



# Historical Biology

An International Journal of Paleobiology



ISSN: (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/ghbi20>

## Large-sized pentadactyl carnivore footprints from the early Miocene fossil track site at Ipolytarnóc (Hungary): 3D data presentation and ichnotaxonomical revision

Gábor Botfalvai, János Magyar, Veronika Watah, Imre Szarvas & Péter Szolyák

To cite this article: Gábor Botfalvai, János Magyar, Veronika Watah, Imre Szarvas & Péter Szolyák (2022): Large-sized pentadactyl carnivore footprints from the early Miocene fossil track site at Ipolytarnóc (Hungary): 3D data presentation and ichnotaxonomical revision, Historical Biology, DOI: [10.1080/08912963.2022.2109967](https://doi.org/10.1080/08912963.2022.2109967)

To link to this article: <https://doi.org/10.1080/08912963.2022.2109967>

 View supplementary material 

 Published online: 16 Aug 2022.

 Submit your article to this journal 

 View related articles 

 View Crossmark data 



# Large-sized pentadactyl carnivore footprints from the early Miocene fossil track site at Ipolytarnóc (Hungary): 3D data presentation and ichnotaxonomical revision

Gábor Botfalvai<sup>a,b,c</sup>, János Magyar<sup>b,c</sup>, Veronika Watah<sup>d</sup>, Imre Szarvas<sup>e</sup> and Péter Szolyák<sup>d</sup>

<sup>a</sup>Department of Palaeontology and Geology, Hungarian Natural History Museum, Budapest, Hungary; <sup>b</sup>ELKH-MTM-ELTE Research Group for Paleontology, Budapest, Hungary; <sup>c</sup>Institute of Geography and Earth Sciences, Department of Paleontology, ELTE Eötvös Loránd University, Budapest, Hungary; <sup>d</sup>Herman Ottó Museum, Miskolc, Hungary; <sup>e</sup>Subregional leader, Bükk National Park Directorate, Ipolytarnóc, Hungary

## ABSTRACT

Ipolytarnóc is one of the most important Cenozoic fossil trackway sites in Europe. Most of the discovered footprints were investigated in 1985; however, a considerable period has elapsed since those investigations, and during that time significant advances have been made in the field of 3D imaging. Given this fact, the present study was undertaken to carry out a new analysis of the Ipolytarnóc fossil tracks, with a view to present possible revisions of current knowledge. In line with this, detailed ichnotaxonomical analyses were conducted on two large-sized pentadactyl footprint types using high-quality 3D models. As a result of the investigations presented in this paper, the largest pentadactyl footprint-type (previously defined as *Bestiopedia maxima*) was reclassified under the *Platykopus* ichnogenus based on new materials and their 3D models. The *P. maxima* footprints are believed to represent those of large-sized Amphicyonidae. Thorough ichnotaxonomical analyses were performed on other pentadactyl fossil tracks which had been attributed to *Carnivoripeda nogradensis*. The aim of the analyses was to suggest an extension of the morphological characters of these ichnospecies. In contrast to the previously suggested Nimravidae origin, we rather suggest that the *C. nogradensis* footprints belong to a mustelid-like carnivore based on its footprint morphology.

## ARTICLE HISTORY

Received 14 July 2022  
Accepted 31 July 2022

## KEYWORDS

Footprints; trackway;  
mammals; 3D; carnivores

## Introduction

Ipolytarnóc is one of the most diverse and important Miocene fossil track sites in Europe. Over the last 120 years more than 3000 vertebrate footprints belonging to at least eleven species were discovered at this locality (e.g. Böckh 1902; Tasnádi Kubacska 1976; Kordos 1985, 1987; Kordos et al. 2021). The site is situated in the northern Hungarian part of the Carpathian Basin, in Nógrád County, near the Hungarian-Slovakian border. The area is now a main gateway of the Novohrad-Nógrád UNESCO Global Geopark (Szarvas 2007; Figures 1(A-B)).

The first mammal and bird footprints were discovered in 1900 by Hugó Böckh, when he went to Ipolytarnóc in order to study a giant silicified tree trunk embedded in a sandstone–tuff transition (Böckh 1902). After the first discoveries, a large-scale excavation of the footprint bearing-sandstone beds was conducted in 1937 at the Ipolytarnóc site under the leadership of A. Tasnádi Kubacska (from the Hungarian Natural History Museum). This led to the discovery of further traces including the first pentadactyl carnivore traces (Tasnádi Kubacska 1976 and see below). The first carnivore footprint from Ipolytarnóc was mentioned by Abel (1935), who presented a photo and gave a short description of this footprint and interpreted it as a left manus imprint of a large carnivore such as Amphicyon or ‘a large Felidae (Machairodus?)’ (see details below). In 1965, O.S. Vialov (from Lvov, USSR) described rhinoceros footprints from Ipolytarnóc and named them *Rhinoceripeda tasnadyi* (Vialov 1965). The first detailed ichnotaxonomical work was published in 1985 by L. Kordos (Hungarian Geological Institute), who identified four birds (*Ornithotarnocia*

*lambrechti*, *Aviadactyla media*, *Tetraornithopedia tasnadii* and *Passeriopedia ipolyensis*) and six mammalians (*Bestiopedia maxima*, *Carnivoripeda nogradensis*, *Bestiopedia* sp., *Mustelipeda punctata*, *Megapecoripeda miocaenica* and *Pecoripeda* cf. *amalphaea*) ichnotaxa from the Ipolytarnóc area (for further details see Kordos 1985). In the same year – but a few months later – O.S. Vialov also published independently and in parallel with the work of Kordos, another detailed ichnotaxonomical paper about the trace fossils of the Ipolytarnóc site and described three mammals (*Bestiopedia hungarica*, *Bestiopedia böckhi* and *Bestiopedia tarnocensis*) and one reptile (*Paruusipeda gemmea*) ichnospecies (Vialov 1985). Since the ichnospecies name of Kordos (1985) was published a few months earlier than Vialov’s work, the new taxa named by L. Kordos have priority over those of Vialov (1985). However, the ichnotaxonomic results of both authors were summarised by Kordos (1987) and he concluded that:

- *Bestiopedia hungarica* Vialov 1985 is a junior synonym for *Carnivoripeda nogradensis* Kordos 1985, because both names are based on the same holotype.
- *Bestiopedia böckhi* Vialov 1985 is a junior synonym of *B. maxima* Kordos 1985, because both names are based on the same figure as Abel (1935) (see details below).
- *Bestiopedia tarnocensis* Vialov 1985 is a valid name for the tetradactyl carnivore footprints of Ipolytarnóc which was characterised as *Bestiopedia* sp. in Kordos (1985).
- *Paruusipeda gemmea* Vialov 1985 is a junior synonym for *Mustelipeda punctata* Kordos 1985, because Kordos (1987)

suggested these digitigrade pentadactyl footprints originated from a medium-sized mustelid and not from a reptile.

After this summary work, only a few short publications on the Ipolytarnóc traces were published (e.g. Kordos and Morgós 1988; Szarvas 2007; Hágen et al. 2014; Kordos et al. 2021) and only *Pecoripeda* cf. *amalphaea* was reclassified as a new species, named as *Pecoripeda hamori* by Vialov (1986).

Most of the ichnospecies names described from Ipolytarnóc are frequently cited in the international literature (e.g. McDonald et al. 2007; Costeur et al. 2009; Lockley and Harris 2010; Abbassi et al. 2015; Melchor et al. 2019). However, a considerable period of time has elapsed since the description of these trace fossils and the significant advances in 3D imaging capabilities would seem to justify a new examination of the traces from Ipolytarnóc.

The examination of the large-sized pentadactyl carnivore footprints discussed in this paper is of paramount importance, since only contemporary, poor-quality images of these traces were available in the original work of Kordos (1985). These images have often led to misinterpretation of details about the traces (e.g. López et al. 1992; Sarjeant et al. 2002 and see below). Furthermore, research over the past years has led to the discovery of several pentadactyl footprints and trackways that were previously unknown. These have contributed greatly to the understanding of the ichnotaxonomic position and palaeobiological features of the traces described here. Finally, the pentadactyl carnivore tracks from the Ipolytarnóc site are of great scientific significance, as the 17 million-year age of the site (Pálfy et al. 2007) suggests that it is possible to look back to a period in the Earth's history when changes in the composition of carnivore mammal faunas were taking place worldwide (Barry et al. 1985; Eizirik et al. 2010; Werdelin et al. 2010; Domingo et al. 2014 and references therein). With the gradual disappearance of early predators (e.g. Amphicyonidae, Hyaenodontidae, Creodonta), the families Felidae, Canidae and Ursidae (recognised as the modern-day carnivore groups) came to the fore (McLellan and Reiner 1994; Viranta 1996; Peigné 2003; Werdelin et al. 2010; Domingo et al. 2014; Morales et al. 2015; Krapovickas and Vizcaíno 2016 and references therein). In connection with this, a thorough understanding of the taxonomic affiliation of the Ipolytarnóc footprints is relevant for interpreting this transition.

This study focuses on the large-sized plantigrade pentadactyl footprints of the Ipolytarnóc area as represented by two different ichnospecies (*Platykopus maxima* and *Carnivoripeda nogradensis*, see below). The tetradactyl footprint of *Bestiopeda tarnocensis* Vialov 1985 and the small-sized digitigrade footprints of *Mustelipeda punctata* Kordos 1985 are out of the scope of this study because further data are needed in order to be able to examine these footprints in more detail.

Here, many high-quality 3D models are presented of the Ipolytarnóc footprints (including holotypes and new materials), which greatly facilitates detailed examination and possible revision of the knowledge about these shallow traces. After a detailed description of the traces, an emended diagnosis has been added for these ichnospecies, and they are compared with other pentadactyl ichnospecies known from the international literature so that ichnotaxonomical conclusions can be formed. Finally, an attempt is made to determine the possible trackmakers for these ichnospecies.

## Geological Background

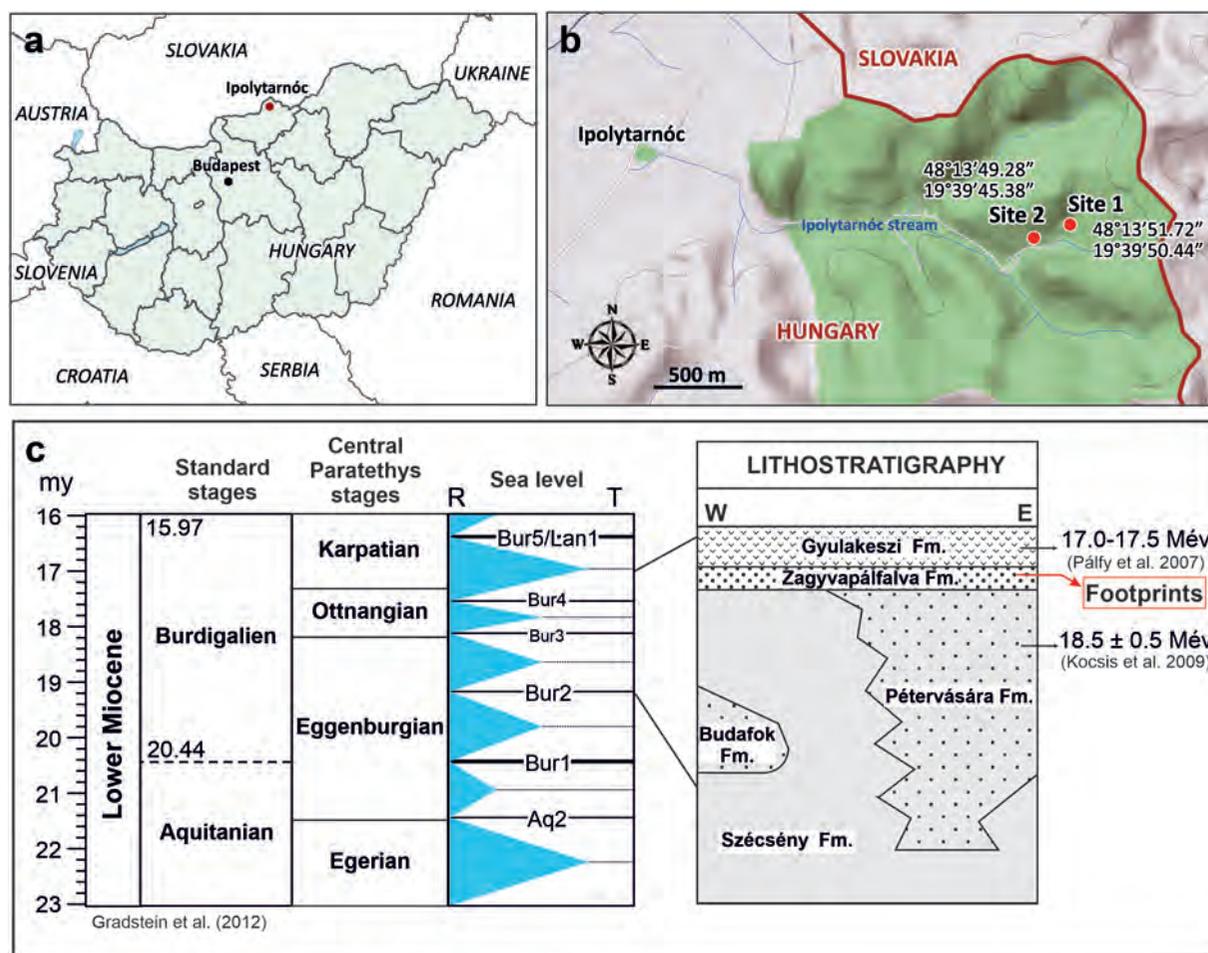
The 510-ha-large Ipolytarnóc Fossil Nature Conservation Area is situated in the North Hungarian zone of the Carpathian Basin (48° 14'12" N; 19°39'25" E; Figures 1(A-B)). It displays a classic

geological sequence of the Lower Miocene and safeguards a uniquely preserved ancient habitat, yielding a large number of high-quality fossils (Szarvas 2007; Kordos et al. 2021). The site has been protected by the state since 1944 and it is managed by the Bükk National Park Directorate.

Results of detailed geological and sedimentological investigations of the Ipolytarnóc area have already been published in several publications (e.g. Vadász 1963; Csepregyhé 1967; Bartkó 1985; Harangi 2001; Kocsis 2007; Pálfy et al. 2007; Karátson et al. 2022). Therefore, in this section of the present paper only a brief overview is given of the main characteristics of the geological background of this area.

The chronostratigraphic framework of the area is based on the Central Paratethys regional stages of the Eggenburgian, Ottnangian and Karpatian, and correlated with the standard Burdigalian stage (see Rögl 1998; Piller et al. 2007; Figure 1(C)). The oldest sediment is the uppermost part of the Szécsény Schlier Formation, which crops out in some places in the area (Bartkó 1985). Siltstone beds of the Szécsény Schlier Formation are interfingered with and overlain by the heterotopic glauconitic sandstone of the nearshore facies of the Pétervására Sandstone Formation (Sztanó 1994). At certain levels, the Pétervására Sandstone contains unusually abundant marine Eggenburgian mollusc fauna and shark teeth assemblages (Csepregyhé 1967; Kocsis 2007). This marine sandstone is in turn overlain by an unconformity – that is, by the terrestrial strata of the Zagyvapálfalva Formation (Bartkó 1985). The latter is represented by 1–8 m of fluvial conglomerate and sandstone overlain by 0–4 m of the track-bearing sandstone (also referred to as ‘the Ipolytarnóc footprint beds’). The whole sequence is capped by a 20–40 m-thick rhyolite called ignimbrite (Gyulakeszi Rhyolite Tuff Formation; Harangi 2001; Karátson et al. 2022). The radiometric measurements (Pálfy et al. 2007) and palaeomagnetic studies (Márton et al. 2007) of the rhyolite tuff of the Gyulakeszi Rhyolite Tuff Formation (which covers the most important footprint-bearing horizon) indicate an age of 17.0–17.5 Myr. This date correlates with the late Ottnangian regional stage of the Central Paratethys and the MN4 Mammal zone (Pálfy et al. 2007). The volcanics are covered by the Nógrádmegyer Member of the Salgótarján Browncoal Formation (rhyolite-tuff-bearing sandstone, variegated clay, and small-grained quartzite gravel conglomerate). Younger rocks have been eroded within the inner core of the investigated area.

The footprint-bearing beds of Ipolytarnóc are part of the uppermost zone of the Zagyvapálfalva Formation (Figure 1(C)), which contains thousands of animal tracks on its footprint horizons (Bartkó 1985; Kordos 1985; Szarvas 2007; Kordos et al. 2021). The alternating thick and thin lamination of the clayish and silty sandstone beds has a wide range of microrelief forms. Furthermore, the occasional dense plant cover around the braided river channel indicates frequent flooding and seasonal water oscillation in a subtropical rainforest environment (Hably 1985). The uppermost layer of the footprint-bearing sandstone is overlain by a thin siliceous limonite coating which easily decays when dried out. The morphology of the footprint sandstone is frequently articulated with slopes and terrace formations, and there is pinching out towards the point bar of the river channel. The strike of the footprint sandstone beds is approximately NW–SE and it displays an undulating surface, while the fault-bordered tectonic blocks dip slightly to the south. There are two main excavation sites (named sites 1 and 2 in this study; see Figures 1(C) and 2) which include ichnofossils, but they represent the same horizon and same age.



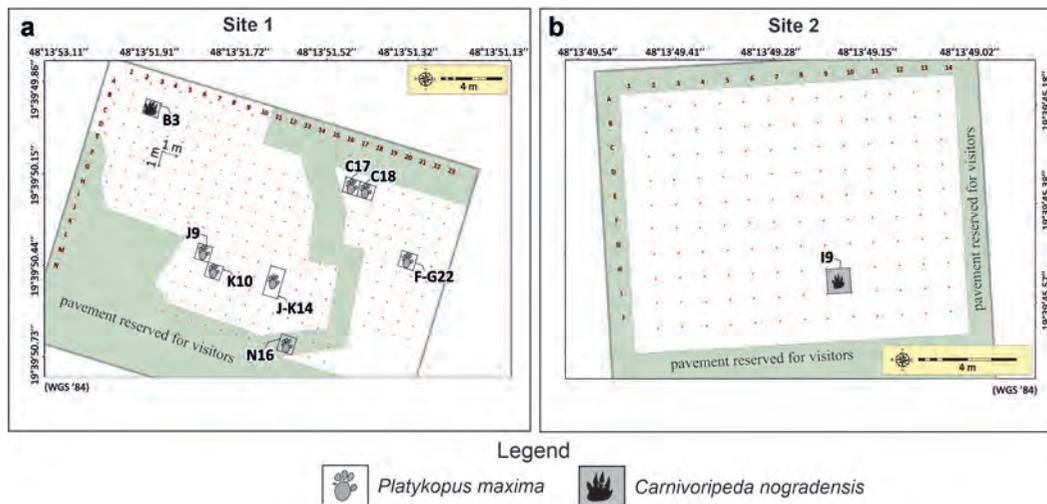
**Figure 1.** Geographic and geological position of the investigated area. (a) Position of Ipolytarnóc locality near the Slovakian-Hungarian border; (b) Location of site 1 and site 2 of the Ipolytarnóc locality. (c) Stratigraphic position of the Lower Miocene formations at Ipolytarnóc Fossils (after Kocsis 2007). Abbreviation: L = Langhian; T = transgression; R = regression.

### Historical overview: the ichnotaxonomy of the large-sized pentadactyl footprints from Ipolytarnóc

The first-mentioned pentadactyl footprint from Ipolytarnóc is in the form of an isolated cast of a large-sized carnivore (figure 144 in Abel 1935). Abel (1935) presented a photo and gave a short description of this footprint and interpreted it as a left manus imprint of a large carnivore such as *Amphicyon* or 'a large Felidae (*Machairodus?*)'. This footprint was discovered by T. Szontagh (Hungarian Geological Institute) in 1900 in Ipolytarnóc, but, unfortunately, it was removed from its original place without detailed documentation and was transported to Vienna, Austria. Consequently, the exact provenance of this trace fossil is unknown (Tasnádi Kubacska 1976; Kordos 1985). Thenius (1948) re-examined this footprint and interpreted it as *Hyaenaelurus* sp. based on its size and mesaxony as well as the number of digital imprints and the retractile claws. The examination contains a more detailed description and comparisons, but the representation of this footprint is only a hand-drawn version of the one presented in the paper of Abel (1935). Thenius (1948) did not find sufficient evidence to place this footprint in a new ichnospecies, mentioning only tangentially that the characters of the footprints most closely resemble those of hyaenodont. Kordos (1985) described this footprint as a new ichnospecies (*Bestiopedia maxima*) and gave the following diagnosis 'Carnivore footprint of great size. Sole impression proximodistally flattened with five separate toe prints of oval plan-view. In

the median of the footprint is the largest (III rd.) toe. The Vth toe is displaced into an extreme position, its proximal end falling in one line with the distal apex of the Vth toe. No trace of claw apex visible'. This diagnosis and the published dimensions of the footprint of this new ichnospecies were limited to the photographs presented in Abel (1935) and Thenius (1948). At that time, no other footprint of this type was known from Ipolytarnóc (see Kordos 1985). In the same year, albeit a few months later, Vialov (1985) also described this footprint as a new ichnospecies (*Bestiopedia böckhi*). However, according to the rules of nomenclature, the name given by Kordos (1985) is considered as the earlier one and is therefore accepted as being valid. Subsequent to these mentioned works, no detailed scientific publications on these footprints have been forthcoming, and there are only a few references to *in situ* footprints of this ichnospecies in the Ipolytarnóc area (e.g. Kordos et al. 2021).

The other large-sized pentadactyl footprint from the Ipolytarnóc locality is the *Carnivoripedia nogradensis*. This was described and named by Kordos (1985). Tasnádi Kubacska (1976) had already mentioned this footprint type from Ipolytarnóc, and he produced a hand-drawn illustration (figure 15 in Tasnádi Kubacska 1976) and a short description of these footprints. However, his work did not include a detailed ichnotaxonomic description, and he did not give a formal ichnotaxonomic name to the footprints. Later, Kordos (1985) re-examined them and gave the following short diagnosis for the *C. nogradensis* ichnospecies: 'Five-toed carnivore footprint. The sole print is laterally wider than longitudinally, being distally



**Figure 2.** Maps of the site 1 and 2 in the Ipolytarnóc locality showing the location of the *P. maxima* and *C. nogradensis* footprints investigated in this study. (a) Map of site 1. (b) Map of site 2. Location of site 1 and site 2 of the Ipolytarnóc locality see Figure 1(B).

impressed. Toe prints elongated, droplet-shaped, ending in an apex. The imprint of the tip of each claw is quite distinct'. In another work, Kordos (1987) mentioned four more *C. nogradensis* footprints from a new excavation site at Ipolytarnóc (site II) and together with these, he classified a total of seven traces in this ichnospecies.

## Material and method

The material investigated for the present paper includes two different, large-sized pentadactyl footprint types located in sites 1 and 2 of the Ipolytarnóc locality (see Figure 1(B)). The exact position of the examined material is shown in Figure 2. The 1 × 1 m square grid system, which is shown in Figure 2, was implemented in the first stage of research in 2021–2022 in order to map the surfaces covered by trace fossils, accurately. For the methods, the tools and software for mapping, see details in Mezei et al. (2022). An analysis is also given of a single replica of the cast of the *Platykopus maxima* holotype (MBFSZ V 2022.1.1) which is housed at the Collection of the Mining and Geological Survey of Hungary (MBFSZ). For the description of footprints and trackways, the nomenclature and methodology of Leonardi (1987) have been used. For measurements on photographs, the software Image J 1.45 (<https://imagej.nih.gov/ij/>) was employed. During the photo documentation, the general procedures discussed in Falkingham et al. (2018) were followed. Photos of the investigated footprints were taken with a Canon EOS 600D DS126311 camera. Three-dimensional models of the footprints were created with an ARTEC LEO 3D HandHeld scanner with structural lights (3D point accuracy: 0.1 mm; 3D resolution: 0.2 mm; see further details in <https://cdn.artec3d.com/pdf/Artec3D-Leo.pdf>). The models were presented and observed using the GOM Suite Software (<https://www.gom.com/en/products/gom-suite/gom-inspect-pro>). 3D scans of the 10 footprints and trackways investigated in this study can be found at [www.sketchfab.com](http://www.sketchfab.com) (see below), where they are all freely downloadable in \*.OBJ format:

### *Platykopus maxima*

Replica of the holotype material (MBFSZ V 2022.1.1): <https://sketchfab.com/3d-models/replica-of-the-holotype-footprint-of-p-maxima-9dfc751ceec4113b2273f3bcfd7f4fd>

C17 of site 1: <https://sketchfab.com/3d-models/p-maxima-footprint-from-c17-quadrate-080a6ec2f9b94e909873ab1df7f63613>

C18 of site 1: <https://sketchfab.com/3d-models/p-maxima-footprint-from-c18-quadrate-dfa40c18529e4491857f6d79eeade6c3>

F-G22 of site 1: <https://sketchfab.com/3d-models/p-maxima-footprints-from-f-g22-quadrate-6639fcb914b04ecd9a54f47b168faa74>

J9 of site 1: <https://sketchfab.com/3d-models/p-maxima-footprints-from-j9-quadrate-82b1848a61954421b5df74458ea41fe0>

J-K14 of site 1: <https://sketchfab.com/3d-models/p-maxima-footprints-from-j-k14-quadrate-033b214603c44c589c3177a51ddc6b65>

K10 of site 1: <https://sketchfab.com/3d-models/p-maxima-footprints-from-k10-quadrate-1fc02ab070974e80844241e46d91b7fb>

N16 of site 1: <https://sketchfab.com/3d-models/p-maxima-footprints-from-n16-quadrate-b08872bf147a4768ac4ba117d08c27ac>

### *Carnivoripeda nogradensis*

B3 of site 1: <https://sketchfab.com/3d-models/holotype-material-of-the-c-nogradensis-29b95a69866b483090c14f97c8f215d5>

I9 of site 2: <https://sketchfab.com/3d-models/c-nogradensis-footprints-from-i9-quadrate-3ad77e744c9045b3a66bb55c26478f8f>

Depth-colour images of the 3D models were generated using GOM Suite software, and these were relative to a horizontal plane which forms a spatial zero plane.

## Systematic Ichnology

### Ichnoorder Carnivora

#### Ichnogenus: *Platykopus* (Sarjeant et al. 2002)

#### Ichnospecies: *Platykopus maxima* (Kordos 1985)

1935 '... die vielleicht von einem Amphicyonherrührt, vielleicht von grossen Feliden' Abel, p. 165, figure 144

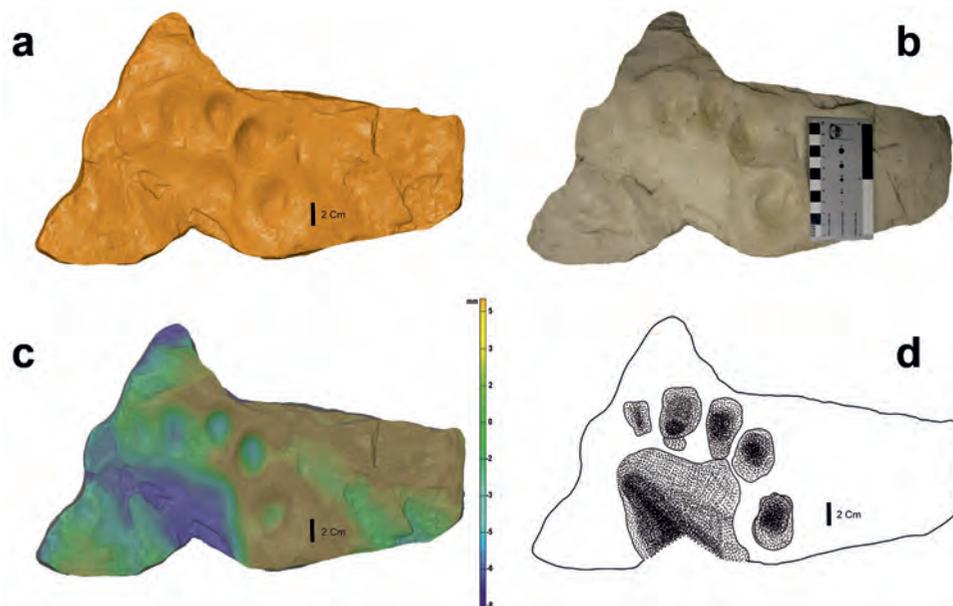
1948 *Hyaenaclurus* sp.; Thenius, p. 225–229, Figure Abb. 1a

1985 *Bestiopedia böckhi*; Vialov, p. 75

1985 *Bestiopedia maxima*; Kordos, p. 281–282

2002 *Felipedia maxima*; Sarjeant et al., p. 44

2021 *Bestiopedia maxima*; Kordos, Figure 4E



**Figure 3.** Replica (V 2022.1.1) of the holotype footprint of *Platykopos maxima* ichnospecies (left manus). (a) Scanned image; (b) General view; (c) Colour-depth image; (d) Interpretative drawing.

**Holotype.** Large pentadactyl footprint presented in figure 144 in Abel (1935), with a subsequent designation by Kordos (1985, p. 367). A replica of this footprint is currently housed and inventoried (V 2022.1.1) in the Collection of Mining and Geological Survey of Hungary and is presented in Figure 3 in this study.

**Remarks.** When Kordos (1985) described the new ichnospecies *Bestiopedia maxima*, he designated the holotype of this ichnospecies as follows: ‘O. Abel (1935), Fig. 144; E. Thenius (1948) Abb. la. Its original was recovered, in 1900, from Ipolytarnóc, by T. Szontagh; neither the original, nor a reproduction of it is known to be available in a Hungarian public collection’. The cited figure of Abel (1935) represents a relatively large pentadactyl footprint on a triangular block; this was identified as a left manus imprint of a large carnivore (*Amphicyon* or a large Felidae). Kordos (1985) assigned only this single footprint (thought to be lost) to this ichnospecies and mentioned no other footprints from Ipolytarnóc that he would classify as being of this species. In 2003, László Kordos found a replica of the holotype footprint cast in the Collection of the Department of Palaeontology of the University of Vienna, but the original footprint (what was presented in Abel 1935) is still missing. László Kordos made an additional replica from this cast, which is currently housed and inventoried (V 2022.1.1) in the Collection of Mining and Geological Survey of Hungary.

#### Emended diagnosis

Large plantigrade footprints with five digits on manus and pes. Digital imprints appear as a separated oval depression. Tips of digits are directed forward without significant rotation. Digits II–V form a symmetrical arc around the pes or manus, while digit I is displaced into medial position and frequently most deeply impressed. Claw imprints are present, but these are short. The palm is antero-posterior oval, and the metacarpal pad is not visible, while in the case of sole, the impression of metatarsal pad is present. Digit I is the strongest imprint, exhibiting variable orientation. The impressions of the hind foot imprints never cover the impressions of the forefoot.

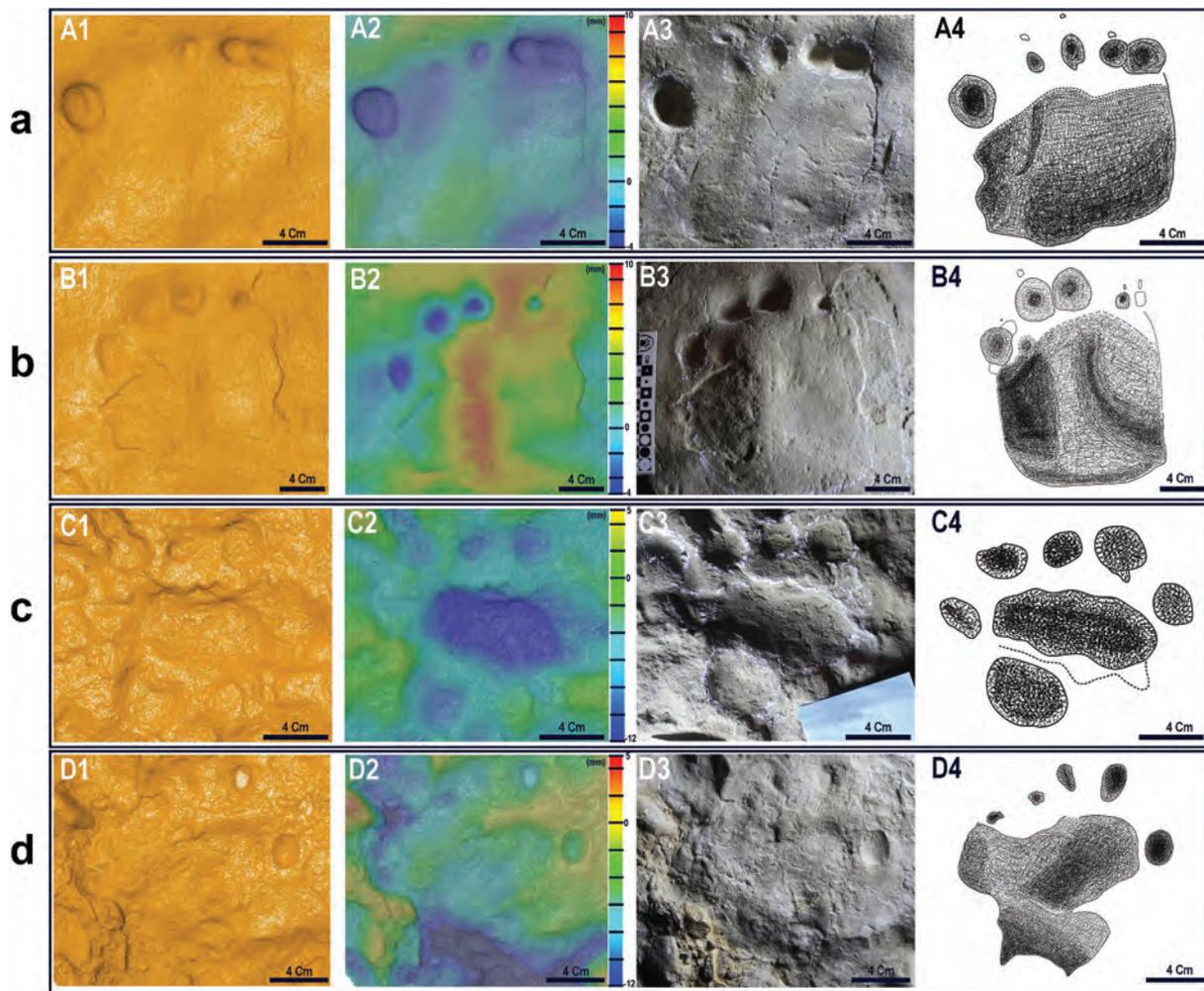
Referred materials: see Table 1, Figures 3–5 and Supplementary I

#### Description

Morphology of *P. maxima* traces varies greatly depending on the moisture of the former substratum (Figure 4), but there are some distinctive morphological features of these footprints that can be used to distinguish them from the other predator tracks of the Ipolytarnóc area. All footprints were considered as *P. maxima*, where a relatively large palm or sole prints (length and width usually larger than 70 mm) were associated with five large-sized ovoidal digital imprints (Figures 3 and 4 and Supplementary I). The coexistence of these features is sufficient to separate the *P. maxima* from the traces of *Carnivoripeda nogradensis* (because these footprints can be characterised by five elongated, sharply clawed digits; see below) and from those of *Bestiopedia tarnocensis* (which are much smaller and only have four digital imprints, see Kordos 1985).

The isolated manus (Figure 4 (A–B)) and pes (Figure 4 (C–D)) imprints can be separated from each other because the manus imprints indicate greater width than length, while the pes traces show the opposite. Both manus and pes exhibit inward rotation to the midline of the trackway (Figure 5); this can help in differentiating the left and the right-side footprints. Furthermore, the characteristic and deep imprints of digit I are always located on the medial side of the footprints (Figures 3–5), a feature which can also be used to separate left and right footprints.

**Manus:** Overall length varies between 79 mm and 171 mm (average = 134), while the overall width varies between 83 mm and 172 mm (average = 134) (Table 1). The palm is frequently square-shaped with two antero-posteriorly elongated palm pes imprints separated by a weak crest at the midline of the palm (Figure 4 A–B). The distal part of the manus imprint is usually more visible and deeper than the proximal part. The metacarpal pad prints are never visible. Imprints of digit I are clearly visible in most cases and often form deeper traces than other digital imprints (Table 1 and Figures 3 and 4 (A–B)). Digit I is not only larger than the other digital imprints but also often forms a deep hollow, which may indicate that this finger was highly mobile and often served as a support when the animal walked on a wet, soft substratum (Figure 4(A)). This high degree of mobility of digit I is supported by the large variability in the angular values measured between digits I and V (see Table 1). The other digital imprints



**Figure 4.** Referred materials of *Platykopus maxima* ichnospecies from the Ipolytarnóc locality. (a) Right manus from the N16 quadrate (N16/1) of site 1 (A1: Scanned image; A2: Colour-depth image; A3: General view; A4: Interpretative drawing); (b) Right manus from the N16 quadrate (N16/4) of site 1 (B1–B4 see above); (c) Right pes from the J-K14 quadrate (J-K14/3) of site 1 (C1–C4 see above); (d) Left pes from the C18 quadrate (C18/1) of site 1 (D1–D4 see above). Position of the different quadrates see Figure 2A.

form a more or less symmetrical arc around the palm, where digits II–IV are of equal size, while digit V usually represents the smallest impression (Table 1). Digit I is always separated from the other digital imprints and situated in an extreme position at the medial side of the palm (Figures 3–4 and Supplementary I). Digits I–V are not closely appressed to palm imprints because they are slightly further away from the palm. Furthermore, the measured interdigital angles exhibit significant variations in the studied material (Table 1), suggesting that all fingers of the forefeet were quite flexible. Claw imprints are only rarely and poorly visible (see Figures 4 (A4 and B4)), indicating the claws of the manus were partly retracted or held above the ground, and only the tips of the claws were impressed.

**Pes:** The pes imprints are of greater length than width due to the impression of the metatarsal pad. The overall length varied between 37 mm and 195 mm (average = 145), while the overall width varied between 83 mm and 164 mm (average = 119) (Table 1). The sole often consists of two parts (Figures 4(C–D)): an oval or rectangular paw print and a much smaller trapezoidal heel print separated by a shallow elevation. In rare cases, where the footprint is not so deep (i.e. the impression has been made in a firmer substratum), the sole forms a kidney-shaped impression where the heel and sole impressions merge (Supplementary I). The pes also has five digits, but in

rare cases only four digital imprints are present. Digit I is situated in a medial position as in the case of the manus, but its imprints are not so prominent here because it is often the same size and depth as the other digital imprints. Imprints of digits II and V are situated further from the palm imprints and located in a distal position (Figures 4 (C–D)). The interdigital angles do not show as much variability as those of the manus (Table 1), suggesting that the pedal digits may have been more rigid. Claws imprints are poorly visible, indicating the claws of the pes were probably partly retracted or held above the ground.

**Trackway pattern** (Figure 5 and Supplementary I): As far as it is known, three partial trackways of *P. maxima* can be described from the Ipolytarnóc area (N16; J-K14 and J9; these abbreviations stand for map coordinates; see Figure 2). In all trackways, the impressions of the hind foot imprints indicate that they never covered the impressions of the forefoot (Figure 5); this can be considered a general character for *P. maxima* traces. These trackways were most likely made by a wide-bodied animal because the left and right footprints have regular and inward orientations.

**N16 trackway** (Figure 5A): This trackway contains the best-preserved and well-studied manus imprints of *P. maxima* from the Ipolytarnóc site (see Figures 4 (A–B)); however, the other data of this trackway cannot be investigated in detail because of the

**Table 1.** Summary of detailed measurements on *Platykopus maxima* footprints from the Ipolytarnóc locality (location data see Figure 2A) (remarks: ? = uncertain data; NA = not available). Close-up of all these footprints is presented in Supplementary 1 and Figures 3–5. See Supplementary 1 for the footprints associated with the serial number.

Location	Serial Number	Position	Footprint		Palm or Sole		Digit Length (mm)					Digit Width (mm)					Divergation of digits								
			Length (mm)	Width (mm)	Length (mm)	Width (mm)	I	II	III	IV	V	I	II	III	IV	V	I–II	II–III	III–IV	IV–V	I–V				
Holotype (Unknown location) C17 of site 1 C18 of site 1 F-G22 of site 1 J9 of site 1	1	Left Manus	155(?)	157	94(?)	107	48	47	53	45	30	32	32	30	34	22	10.5	6.2	5.7	16.6	27.9				
	C17/1	Right Manus	107	119(?)	78(?)	88(?)	25	19	15	22	11	15	16	19	21	20	8.9	3.9	3.7	5.3	21.4				
	C18/1	Left Pes	150	164	124	139	26	31	20	10	7(?)	21	19	11	11	11	7.2	6.3	3.8	6.1	24.4				
	F-G22/1	Partial Left Pes(?)	136	118	105	120	NA	NA	26	17	24	NA	NA	13	14	21	NA	NA	NA	4.9	6.4	NA			
	F-G22/2	Partial Right Pes(?)	172(?)	145	116	133	NA	NA	NA	38	29	NA	NA	NA	24	19	NA	NA	NA	NA	10.5	NA	NA		
	J9/1	Left Pes	100	48	100	48	10	NA	NA	NA	NA	10	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
	J9/2	Right Pes	87	37	87	37	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
	J9/3	Left Manus	93(?)	130	69	95	27	15	21	18	16	25	18	16	15	23	48.7	23.0	12.0	15.7	93.7				
	J9/4	Right Pes	111	107	97	77	NA	18	19	NA	NA	NA	19	10	NA	NA	NA	14(?)	NA	NA	NA	NA	NA	NA	
	J9/5	Left Manus(?)	139	121	93	73(?)	NA	NA	33	28	NA	NA	NA	21	23	NA	NA	NA	26(?)	NA	NA	NA	NA	NA	NA
	J9/6	Right Manus	171	158	97	110	33	33	29	29	20	21	22	28	33	19	17.3	17.8	20,1(?)	11.7	67,8(?)				
	J9/7	Right Manus or Pes	113	83	86	83	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	J9/8	Left Manus(?)	150	121	117	121	38	NA	NA	NA	NA	NA	NA	25	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	J-K14 of site 1	J-K14/1	Right Pes	158	126	106	84	45	NA	39	40	42	25	NA	26	18	27	NA	NA	7.5	10.7	26.9			
	J-K14/2	Left Manus	79(?)	121(?)	46(?)	95(?)	NA	18	31	25	NA	NA	11	32	26	NA	NA	13.7	19.7	NA	NA				
	J-K14/3	Left Pes	142	128	94	99	23	26	26	19	14	27	31	21	27	17	16.9	9.6	11.7	13(?)	38,4(?)				
K10 of site 1	K10/1	Right Pes	178	152	85(?)	115(?)	46	38	18	36	NA	37	40	23	37	NA	26.3	10.9	11.0	NA	NA				
	K10/2	Left Manus(?)	167	154	122	134	32	39	19	32	NA	43	33	16	36	NA	17.9	9.5	9.5	NA	NA				
	N16/1	Right Manus	123	138	91	116	30	10	14	15	14	26	10	11	16	12	25.1	12.9	13.9	8.2	52.9				
N16 of site 1	N16/2	Right Pes	195(?)	134	156	118	25	NA	NA	NA	NA	22	NA	NA	NA	NA	NA	NA	NA	NA	NA				
	N16/3	Pes(?)	170	151	135	151	NA	32	21	22	7	NA	26	29	11	9	NA	13.1	11.0	3.8	NA				
	N16/4	Right Manus	177	172	108(?)	165	41	46	46	16	14	31	33	38	13	6	16.2	10.7	18.4	5.3	33.1				

Summary of detailed measurements on *Platykopus maxima* from Ipolytarnóc locality

sharp bend of the midline of the trackway. Furthermore, the examination of the footprints is made more difficult by the fact that they are located under a pavement reserved for visitors and thus their examination is limited (see Figure 2(A)). This trackway contains two well-preserved right manus imprints with two poorly preserved footprints (probably pes imprints) between them. In addition to these footprints, there are other isolated and very deep digital imprints (some of these can reach a depth of 1 cm) without palm or sole prints. The depth of the digital imprints associated with the manus is also much greater than those of the other footprints investigated in this study; furthermore, the claw prints are also more robust in these cases (see Supplementary I). The depth of the fingerprints suggests that the surface may have been highly moist, and the animal may have pushed its fingers deeply into the substrate to keep its balance during its gait. The available information indicates that only the left-side footprints of this trackway can be studied – i.e. those which curve along an S-shaped midline.

J-K14 trackway (Figure 5(B)): This trackway shows three successive footprints: two of the hind feet and one of the forefeet (for more detailed images see Supplementary I), probably of a bear-sized animal travelling across a surface sufficiently moist for its weight to create pressure mounds around the prints (see also Figure 4(C)). The external trackway width is ca. 287 mm; the width of pace (feet) is ca. 141 mm, the length of pace (feet) 691 mm, while the distance between the manus and pes is about 421 mm (based on the methods of Leonardi 1987). Both manus and pes exhibit inward rotation (Figure 5(B)). The most distal footprint (left pes; presented in Figure 4(C)) was impressed into a very moist substratum because its contours are blurred and spread. Furthermore, following the formation of the footprint, it is likely that water flowed inside to the sole from the digital imprints through small channels.

J9 trackway (Figure 5(C)): This trackway exhibits a left-turning series as a result of which footprints are significantly crowded in the direction of the bend, making it difficult to investigate the trackway pattern. In addition to the blurred and faintly visible partial footprints and digital imprints, the trackway contains a minimum of six relatively well-preserved footprints (two of the hind feet and four of the forefeet, see details in Supplementary I). Measurements of different trackway patterns were made on the first two pes imprints (left and right), because in this case, the midline is still relatively straight. The external trackway width is ca. 177 mm, the width of pace (feet) is ca. 108 mm, and the length of pace (feet) 469 mm, while the distance between the manus and pes is about 301 mm. These values are one and a half times smaller than for the J-K14 trackway, which is consistent with the differences in the size of the pes imprints in the two series (pes prints of the J-K14 series are one and a half times larger than those of the J9). Characterisation of the most distal footprints is problematic because their orientation and position cannot be determined due to their poorly visible contours. They appear to form a single print (right manus?), but in this case the resulting size data would be very high (e.g. total width = 188 mm) compared to the other footprints in this trackway and the other investigated footprints in this study. It is suggested here that this imprint consists of two footprints placed side by side, but the details of these footprints are not available for study.

#### Comparison with other relevant Tertiary pentadactyl footprints

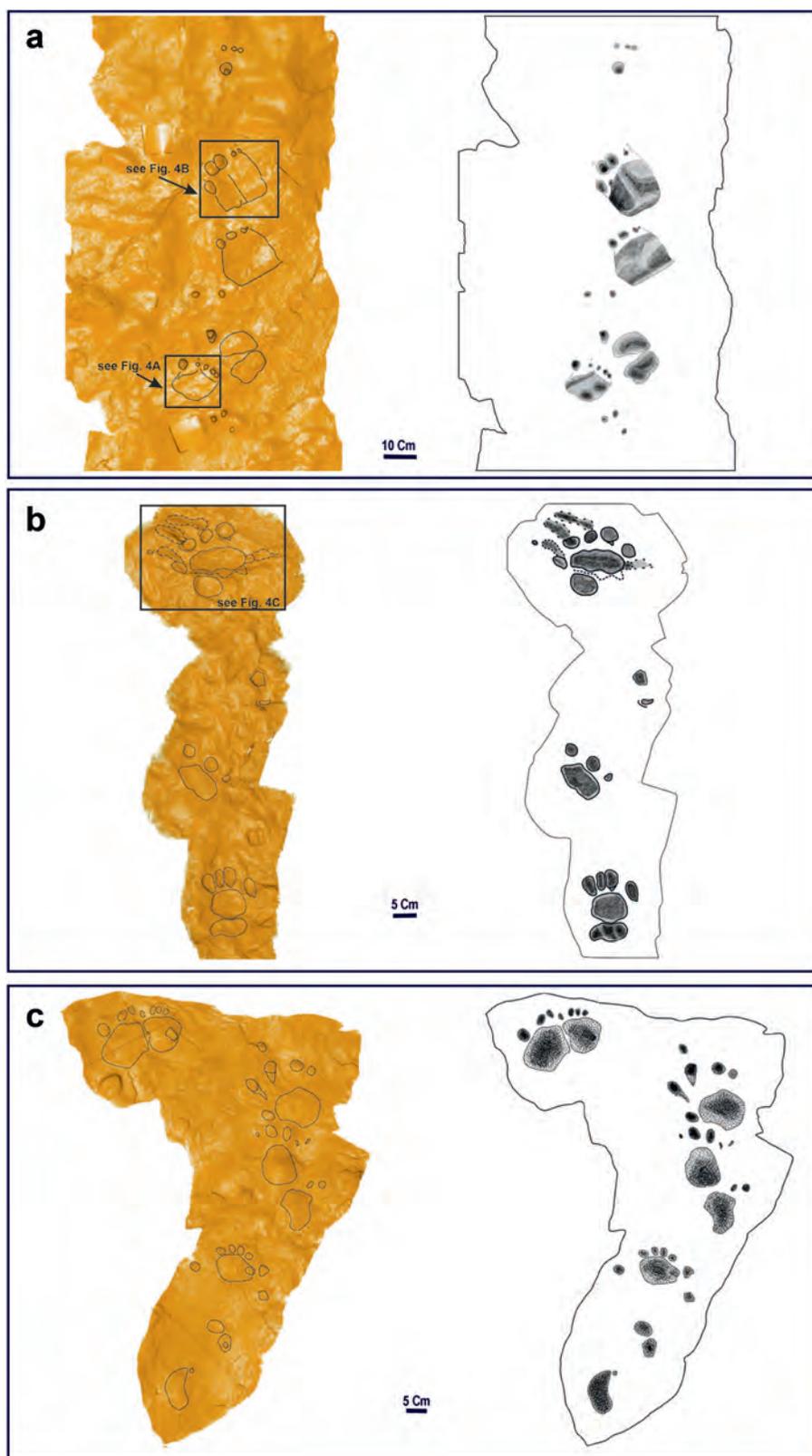
The *Platykopus maxima* footprints are clearly different from the *Carnivoripeda nogradensis* (i.e. the other pentadactyl footprint from Ipolytarnóc; see below) because the digital imprints are oval and not elongated. The claw imprints are only slightly visible, and the *P. maxima* prints are generally wider than long, as opposed to *Carnivoripeda* which are longer than wide

(see below). The size of the *Bestiopeda tarnocensis* traces is half of the *P. maxima*, and these are tetradactyl footprints and not pentadactyl (see Kordos 1985).

This ichnospecies does not resemble the creodont *Zanclonychopus cinicalcator* traces (Late Eocene tuff, Presidio County, Texas, USA; Sarjeant and Langston 1994) because they are much larger, and the characteristic curving fingers seen in *Zanclonychopus* are not observed in *P. maxima* footprints. Another Eocene creodont trace fossil was described from the Célas Sandstone deposit of south France and named *Hyaenodontipus praedator* (Ellenberger 1980). The poor preservation of these traces and the lack of detailed illustrations make it difficult to compare them with the Ipolytarnóc footprints. However, besides the significantly different ages of the two trace fossils, there is also a difference in that the trackways of *H. praedator* are described as heteropodous with pentadactyl manus and tetradactyl pes, while the *P. maxima* has pentadactyl pes. The creodont-like footprint of *Sarcotherichnus enigmaticus* (Oligocene, Vaucluse, south-eastern France) is clearly different from the Ipolytarnóc traces, based on the orientation of digits I and V (see Demathieu et al. 1984). *Sarjeantipes whitea* was described by McCrea et al. (2004) based on heteropodous trackways (tetradactyl manus and pentadactyl pes) where the manus prints are partially or completely overprinted by pes prints; thus, this ichnospecies is different from the *P. maxima* (see Figure 5).

Two species of the amphicyonid *Axiciapes* were described by Sarjeant and Langston (1994) from the Late Eocene tuff in Presidio County (west Texas, USA). The first is *Axiciapes ferox* which has five digits on the manus and only four on the pes, so this ichnospecies is different from *P. maxima*. Furthermore, the pattern of *Axiciapes ferox* tracks shows a regular superposition of hind foot imprints on those of the forefoot. Such a pattern is not detectable from the tracks of *P. maxima* (see Figure 5). The other ichnospecies of the genus *Axiciapes* is *A. curvidigitatus* which is characterised by a strong inward curvature of digits I to IV (Sarjeant and Langston 1994), which is not observed in the case of the Ipolytarnóc traces. *P. maxima* is clearly different from the *Hirpexipes alfi* because of the absence of the characteristic sharp claws and the long and slender digits of the pes (see Sarjeant et al. 2002). An animal with a heteropodous trackway with pentadactyl manus and tetradactyl pes was described as *Bestiopeda amphicyonides* by Thenius (1967). It was found in the Pliocene Rohrbacher Conglomerates of the Vienna Basin. These footprints are different from those of *P. maxima*, because in the case of *B. amphicyonides* the digital imprints are situated very close to each other; digit I is not in a lateral position and the impression of the hind foot is tetradactyl. Elongate digits and the marked claw imprints of *Carnotipus solitarius* (Monte el Cristo, Spain, Lower Miocene; López et al. 1992) are clearly different from *P. maxima* footprints.

Rich and variable samples of ursid-like trace fossils were identified as *Ursichnus europaeus* ichnospecies from the Upper Pleistocene cave sediments of Urşilor Cave in the western Carpathians, Romania (Diedrich 2011). These footprints differ from *P. maxima* because the palm imprints are kidney-shaped, an ovoidal heel imprint has been made by the front paw, and all digital imprints are situated in front of the pad. Another ichnospecies of *Ursichnus* ichnogenus is the *U. sudamericanus* described from the late Pleistocene palaeoichnological sites of Pehuen Co, Buenos Aires province, Argentina (Aramayo et al. 2015). The Ipolytarnóc traces differ from the footprints of *U. sudamericanus* because the digit imprints do not show inward rotation, claw prints are only slightly visible, the palm impression is not separated from the digital pad impressions by a marked ridge, and the length of digit III is not significantly different from the other digital imprints.



**Figure 5.** *Platykopus maxima* trackways. (a) trackway located in the N16 quadrat of site 1; (b) trackway located in the J-K14 quadrat of site 1; (c) trackway located in the J9 quadrat of site 1. Position of the different quadrates see Figure 2A and see Supplementary I for a close-up of the different footprints on these trackways.

Another ichnogenus with an ursid-like track is *Platykopus* (see Sarjeant et al. 2002; Lucas and Schultz 2007). This exhibits a high similarity with the Ipolytarnóc traces based on the diagnosis of Sarjeant et al. (2002) because (1) these are large-sized plantigrade footprints with five digits on manus and pes; (2) digital imprints

appear as separated oval depressions; (3) digits II–V form a symmetrical arc around the pes or manus; (4) digits I to IV are similar in size, while digit V is shorter than the other; and (5) the pes is longer and narrower than the manus due to the metatarsal pad. Based on the diagnosis of the *Platykopus* ichnogenus given by

Sarjeant et al. (2002), the *Ipolytarnóc* traces are classified under this genus. Two ichnospecies of *Platykopos* are known: one is *P. ilycalicator* (type ichnospecies of the ichnogenus; Late Miocene, Nevada USA) described by Sarjeant et al. 2002 and the other is the *P. stuartjohnstoni* from the Upper Miocene strata of Ogallala Formation, Texas, USA (Lucas and Schultz 2007). The *Ipolytarnóc* traces are different from the *P. ilycalicator* because the morphology, size, and orientation of digit I are different, digital pads are situated further from the metatarsal/metacarpal pads, and the impression of the claws is only slightly visible and there are no strong tips at the end of the digital pads (see the diagnosis of Sarjeant et al. 2002). Further tracks of *P. ilycalicator* were identified at the Miocene Upper Red Formation in the Shokorchi area, west Zanjan, NW Iran (Abbassi 2010). These imprints are half the size of the type ichnospecies of *P. ilycalicator* but represent the same species in terms of morphological characters (see further details in Abbassi 2010). However, in the case of the *P. ilycalicator* of the Upper Red Formation, the tips of manus digits are rounded without claw traces; this indicates a difference from the type ichnospecies and similarities with the *P. maxima* of the *Ipolytarnóc* locality. Apart from this similarity, the footprints of *P. maxima* differ from the *P. ilycalicator* of the Upper Red Formation because 1) there is a greater distance between the pes and manus imprints in a trackway; 2) The pes and manus imprints display the same quality of preservation; 3) the *Ipolytarnóc* footprints are clearly plantigrade and not semiplantigrade (see Abbassi 2010). Footprints of *P. maxima* differ from *P. stuartjohnstoni* because the pes has five digital imprints, the breadth of the pes is less than that of the manus, and the digit imprints are oval and not triangular (see Lucas and Schultz 2007).

### Comments

These footprints were earlier described by Kordos (1985) as those of *Bestiopedina maxima*. However, this ichnogenus name can be misleading (for further details, see Sarjeant et al. 2002; Melchor et al. 2019) because the observed footprints are pentadactyl, while the *Bestiopedina* nomenclature was originally applied to tetradactyl footprints (Vialov 1965, 1966; Sarjeant and Langston 1994; Sarjeant et al. 2002; Melchor et al. 2019). Although Vialov (1965, p. 112) proposed the ichnogenus name *Bestiopedina* (with the type ichnospecies being *B. bestia*) to imprints with four digits, *Bestiopedina* was later applied to pentadactyl footprints (Thenius 1967; Costeur et al. 2009) and heteropodous trackways with pentadactyl manus and tetradactyl pes (Thenius 1967) as well (see detailed in Melchor et al. 2019). The problems with the *Bestiopedina* name primarily originated with Vialov (1965, 1966) because he did not present a diagnosis for this ichnogenus, and he proposed this ichnogenus name as a neutral generic one for all paw prints of predators (Melchor et al. 2019). Furthermore, based on the detailed taxonomic revision of the tetradactyl footprints, Melchor et al. (2019) suggested that the two ichnospecies (*B. sanguinolenta* and *B. gracilis*) of *Bestiopedina* should be considered as *Canipedia*, while the type ichnospecies (*B. bestia*) of *Bestiopedina* should be regarded as a hyaena-like fossil footprint. Therefore, the use of the *Bestiopedina* ichnogenus name for the pentadactyl footprint of the *Ipolytarnóc* site is highly problematic because 1) no diagnosis of this ichnogenus is available and 2) all the species classified by Vialov (1965) in the ichnogenus *Bestiopedina* are tetradactyl footprints and thus this name is not applicable to pentadactyl prints (Melchor et al. 2019). Considering the nomenclature problems of the *Bestiopedina* ichnogenus, here these footprints have been classified under *Platykopos*, based on listed features in the diagnosis above.

Kordos et al. (2021) mentioned a further nine *Bestiopedina maxima* ‘unpublished’ footprints (Table 1 in Kordos et al. 2021) which

were discovered between 1983 and 1988. Unfortunately, this recent work of Kordos does not provide information about the position of these *Bestiopedina maxima* footprints and does not contain descriptions of their traces; consequently, it is impossible to identify and compare them with the footprint investigated in this study. Only one footprint was depicted from the mentioned nine traces (Figure 4 in Kordos et al. 2021), which presumably corresponds to Figure 4(B) footprint presented in the study.

## Ichnogenus *Carnivoripedia* (Kordos 1985)

### Ichnospecies: *Carnivoripedia nogradensis* (Kordos 1985)

1974 ‘... Amphicyonidae footprint’ Tasnádi Kubacska, p. 93, Figure 15

1985 *Bestiopedina hungarica*; Vialov, p. 73, Plate II

1987 *Carnivoripedia nogradensis*, Kordos, p. 458–460, Figure 1

**Holotype.** Three footprints belonging to one individual located in the B3 square grid (see Figure 2A) of site I of the *Ipolytarnóc* locality. These footprints were first depicted in Tasnádi Kubacska (1976), and later in Kordos (1985). The same footprints are presented in Figure 6 in this study.

### Emended diagnosis

Plantigrade footprints with five elongated, sharply clawed digits on the manus and pes. Imprints of the manus and pes are longer than they are wide. Digits III–V point forwards, while digits I and II outwards in the case of the manus. In the case of the pes, the central digits (II, III, IV) are parallel and the outer digits (I and V) are offset, at an angle pointing slightly outwards. Digits II and IV of the pes curve towards digit III. Imprints of claws are distinct. Digit III represents the largest digital imprint. The palm and sole are of greater width than length and form a relatively deep, kidney-shaped impression. The impressions of the hind foot imprints never cover the impressions of the forefoot.

### Referred materials:

see Table 2 and Figures 6–7

### Descriptions

The tracks of *Carnivoripedia nogradensis* appear to be of a large plantigrade carnivore with mesaxononic feet and hands. These footprints can be distinguished from the other carnivore footprints from the *Ipolytarnóc* site based on their large-sized elongated digital imprints (five on the manus and pes) and the deeply impressed claws.

**Manus** (Figures 6(B) and 7(C and E)): Overall length varied between 96 mm and 142 mm (average = 116), while the overall width varied between 83 mm and 100 mm (average = 89) (Table 2). A well-preserved and deeply impressed manus imprint can be investigated in the B3 quadrat of site I (holotype material; see Figure 6(B)), while the manus imprints are poorly preserved with blurred contours in the trackway of the I9 quadrat of site II (see Figures 7 (C and E)). Accordingly, the description here (and the description of the pes later) is limited to the holotype material (B3 quadrat). The proximal ends of the digital imprints form a symmetrical arc around the palm, where digits III–V point forward, while digits I and II point outwards. The digital imprints are straight and oriented outwards from the centre of the sole. Digits I and V bear single elongated phalangeal pads, while digits II–IV appear to bear two or three pads (Figure 6 (B1)). The palm impression is separated from the imprints of digits II–V by a marked ridge,

**Table 2.** Summary of detailed measurements on *Carnivoripeda nogradensis* footprints from the Ipolytarnóc locality (location data see Figure 2) (remarks: ? = uncertain data; NA = not available). Close-up of all these footprints is presented in Supplementary I and Figures 6–7. See Supplementary I for the footprints associated with the serial number.

Summary of detailed measurements on <i>Carnivoripeda nogradensis</i> from Ipolytarnóc locality																					
Location	Serial Number	Position	Footprint		Palm or Sole		Digit Length (mm)					Digit Width (mm)					Divarication of digits				
			Length (mm)	Width (mm)	Length (mm)	Width (mm)	I	II	III	IV	V	I	II	III	IV	V	I–II	III–IV	IV–V	I–V	
B3 of site 1	B3/1	Right Pes	91	79	41	60	26	32	42	30	41	15	11	12	11	14	19.4	15.0	13.5	17.9	65.4
	B3/2	Left Manus	111	83	40	60	20	26	36	28	27	12	15	13	13	12	30.9	25.6	16.4	15.6	86.8
	B3/3	Right Pes?	66(?)	75	NA	NA	24	27	32	24	23	12	10	16	16	12	14.6	16.0	17.3	19.4	52.3
I9 of site 2	I9/1	Right Pes	149	126	62	72	NA	61	62	52	39	NA	15	20	25	13	NA	25.1	17.6	19.7	NA
	I9/2	Right Manus	142	100(?)	62	53	NA	53.9	66.5	NA	NA	NA	NA	NA	NA	NA	NA	17.7	NA	NA	NA
	I9/3	Left Pes	160	120(?)	65	87(?)	47	80	68	56	NA	15	29	25	15	NA	13.6	16.8	14.8	NA	NA
	I9/4	Left Manus	96(?)	85(?)	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

while the imprint of digit I merges with the palm (Figure 6(B)). The palm is kidney-shaped and contains three roughly trapezoidal palm pad imprints. The claw imprints of all digits are visible. The distal and proximal parts of the manus imprint are approximately equal with respect to depth and preservation (Figure 6 (B2)); the metacarpal pad prints are not visible. Manus imprints of the trackway of the I9 quadrate of site II are poorly preserved, and thus only the palm prints and the outline of digits II and III (with claw imprints) can be studied (Figure 7 (C and E)). Its size is approximately one and a half times that of the manus impression of the B3 quadrate of site I.

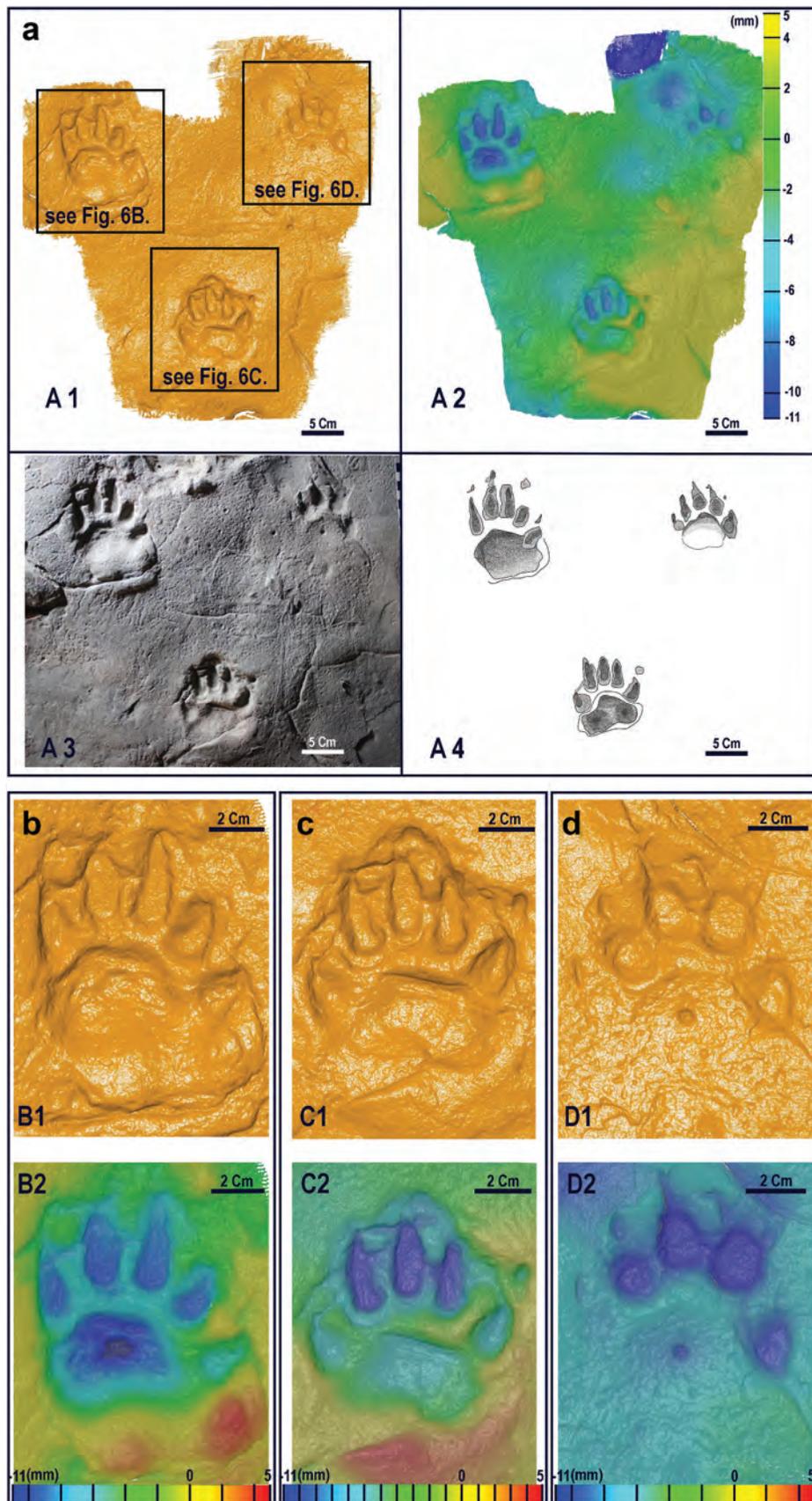
*Pes* (Figures 6(C–D) and 7(B and D)): The pes seems to be of a size equal to that of the manus. Its overall length varies between 91 mm and 160 mm (average = 116), while the overall width is between 75 mm and 126 mm (average = 100) (Table 2). Digits II and IV curve inward towards the axis of digit III, while the outer digits (I and V) are offset and angled slightly outwards (Figure 6(C)). All digits have marked and deeply impressed claw imprints. Digit III is the largest digital imprint situated in the median of the footprint. The impression of the sole is separated from the imprints of digits II–IV by a marked ridge, while in the case of digits I and V, this ridge is not so prominent (Figure 6(C)). This impression is proximodistally flattened and contains three ovoidal to trapezoidal palm pad imprints separated by a weak crest (Figure 7 (C2)). The values of divarication of the digits are lower than the values measured at the manus (Table 2). The distal and proximal parts of the pes imprint are of approximately equal depth, while the metatarsal pad prints are not visible (Figure 6(C)). The pes imprints of the trackway of the I9 quadrate of site II are large and contain long claw imprints (Figure 7(B and D)). The digit imprints are completely fused and only the claws form deep grooves at the end of the toes. The imprints of the sole contain three ovoidal palm pad imprints separated by a relatively high crest.

*Trackway pattern*: Each of the footprints described above is present in two different trackways (Figures 6(A) and 7(A)), and there appear to be no other *C. nogradensis* footprints in the area apart from these tracks. All the trackways indicate that the impressions of the hind foot imprints never cover the impressions of the forefoot.

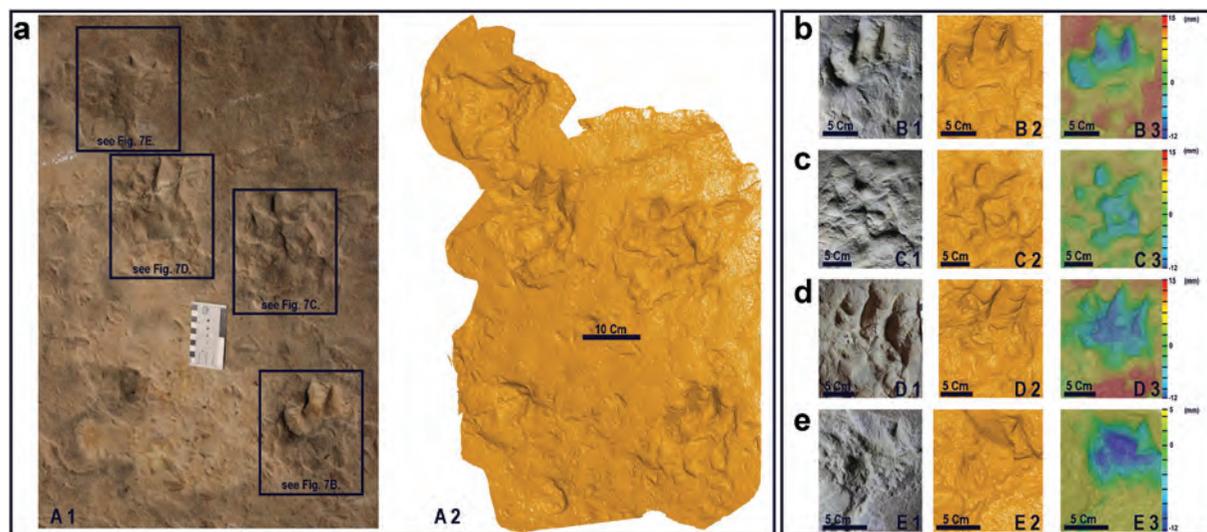
B3 trackway (holotype material; Figure 6(A)): This trackway contains three footprints, where the footprint in the upper left position represents the imprint of a left manus, while the footprint underneath can be interpreted as the imprint of

a right pes (see also Kordos 1985). The third imprint is a partial footprint, of which only the distal part can be studied (Figure 6(D)). Kordos (1985) interpreted this partial footprint as a right manus, but its position in the trackway does not support this suggestion. If this interpretation of the third impression were to be accepted, then the relative positions of the three footprints would form a roughly equilateral triangle, where the left and right manus are situated side by side, but very far apart compared to the distance of the left manus and right pes. Furthermore, if the upper footprints were interpreted as left and right manus imprints, then the position of the lower footprint (right pes) would be uninterpretable, as it would fall in the middle of the distance between the two handprints. However, if the I9 series from site II is observed, it can clearly be seen that the manus and pes imprints on the same side are below each other, while the distance between the left and right footprints is the same for both the manus and the pes (see Figure 7(A)). Thus, the evidence indicates that this pattern (which is general for the large-bodied quadruped carnivores) is not compatible with the assumption proposed by Kordos (1985) – i.e. that the upper two footprints represent an impression of the left and right manus. Unfortunately, the trackway series does not contain more footprints, so it is not possible to reconstruct the direction of the animal's movement. Theoretically, it is possible that the problematic footprint represents the second impression of the right pes, which was imprinted when the animal turned to the right. This hypothesis can be supported by the fact that the morphology (e.g. respective positions of digits II–IV; divarication of digits; and inward orientations) and the size of these two footprints are very similar to each other and they do not exhibit any characters (e.g. size and orientation of digital imprints) which are indicative of the manus imprint.

I9 trackway (Figure 7(A)): This trackway was first mentioned by Kordos (1987) as showing *C. nogradensis* footprints, and he gave a short description of them. It contains four successive footprints (two of the hind feet and two of the forefeet) of a large-sized animal travelling across a very moist surface. Due to this moist substrate, the animal's feet sank deeply into the substrate and thus the original contours of these footprints are noticeably blurred. Trackway pattern can be characterised as follows: (1) The external trackway width is ca. 373 mm, (2) the width of pace (feet) is ca. 283 mm, (3) the length of pace (feet) is 338 mm, (4) the width of pace (hands) is ca. 242 mm, (5) the length of pace (hands) is ca. 240 mm



**Figure 6.** Holotype footprints of *Carnivoripeda nogradensis* ichnospecies (located in the B3 quadrat of site I). (a) Trackway of holotype material (A1: Scanned image; A2: Colour-depth image; A3: General view; A4: Interpretative drawing). (b) Left manus from the holotype trackway (B1: Scanned image; B2 Colour-depth image). (c) Right pes from the holotype trackway (C1: Scanned image; C2 Colour-depth image). (d) Partial imprint of right pes from the holotype trackway (D1: Scanned image; D2 Colour-depth image).



**Figure 7.** Referred material of *Carnivoripeda nogradensis* ichnospecies (located in the I9 quadrante of site 2). (a) *Carnivoripeda nogradensis* (A1: General view; A2: Scanned image); (b) Right pes (B1: General view; B2: Scanned image; B3: Colour-depth image); (c) Right manus (C1-C3 see above); (d) Left pes (D1-D3 see above); (e) Left manus (E1-E3 see above). Position of the I9 quadrante of site 2 see Figure 2B.

and (6) the respective distances between the manus and pes are about 353 mm (right side) and 250 mm (left side) (these measures are based on the methods of Leonardi 1987). The impressions of the hind foot imprints do not cover the impressions of the forefoot.

#### Comparison with other relevant Tertiary pentadactyl footprints

The footprint of *C. nogradensis* is different from that of *Zanclonychopus cincalcator* because it is much larger, and the inner digits do not curve outwards (see Sarjeant and Langston 1994). Creodont-like tracks of *Dischidodacylus stevensi* have been reported from the latest Eocene sediments of the Skyline Channels of Trans-Pecos Texas, USA (Sarjeant and Wilson 1988), but these have very unusual features, for example, digit IV of the pes is distally divided and has two claws, while digits III and IV of the manus are sometimes distally divided and may have two sets of claws. Thus, these are clearly different from the Ipolytarnóc traces. *C. nogradensis* differs from the footprint of *Sarcotherichnus enigmaticus* because the digital imprints are elongated, the claw marks are present and the orientation of digits I and V is significantly different (based on the description of Demathieu et al. 1984). *Sarjeantipes whitea* clearly differs from the Ipolytarnóc traces because the manus imprints of *C. nogradensis* are also pentadactyl and the manus prints are never overlain by pes prints (see McCrea et al. 2004). López et al. (1992) presented several footprints of *Carnotipus solitarius* from lower Miocene sediments at Monte el Cristo, Spain, and these exhibit four or five elongate digital imprints with a square to trapezoidal palm and sole. The remains of *C. solitarius* are similar in age (Miocene) and also have many similarities in their diagnostic characters to the footprints of *C. nogradensis* from Ipolytarnóc (e.g. size, elongated and radially orientated digital imprints, and claw impressions; for a diagnosis see López et al. 1992). Unfortunately, the poor preservation of *C. solitarius* footprints and consequently the quality of the presented figures of these traces do not allow a more detailed comparison with the *C. nogradensis* footprint. However, based on the diagnosis provided for *C. solitarius* by López et al. (1992), *Carnotipus* is considered a junior subjective synonym of *Carnivoripeda*.

Footprints of *Axiciapes ferox* do not match the Ipolytarnóc traces, because five digits are also present on the pes, the claws of the manus are present, and the manus and the pes imprints in the trackways never cover each other (see Sarjeant and Langston 1994; Plate 17). This ichnospecies does not resemble the *Axiciapes curvigitatus*, because the curvature of the digital impressions is different, the claws of the hands were not retracted, the pes and manus are equal in size, five digits are present on the pes, and the pes imprints are not shovel-shaped (see description in Sarjeant and Langston 1994). The other amphicyonid footprint, *Hirpexipes alfi* (Sarjeant et al. 2002) is also different from that of *C. nogradensis*, because digit III is the longest compared to the other digits, and the metacarpal or metatarsal pads did not make an impression, and the digits of the pes are much shorter.

The footprints of *Ursichnus europaeus* Diedrich 2011 are different because they are much larger, the pes imprints have different shapes, and the manus are of greater width than length. Furthermore, *C. nogradensis* differs from all ichnospecies of *Platykopos* because the digital impressions are elongated and not oval (for a detailed description of *Platykopos* ichnogenus, see above and in Sarjeant et al. 2002; Lucas and Schultz 2007; Abbassi 2010).

*C. nogradensis* exhibits the closest resemblance to the mustelid-like carnivore footprints of *Phacelopus therates* (Late Eocene tuff, Presidio County, Texas, USA; Sarjeant and Langston (1994)). This assertion is based on the similarity of their respective general shapes, sizes, and the inward rotation of the digital impressions (see Sarjeant and Langston 1994). A notable difference is the position of digit I which is situated in a lateral position in the case of the Ipolytarnóc traces, as opposed to *P. therates* where digit I is directed forward, in a similar way to the other digits. Furthermore, the length of the digital imprint of *P. therates* is proportionally longer than that of *C. nogradensis* and the shape of the palm imprint is also different. Another mustelid-like carnivore footprint was described from the Pliocene Rohrbacher Conglomerates of the Vienna Basin by Thenius (1967) and this was cited as being that of *Bestiopeda guloides*. This footprint is different from the Ipolytarnóc traces because the digital imprints are elongated and not oval. Costeur et al. (2009) mentioned an isolated pentadactyl footprint (named *Bestiopeda* sp.) from the Oligocene sediments of the Regional

Natural Park of Luberon, France, showing resemblances in morphology and size with *Bestiopeda guloides*. This footprint also differs from *C. nogradensis* because of its ovoid-shaped digital imprints. Pleistocene footprints of *Mustelidichnum* (*M. enigmaticum* and *M. vallecitoensis*; see Remeika 2001) were interpreted as those of an aquatic mustelid, based on the webbing impression between the central digits. This feature is missing in the case of *C. nogradensis* and thus the relationship between these two ichnospecies can be ruled out.

## Discussion

The Ipolytarnóc site is considered to have been a drinking place for animals (e.g. Kordos 1985; Szarvas 2007, 2021). The site provided several spring waters which constituted a valuable source under a relatively hot subtropical climate (Bartkó 1985; Hably 1985; Kordos 1985). Since the channel-fill sediments are only detectable in older layers, it was suggested that the water holes may have been fed by veins flowing from intermittent springs (Bartkó 1985). Animal footprints can be found at several levels on the surface of successive sandstone layers, where traces have been well preserved around water holes which were subject to periodical drying out on relatively silty sediment surfaces.

Footprints of carnivores are rare at the Ipolytarnóc site and account for less than 3% of the footprints documented in the area (based on Kordos et al. 2021, and this study). The most frequent carnivore footprints are the tetradactyl ones of *Bestiopeda tarnocensis* (~33 samples, in Kordos et al. 2021), followed by pentadactyl footprints of *P. maxima* (22 samples), while the rarest are those of *C. nogradensis* (7 samples).

The largest carnivore footprints of the Ipolytarnóc locality belong to the *P. maxima* which over many years have been regarded as footprints of an amphicyonid carnivore (Abel 1935; Thenius 1948; Kordos et al. 2021). The first description of this footprint type was produced by Abel (1935) and at that time he suggested that these large pentadactyl footprints from Ipolytarnóc could have belonged to an amphicyon-like carnivore; however, he also did not rule out its origin as coming from a 'large *Felidae* (*Machairodus?*)'. Thenius (1948) came to the same conclusion as Abel (1935) and he also defined this footprint as being one left by an amphicyonid carnivore. Kordos (1985) makes no mention of the origin of this large-sized pentadactyl footprint, but in his later work he also suggested that these footprints most likely belonged to a large-sized bearded dog (e.g. Kordos et al. 2021).

In this study, based on the morphological characters of this footprint type, the authors suggest that these footprints belong to the *Platykopus* ichnogenus, because all diagnostic characteristics of this ichnogenus can be recognised on them (see above). All *Platykopus* footprints are considered to represent those of a large bear-like animal (Sarjeant et al. 2002; Lockley et al. 2007; Abbassi 2010; Diedrich 2011; Aramayo et al. 2015). During the early Miocene, there was no large-sized Ursidae present in Europe (see McLellan and Reiner 1994; Jiangzuo and Flynn 2020). Thus, this group can probably be excluded as a trackmaker for the *P. maxima* footprints. The most common Early and Middle Miocene bears are usually classified as Hemicyoninae. However, the small-sized (the Early Miocene forms were approximately raccoon-sized) and digitigrade gait, along with the elongated limbs of these animals, is not compatible with the tracks from Ipolytarnóc (Frick 1926; McLellan and Reiner 1994; Ginsburg and Morales 1998; Jiangzuo and Flynn 2020). Evidence of *Ursavus* (e.g. *U. brevirohinus*; *U. elemensis*) already appears in the Early Miocene (Burdigalian) but their size was no larger than that of a wolf (McLellan and Reiner 1994; Jiangzuo and Flynn 2020). Therefore, their footprints would be

much smaller than the *P. maxima* traces of the Ipolytarnóc locality. The genus *Indarctos* comprises extinct bears of moderate and large size with plantigrade limbs, but their appearance may have been later (Middle to Late Miocene) than the suggested date (Early Miocene) of the formation of the Ipolytarnóc traces (see Petter and Thomas 1986; McLellan and Reiner 1994; Baryshnikov 2002; Viranta 2004).

This study agrees with the former suggestion (i.e. in agreement with Abel 1935; Thenius 1948), and also accepts that the most likely trackmaker for the *P. maxima* footprints is a large-sized Amphicyonidae. The species diversity of the family of Amphicyonidae was reduced in the Miocene, but it still formed a vital part of the carnivore guilds of that period (Viranta 1996). Unfortunately, many of the European specimens are known only from dental material; thus, reconstruction of the mode of locomotion is frequently problematic. However, there are a few postcranial skeletal parts of amphicyonids, and the palaeobiological studies of which provide important information about the stance and gait of amphicyonid species. Such studies have greatly increased our current knowledge of the locomotion mode of this animal (e.g. Olsen 1958; 1960; Ginsburg 1961; Kurtén 1976; Viranta 1996; Argot 2010 and references therein).

The Amphicyonidae origin of the *P. maxima* footprints is based on the following anatomical evidence which features characteristics to the majority of Miocene Amphicyonidae species: 1) the ungual phalanges are similar to those of bears (see Olsen 1960); 2) the body was long, and the limbs short and stout (Ginsburg 1961); 3) the manus and the pes were pentadactyl (Viranta 2004; Argot 2010); 4) the stance was plantigrade (Viranta 2004; Argot 2010); 5) they have short phalanges; 6) the body size varies significantly, but larger Miocene forms (such as *Amphicyon major*) were accomplished predators reaching the size of the existing American grizzly bear (*Ursus arctos*) (Ginsburg 1961; Kurtén 1976; Viranta 2004). Based on these listed features, it can be assumed that Amphicyonid carnivores could have left similar footprints as those of the ichnospecies *P. maxima*. The *Amphicyon major* seems the best candidate as the maker of the *P. maxima* traces because the body size of this species is roughly compatible with the size of the Ipolytarnóc footprints (Viranta 1996; Argot 2010). Furthermore, this species was probably present in the Carpathian Basin at the time of the formation of the Ipolytarnóc traces (e.g. Sabol 2000).

Studies into the possible trackmaker of the *C. nogradensis* footprints are not particularly extensive in scope, and only two hypotheses have been put forward as to the origin of these traces. Tasnádi Kubacska (1976) mentioned that these footprints might have belonged to an amphicyonid carnivore. However, the anatomical features (e.g. short phalanges) and ichnotaxonomic ones (e.g. bear-like footprint-type) discussed for the *P. maxima* footprints suggest that a possible amphicyonid origin of the *C. nogradensis* footprints can with high probability be excluded. A long-standing notion is that the *C. nogradensis* footprints may have been made by a nimravid (i.e. a family of sabre-tooth predators). This theory often appears in museum information materials and scientific publications (Kordos et al. 2021). However, the nimravid origin can almost certainly be excluded since all sabre-tooth predators had fully retractile claws (Gonyea 1976; Bryant 1991; Sarjeant and Langston 1994; Christiansen and Adolfssen 2007; Wroe et al. 2008). However, in the case of the *C. nogradensis* footprints, the claw imprints are markedly present regardless of substratum moisture content (Figures 6 and 7).

It would seem more feasible that a medium- to large-size Mustelidae is a possible candidate for the trackmaker of the *C. nogradensis* footprints because the size and morphology of these traces exhibit strong affinities with modern mustelid

footprints, in particular with the footprints of wolverines (e.g. *Gulo gulo*; see Olsen 2013). Moreover, the morphology of the *C. nogradensis* ichnospecies exhibits similarities with the Late Eocene *Phacelopus therates* (see above). This ichnospecies was also interpreted as having a footprint type of a mustelid-like carnivore (Sarjeant and Langston 1994). Remeika (2001) suggests that the asymmetric placement of digits and the inward rotation of the digital imprints are diagnostic characteristics of the carnivoran family Mustelidae. The inward rotation of the digital imprints can be clearly seen in the case of the *C. nogradensis* footprints. Moreover, the placement of digital imprints is also asymmetric because the orientation of the digital imprints varies considerably between the outer and inner digits; thus, all these features point to a Mustelidae origin (see also Sarjeant and Langston 1994; Remeika 2001). If a mustelid origin is accepted for the *C. nogradensis* footprints, then the wolverine-sized mustelid *Ischyriactis* could be a potential candidate. This genus is known from several middle to late Miocene European localities ranging from 18.5 to 8.0 Ma, and it is recognised as a terrestrial predator that foraged mostly on the ground (Salesa et al. 2020 and references therein). Unfortunately, most of the *Ischyriactis* material is represented by cranial and dental remains and thus their locomotor adaptations and ecological role are still basically unknown (Salesa et al. 2020). Another large European mustelid is the *Hoplictis*, known from 17 to 11 Ma (Valenciano et al. 2019; Salesa et al. 2020). The earliest specimens of *Hoplictis* appeared in Western and Central Europe during the late early Miocene (Mayet 1908; Valenciano et al. 2019), so this group could also be considered as a conceivable contender as a trackmaker for the *C. nogradensis* footprint. However, the postcranial remains of *Hoplictis* are unknown and thus, with our present knowledge, the assignment of this genus to *C. nogradensis* cannot be verified. During the late Miocene, many large mustelids are known to have roamed Europe including *Mellalictis*, *Ekorus* and *Eomellivora* (see Ginsburg 1977; Tseng et al. 2009; Salesa et al. 2020 and references therein). However, apart from the almost complete skeleton of *Ekorus ekakeran* (Lothagam, Kenya), postcranial skeletons of these genera are very rare and little is known about them. *Eomellivora* was a giant mustelid in the late Miocene of Europe, and remains of this species are known from the Carpathian Basin as well (Kretzoi 1942; Valenciano et al. 2015). Given this fact, the early relatives of this animal may also be possible trackmakers of the *C. nogradensis* footprints.

Summarising the above-mentioned details, it can be said that despite earlier suppositions, a nimravid origin for the *C. nogradensis* footprints can be excluded. This is because the claw imprints are always clearly visible, while the sabre-tooth predators had fully retractile claws. Given the evidence available so far, the present authors would prefer a mustelid origin for this ichnospecies. This is based primarily on the fact that the morphology of these footprints does suggest this group, although the available skeletal materials do not provide sufficient biodata for a more precise identification.

## Conclusion

Ipolytarnóc is the most diverse Early Miocene trackway site in Europe, from where more than two thousand footprints belonging to at least eleven ichnospecies have been discovered during the last 120 years. Detailed 3D data presentation and ichnotaxonomical analyses of two plantigrade, pentadactyl carnivore footprint types (*Platykopus maxima* and *Carnivoripeda nogradensis*) were performed with the aim of contributing to a deeper understanding of the taxonomic affiliation of these tracks.

3D documentation of footprints is now an indispensable part of international ichnotaxonomic research, as it is the only way to guarantee comparison with other footprints and to preserve footprint sequences for future research. We are the first to present 3D models from the footprints of the Ipolytarnóc locality. These images have greatly contributed to the morphological comparison and taxonomic identification of the footprints studied here.

Due to the 3D documentation, the largest pentadactyl carnivore track previously defined as *Bestiopeda maxima* by Kordos (1985) was reclassified under the *Platykopus* ichnogenus. This is because the *Bestiopeda* ichnogenus was originally applied to tetradactyl and not pentadactyl footprints. Considering the nomenclature problems of the *Bestiopeda* ichnogenus, the present study now classifies these footprints under *Platykopus* because all the morphological features mentioned in the diagnosis of the *Platykopus* ichnogenus can be recognised on the Ipolytarnóc traces. Furthermore, only one isolated footprint was previously known which belonged to this ichnospecies. However, during this study, additional footprints and several trackways were determined as *P. maxima* ichnospecies, and this greatly complements the morphological markers of the footprints belonging to this ichnospecies. *P. maxima* footprints are considered to represent the footprints of large-sized Amphicyonidae.

The other pentadactyl ichnospecies from Ipolytarnóc is known as *Carnivoripeda nogradensis*. A detailed ichnotaxonomical investigation was conducted on these traces and this contributed to a better recognition of the morphological characteristics of this ichnospecies. During this study, 3D models were taken from the holotype and another trackway, thus representing the first high-resolution images of this ichnospecies. In contrast to the previously suggested Nimravidae origin, the new morphological characters suggested here that the *C. nogradensis* footprints belong to a mustelid-like carnivore.

This study represents only a first step in the 3D digitalisation and ichnotaxonomical revision of the Ipolytarnóc track site and it will be followed by further papers describing and presenting other footprint types from this famous locality.

## Acknowledgments

We thank Márton Rabi, Tünde Mezei, Mihály Gasparik and Eszter Hankó for scientific discussions, and thank 3D IPAR Ltd. for their help in the 3D scanning procedure. The research was supported by the SKHU/1902/1.1/037 INTERREG project of the Bükk National Park Directorate, the Herman Ottó Museum of Miskolc, the Hungarian Natural History Museum, Eötvös Loránd Research Network, the Hungarian National Research, Development and Innovation Office (project NKFIH/OTKA PD 131557), the ÚNKP-21-4 New National Excellence Program of the Ministry for Innovation and Technology from the source of the National Research (ÚNKP-21-4-II-ELTE-218), Development and Innovation Fund, and the János Bolyai Research Scholarship of the Hungarian Academy of Sciences to G.B. ELKH-MTM-ELTE Paleo Contribution [no. 367]. The authors would like to thank Dr Nasrollah Abbasi and Dr Spencer G. Lucas reviewers, as well as the Chief Editor (Dr Gareth Dyke), for their insightful and constructive comments on a previous version of this manuscript which improved the standards of this study.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

## Funding

This work was supported by SKHU/1902/1.1/037 INTERREG project of the Bükk National Park Directorate; National Research, Development and Innovation Office of Hungary (project NKFIH/OTKA PD 131557); ÚNKP-21-4 New National Excellence Program of the Ministry for Innovation and Technology from the source of the National Research, Development and Innovation Fund (ÚNKP-21-4-II-ELTE-218); János Bolyai Research Scholarship of the Hungarian Academy of Sciences BO/00024/19/10

## ORCID

Gábor Botfalvai  <http://orcid.org/0000-0002-5479-9036>  
 János Magyar  <http://orcid.org/0000-0002-2072-0174>

## References

- Abbassi N. 2010. Vertebrate footprints from the Miocene upper red formation, Shokorchí area, Zanjan Province, NW Iran. *Ichnos*. 17(2):115–126. doi:10.1080/10420941003659493.
- Abbassi N, Kundrát M, Mirzaie Ataabadi M, Ahlberg PE. 2015. Avian ichnia and other vertebrate trace fossils from the Neogene red beds of Tarom valley in north-western Iran. *Hist Biol*. 28(8):1075–1089. doi:10.1080/08912963.2015.1104306.
- Abel O. 1935. *Vorzeitliche lebensspuren*. Jena: Jena Verlag von Gustav Fischer; p. 165.
- Aramayo SA, de Bianco TM, Bastianelli NV, Melchor RN. 2015. Pehuen Co: updated taxonomic review of a late Pleistocene ichnological site in Argentina. *Palaeogeogr Palaeoclimatol Palaeoecol*. 439:144–165. doi:10.1016/j.palaeo.2015.07.006
- Argot C. 2010. Morphofunctional analysis of the postcranium of Amphicyon major (Mammalia, Carnivora, Amphicyonidae) from the Miocene of Sansan (Gers, France) compared to three extant carnivores: *ursus arctos*, *Panthera leo*, and *Canis lupus*. *Geodiversitas*. 32(1):65–106. doi:10.5252/g2010n1a2.
- Barry JC, Johnson NM, Raza SM, Jacobs LL. 1985. Neogene mammalian faunal change in southern Asia: correlations with climatic, tectonic, and eustatic events. *Geology*. 13(9):637–640. doi:10.1130/0091-7613(1985)13<637:NMFCS>2.0.CO;2.
- Bartkó L. 1985. Geology of Ipolytarnóc. *Geologica Hungarica Series Palaeontologica*. 44:49–71.
- Baryshnikov GF. 2002. Late Miocene *Indarctos punjabiensis atticus* (Carnivora, Ursidae) in Ukraine with survey of Indarctos records from the former USSR. *Russian J Theriol*. 1(2):83–89. doi:10.15298/rusjtheriol.01.2.02.
- Böckh H. 1902. Report of the director. Magyar Királyi Földtani Intézet Jelentése 1900-ról. p. 33–34. (in Hungarian).
- Bryant HN. 1991. Phylogenetic relationships and systematics of the Nimravidae (Carnivora). *J Mammal*. 72(1):56–78. doi:10.2307/1381980.
- Christiansen P, Adolfsen JS. 2007. Osteology and ecology of *Megantereon cultridens* SE311 (Mammalia; Felidae; Machairodontinae), a sabrecat from the Late Pliocene-Early Pleistocene of Senéze, France. *Zool J Linn Soc*. 151(4):833–884. doi:10.1111/j.1096-3642.2007.00333.x.
- Costeur L, Balme C, Legal S. 2009. Early Oligocene mammal tracks from south-eastern France. *Ichnos*. 16(4):257–267. doi:10.1080/10420940902953197.
- Csepregyhé MI. 1967. Az Ipolytarnóci Burdigalái fauna. *Földtani Közlöny*. 97:177–185.
- Demathieu G, Ginsburg L, Guerin C, Truc G. 1984. Étude paléontologique, ichnologique et paléocéologique du gisement oligocène de Saignon (Bassin d'Apt, Vaucluse). *Bulletin du Muséum national d'histoire naturelle Section C, Sciences de la terre, paléontologie, géologie, minéralogie*. 6(2):153–183.
- Diedrich CG. 2011. An overview of the ichnological and ethological studies in the Cave Bear Den in Ursilor Cave (Western Carpathians, Romania). *Ichnos*. 18(1):9–26. doi:10.1080/10420940.2011.552578.
- Domingo MS, Badgley C, Azanza B, DeMiguel D, Alberdi MT. 2014. Diversification of mammals from the Miocene of Spain. *Paleobiology*. 40:197–221. doi:10.1666/13043
- Eizirik E, Murphy WJ, Koepfli K, Johnson WE, Dragoo JW, Wayne RK, O'Brien SJ. 2010. Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. *Mol Phylogenet Evol*. 56(1):49–63. doi:10.1016/j.ympev.2010.01.033.
- Ellenberger P. 1980. Sur les empreintes de pas de gros mammifères de l'Éocène supérieur de Garrigues-Ste-Eulalie (Gard). *Paleovertebrata, Mémoire* Jubilé R. Lavocat. p. 37–78.
- Falkingham PL, Bates KT, Avanzini M, Bennett M, Bordy EM, Breithaupt BH, Castanera D, Citton P, Diaz-Martinez I, Farlow JO, et al. 2018. A standard protocol for documenting modern and fossil ichnological data. *Palaeontology*. 61(4):469–480. doi:10.1111/pala.12373.
- Frick C. 1926. The Hemicyoninae and an American tertiary bear. *Bull Am Museum Nat Hist*. 56:1883–1965.
- Ginsburg L. 1961. Plantigradie et digitigradie chez les carnivores fissipedes. *Mammalia*. 25(1):1–21. doi:10.1515/mamm.1961.25.1.1.
- Ginsburg L. 1977. Les carnivores du Miocène de Beni Mellal (Maroc). *Géologie Méditerranéenne*. 4(3):225–239. doi:10.3406/geolm.1977.1005.
- Ginsburg L, Morales J. 1998. Les Hemicyoninae (Ursidae, Carnivora, Mammalia) et les formes apparentées du Miocène inférieur et moyen d'Europe occidentale. *Annales de Paléontologie*. 84:71–123. doi:10.1016/S0753-3969(98)80003-7
- Gonyea WJ. 1976. Behavioral implications of saber-toothed felid morphology. *Paleobiology*. 2(4):332–342. doi:10.1017/S0094837300004966.
- Gradstein FM, Ogg JG, Schmitz M. 2012. *The geological time scale 2012*. Oxford: Elsevier Science Ltd. Vol. 2 (28). p.855–921.
- Hably L. 1985. Early Miocene plantfossils from Ipolytarnóc, N Hungary. *Geologica Hungarica, Series Geologica*. 45:73–255.
- Hágen A, Horváth D, Stromp M. 2014. Dynamics of the terrestrial mammals of Ipolytarnóc (Northern Hungary). *Ichnos*. 21(3):205–210. doi:10.1080/10420940.2014.934450.
- Harangi S. 2001. Neogene to Quaternary volcanism of the Carpathian-Pannonian region – a review. *Acta Geologica Hungarica*. 44:223–258.
- Jiangzuo Q, Flynn JJ. 2020. The Earliest ursine bear demonstrates the origin of plant-dominated omnivory in Carnivora. *Iscience*. 23(6):101235. doi:10.1016/j.isci.2020.101235.
- Karátson D, Biró T, Portnyagin M, Kiss B, Paquette JL, Cseri Z, Hencz M, Németh K, Lahitte P, Márton E, et al. 2022. Large-magnitude (VEI ≥ 7) 'wet' explosive silicic eruption preserved a Lower Miocene habitat at the Ipolytarnóc Fossil Site, North Hungary. *Sci Rep*. 12:9743. doi:10.1038/s41598-022-13586-3
- Kocsis L. 2007. Centralparatethyan shark fauna (Ipolytarnóc, Hungary). *Geologica Carpathica-Bratislava*. 58(1):27–40.
- Kocsis L, Vennemann TW, Hegner E, Fontignie D, Tütken T. 2009. Constraints on Miocene oceanography and climate in the Western and Central Paratethys:  $\delta^{18}O$ , Sr-, and Nd-isotope compositions of marine fish and mammal remains. *Palaeogeogr Palaeoclimatol Palaeoecol*. 271:117–129. doi:10.1016/j.palaeo.2008.10.003.
- Kordos L. 1985. Footprints in the Lower Miocene sandstone of Ipolytarnóc. *Geol Hung Ser Geol*. 46:257–415.
- Kordos L. 1987. Újabb Adatok az Ipolytarnóci Alsó-Miocén Homokkő Lábnymaihoz. *Annual Report of the Hungarian Geological Institute of 1985*. p. 453–466.
- Kordos L, Mészáros I, Szarvas I. 2021. Tracking a “Prehistoric Pompeii”, Rhinoland and Crocodilia: new discoveries and interpretations of Ipolytarnóc (N Hungary) Lower Miocene track site. *Geoconserv Res*. 4(2):621–634. doi:10.30486/gcr.2021.1914158.1062.
- Kordos L, Morgós A. 1988. Lower Miocene footprints as studied at Ipolytarnóc in 1986. *Annual Report of the Hungarian Geological Institute of 1986*. p. 493–451.
- Krapovickas V, Vizcaíno S. 2016. The Cenozoic radiation of mammals. In: Mángano M, Buatois L, editors. *The trace-fossil record of major evolutionary events*. Topics in geobiology. Vol. 40. Dordrecht: Springer Nature; p. 371–410.
- Kretzoi M. 1942. *Eomellivora* von Polgárdi und Csákvár. *Földtani Közlöny*. 72(4–12):318–323.
- Kurtén B. 1976. Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. *Notes du Service Géologique de Tunisie*. 42:177–214.
- Leonardi G. 1987. Glossary and manual of tetrapod footprint paleoichnology. Brasília ((Brazil)): Departamento Nacional de Produção Mineral; p. 1–75.
- Lockley MG, Harris JD. 2010. On the trail of early birds: a review of the fossil footprint record of avian morphological and behavioral evolution. In: Ulrich PK, Willard JH, editors. *Trends in ornithology research: birds - evolution, behavior and ecology*. New York: Nova Science Publishers; p. 1–63.
- Lockley MG, Reynolds R, Milner AC, Varhalmi G. 2007. Preliminary overview of mammal and bird tracks from the white narrows formation, Southern Nevada. *New Mexico Museum Nat Hist Sci Bul*. 42:91–96.
- López G, Mayoral E, Muñoz A, Pérez A, Santamaría R. 1992. Nuevas incitas de mamíferos carnívoros en el Mioceno Inferior del sector occidental de la depresión del Ebro (Logroño, La Rioja). *Revista de la Sociedad Geológica de España*. 5:31–51.
- Lucas S, Schultz G. 2007. Miocene vertebrate footprints from the Texas Panhandle. *Cenozoic vertebrate tracks and traces*. New Mexico Museum Nat Hist Sci Bul. 42:177–183.
- Márton E, Vass D, Tunyi I, Marton P, Zelenka T. 2007. Paleomagnetic properties of the ignimbrites from the famous fossil footprints site, Ipolytarnóc (close to the Hungarian-Slovak frontier) and their age assignment. *Geologica Carpathica-Bratislava*. 58(6):531.
- Mayet L. 1908. Études de Mammifères miocènes des sables de l'Orléanais et des faluns de la Touraine. *Annales de l'Université de Lyon, Nouvelle Série*. 24:1–336.
- McCrea RT, Pemberton SG, Currie PJ. 2004. New ichnotaxa of mammal and reptile tracks from the Upper Paleocene of Alberta. *Ichnos*. 11(3–4):323–339. doi:10.1080/10420940490442313.
- McDonald HG, White R, Lockley M, Mustoe G. 2007. An indexed bibliography of Cenozoic vertebrate tracks. *Cenozoic Vertebrate Tracks and Traces: Bulletin*. 42:275–302.
- McLellan B, Reiner DC. 1994. A review of bear evolution. *Bears: Their Biol Manage*. 9(1):85–96. doi:10.2307/3872687.

- Melchor RN, Feola SF, de Bianco TM. 2019. Canid paleoichnology: taxonomic review and producers of Canipeda from the late Pleistocene of Argentina. *Ichnos*. 26(2):85–107. doi:10.1080/10420940.2018.1447466.
- Mezei T, Szolyák P, Watah VE, Botfalvai G. 2022. Az ipolytárnóci nyomfossziliás őslénylelőhely új térképi feldolgozása. Abstract book of the 25th Hungarian Palaeontological Meeting in Tótvárzsony, Hungary. p. 25
- Morales J, Cantalapiedra JL, Valenciano A, Hontecillas D, Fraile S, García Yelo BA, Montoya P, Abella J. 2015. The fossil record of the Neogene Carnivore mammals from Spain. *Palaeobiodiversity and Palaeoenvironments*. 95(3):373–386. doi:10.1007/s12549-015-0206-z.
- Olsen SJ. 1958. The fossil carnivore *Amphicyon intermedius* from the Thomas Farm Miocene Part I. Skull and dentition. *Bull Museum Comparative Zool*. 123:1–44.
- Olsen SJ. 1960. The fossil carnivore *Amphicyon longiramus* from the Thomas Farm Miocene, Part II. Postcranial skeleton. *Bull Museum Comparative Zool*. 123:1–44.
- Olsen L-H. 2013. Tracks and signs of the animals and birds of Britain and Europe. New Jersey: Princeton University Press. doi:10.1515/9781400847921
- Pálffy J, Mundil R, Renne PR, Bernor RL, Kordos L, Gasparik M. 2007. U–Pb and <sup>40</sup>Ar/<sup>39</sup>Ar dating of the Miocene fossil track site at Ipolytárnóc (Hungary) and its implications. *Earth Planet Sci Lett*. 258(1–2):160–174. doi:10.1016/j.epsl.2007.03.029.
- Peigné S. 2003. Systematic review of European Nimravinae (Mammalia, Carnivora, Nimravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zool Scr*. 32:199–229. doi:10.1046/j.1463-6409.2003.00116.x
- Petter G, Thomas H. 1986. Les Agriotheriinae (Mammalia, Carnivora) néogènes de l’Ancien Monde présence du genre *Indarctos* dans la faune de Menacer (Ex-Marceau), Algérie. *Geobios*. 19(5):573–586. doi:10.1016/S0016-6995(86)80055-9.
- Piller WE, Harzhauser M, Mandic O. 2007. Miocene Central paratethys stratigraphy—current status and future directions. *Stratigraphy*. 4(2/3):151–168.
- Remeika P. 2001. The Fish Creek Canyon ichnofauna: a pliocene (blancan) vertebrate footprint assemblage from Anza-Borrego Desert State Park, California. In: Santucci VL, McClelland L, editors. Proceedings of the 6th fossil resource conference. Lakewood (Colorado): Geologic Resources Division Technical Report; p. 55–75.
- Rögl F. 1998. Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien*. 99A:279–310.
- Sabol M. 2000. Neogene carnivores of Slovakia. *Slovak Geological Magazine*. 6 (2–3):124–126.
- Salesa MJ, Siliceo G, Antón M, Fabre A-C, Pastor JF. 2020. Functional inferences on the longbones of *Ischyriactis zibethoides* (Blainville, 1841) (Carnivora, Mustelidae) from the middle Miocene locality of Sansan (Gers, France). *Geodiversitas*. 42(1):1–16. doi:10.5252/geodiversitas2020v42a1.
- Sarjeant WAS, Langston JW. 1994. Vertebrate footprints and invertebrate traces from the Cadronian (LateEocene) of Trans-Pecos Texas. *Texas Memorial Museum Bulletin*. 36:1–86.
- Sarjeant WAS, Reynolds RE, Kissell-Jones MM. 2002. Fossil creodont and carnivore footprints from California, Nevada, and Wyoming. In: Reynolds RE, editor. Between the basins: exploring the Western Mojave and Southern Basin and Range Province. Desert studies consortium, Fullerton. Fullerton: California State University; p. 37–50.
- Sarjeant WAS, Wilson JA. 1988. Late Eocene (Duchesnean) mammal footprints from the Skyline Channels of Trans-Pecos Texas. *Texas J Sci*. 40(4):439–446.
- Szarvas I. 2007. Cases study of the Ipolytárnóc track site, Hungary. In: Lucas SG, Spielmann JA, Lockley Meditors. Cenozoic vertebrate tracks and traces. New Mexico Museum Nat Hist Sci Bul. 42:303–307.
- Sztánó O. 1994. The tide-influenced Pétervására sandstone, early Miocene, Northern Hungary: sedimentology, palaeogeography and basindevelopment. *Geologica Ultraiectina*. 120:1–155.
- Tasnádi Kubacska A. 1976. Traces of Prehistoric Life in the Sandstone with Footprints at Ipolytárnóc Village (N Hungary). Annual Report of the Geological Institute of Hungary. p. 77–94
- Thenius E. 1948. Bemerkungen über die angeblichen *Anchitherium*-und *Amphicyoniden*fährten aus dem Burdigal von Ipolytárnóc: ungar. Sitzungsberichteder Akademieder Wissenschaften in Wien Kl I. 157:223–230.
- Thenius E. 1967. Säugetierfährten aus dem Rohrbacher Konglomerat (Pliozän) von Niederösterreich. *Annalen des Naturhistorischen Museums in Wien*. 71:363–379.
- Tseng ZJ, O’Connor JK, Wang X, Prothero DR. 2009. The first old world occurrence of the North American mustelid *Sthenictis* (Mammalia, Carnivora). *Geodiversitas*. 31(4):743–751. doi:10.5252/g2009n4a743.
- Vadász E. 1963. Magyarországi megkövesedett famaradványok földtani kérdései. *Földtani Közlöny*. 93(4):505–545.
- Valenciano A, Abella J, Sanisidro O, Hartstone-Rose A, Álvarez-Sierra MÁ, Morales J. 2015. Complete description of the skull and mandible of the giant mustelid *Eomellivora piveteaui* Ozansoy, 1965 (Mammalia, Carnivora, Mustelidae), from Batallones (MN10), late Miocene (Madrid, Spain). *J Vertebrate Paleontol*. 35(4):e934570. doi:10.1080/02724634.2014.934570.
- Valenciano A, Jiangzuo Q, Wang S, Li C, Zhang X, Ye J. 2019. First record of hoplictis (Carnivora, Mustelidae) in East Asia from the Miocene of the Ulungur River Area, Xinjiang, Northwest China. *Acta Geologica Sinica-English Edition*. 93(2):251–264. doi:10.1111/1755-6724.13820.
- Vialov OS. 1965. Stratigrafiya Neogenovykh molass Predkarpatskovo progriba [Stratigraphy of the Neogene molasse of the PreCarpathian basin]. Kiev, Naukova Dumka (Akademiya Nauk Ukrainskoy SSR Institut Geologii I Geokhimii Goryuchikh Iskopayemykh). p.165.
- Vialov OS. 1966. Sledy zhiznedeyatelnosti organizmov I ikh paleontologicheskoe znachenie [Traces of the vital activity of organisms and their paleontological significance]. *Akademiya Nauk Ukrainian SSR*. p. 29.
- Vialov OS. 1985. Sledy pozvonochnykh iz nizhnevo Miotsena Vengrii [Tracks of vertebrates from the lower Miocene of Hungary]. *Paleontologicheskyy Sbornik*. 22:71–78.
- Vialov OS. 1986. Artiodactyla’s traces from the Lower Miocene of Hungary. *Paleontologicheskii Sbornik*. 23:63–69.
- Viranta S. 1996. European Miocene Amphicyonidae: taxonomy, systematics and ecology. *Acta Zoologica Fennica Finnish Zool Botanical Publ Board*. 204:1–61.
- Viranta S. 2004. Habitat preferences of European Middle Miocene omnivorous ursids. *Acta Palaeontologica Polonica*. 49(2):325–327.
- Werdelin L, Yamaguchi N, Johnson WE, O’Brien SJ. 2010. Phylogeny and evolution of cats (Felidae). In: Macdonald DW, Loveridge AJ, editors. Biology and conservation of wild felids. New York: Oxford University Press; p. 59–82.
- Wroe S, Lowry MB, Anton M. 2008. How to build a mammalian super-predator. *Zoology*. 111(3):196–203. doi:10.1016/j.zool.2007.07.008.