Negative values indicate inward rotation.

Museum collection number	MBCN27438 (mould and cast). Holotype (Fig. 2)				MBCN27441, MBCN27442 (moulds and casts). Referred trackway (Fig. 5B)		
Field number	NA-77.5-01 (field identificator of track surface)				NA-77.5-02 (field identificator of track surface)		
Pace angulation pes (°)	148	132			140		
Pace angulation manus (°)	159	151?			–		
Divarication pes (°)	-7	10	-5	7	-6	-7	-37
Divarication manus (°)	-15	-24?	-14	–	–	–	–
Stride pes (mm)	482	449			469		
Stride manus (mm)	471	442?			–		
Pace pes (mm)	240	261	229		268	230	
Pace manus (mm)	195	284	170		–	–	
Length pace pes (mm)	230	241	207		257	213	
Length pace manus (mm)	190	279	162?		–	–	
Width pace pes (mm)	69	99	99		83	86	
Width pace manus (mm)	41	52	52?		–	–	
Manus-pes distance (mm)	81	40	74	50?	–	–	–
Manus-pes divarication (°)	9	33	7	–	–	–	–
External trackway width (mm)	145	148	182		153	148	
Gleno-acetabular distance (mm)	295	276			–		

preserving five digits (Figs. 3D, 4C, 5A).

Pes: Imprints of the pes (67–106 mm long, 65–130 mm wide) are notably larger and generally better preserved than those of the manus (Table 1). Pes tracks are semiplantigrade to plantigrade and pentadactyl, with digit impressions being the most prominent part of the ichnites. Digit imprints increase in length from I to IV, and digit V imprint is slightly shorter than digit III. The relative depth of the digit imprints parallels their relative length: I < II < III < V < IV; though occasionally the digit V imprint is the deepest (Fig. 4B). All digit imprints are curved inwards, with the tip imprint more markedly bent. The tips display large and deep claw traces that are anteroposteriorly elongated, giving an overall hook shape to the digit tip imprints. In addition to their large size, claw traces are also the deepest part of the digit imprints, followed by the distal third of the phalangeal region (Figs. 3, 4B–D, 5A), somewhat similar to the manus tracks, which usually show digit tips deeper than the rest of the digit imprints. The digit imprints are generally well-defined, except for digit I, which is mostly only represented by a shallow imprint of the tip (the claw) and a very faint impression (if present) of the distal phalangeal portion. The same is true for the proximal half of digit II, usually not preserved or only shallowly impressed. In the best-preserved pes track (Fig. 4B), the digit V imprint displays laterally elongated creases (*i.e.*, perpendicular to the digit axis), more developed to the inner side and forming blocky rectangular reliefs; they most likely correspond to skin creases (similar to those found in *Dimetropus*: Calábková et al., 2023). The digit imprints are radially distributed from the sole imprint, which is mainly represented by the impressions of the basal pad of each digit, corresponding to the metatarsal-phalangeal joint. Each basal pad is circular and altogether form a tight bulbous impression, being deepest below digit IV and usually not imprinted below digit I. In most of the pes tracks, a separate, slightly anteroposteriorly elongated oval-shaped imprint is present; it is usually well-defined, even surrounded by an expulsion rim. This oval-shaped imprint represents the most proximal part of the pes tracks, and most likely corresponds to the impression of the tarsal pad. This imprint may appear connected to the basal pad of digit V by a shallow, faint relief that would correspond to the tarsal bones associated to digits IV and V. The inner-proximal part of the sole is not imprinted. Considering the imprinted parts of the sole and the relative depth pattern of the digit imprints (with imprints of digits IV and V being the deepest), pes tracks indicate a marked lateral functional prevalence of the autopodium.

Trackway: Tracks are arranged in couples or sets, with pes tracks immediately behind or partially overstepping (overprinting) manus tracks (Fig. 2). The divergence angle between manus and pes tracks ranges between 7° and 33°. Manus tracks are slightly closer to the midline than pes tracks. Trackways are composed of completely alternating manus-pes sets, they are relatively narrow, with a high pace angulation (132–148° for the pes, 151° and 159° for the manus) and long paces and strides (pace: 269–268 mm for the pes, 170–284 mm for the manus; stride length: 449–482 mm for the pes, 442 and 471 mm for the manus; foot length/stride length ratio: 0.156–0.185). No tail nor belly traces are preserved. All these features (Table 2) indicate a narrow gauge and a relatively upright posture of the limbs of the trackmaker, denoting a parasagittal locomotion (see discussion below). The gleno-acetabular distance of the trackmaker inferred from the trackways is of 276 to 295 mm. Pes tracks are rotated inwards or subparallel to the trackway midline; manus tracks are rotated inwards. In the trackways, pes imprints are notably much better preserved than manus imprints (Figs. 2, 5B).

5. Discussion

5.1. Ichnotaxonomic remarks

The size range of the tracks herein studied is relatively wide (Table 1), yet their morphology and trackway parameters remain quite consistent (Figs. 2–5; Table 2). Therefore, all these tracks are referred to the same morphotype: *Algarpes ferus* igen. *et* isp. nov.

The combination of features from both tracks and trackways from Mallorca herein described show that they were produced by quadrupedal tetrapods with marked heteropody, with both manus and pes being pentadactyl and with clawed digits. This readily rules out *Batrachichnus*, *Limnopus*, and *Matthewichnus*, which have a tetradactyl manus, clawless digit imprints, and are attributed to non-amniotes (usually temnospondyls and/or lepospondyls) (Voigt, 2005; Marchetti et al., 2025). The presence of claw traces also rules out *Amphisauropus* and *Ichniotherium*, which have a pentadactyl manus but are clawless. Besides, these ichnogenera display a notably different morphology of both manus and pes, and a much weaker heteropody than the tracks from Mallorca. In the same way, the strong heteropody (pes much larger than manus tracks) plus the weak ectaxony of the tracks from Mallorca differ from coeval (or similarly aged) ichnotaxa such as *Hyloidichnus* (represented by two morphotypes on Mallorca, see Matamales-Andreu et al., 2022, 2023), "*Merifontichnus*" (recently found as a junior synonym of *Hyloidichnus*: Marchetti et al., 2025), *Varanopus*, *Erpetopus*, *Dromopus* (also present on Mallorca, see Matamales-Andreu et al., 2022), and *Rhynchosauroides*. The tracks studied herein also differ from *Pachypes* (potentially present on Mallorca, see Matamales-Andreu et al., 2022) because tracks of this ichnogenus (correlated to pareiasauromorphs) display relatively short and wide digit imprints (Marchetti et al., 2021). Another major difference is in the relative depth pattern: in the

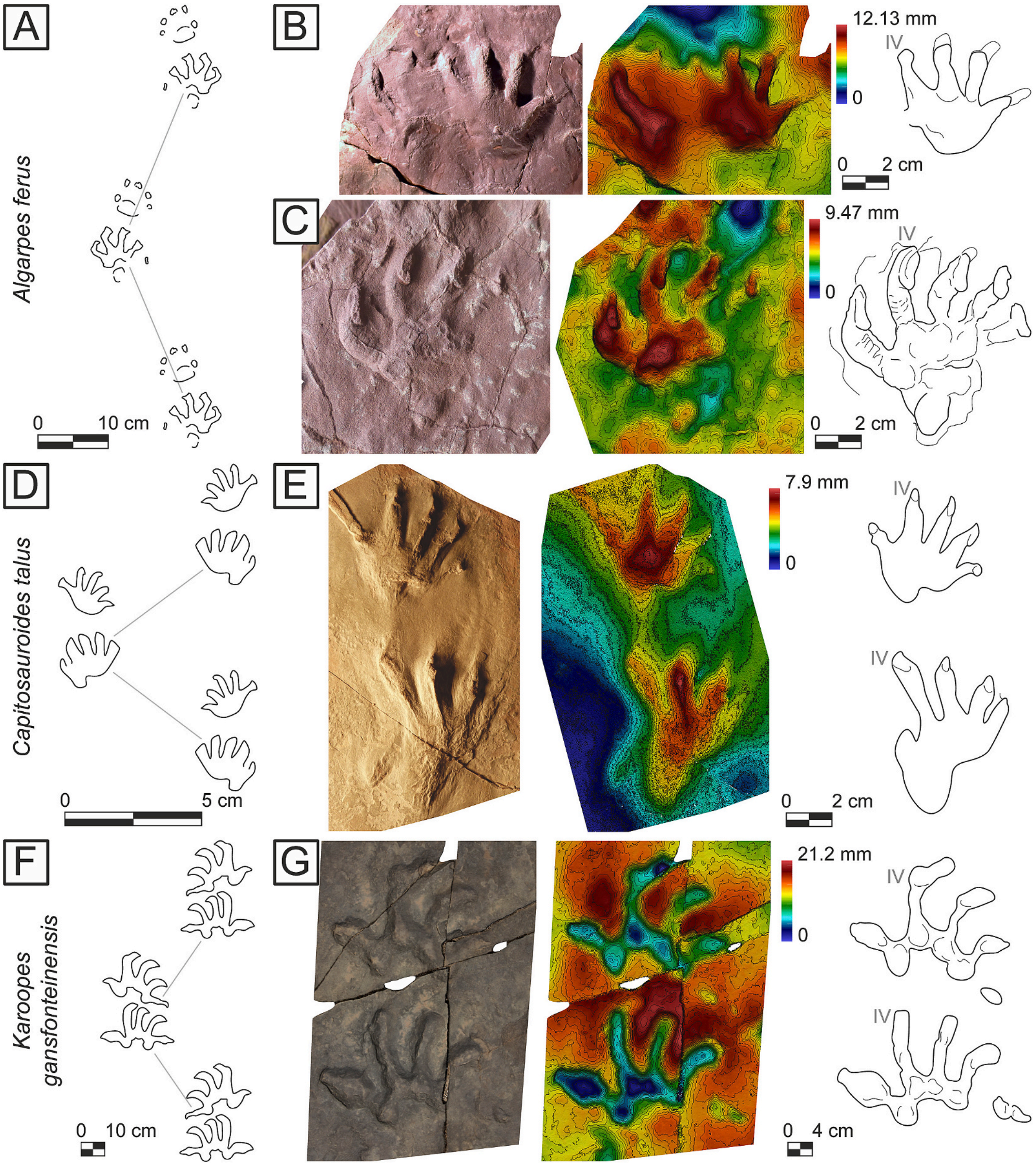

Fig. 6. Comparison of *Algarpes ferus* igen. *et* isp. nov. (A–C) with *Capitosauroides talus* (D, E) and *Karoopes gansfonteinensis* (F, G), including idealised trackways (A, D, F) and exemplary manus and pes tracks (B, C, E, G) of the three ichnotaxa. Specimens in B and G are mirrored for a better comparison. Idealised trackways of *C. talus* (D) and *K. gansfonteinensis* (F) modified from Matamales-Andreu et al. (2021). 3D model of *K. gansfonteinensis* (G) modified from Marchetti et al. (2019a) and Mujal et al. (2020), photograph of *C. talus* (E) modified from Marchetti et al. (2022).

specimens from Mallorca, manus imprints are deeper median-laterally, and pes imprints are notably deeper laterally, whereas tracks attributed to all aforementioned ichnotaxa are deeper medially or median-medially (see Mujal et al., 2020). As discussed by these authors, relative depth patterns of the tracks may correlate to the functional prevalence of autopodia, which may be linked to phylogeny. In this sense, the tracks of Mallorca indicate a lateral (or median-lateral) functional prevalence of autopodia, which is a state generally attributed to synapsids (Mujal et al., 2020). Indeed, this is in agreement with the anatomical features of the studied tracks that, as detailed below, are comparable to those observed in ichnotaxa correlated to synapsid, and, more specifically, therapsid trackmakers.

The morphologies of both manus and pes tracks of *Algarpes ferus* differ from most Permian/Triassic ichnotaxa correlated to synapsid trackmakers (*e.g.*, Marchetti et al., 2019a: fig. 9; Matamales-Andreu et al., 2021: fig. 4; Marchetti et al., 2025). *Dimetropus* presents proportionally longer sole imprints, thinner and straight digit imprints, usually with only the distal part well impressed (although this latter feature resembles some manus imprints here described: Figs. 3D, 4C, 5A). *Tambachichnium* presents low heteropody, a very well-marked ectaxony, relatively long digit imprints (giving an overall elongated and slender morphology to the tracks), and a digit V imprint in both manus and pes rotated outwards and proximally positioned, separated from the rest of the digit imprints. *Brontopus giganteus*, *Dolomitipes* and *Dicynodontipus* generally show a much lower degree of heteropody (even with the manus larger than the pes in some *Dolomitipes*), relatively shorter and more rounded digit imprints, and no overstepping, with the manus imprint always anteriorly positioned with respect to the pes imprint. *Brontopus antecursor* presents high heteropody, but the other features of this morphotype are like those of the aforementioned ichnotaxa, and the pes tracks of this ichnospecies have a characteristic hourglass shape (Marchetti et al., 2019a; De Jaime-Soguero et al., 2023), differing from the almost equidimensional, or even wider than long pes tracks of Mallorca. Therefore, the tracks from Mallorca cannot be attributed to any of these ichnotaxa either.

Among tracks correlated to therapsid synapsid trackmakers, *Algarpes ferus* is most similar to the ichnospecies *Capitosauroides talus* and *Karoopes gansfonteinensis* (Fig. 6), known from the Permian of central and southern Pangaea, respectively (Marchetti et al., 2019a, 2019c, 2022; Buchwitz et al., 2020). These ichnotaxa show some anatomical characters and relative depth patterns consistent with biarmosuchian, dinocephalian, gorgonopsian, and therocephalian trackmakers, but their absolute sizes, degrees of heteropody and age ranges suggest that *Capitosauroides* was produced by therocephalians and *Karoopes* by gorgonopsians (Marchetti et al., 2019a; but see Jones et al., 2021, who alternatively suggested dinocephalians as the potential trackmakers of *Karoopes*). Manus and pes track morphology, and trackway pattern of *C. talus* and *K. gansfonteinensis* are here compared in detail with the Mallorcan specimens. Despite superficial similarities among these three track morphtypes (Fig. 6), their analysis reveals key anatomical differences. The identified similarities are most probably related to the potential trackmakers, all corresponding to therapsids (see also section 5.2 below).

The shape of the manus tracks from Mallorca is somewhat similar to that of *Capitosauroides talus*, known from the Guadalupian of Saxony-Anhalt, Germany, and the Massif Central, France (Buchwitz et al., 2020; Marchetti et al., 2022) and the Lopingian of the Italian Alps (Marchetti et al., 2019c, 2022). They present a similar overall shape, with slender digit imprints and a deeply impressed palm (Fig. 6B, E); also, both display a digit V imprint only slightly longer than digit I. In both *C. talus* and the tracks of Mallorca manus imprints are weakly ectaxonic, although not all specimens of *C. talus* display a slightly longer digit IV (see parameters in Buchwitz et al., 2020 and Marchetti et al., 2022). The main difference is in the morphology of the proximal margin of the palm imprint, which is concave in *C. talus* and convex in the tracks of Mallorca. In addition, most of the manus tracks of Mallorca are mainly composed of round to oval digit tip and palm imprints (with only one exception; Fig. 4A), whereas manus tracks of *C. talus* usually preserve the complete imprint of the digits.

The pes tracks of *Algarpes ferus* are morphologically reminiscent of those of *Karoopes gansfonteinensis* from the uppermost Guadalupian of South Africa (Marchetti et al., 2019a). However, significant differences exist in the pes track morphology of both *K. gansfonteinensis* and *C. talus* (Marchetti et al., 2019a, 2022, 2025; Buchwitz et al., 2020; Fig. 6C, E, G), indicating that they were produced by animals with a different pes anatomy: (1) The relative position, proportions and shape of digit V is notably different; in the tracks of Mallorca the digit V is more proximally positioned (close to digit IV, not separated from the group I-IV as it is in *K. gansfonteinesis* and *C. talus*), longer than digit III (whereas digit V is as long as digit I in *C. talus*, and as long as digit III in *K. gansfonteinensis*), anteriorly oriented, and curved inwards (being straight or curved outwards, and directed outwards in both *K. gansfonteinensis* and *C. talus*). (2) The pes of *Algarpes ferus* displays an oval-shaped imprint proximolaterally positioned (at the height of digit V), which is generally well separated from the rest of the track (even from the metatarsal-phalangeal pad impression), and may correspond to the impression of the calcaneum (see section 5.2 below); in both *K. gansfonteinensis* and *C. talus* such proximolateral imprint may also be present, but, when present, it is always connected to the rest of the pedal imprint through the outer side of the metatarsal-phalangeal joint. (3) The digit imprints of the pes tracks of Mallorca are more inwardly curved than those of *K. gansfonteinensis* and, especially, *C. talus*. (4) The digit tips of the pes tracks of Mallorca are characterised by notably large and deep claw traces, which are oval-shaped and located in the inner side of the digits, giving a hook shape to the digit tip imprints; instead, in *K. gansfonteinensis* claw traces are smaller and less well-differentiated from the rest of the digit imprints, and in *C. talus*, claw traces are circular to triangular (generally much more equidimensional than in the tracks of Mallorca) and located anteriorly to the digit imprints. The relative depth pattern of the pes tracks is more similar between *Algarpes ferus* and *K. gansfonteinensis* (tracks markedly deeper laterally) than with *C. talus* (tracks deeper median-laterally). The overall set of differences is most likely linked to the anatomy of the autopodium, and position of limbs, rather than to different locomotion gaits. Of note, even if pes tracks are somewhat reminiscent of those of *K. gansfonteinensis*, the manus track morphology is markedly different. In this ichnospecies, manus and pes tracks are of similar morphology and size (Fig. 6G), whereas *Algarpes ferus* is strongly heteropodic and the overall morphology and proportions between manus and pes imprints are different (Table 1).

The trackways of *Algarpes ferus* (Figs. 2, 5B, 6A) show a combination of features that are not observed in any other Permian/Triassic ichnotaxon correlated to synapsid trackmakers (including also *Karoopes gansfonteinsensis* and *Capitosauroides talus*), which generally present a relative depth pattern that indicates a lateral, and/or median-lateral, functional prevalence of autopodia (see Mujal et al., 2020). This unique combination of features includes: (1) marked heteropody, with pes tracks notably larger than manus tracks, as well as with a different morphology, (2) narrow gauge with high pace angulation, (3) long strides and paces, and (4) manus tracks rotated inwards and pes tracks slightly rotated inwards to subparallel to the midline (Fig. 6A; Table 2). The morphological consistency of all the tracks and trackway patterns, with important size differences (67–106 mm pes length; Table 2), suggests that the unique morphology of *Algarpes ferus* is not a result of trackmaker size, ontogeny, extramorphology, or peculiar gait, but represents a strong anatomical signal of the producer. Conversely, in trackways of *Capitosauroides talus* the pes is parallel to rotated outwards to the midline, the pace angulation is relatively low, resulting in short stride lengths and an overall wide trackway (Fig. 6D; Buchwitz et al., 2020), being significantly different to *Algarpes ferus* (Fig. 6A). *Karoopes gansfonteinensis* trackways are also narrow and with high pace angulation (Fig. 6F), some trackways show a partial to complete overstepping of the manus by the pes, and the pes is parallel to slightly rotated otwards to the midline (Marchetti et al., 2019a, 2025); however, as stated above, manus and pes tracks of *K. gansfonteinensis* are very similar in morphology and size (homopody), features differing from *Algarpes ferus* (heteropody).

For all the reasons above, the attribution of the morphotype herein studied to *Capitosauroides* or *Karoopes* is ruled out (*Karoopes* is so far monospecific, and the other ichnospecies of *Capitosauroides*, *C. bernburgensis* from the Triassic of the Central European Basin, displays a notably different track morphology, especially in the manus imprints, see Buchwitz et al., 2020). This suggests that most of (if not all) the described features reflect the anatomy of the autopodia and bauplan of the trackmaker, and thus no extramorphological features nor locomotion or gait play a significant role in the described tracks and trackways. Therefore, considering also the morphological preservation (*sensu* Marchetti et al., 2019b) of the track sample (Table 1), and the presence of two trackways (plus partial step cycles: Fig. 5B) with a consistent pattern (Table 2), all the specimens from Mallorca herein described are here attributed to the new ichnotaxon *Algarpes ferus*. In the following section, these tracks are correlated to the potential trackmakers, gorgonopsian therapsids.

5.2. Track-trackmaker correlation

The relatively good morphological preservation (*sensu* Marchetti et al., 2019b) of most of the pes tracks and a few manus tracks (Table 1), as well as the presence of complete step cycles, makes it possible to propose a detailed anatomy-based correlation to the potential producer (s) (Fig. 7). This has been done for other Permian ichnotaxa, such as *Amphisauropus*-seymouriamorphs (Marchetti et al., 2017), *Ichniotherium*-diadectomorphs (Voigt et al., 2007; Buchwitz and Voigt, 2018; Mujal and Marchetti, 2020), *Hyloidichnus*-captorhinomorphs (Logghe et al., 2021), *Hyloidichnus*-moradisaurine captorhinids (Matamales-Andreu et al., 2023), and *Pachypes*-pareiasauromorphs (Marchetti et al.,

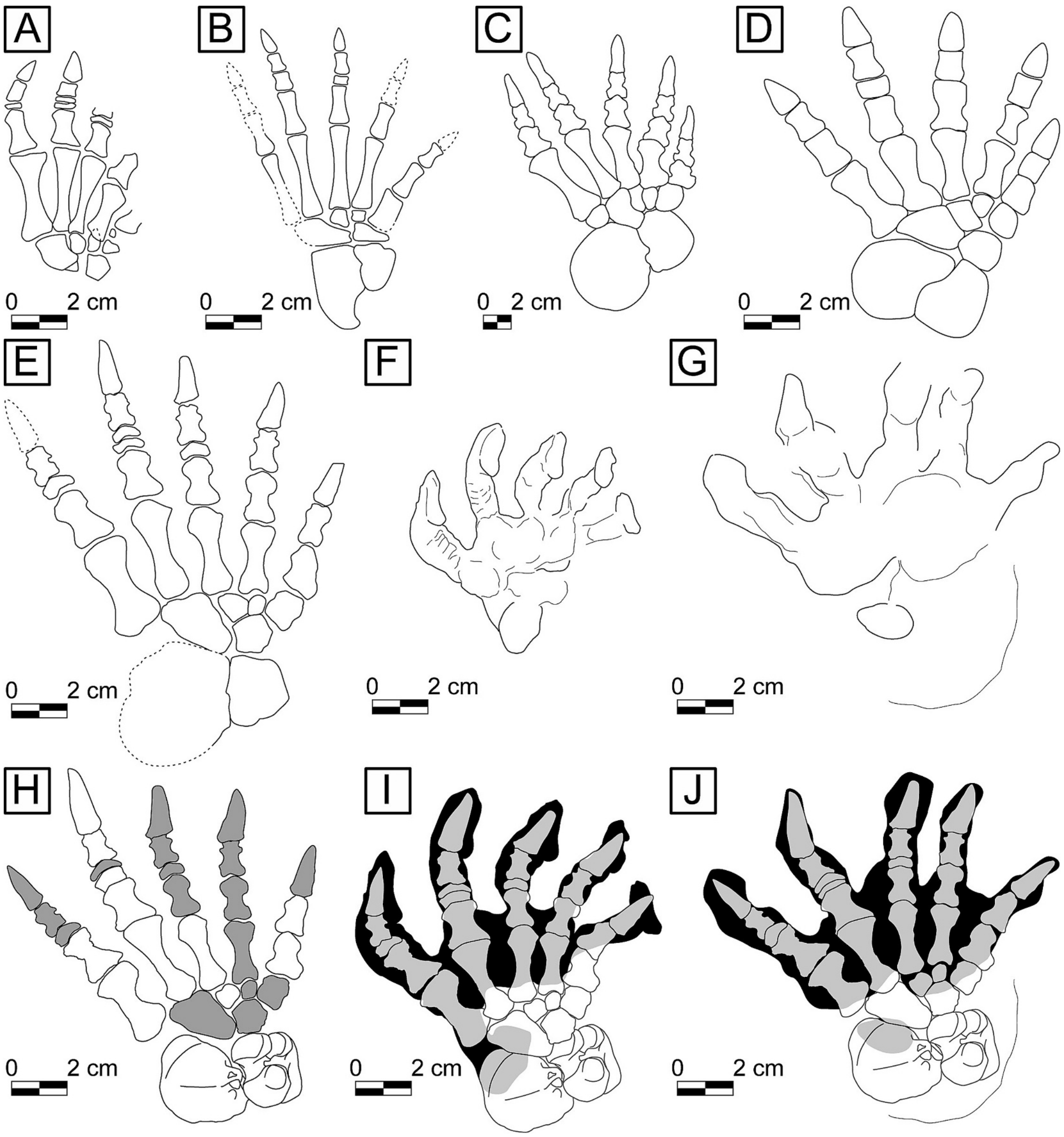

Fig. 7. Track-trackmaker correlation of *Algarpes ferus* igen. *et* isp. nov. with therapsids. A–E: Left pedes of biarmosuchian *Biarmosuchus tener* (A, redrawn and mirrored from Sigogneau and Tchudinov, 1972), biarmosuchian *Hipposaurus boonstrai* (B, redrawn and mirrored from Boonstra, 1965), dinocephalian *Titanophoneus potens* (C, redrawn and mirrored from Orlov, 1958), gorgonopsian *Lycaenops ornatus* (D, redrawn from Colbert, 1948), Gorgonopsia indet. (E, drawn and mirrored from Sidor, 2022). F, G: Pes tracks of *Algarpes ferus*, including the best-preserved (F) and largest (G) specimens. H: Reconstructed left pes of the gorgonopsian from Mallorca (DA21/17–01-01, some elements are mirrored, elements in grey are missing from the original specimen; see details in Matamales-Andreu et al., 2024). I, J: Correlation and reconstruction of the gorgonopsian pes from Mallorca overlapping pes tracks of *Algarpes ferus* (those in F and G); note that track in I is enlarged to fit with the bones, and that track and bones in J are at the same scale.

2021). The lateral and median-lateral functional prevalence inferred from the tracks herein studied points to synapsids as the potential trackmakers (Mujal et al., 2020), and this is in accordance with the resemblance of *Algarpes ferus* igen. *et* isp. nov. with *Capitosauroides talus* and *Karoopes gansfonteinensis* (see section 5.1 above), which have been correlated to theriodont therapsids (Marchetti et al., 2019a, 2022; Buchwitz et al., 2020). Indeed, the relative length of the imprints of the pes digits of *Algarpes ferus*, their proportions with respect to the sole impression, and the oval-shaped impression posterolaterally positioned are consistent with the pedal morphology of several groups of early therapsids such as biarmosuchians, dinocephalians, gorgonopsians and therocephalians (*e.g.*, Colbert, 1948; Romer, 1956; Orlov, 1958; Boonstra, 1964, 1965, 1966; Sigogneau and Tchudinov, 1972; Sigogneau-Russell, 1989; Gebauer, 2014; Sidor, 2022; Bendel et al., 2023; Fig. 7A–E). Detailed features of *Algarpes ferus* include: (1) ectaxony, with pedal digit IV being the longest, and a relative long digit V (only slightly shorter than digit IV); (2) large claw impressions that fit well with the large unguals of those groups; (3) deeply impressed metatarsal-phalangeal joint (characteristic of synapsid tracks) that corresponds to the wide ends of the metatarsals, particularly those of digits III to V; (4) oval-shaped impression posterlaterally positioned in the sole that agrees with the large calcaneum and its position in those groups (Fig. 7F, G). Attributing *Algarpes ferus* to one of the early therapsid groups mentioned above is no easy task, as the autopodial morphology remains undescribed for most of their species. Moreover, even considering the taxa in which the autopodia are well-known, they appear to have a fairly conserved morphology, showing a remarkably similar general structure. In such cases, resorting to the co-occurring body fossil record is the only way to shed some light on this question (*e.g.*, Voigt et al., 2007; Matamales-Andreu et al., 2023).

Apart from tetrapod tracks, the Port des Canonge Formation contains several bone beds that have produced remains of different tetrapod taxa

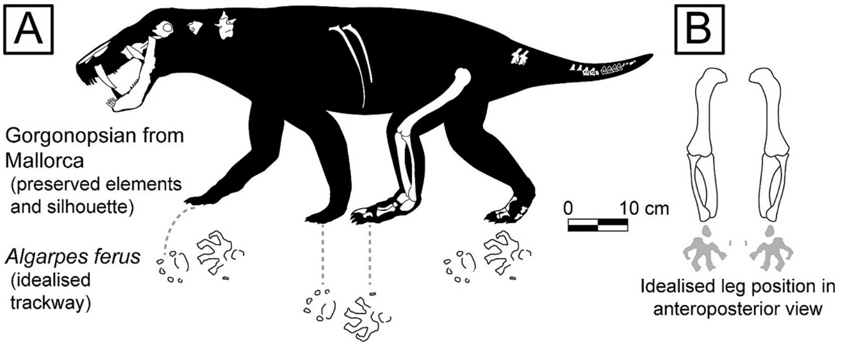

Fig. 8. Trackmaker posture during locomotion inferred from *Algarpes ferus* igen. *et* isp. nov. A: Correlation of the idealised trackway with the interpretative silhouette and skeletal elements of the gorgonopsian from Mallorca (silhouette modified from Matamales-Andreu et al., 2024). B: Inferred position of the legs of the trackmaker, based on the distance between consecutive pes tracks in the trackways; outlines of femur, tibia and fibula based on the preserved elements of the gorgonopsian from Mallorca.

(Matamales-Andreu et al., 2023, 2024). Particularly interesting is a partial skeleton of a gorgonopsian therapsid that has been found 46 m stratigraphically below the tracksite containing *Algarpes ferus* (Matamales-Andreu et al., 2024; Fig. 1B). This specimen (DA21/17-01-01) preserves several elements of the left and right pedes, allowing for a nearly complete reconstruction of the pes (Fig. 7H). Such reconstruction, with the missing elements taken from the gorgonopsian pes studied by Sidor (2022), fits exactly with the tracks of *Algarpes ferus*. The preserved skeletal elements in the gorgonopsian from Mallorca (Matamales-Andreu et al., 2024), all fitting with the tracks include an almost complete digit IV, metatarsal and first phalange of both digits I and V, metatarsal 3, and the calcaneum. Noteworthy, the wide distal end of the metatarsals matches the deep impression of the metatarsal-phalangeal area in *Algarpes ferus*. In addition, even if the restored pes of the Mallorcan gorgonopsian using elements from the specimen of Sidor (2022) is hypothetical, the size and proportions in the shared elements is almost the same, and reconstructed elements fit also with the tracks. Remarkably, in the holotype trackway and paratype pes (Figs. 2, 3, 4B) the only difference is size (Fig. 7I) but, in the largest tracks (Fig. 5), the bones fit also in size (Fig. 7J).

Overall, these comparisons provide a reasonably confident correlation of the pes tracks and the skeletal remains. In addition, the partial overstepping of some pes tracks to manus tracks of *Algarpes ferus* and the inward rotation of the manus and inward rotation to subparallel orientation of the pes with respect to the trackway midline (Table 2) suggest an upright posture for the gorgonopsian of Mallorca (Fig. 8).

5.3. Locomotion

Therapsid synapsids developed a suite of morphological innovations from the basal 'pelycosaur' body plan. Those affected different aspects of their biology, including, among others, a more specialised dentition, the possible presence of a soft secondary palate and more complex nasoturbinals, the beginning of reorganisation of the bones associated to sound reception, and the modification of girdle joints, shifting from a sprawled to a more upright posture (Kemp, 2006).

This change of posture had a profound impact on the locomotion and, as a consequence, on the track arrangement in the produced trackways (Kubo and Benton, 2009; Jones et al., 2021). The study of the girdle joints of early therapsids suggests that their front limbs were still anatomically constrained to adopt a sprawled posture, whereas the hind limbs could facultatively switch between a sprawled and a more upright posture (Kemp, 1982, 2005). Therefore, early therapsids could produce trackways with low pace angulation values and wide gauges, similar to those made by 'pelycosaurs' and other amniotes, but they also were able to move with a narrower gauge and a wider pace angulation (Marchetti et al., 2019a; see also discussion in Jones et al., 2021).

The trackways of the new ichnotaxon described herein, *Algarpes ferus* igen. *et* isp. nov., show a distinctly narrow gauge and a very high pace angulation (Figs. 2, 5B; Table 2), especially when compared to other latest Cisuralian–early Guadalupian ichnotaxa attributed to synapsids (see Marchetti et al., 2019a). The relatively long stride, together with very high pace angulation and the pes parallel to slightly rotated inwards, which characterise the trackways of *Algarpes ferus*, most probably show that the trackmaker moved on an upright posture and a low (if any) lateral bending of the trunk. This is in contrast with what is observed in more primitive synapsids, the trackways of which (*e.g.*, *Dimetropus*) show low stride length and pace angulation, which would have been compensated with a lateral bending of the trunk (Hopson, 2015). At the same time, this is in line with the findings of Jones et al. (2021), who suggested a new, more complex paradigm for the evolution of mammalian locomotion. This would include an increase in the sagittal bending of the posterior portion of the trunk, plus a general regionalisation of the vertebral column (Jones et al., 2021), a set of characteristics that seem to be hinted at the trackways of *Algarpes ferus*.

The Permian ichnogenera *Capitosauroides* and *Karoopes*, with tracks reminiscent to *Algarpes ferus* (Fig. 6), show trackway values indicative of a different locomotion style (see Marchetti et al., 2019a, 2022, 2025; Buchwitz et al., 2020), possibly with a more sprawled posture in both the front and hind limbs. Especially, the relatively low pace angulation and stride length observed in *C. talus* would indicate that the potential trackmakers, even if those were (early) therapsids, still had a sprawling posture and performed lateral bending of the trunk as suggested for primitive synapsids (Hopson, 2015). Similarly, Jones et al. (2021) suggested also a lateral bending of the trunk for the trackmaker of *Karoopes*. This would indicate that, hypothetically, in the early steps of their evolution, therapsids had a relatively diverse locomotor repertoire.

Overall, such trackway variability in an otherwise morphologically conservative group is striking, but it could be explained by the effect of size and stoutness, as well as by slight morphological variations on the limb and manus/pes structure among gorgonopsian species. Most of the studies on gorgonopsian anatomy have focused on the skull remains, and the postcrania of most species remain undescribed or are yet to be found, so this question cannot be solved at present. In any case, the correlation of *Algarpes ferus* to gorgonopsian trackmakers proposed herein confirms that the ability to walk in a primitive upright posture had been already acquired in the early/?middle Permian by, at least, some species of medium-sized gorgonopsians.

6. Conclusion

In this paper, we have described a new tetrapod ichnotaxon from the palaeoequatorial Permian of Mallorca (western Mediterranean), *Algarpes ferus* igen. *et* isp. nov., correlating it to potential gorgonopsian therapsid trackmakers. This attribution has been possible thanks to the gorgonopsian pes bones present in the same section and formation, which match the pes tracks in terms of morphology and proportions, and in some cases also in size. The tracks herein described are among the oldest ichnofossils confidently attributed to therapsid trackmakers, as they date to the lower/?middle Permian. Despite its age, the trackway parameters, with narrow gauges and wide pace angulation values, show that the trackmakers walked in a relatively upright posture and parasagittal gait. This suggests that early/?middle Permian therapsids had already acquired part of the anatomical modifications that contributed to the shift from sprawled posture, typical of sauropsids and 'pelycosaur'-grade synapsids, to the upright posture that would characterise the derived therapsids, *i.e.*, mammals and their kin.

CRediT authorship contribution statement

Rafel Matamales-Andreu: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Eudald Mujal:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Àngel Galobart:** Writing – review & editing, Validation, Methodology, Funding acquisition. **Josep Fortuny:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors of the present paper thank Sebastià Matamalas, Josep Juárez and Chabier De Jaime-Soguero for aid in fieldwork. Alejandro Serrano-Martínez (ICP) and Lucrezia Ferrari (SMNS) are thanked for help in the processing of the 3D photogrammetric models. We acknowledge Marina Rull and Xènia Aymerich for technical support in the creation of casts at the ICP lab. We are grateful to Lorenzo Marchetti and Christian F. Kammerer for fruitful discussions. We thank the comments by Sebastian Voigt, Christian Sidor and an anonymous reviewer, which helped to improve a previous version of the manuscript, as well as the editor Howard Falcon-Lang for handling the manuscript. To the Comissió Insular de Patrimoni Històric and Servei de Patrimoni Històric (Consell de Mallorca) for granting us the excavation permits (file number 75/2021). R.M.A. was supported by the predoctoral grant FPU17/01922 (Ministerio de Ciencia, Innovación y Universidades) and the grant Synthesys+ DE-TAF-23 (European Commission). This work has been further supported by the Generalitat de Catalunya (consolidated research groups 2021 SGR 01184 to J.F. and 2021 SGR 01192 to À.G., and the CERCA programme [ICP]). This work is part of the Ramón y Cajal grant to J.F. [RYC2021–032857-I] financed by MCIN/AEI/10.13039/501100011033 and the European Union 'NextGenerationEU'/PRTR. We acknowledge support from the projects "Mallorca abans dels dinosaures: estudi dels ecosistemes continentals del Permià i Triàsic amb especial èmfasi en les restes de vertebrats" (ref. 15–619/2020) and "Els primers avantpassats dels mamífers i els moscards més antics del món: paleoecosistemes del Permià i Triàsic de Mallorca" (ref. 8–2024) based at the Institut Català de Paleontologia Miquel Crusafont and funded by the Departament de Cultura i Patrimoni (Consell de Mallorca).

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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