Quaternary Science Reviews 265 (2021) 107028

Contents lists available at ScienceDirect

Quaternary Science Reviews

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

First small-sized *Dinofelis*: Evidence from the Plio-Pleistocene of North Africa

Joan Madurell-Malapeira [a, *], Antonio Rodríguez-Hidalgo [b, c, d], Hassan Aouraghe [e], Hamid Haddoumi [e], Saverio Bartolini Lucenti [f], Aïcha Oujaa [g], Palmira Saladié [c, h, i], Said Bengamra [e], Juan Marín [c, k], Mohamed Souhir [e], Mourad Farkouch [c, e], Hicham Mhamdi [e], Al Mahdi Aissa [c, e], Lars Werdelin [j], M. Gema Chacón [c, h, k], Robert Sala-Ramos [c, h]

[a] *Institut Català, de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193, Cerdanyola del Vallès, Barcelona, Spain*
[b] *Departamento de Prehistoria, Historia Antigua y Arqueología, Universidad Complutense de Madrid, Facultad de Geografía e Historia, C/ Prof. Aranguren s/n, 28040, Madrid, Spain*
[c] *Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), Tarragona, 43007, Spain*
[d] *Instituto de Evolución en África (IDEA, Madrid), C/ Covarrubias 36, 28010, Madrid, Spain*
[e] *Université Mohamed Premier, Faculté des Sciences, Département de Géologie, BV Mohammed VI, Hay Al Qods, 60000, Oujda, Morocco*
[f] *Dipartimento di Scienze della Terra, Paleo[Fab]Lab, Università degli Studi di Firenze, Via G. La Pira 4, 50121, Firenze, Italy*
[g] *Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Av. Allal El-Fassi, Hay Riad, 6828, Rabat, Morocco*
[h] *Universitat Rovira i Virgili, Departament d'Història i Història de l'Art, Avinguda de Catalunya 35, 43002, Tarragona, Spain*
[i] *Unidad Asociada al CSIC. Departamento de Paleobiología. Museo Nacional de Ciencias Naturales, C/ José Gutiérrez Abascal, 2, 28006, Madrid, Spain*
[j] *Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, SE-104 05, Stockholm, Sweden*
[k] *UMR7194-HNHP (CNRS-MNHN-UPVD-Sorbonne Universités), Musée de l'Homme, Palais Chaillot, Place du Trocadéro 17, 75016, Paris, France*

ARTICLE INFO

Article history:
Received 15 October 2020
Received in revised form
7 May 2021
Accepted 7 June 2021
Available online 25 June 2021

Handling Editor: Danielle Schreve

Keywords:
North africa
Morocco
Plio-Pleistocene
Carnivora
Felidae
Machairodontinae
Dinofelis

ABSTRACT

We describe small-sized specimens of the metailurine felid *Dinofelis* from a new Plio-Pleistocene site in North Africa. *Dinofelis* is a genus of saber-toothed cats mainly recorded from East and South Africa with numerous leopard to jaguar-sized species. The described specimens, clearly smaller than all the other African *Dinofelis*, resemble isolated remains from the Late Pliocene of France and the Early Pleistocene of Africa. Present evidence suggests that our form represents a new species and/or new lineage of *Dinofelis*, smaller and probably occupying a different ecological niche compared to the previously known members of the genus, and thus it adds complexity to the high intraspecific competition among large carnivorans in the Plio-Pleistocene of Africa.

© 2021 Elsevier Ltd. All rights reserved.

1. Introduction

Metailurines are a group of saber-toothed felids (Subfamily Machairodontinae, Tribe Metailurini) with generally intermediate characteristics between Pantherinae and Machairodontinae felids, with certain forms resembling the former and others the latter. Metailurines possess shorter and less flattened upper canines as compared with other machairodontines, an only slightly derived mastoid region, the glenoid not lowered, a ventrally flattened mandibular corpus without mental flange, and no reduction of the coronoid process (Antón, 2013). Several genera of metailurines are

* Corresponding author.
E-mail address: joan.madurell@icp.cat (J. Madurell-Malapeira).

https://doi.org/10.1016/j.quascirev.2021.107028
0277-3791/© 2021 Elsevier Ltd. All rights reserved.

known from Late Miocene–Early Pleistocene sites of Europe, Asia, Africa, and North America. These include: *Dinofelis, Metailurus, Adelphailurus, Stenailurus* and *Fortunictis* (Roussiakis et al., 2006; Li, 2014; Spassov and Geraads, 2015; further discussion in Werdelin and Lewis, 2001 and references therein). *Metailurus* and *Dinofelis* are the best-known genera of metailurines. Their records respectively characterize the Late Miocene of Eurasia (Spassov et al., 2018) and the Plio-Pleistocene of Africa (Werdelin and Peigné, 2010).

Metailurus was erected by Zdansky (1924) based on craniodental specimens from the Late Miocene of China. Later finds come from the classic Turolian Greek localities (e.g., Pikermi and Samos). Such records expanded the known geographical range of this genus (Roussiakis et al., 2006 and references therein). In his study of carnivorans from China, Zdansky (1924) erected two species of *Metailurus*, *M. major* and *M. minor* (the latter today considered a junior subjective synonym of *Metailurus parvulus*). The first was more or less of the size of a puma and the second slightly smaller and more gracile. As the original description was based only on craniodental specimens, the postcranial anatomy was not known until recently, when two complete skeletons of the species were found in the Turolian of Bulgaria (Kovatchev, 2001) and Greece (Roussiakis et al., 2006). The limb proportions of *M. major* are close to those of a male puma, although its hind limbs were more elongated. *Metailurus parvulus* also had forelimb proportions comparable to those of a puma, yet its hindlimbs were long, slender and gracile, like those of an extant snow leopard.

The genus *Dinofelis*, in turn, includes a small number of large-sized species characterized by slightly compressed upper canines lacking serrations but retaining anterior and posterior edge crests (see Werdelin and Lewis, 2001). This genus was also described by Zdansky (1924) on the basis of craniodental specimens from the 'Pontian' of China. Although the age of the holotype specimen was historically considered to be Late Miocene, more recent hypotheses have reassigned the type locality (Henan; Lok. B) to the Pliocene (Werdelin and Lewis, 2001). The latter authors described *Dinofelis* as a genus of large-sized felids which putatively preferred mixed or closed habitats, as their appendicular skeleton has short distal elements, characteristic of less cursorial species not adapted to open habitats. Werdelin and Lewis (2001) recognized as valid eight species of *Dinofelis*: *D. cristata* (from the Pliocene of the Indo-Pakistani Siwaliks and Henan, China); *D. diastemata* (from the Pliocene of Serrat d'en Vaquer, France); *D. barlowi* (from the Late Pliocene-Early Pleistocene, Sterkfontein, Bolt's Farm, Swartkrans and Kromdraai B, South Africa); *D. paleoonca* (Early Pleistocene of the Blanco Local Fauna, U.S.A.); *D. darti* (Late Pliocene, Makapansgat, South Africa): *D. piveteaui* (Early Pleistocene of Kromdraai A and Koobi Fora, South Africa and Kenya); *D. petteri* (Late Pliocene, Kanapoi, Laetoli and Omo, Kenya and Tanzania) and *D. aronoki* (Late Pliocene-Early Pleistocene, Koobi Fora and Lothagam, Kenya) (Werdelin and Lewis, 2001).

Here we describe some dentognathic and postcranial specimens of a small-sized *Dinofelis* from the latest Pliocene-earliest Early Pleistocene of Guefaït-4 (ca. 2.5 Ma; Morocco, North Africa), comparing them with selected known species of metailurines.

2. Age and geological setting

The paleontological site of Guefaït-4 is located near the homonymous village in eastern Morocco (Fig. 1). Since 2006, a Moroccan-Spanish interdisciplinary project has carried out several field surveys in the Aïn Beni-Mathar/Guefaït region (Jerada Province, Eastern Morocco), with the aim of mapping archaeo-palaeontological sites, establishing their geochronological context and the evolution of human peopling in the region (Aouraghe et al., 2016; Chacón et al., 2016). Systematic surveys have led to the discovery of several Pleistocene archaeological sites and some paleontological localities ranging from the Late Miocene (Blain et al., 2013) to the Plio-Pleistocene boundary (Piñero et al., 2019).

Situated in the High Plateau Region, the Aïn Beni-Mathar/Guefaït basin preserves a ca. 150 m thick succession of alluvial and lacustrine/palustrine deposits described through various regional stratigraphic sections. Specifically, the Dhar Iroumyane (DI) stratigraphic section, ca. 120 m thick, includes the localities of Guefaït-4.1, −4.2 and −4.3 along the same fossiliferous layer. This layer is formed by green marls and white micritic limestones and contains abundant remains of micro- and macro-vertebrates. It extends for several hundred meters on the eroded slope of the continental deposits. During the 2017–2019 seasons, more than 3200 fossil remains of macro-vertebrates were recovered from Guefaït-4.2, in a ca. 2 m thick trench covering 28 m^2.

The preliminary analysis on the unearthed remains enables the identification of several dentognathic and postcranial specimens of *Hipparion* sp., the most abundant taxon. Few other fossils corresponding to Rhinocerotidae indet. are currently under study. The second most abundant group identified in the site are bovids. Remains of a small gazelle are particularly relevant in number, while specimens of a tragelaphine and of a bovid of intermedium sized are less abundant. A carpal is attributable to Giraffidae. Few dental remains belong to Suidae and several dental and postcranial remains to a primitive hippopotamus, the size of the living species. Several dental specimens indicate the presence of *Anancus* sp. in the assemblage. In addition to the carnivore remains presented in this paper, we found some small to medium-sized elements of a canid. *Macaca* cf. *M. sylvanus* (Alba et al., 2021) and Leporidae indet. complete the sample of mammals identified. Among the non-mammalian species, we have documented Testudinae cf. *T. hermanii*/*graeca*-sized tortoise, a giant tortoise (*Centrochelys*?) and some fish remains.

Although fragmentary in some cases, the composition of the fauna of Guefait-4 allows tentative biochronological interpretations. The micromammals from Guefaït have been published and the murid assemblage allows the biostratigraphic correlation with other sites from Northern Africa, according to the biochronological scale proposed by Stoetzel (2013), indicating an age close the Plio-Pleistocene boundary (Agustí et al., 2017; Piñero et al., 2019). This is corroborated by the large vertebrates. The absence of *Equus* compared to the abundance of hipparion indicates an age older than 2.44 Ma, (Sahnouni et al., 2018), Other elements, such as the primitive hippopotamus, the proboscidean *Anancus* sp., the giant tortoise (*Centrochelys* indet.) and the jackal-like canid suggest an age close to or even older than Ahl al Oughlam (Aouraghe et al., 2019; Alba et al., 2021). However, more research, such as radiometric ages (currently not available), will help to establish a more time-constrained chronology. The felid remains presented in this paper, which could belong to a single individual, were located in an area of less than 12 square meters, in clear anatomical association in some cases (Fig. 1E).

3. Materials and methods

This work is based on the comparative morphological and biometrical analysis of the small-sized *Dinofelis* from Guefaït-4 and other metailurine species of the Old World. We excluded the poorly known or stratigraphically unclear species and the American species *Dinofelis paleoonca.* The described fossils are housed in Faculté de Sciences, Département de Géologie, Université Mohamed Premier (Oujda, Morocco).

Cranial and dental measurements were taken with digital

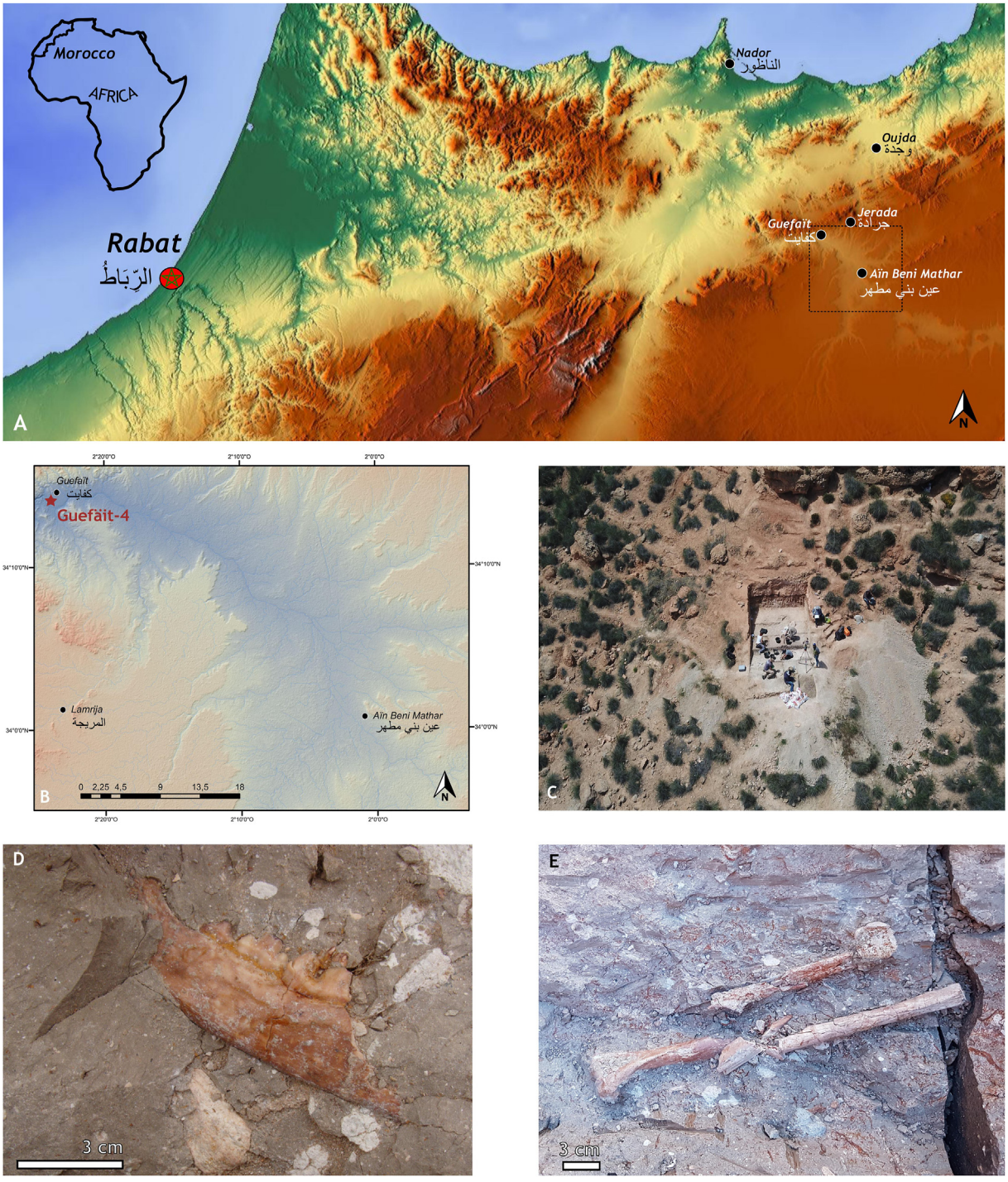


Fig. 1. Location of the Guefaït-4 site and −4.2 locality. **A,** Partial map of Morocco with the area of interest (dotted box). Data extracted from Map Tile 7_61/62/63−50 & 7_61/62/63−510 (CC BY-SA). OpenStreetMap© licensed under ODdL 1.0 (https://www.openstreetmap.org/copyright) by the OpenStreetMap Foundation (OSMF). ©OpenStreetMap contributors (https://www.openstreetmap.org/), **B,** Location of the Guefaït-4 site (Base Map ArcGIS), **C,** Locality 4.2, **D,** *Dinofelis* sp. mandible in situ, **E,** Distal humerus and proximal ulna of *Dinofelis* sp. in situ (pictures by Alfonso Benito-Calvo and Antonio Rodríguez-Hidalgo).

calipers to the nearest 0.1 mm.

As comparative fossil material we used Miocene to Pleistocene fossil collections from Eurasian sites housed at the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain). The relevant literature regarding Miocene, Pliocene and Pleistocene metailurines was also used for comparative purposes and biometrical analyses (Zdansky, 1924; Colbert, 1939; Chang and Liu, 1964; Kurtén, 1973; Cooke, 1991; Kovatchev, 2001; Werdelin and Lewis, 2001, 2013; Werdelin, 2003a, 2003b; Lacruz et al., 2006; Roussiakis et al., 2006; Li, 2014; Adams et al., 2015; Spassov and Geraads, 2015).

4. Results

Order Carnivora Bowdich, 1821

Family Felidae Fischer, 1817.
Subfamily Machairodontinae Gill, 1872
Tribe Metailurini Turner, 1997
Genus *Dinofelis* Zdansky, 1924.
Dinofelis sp.
Figs. 2 and 3.

Referred specimens—**GFT4.2′19-1-S14**–**6**, partial right corpus with broken c1 and p3 and complete p4-m1; **GFT4.2′19-1-T15**–**8**, distal fragment of right humerus; **GFT4.2′19-1-T15**–**6,** proximal fragment of right ulna; **GFT4.2′19-1-S15**–**128,** left i1; **GFT4.2′19-1-R15**–**35,** distal fragment of right proximal phalanx; **GFT4.2′19-1-Q14**–**96,** distal fragment of right proximal phalanx; **GFT4.2′19-1-T13**–**37,** complete left medial phalanx.

Measurements—See Table 1.

Description—GFT4.2′19-1-S14-6 is a fragment of a low corpus broken off at the anterior end of the masseteric fossa as seen in buccal view (Fig. 2B). The symphysis is more vertical than in pantherines, with an 115° angle with the ventral margin of the corpus, similar to other machairodonts (Christiansen, 2006), and with a marked mental crest but no mental flange. The ventral margin of the corpus is straight and only slightly convex ventrally. The diastema between c1 and p3 is long (14.8 mm; Table 1). The c1 is broken diagonally at the base of the crown. Three mental foramina are visible, the rostral two are small and are placed at the level of the diastema. The third, which is the largest, is placed at the level of the mesial root of p3. The p3 is broken, only preserving the distolingual part (Fig. 2B). In occlusal view, the p3 alveolus is not in line with the alveoli of p4 and m1, but oriented diagonally to them. Compared to the p4, the p3 is very reduced in mesiodistal length, showing a small distal accessory cuspid and a marked distal cingulid. The p4 bears mesial and distal accessory cuspids, of which the mesial one is particularly high. A marked cingulid bounds the buccal and distal parts of the p4. The m1 has a mesiodistally shorter paraconid compared to the protoconid (Fig. 2C). A marked but small m1 metaconid is visible in lingual view (Fig. 2A). The m1 also bears a small talonid that represents the continuation of small lingual cingulid arising at the base of the protoconid. GFT4.2′19-1-T15-8 is a slender distal fragment of a right humerus (Fig. 3A). The lateral epicondyle is small cranially and the trochlea is narrow proximodistally (Fig. 3F). The medial epicondyle is well-developed, triangular and placed roughly at the same height as the trochlea. The medial epitrochlea is more projected distally compared to the lateral one, the proximal margin of the trochlea is straight and rectilinear in the mediolateral direction. The coronoid fossa is oval and deep. The epicondylar foramen is broken, yet completely distinct from the epicondyle. Palmarly, the olecranon fossa is rounded and deep, although not especially wide distally. Distally, the trochlea is wide craniopalmarly and short mediolaterally, with a very shallow incision between the epitrochleas. The other identified remains, the partial ulna and the partial phalanx (Fig. 3C-O), are damaged and too fragmentary to be described in detail. No distinguishing features can be recognized on them.

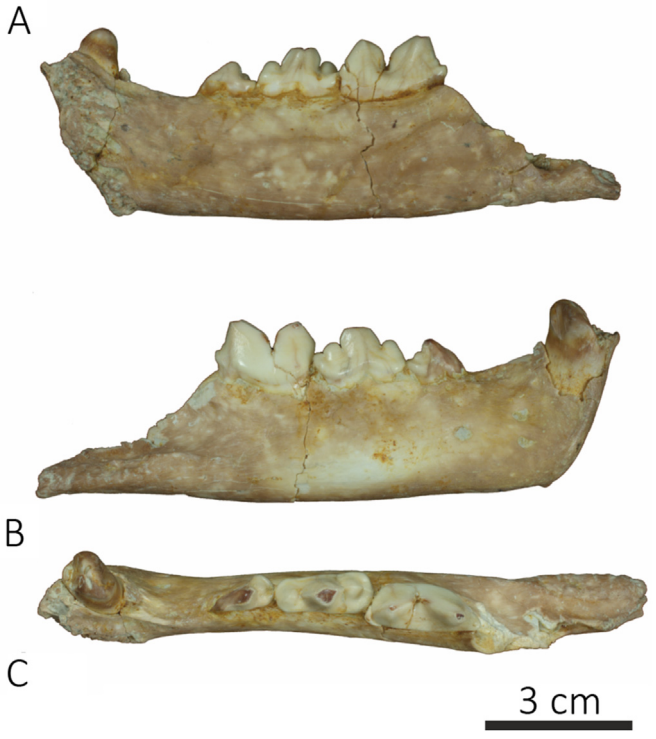


Fig. 2. *Dinofelis* sp. dentognathic remains from Guefaït-4. GFT4.2′19-1-S14-6, right corpus in **A,** lingual view; **B,** buccal view and **C,** occlusal view.

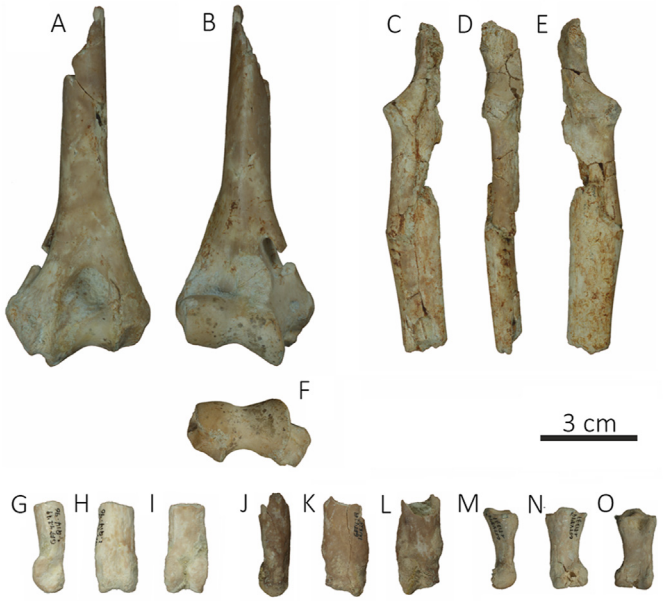


Fig. 3. *Dinofelis* sp. postcranial remains from Guefaït-4. GFT4.2′19-1-T15-8, distal fragment of right humerus in **A,** posterior view; **B,** anterior view and **F**, distal view. GFT4.2′19-1-T15-6, proximal fragment of right ulna in **C,** medial view; **D**, anterior view and **E**, lateral view. GFT4.2′19-1-Q14-96, distal fragment of proximal phalanx in **G**, lateral view; **H**, dorsal view and **I**, palmar view GFT4.2′19-1-R15-35, distal fragment of proximal phalanx in **J**, lateral view; **K**, dorsal view and **L**, palmar view. GFT4.2′19-1-T13-37, complete medial phalanx in **M,** lateral view; **N**, dorsal view and **O**, palmar view.

5. Discussion

5.1. Morphological dentognathic comparisons with other Dinofelis

5.1.1. Morphological dentognathic comparisons with African Dinofelis

In the only revision to date of the genus *Dinofelis*, Werdelin and Lewis (2001) distinguished two different lineages, both departing from the basal Mio-Pliocene specimens of Lothagam.

East African lineage—Werdelin and Lewis (2001) identified a succession of three species *D. petteri-D. aronoki-D. piveteaui* from the Early Pliocene to the latest Early Pleistocene (ca 4.2–1.0 Ma). This lineage, best recorded in the Koobi Fora sequence, is characterized by an increase in machairodontid affinities, e.g., reduced p3 and p4, elongated m1 and the increased mandibular corpus

Table 1
Measurements of the studied corpus and humerus of *Dinofelis* sp. from Guefait.

	c1		p3		p4		m1								
Rec. num.	L	W	L	W	L	W	L	W	Lpa	Lpr	Ld	Lp3-m1	Hp4	Hm1	Hd
S14-L1-6	10.2	8.5	9.9	5.3	16.4	7.0	19.1	7.8	9.6	9.0	14.8	45.3	23.2	20.8	22.3
Rec. num.	**MLMD**	**MLDD**	**APMD**	**APDD**											
T15-L1-8	12.5	40.7	15.2	23.1											

Abbreviations: **Hd:** height of the corpus below diastema; **Hp4:** height of the corpus below p4; **Hm1:** height of the corpus below m1; **L:** mesiodistal length; **Ld:** mesiodistal length of diastema; **Lpa:** mesiodistal length of m1 paraconid; **Lpr:** mesiodistal length of m1 protoconid; **Lp3-m1:** mesiodistal length from mesial margin of p3 to distal margin of m1; **W:** buccolingual width.

robustness.

Dinofelis aronoki from Koobi Fora (Karari Ridge; specimen ER3880R) and specially *D. piveteaui* from Koobi Fora (Okote Member; specimen ER40482C) clearly display more machairodontine affinities than does the Guefaït-4 specimen. Moreover, they possess thicker and higher corpuses, sharper, buccolingually compressed check teeth, a longer (in *D. aronoki*) and shorter (in *D. piveteaui*) c1-p3 diastema, reduced p3 (especially in *D. piveteaui*), more slender p4, and mesiodistally long and low m1 with enlarged protoconid (Werdelin and Lewis, 2013).

On the other hand, the older and widely recorded *Dinofelis petteri* from Late Pliocene-Early Pleistocene sites (see Werdelin, 2003a,b; Werdelin and Lewis, 2001, 2013) is the smallest of the known African *Dinofelis*. In this regard, it similar to Guefaït-4. Nevertheless, the mandible KNM-ER-30397 from Kanapoi differs from the Moroccan specimen in the broad and thick corpus, the longer diastema (ca. 20 mm), the absence of distal accessory cuspulids on p3, the slender and proportionally longer p4 with more vertical mesial accessory cuspulids and weakly developed distal cingulid, the longer m1 protoconid, and absence of the m1 metaconid.

Finally, fragmentary specimens of *Dinofelis* sp. were recorded from the Late Miocene of the Middle Awash, Ethiopia, in sites that are roughly contemporaneous with Lothagam (Haile-Selassie and Howell, 2009). The best-preserved specimen, AME-VP-1/1, consists of a corpus with p3-m1. It is small in size, close to that of KNM-ER-30397 from Kanapoi, and only slightly larger than the Guefaït-4 specimen (Table 1). In its general morphology, this specimen is similar to the one described here. Some similarities include, e.g., a moderately long diastema, p3 with small distal accessory cuspulid. Moreover, AME-VP-1/1 has a slender p4 with low accessory cuspulids and distal cingulid, and a moderately long m1 without metaconid.

South African lineage—This second lineage, according to Werdelin and Lewis (2001), evolved from a leopard-like form from the Late Miocene of Lothagam and Mio-Pliocene of Langebaanweg into the lion-sized *Dinofelis barlowi*. This lineage displays more pantherine characters as compared with the former one.

The Mio-Pliocene Langebaanweg specimens were included by Hendey (1974) in *D. diastemata* and by Werdelin and Lewis (2001) in *Dinofelis* cf. *diastemata*. The best-preserved mandible (L20284, Fig. 36 in Hendey, 1974) displays slightly larger cheek teeth compared to Guefaït-4, a much longer diastema (ca. 27 mm), higher and more robust corpus (ca. 34 mm below m1), more slender p4 with smaller and more individualized accessory cuspulids. As in Guefaït-4, the m1 of *D. diastemata* is not elongated mesiodistally, and possesses a vestigial talonid. Nevertheless, it should be noted that a second Langebaanweg mandible (L20685) is considerably smaller. Hendey (1974) explained this difference in size as due to sexual dimorphism.

Dinofelis barlowi is a Late Pliocene to Early Pleistocene (ca. 3.5–2 Ma) large-sized species recorded in South African sites as Sterkfontein, Bolt's Farm and Swartkrans among others (Broom, 1937; Ewer, 1955; Hemmer, 1965; Cooke, 1991). As compared to the Guefaït-4 specimen, this species is definitely larger in size. Moreover, the corpus in buccal view is high, stoutly-built and convex. Other dentognathic differences include the relatively longer postcanine diastema, the relatively reduced p3, the sharp and slender p4 with more verticalized mesial accessory cuspulid, and the relatively longer m1 with sharper cuspids.

North African Dinofelis—The large felid remains from the site of Ahl al Oughlam (ca. 2.5 Ma) were initially included by Geraads (1997) in *Panthera* nov. sp., aff. *P. leo*. Later, the same author included them in *Dinofelis* sp. cf. *D. cristata* (Geraads, 2004). According to the first identification, these Moroccan remains show strong affinities with pantherine felids. They are considerably larger those from Guefaït-4 – close to the size of an extant lion. The best-preserved corpus (AoO-4120) is more stoutly-built and higher compared to our specimen. It also has a proportionally smaller p3, slenderer p4 with strong distal cingulid, and m1 with mesiodistally longer protoconid bearing a vestigial talonid and metaconid.

To summarize, the specimen from Guefaït-4, despite its small dimensions, can be referred to a metailurine with more pantherine than machairodontine-like characters. Such features include: the only slightly convex, slenderly-built and low corpus; the bulbous dentition compared to the buccolingually compressed or sharp morphology of the latter group; the m1 that is not mesiodistally elongated, the rather short m1 protoconid; the relatively enlarged p3, and the long c1-p3 diastema. Altogether these features suggest affinity with the early African forms of *Dinofelis* from the Mio-Pliocene such as those of Langebaanweg and Middle Awash.

5.1.2. Morphological dentognathic comparisons with Eurasian *Dinofelis*

Dinofelis cristata—recorded in Early to Late Pliocene Asian sites such as the Indo-Pakistani Siwaliks and Lok. B in China (Werdelin and Lewis, 2001). This form is the largest recorded of the genus and also the most pantherine of all the *Dinofelis* species. The type specimen of Zdansky (1924; plate XXXI; Figs. 3 and 4), as compared to the Guefaït-4 dentognathic specimen, displays very large dimensions, higher and stouter mandibular corpus, less verticalized mandibular symphysis, longer c1-p3 diastema, proportionally mesiodistally shorter p3, slenderer and buccolingually compressed p4 with sharper and more vertical mesial accessory cuspulid, and stouter m1 with buccolingually enlarged distal part and slightly mesiodistally elongated protoconid.

Dinofelis diastemata—erected by Astre (1929) on the basis of poorly-preserved dentognathic material from the Early Pliocene of Serrat d'en Vaquer (France). As compared with the species from Guefaït-4 the diastema is proportionally longer, the p3 and p4 are similarly developed and proportioned, and the m1 does not show either metaconid or talonid (Hemmer, 1965, pp. 78, 80).

Balaruc II—A *Dinofelis* sp. hemimandible from the Late Pliocene/Early Villafranchian of Balaruc II (France, de Beaumont, 1983) appears very similar to the studied material, in its reduced dimensions and overall morphology. Unfortunately, the French

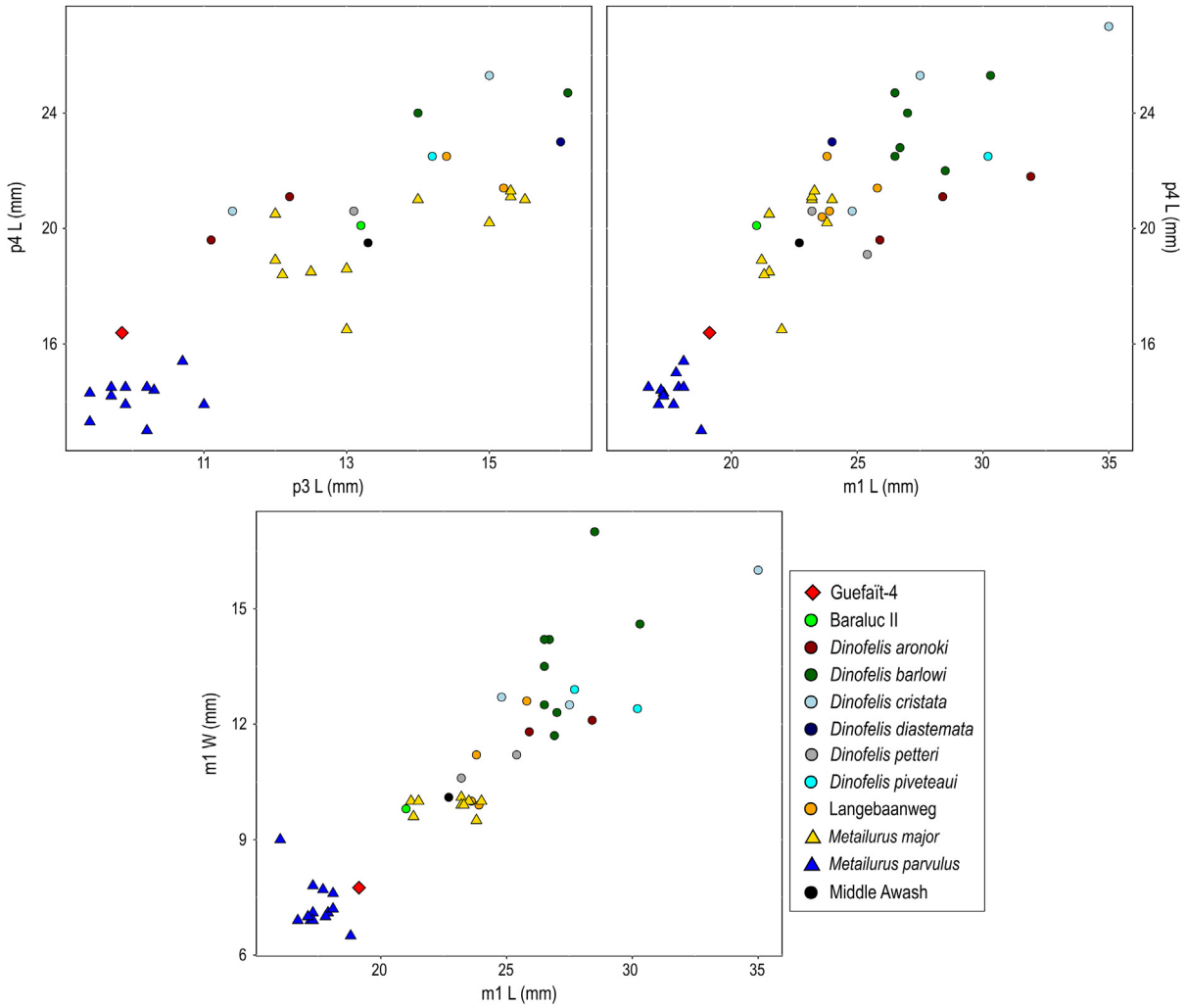


Fig. 4. Biplot of selected dental measures in the considered fossil metailurines. **A**, plot of p3 length and p4 length; **B**, m1 length with p4 length; **C**, plot of m1 length and width.

specimen is broken in its mesial part and the symphysis is not visible. This specimen shares with the Guefaït specimen the low and only slightly convex corpus in buccal view and the proportionally similar c1-p3 diastema. The p3 is also only slightly reduced and with marked distal cingulid; the p4 is narrow with a clear 'fleur-de-lys' morphology and more vertically placed mesial accessory cuspulid; the m1 is also bulbous with higher paraconid. The mesiobuccal and distobuccal cingulids are not present in buccal view of the French specimen.

5.2. Morphological dentognathic comparisons with Eurasian *Metailurus*

5.2.1. Morphological dentognathic comparisons with Eurasian *Metailurus parvulus*

Metailurus parvulus is the only metailurine species comparable to or smaller than the Guefaït-4 specimen. They are also share some similarities, e.g., the verticalized symphysis, the mental crest, the low and slender corpus, the p3 with distal accessory cuspid and cingulid, the p4 with 'fleur-de-lys' morphology and with a strong distal cingulid, and the m1 not mesiodistally elongated. However, there are also some differences. These include a convex corpus, the clearly shortened c1-p3 diastema, the presence of a dorsal ridge on the diastema, the larger p3 with more developed distal accessory cuspid, the p4 with more buccolingually compressed accessory cuspids and a more verticalized mesial accessory cuspid, and the m1 with slightly elongated protoconid and marked metaconid-talonid.

5.2.2. Morphological dentognathic comparisons with Eurasian *Metailurus major*

As we stated above the Guefaït-4 corpus displays many similarities with the most primitive or pantherine-like *Dinofelis* which are also similar to the genus *Metailurus* in several traits. Specifically, the *Metailurus major* holotype (Zdansky, 1924; plate XXIX, Figs. 3 and 4) is a leopard-sized species with unspecialized morphology sharing several traits in common with the studied material, such as the vertical symphysis with mental crest, the relatively unreduced or unelongated diastema, the bulbous pantherine-like dentition with the p3 showing a distal accessory cuspulid, the p4 with 'fleur-de-lys' morphology and marked distal cingulum, and the m1 with protoconid slightly larger than paraconid and vestigial metaconid and talonid. Nevertheless, *M. major* displays several differences, such as the higher and more robust corpus, relatively larger p3 and p4, and m1 with longer protoconid.

5.3. Morphological dentognathic comparisons with early Machairodontinae

In the paleontological literature, the subfamily Machairodontinae has traditionally been subdivided into three tribes: Homotherini, Smilodontini and Metailurini (see Turner, 1997; Werdelin et al., 2010). However, the phylogenetic relationships between these three tribes and the possible existence of polyphyletic genera have led to other interpretations based on recent cladistic analyses (see Christiansen, 2013; Wallace and Hulbert, 2013). These analyses highlight doubts regarding the placement of more basal machairodontines such as *Machairodus* and *Paramachairodus* in any of the three tribes and the phylogenetic relationships among *Metailurus* and *Dinofelis,* suggesting a more complex phylogenetic history for the Machairodontinae than traditionally envisaged (Christiansen, 2013; Wallace and Hulbert, 2013).

Metailurini s.l. share several similarities with this early sabertooth stock from the Late Miocene. Specifically, the genus *Paramachaerodus* (including *Promegantereon*) from Late Miocene Eurasian sites (Salesa et al., 2010; Li and Spassov, 2017) shares some traits with the Guefaït-4 *Dinofelis* specimen, namely: clear mental ridge, absence of mental flange, low corpus in buccal view, reduced p3 and bulbous dentition with mesiodistally unelongated m1 with metaconid (Li and Spassov, 2017). However, *Paramachaerodus,* as well as the American Pliocene species *Rhizosmilodon* (a putatively basal member of the Smilodontini; Wallace and Hulbert, 2013), are slightly larger in size compared to the specimen from Guefaït-4. Moreover, the diastema is mesiodistally shorter in comparison with the studied specimen. Similarly, the slightly developed mental flange in the *Rhizosmilodon* is not present in the Moroccan material.

The above-mentioned similarities between these basal machairodontines and the Guefaït-4 specimen, despite their Miocene and Early Pliocene origin, may support the idea of a more complex history for the Subfamily Machairodontinae than traditionally anticipated. Additional in-depth studies on the whole subfamily may shed light in this topic.

5.4. Morphological comparisons of postcranial elements between Dinofelis and Metailurus

Unfortunately, no complete or partial humeri have been described for the Eurasian species *Dinofelis cristata* and *D. diastema*, or for Balaruc-II. Concerning African forms, several humeri were described in detail by Werdelin and Lewis (2001). We agree with these authors regarding the distinctive features of the *Dinofelis* humerus. The specimen GFT4.2′19-1-T15-8 from Guefaït-4, in keeping with other *Dinofelis*, displays an anteroposteriorly wider distal articular surface relative to mediolateral width as compared with pantherines (e.g., a small leopard; Fig. 3F). The shape of the olecranon fossa, especially its proximal end, is positioned more laterally as compared with other machairodontines, such as *Homotherium* (Werdelin and Lewis, 2001). Additionally, the incision between epitrochleas is very shallow in our specimen, whereas it is marked in *Homotherium* and highly variable in pantherines. Finally, in distal view the medial epicondyle is markedly projected medially as in other *Dinofelis, Smilodon* and *Megantereon*, whereas it is less projected in *Homotherium* and projected palmarly in pantherines (e.g., *Panthera leo* and *P. onca*; Fig. 3F).

Regarding *Metailurus*, only postcranial remains of *M. major* from Bulgaria and *M. parvulus* from Kerassia have been published (Kovatchev, 2001; Roussiakis et al., 2006). The descriptions and figures of the Bulgarian specimen are insufficient for a valid comparison with our specimen. On the other hand, the detailed description of the Greek skeleton enables us to appreciate the numerous similarities with the studied specimen from Guefaït-4. *Metailurus parvulus* has a craniopalmarly wider distal trochlea as compared with mediolateral width; additionally the morphology of the olecranon fossa is also similar. Unfortunately, the projection of the medial epicondyle is not visible (Roussiakis et al., 2006).

5.5. Biometrical comparisons with Dinofelis and Metailurus

In general size and dental biometrical proportions, the studied mandibular corpus is smaller as compared to all presently-known specimens of *Dinofelis* (see summary in Werdelin and Lewis, 2001, Table 1). Indeed, the specimen from Guefait-4 is clearly smaller if compared to the French Late Pliocene specimen from Balaruc II (de Beaumont, 1983) and the specimens from the Late Miocene of Middle Awash (Haile-Selassie and Howell, 2009). This size difference is also evident from the biplots of Fig. 4. In general, it is evident that *Dinofelis* from Guefaït-4 is intermediate between the small *M. parvulus* and the group of *M. major-Dinofelis* spp. This is especially clear in Fig. 4B–C. The variability in mesiodistal length in the teeth of the considered species is higher if we plot measures of lower premolars (Fig. 4A) as opposed to the m1 (Fig. 4B–C). Compared to *Metailurus*, *Dinofelis* spp. show a greater degree of variation in m1 W (Fig. 4C).

Some interesting patterns can be seen in dental ratios (Fig. 5). The W/L ratio of the third lower premolar (Fig. 5A) shows the presence of three distinct groups within *Dinofelis*. *Dinofelis piveteaui* and the sample from the Middle Awash possess low ratios, whereas *D. cristata* and *D. aronoki* have higher ratios, although *D. cristata* has a particularly wide range of variation. Intermediate between these extremes lie the majority of the species: *D. barlowi*, *D. petteri*, the samples from Balaruc II and from Langebaanweg. Guefaït-4 belongs to this cluster. The two *Metailurus* species are distinct in terms of medians, yet their ranges overlap greatly. Considering the ratio between third and fourth premolars (Fig. 5B), *Dinofelis* is characterized by two clusters: lower ratios are found in *D. cristata*, *D. barlowi*, *D. petteri*, *D. aronoki* and *D. piveteaui* and higher values in the Langebaanweg, Middle Awash and Balaruc II samples, and *D. diastemata*. Guefaït-4 belongs to the former group. In this ratio *Metailurus* is characterized by a great degree of variation. Fig. 5C shows the values of the W/L dental ratios of m1. The range of variation is more limited compared to the previous ratios (with the exception of *D. barlowi*, as also seen in in Fig. 4C). Here Guefaït-4 shows the lowest value of the m1 ratio of all *Dinofelis,* close to the median of *M. parvulus*.

5.6. Taxonomical and morphological considerations of the Guefaït-4 Dinofelis

Most scholars dealing with felid evolution have considered *Dinofelis* and *Metailurus sensu lato* (including *Yoshi*; Spassov and Geraads, 2015) as forming a monophyletic clade within Machairodontinae, the Metailurini (Werdelin et al., 2010; see also section 5.3), that also includes a small number of other genera. Nevertheless, published phylogenetic analyses have failed to retrieve this topology (Werdelin and Flink, 2018). Despite the uncertain relationship between them, *Dinofelis* and *Metailurus* were very similar in overall morphology, especially dentally, and presumably had a similar role in the ecosystems of the Plio-Pleistocene and Miocene, respectively. There was, however, little overlap in size between the two genera, with the largest *Metailurus* (e.g., *Metailurus major*) being similar in size to the smallest *Dinofelis* (e.g., *Dinofelis* sp. from Langebaanweg; Werdelin and Lewis, 2001). The felid from Guefaït-4 therefore presents a conundrum: is it a very small *Dinofelis* or is it a very late (the first post-Miocene) *Metailurus*?

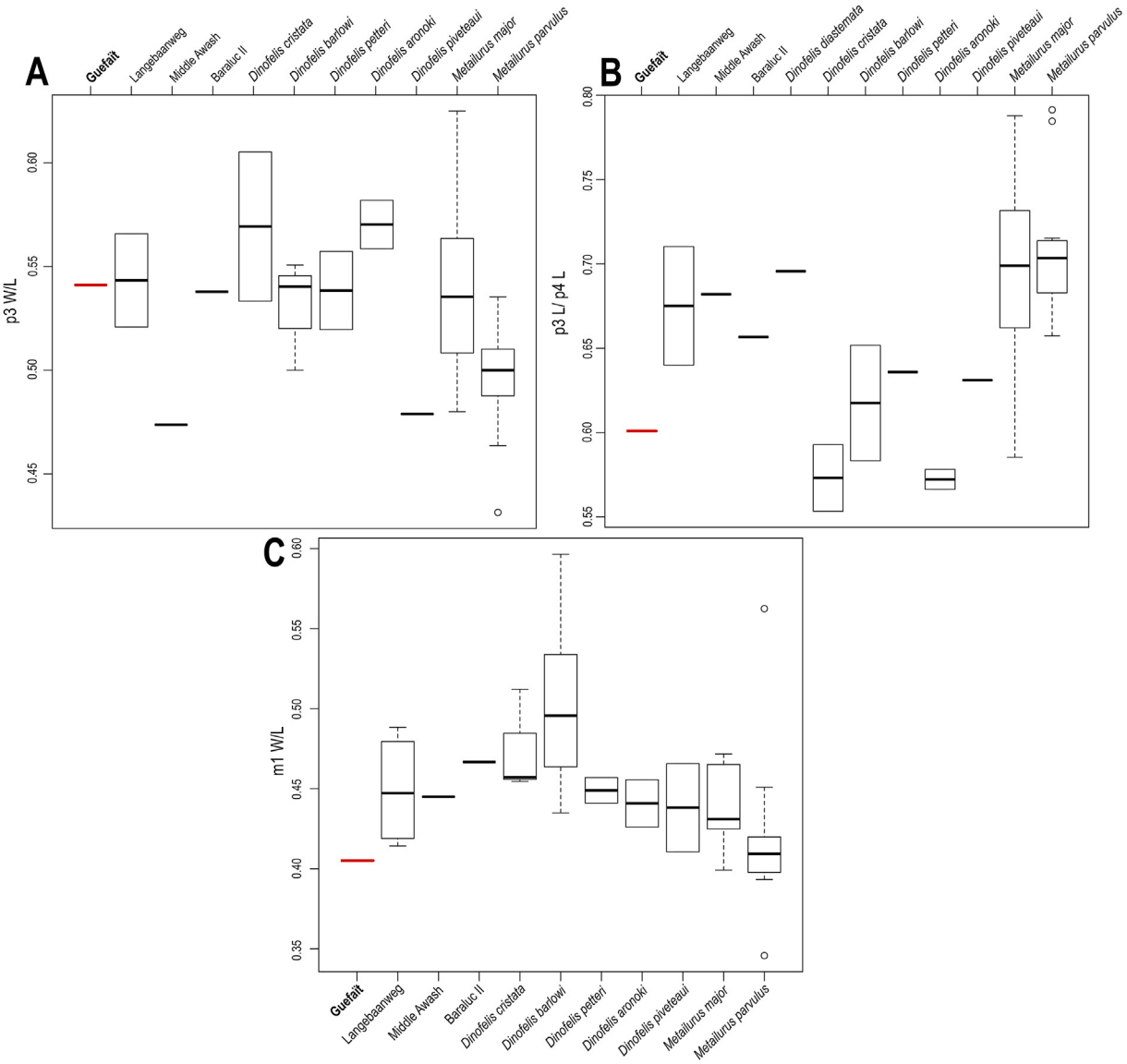


Fig. 5. Boxplots on selected dental ratios. **A**, ratio between p3 width and length. **B**, ratio between p3 length and p4 length; **C**, ratio between m1 width and length.

All the analyses of dental morphology and metrics place the Guefaït-4 felid among specimens of *Metailurus parvulus* (Figs. 4 and 5). Taking only this fact into consideration would seem to answer the question above, identifying the Guefaït-4 felid as a late surviving *Metailurus*. However, dental metrics are not reliable indicators of relationship among felids because of the reduced nature of their dentition and its extreme specialization for carnivory. Allometric features may also affect these results. Therefore, we have looked for non-dental characters that differentiate between the two genera. We have especially looked at characters that differentiate the Guefaït-4 felid from *Metailurus parvulus* (=*Yoshi minor*) which is the *Metailurus* s.l. that it is closest in size to Guefaït-4. These are few, but we have identified three distinct, albeit potentially associated, such characters. First is the angle of the symphysis, which is more vertical in *Dinofelis* than in *M. parvulus*, as shown in Fig. 6. The second is the length of the c-p3 diastema, which is long in *Dinofelis* and short in *M. parvulus* (Fig. 6) The third is the dorsal ridge on the diastema seen in *Dinofelis* (and some *Metailurus major*), but never in *Y. minor*. In all these characters, the Guefaït felid conforms to the morphology of *Dinofelis*. We consider these characters more reliable elements for phylogenetic relatedness compared to dental metrics among these felids and therefore assign the Guefaït-4 felid to *Dinofelis*. The specimen is clearly an adult, as evidenced by dental wear and equally clearly can be assigned to a new species of *Dinofelis*.

A somewhat younger specimen assigned to ?*Metailurus* was reported by Petter (1973) from Bed II at Olduvai (ca. 1.7 Ma). This specimen consists of an upper canine in the process of erupting. It is much smaller than other remains of *Dinofelis* from Olduvai (Werdelin and Lewis, 2001), but given the presence at Guefaït-4 of a small *Dinofelis*, perhaps the Olduvai specimen can also be assigned to that genus and potentially to the same species, although there are obviously no features that would support this.

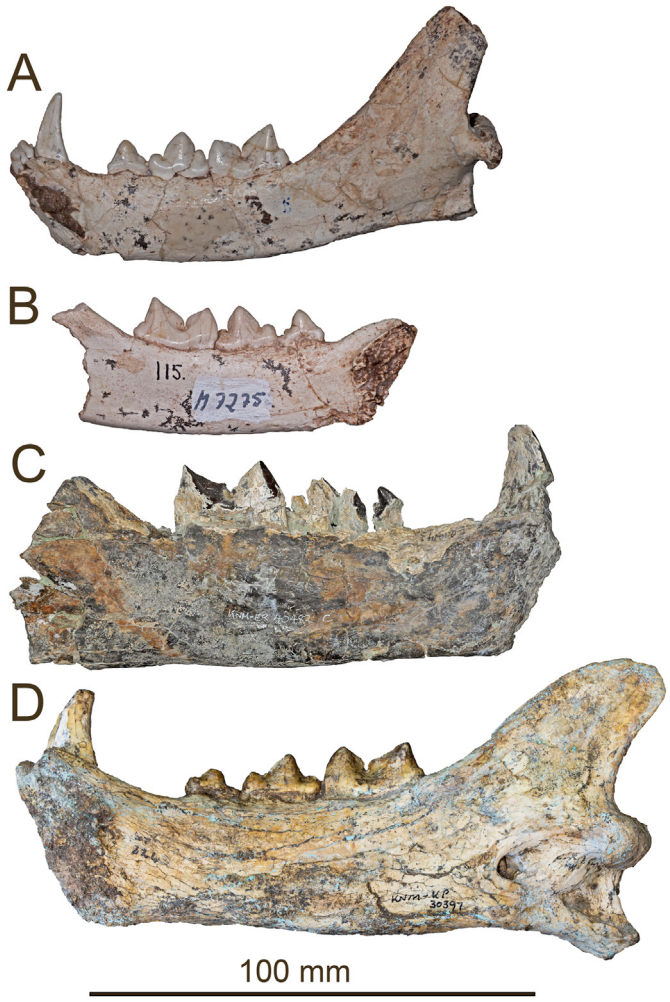


Fig. 6. Photos of specimens of *Metailurus parvulus* (**A**, **B**) and *Dinofelis* spp. (**C**, **D**) showing differences in symphysis angle and diastema length. **A**, *M. parvulus*, PMU M72, Loc 30, Baode, Shanxi, China, (Zdansky, 1924: pl. 29, Fig. 5; pl. 30, Fig. 3). **B**, *M. parvulus*, PMU M7275, Loc 115, Baode, Shanxi, China, (Zdansky, 1924). **C**, *D. piveteaui*, KNM-ER 40482, Okote Member, Koobi Fora Formation, Kenya, (Werdelin and Lewis, 2013: Fig. 8.19b). **D**, *D. petteri*, KNM-KP30397, Kanapoi, Kenya, (Werdelin, 2003: Fig. 6). All specimens have been aligned so that the cheek tooth row is horizontal.

6. Conclusions

The studied specimens of *Dinofelis* from Guefaït-4 (ca. 2.5 Ma) clearly possess more pantherine than machairodontine characters, displaying affinities with considerably older African Mio-Pliocene specimens and being similar to the roughly contemporaneous Late Pliocene European or Early Pleistocene East African isolated findings. The overall small dimensions of these specimens as compared with other *Dinofelis*, are in any case not ascribable to sexual dimorphism or interspecific variability, but represent the smallest recorded *Dinofelis*, with the size of a large Eurasian lynx or small puma.

Although the material from Guefaït-4 is not inconsiderable and almost certainly represents a new taxon, the absence of properly diagnostic craniodental material, specifically complete or partial crania, advises caution before erecting a new species. The evidence reported here, combined with other isolated findings from Africa and Europe (e.g. Olduvai), can be putatively related to a previously unknown lineage of small-sized *Dinofelis*, with two different forms of clearly different size. In any case, this new form/species adds more complexity to the already high variety and intraspecific competition between African carnivorans in Plio-Pleistocene time.

Author contributions

J.M.-M, A. R-H., S. B. L. and L. W. conceived the research and wrote the paper; J.M.-M, S. B. L. and L. W. performed the analysis; J.M.-M, A. R-H., H. A., H. H., S. B. L., A. O., P. S., S. B., J. M., M. S., M. F., H. M., M. A., L. W., M. G. CH. and R. S. revised all the manuscript versions and make improvements in the research.

Declaration of competing interest

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

Acknowledgments

We thank the Jerada Government and Local Authorities of Aïn Béni Mathar and Guefaït for local permits to develop geological, archaeological and paleontological fieldworks in the region. The authors thank Prof. S. Roussakis, who sent us pictures and measurements of Greek *Metailurus* specimens and Elena Moreno for the preparation of the fossils. For access to the surface scan data of *Dinofelis barlowi* and *D. piveteaui*, we thank Ditsong National Museum of Natural History, South Africa and Justin Adams of the Department of Anatomy and Developmental Biology, Monash University, Australia. This work has been funded by Palarq Foundation, Spanish Ministry of Culture and Sport (Ref: 42-T002018N0000042853 and 170- T002019N0000038589), Direction of Cultural Heritage (Ministry of Culture and Communication, Morocco), Faculty of Sciences (Mohamed 1r University of Oujda, Morocco), INSAP (Institut National des Sciences de l'Archéologie et du Patrimoine), Ministry of Science, Innovation and Universities (Ref: CGL2016-80975-P, CGL2016-80000-P, PGC2018-095489-B-I00 and PGC2018-093925-B-C31), Agencia Estatal de Investigación—European Regional Development Fund of the European Union (CGL2017-82654-P, AEI/FEDER-UE), the Generalitat de Catalunya (CERCA Program) which is financed by European Community Research Infrastructure Action under the FP7 "Capacities" Program and Research Groups Support (2017 SGR 836 and 2017 SGR 859). R.S-R, M.G.CH., and P.S. research is funded by CERCA Programme/Generalitat de Catalunya. J.M.-M. is member of consolidated research group 2017 SGR 116 (AGAUR, Generalitat de Catalunya). A.R.-H. is the beneficiary of a postdoctoral scholarship from the MICINN, Subprograma Juan de la Cierva (IJC-037447-I) and member of the Consolidated Research Group 2017 SGR 1040 of the Generalitat de Catalunya. A.M.A and M.F. are beneficiaries of a fellowship from the Erasmus Mundus Program to do the Master in Quaternary and Prehistory at the Universitat Rovira i Virgili (Tarragona, Spain). The Institut Català de Paleoecologia Humana i Evoluciò Social (IPHES-CERCA) has received financial support from the Spanish Ministry of Science and Innovation through the 'María de Maeztu' program for Units of Excellence (CEX2019-000945-M).

References

Adams, J.W., Olah, A., McCurry, M.R., Potze, S., 2015. Surface model and tomographic archive of fossil primate and other mammal holotype and paratype specimens of the Ditsong National Museum of Natural History, Pretoria, South Africa. PloS One 10 (10), e0139800.

Agustí, J., Piñero, P., Blain, H.-A., Aouraghe, H., Haddoumi, H., El Hammouti, K., Chacón, G., Sala, R., 2017. The Early Pleistocene small vertebrates from Guefaït 4 (Jerada, Morocco). In: La 9_eme Rencontre des Quaternaristes Marocains (RQM9). Recueil des Résumes. "Programme et Guide de l'Excursion". Cadi Ayyad

University, Faculté Polydisciplinaire, Safi, p. 54.
Alba, D.M., Rodríguez-Hidalgo, A., Aouraghe, H., van der Made, J., Oujaa, A., Haddoumi, H., Saladié, P., Al Mahdi, A., Marín, J., Farkouch, M., Lorenzo, C., Bengamra, S., Delson, E., Chacón, M.G., Sala-Ramos, R., 2021. New macaque fossil remains from Morocco. J. Hum. Evol. 153, 102951.
Antón, M., 2013. Sabertooth. Indiana University Press.
Aouraghe, H., Sala, R., Chacón, M.G., 2016. Bilan de dix ans de recherches archéologiques dans la région de Jerada (Maroc Oriental). In: 10 Ans de Recherches & de Coopérations Scientifiques Maroco-Espagnole dans la Province de Jerada (Maroc Oriental). Séminaire International sur le Patrimoine Archéologique de la Province de Jerada. Recueil du Séminaire, Jerada, 2016, pp. 8–9.
Aouraghe, H., Haddoumi, H., Rodríguez-Hidalgo, A., Van der Made, J., Piñero, P., Agustí, J., Álvarez, C., Benito-Calvo, A., Blain, H.-A., Duval, M., El Hammouti, K., Expósito, I., Marín, J., Mejías, D., Oujaa, A., Parés, J.M., Pla, S., Ramírez-Pedraza, I., Rivals, F., Saladié, P., Tornero, C., Chacón, M.G., Sala-Ramos, R., 2019. Nouvelles données sur le site du Pliocène Final/Pléistocène Inférieur de Guefaït 4: mission 2019. In: 10ème Rencontre des Quaternaristes Marocains. Recueil des Résumés, pp. 47–48.
Astre, G., 1929. Sur un félin a particularités ursoïdes des limons Pliocènes du Roussillon. B. Soc. Geol. Fr. 29, 199–204.
de Beaumont, G., 1983. Une mandibule de *Dinofelis* (mammifère, carnivore, félidé) du Villafranchien inférieur de Balaruc II, hérault, France. Arch. Sci. 36, 469–477.
Blain, H.-A., Agustí, J., López-García, J.M., Haddoumi, H., Aouraghe, H., El Hammouti, K., Pérez-González, A., Chacón, M.G., Sala, R., 2013. Amphibians and squamate reptiles from the late Miocene (Vallesian) of eastern Morocco (Guefaït- 1, Jerada Province). J. Vertebr. Paleontol. 33, 804–816.
Broom, R., 1937. On some new fossil mammals from limestone caves of the Transvaal. South Afr. J. Sci. 33, 750–769.
Chacón, M.G., Aouraghe, H., Agustí, J., Álvarez, C., Arnold, L., Benito-Calvo, A., Iaín, H.-A., Carrancho, A., de Lombera, A., Duval, M., El Hammouti, K., El Harradji, A., Haddoumi, H., Menéndez, L., Parés, J.M., Piñeiro, P., Tarriño, A., Villalaín, J.J., Sala, R., 2016. Ten years of archaeological research in the Aïn Beni-Mathar/Guefaït region (Eastern Morocco): results and perspectives. In: 58th Annual Meeting in Budapest. March 29th-April 2nd, 2016. Hugo Obermaier-Gesellschaft für Erforschung des Eiszeitalers und der Steinzeit E.V., Erlangen, pp. 21–22.
Chang, H., Liu, H., 1964. On specimens of *Metailurus* from Yushe. Shansi. Vert. PalAs. 2, 5–11.
Christiansen, P., 2013. Phylogeny of the sabertoothed felids (Carnivora: Felidae: Machairodontidae). Cladistics 29, 543–559.
Christiansen, P., 2006. Sabertooth characters in the clouded leopard (*Neofelis nebulosa* Griffiths 1821). J. Morphol. 267, 1186–1198.
Colbert, E.H., 1939. Carnivora of the Tung Gur formation of Mongolia. Bull. Am. Mus. Nat. Hist. 76, 47–81.
Cooke, H.B.S., 1991. *Dinofelis barlowi* (mammalia, carnivora, Felidae) cranial material from Bolt's Farm, collected by the university of California african expedition. Palaeontol. Afr. 28, 9–21.
Ewer, R.F., 1955. The fossil carnivores of the Transvaal caves: Machairodontinae. Proc. Zool. Soc. Lond. 125, 587–615.
Geraads, D., 1997. Carnivores du Pliocène terminal de Ahl al Oughlam (Casablanca, Maroc). Geobios 30, 127–164.
Geraads, D., 2004. First record of *Dinofelis* (Felidae, mammalia) from North Africa. Neues Jahrbuch Geol. Palaontol. Abhand. 308–320.
Haile-Selassie, Y., Howell, F.C., 2009. Carnivora. In: Haile-Selassie, Y., WoldeGabriel, G. (Eds.), *Ardipithecus kadabba*. Late Miocene Evidence from the Middles Awash, Ethiopia. University of California Press, Berkeley, pp. 237–276.
Hemmer, H., 1965. Zur Nomenklatur und Verbreitung des Genus *Dinofelis* Zdansky, 1924 (*Therailurus* Piveteau, 1948). Palaeontol. Afr. 9, 75–89.
Hendey, Q.B., 1974. The late Cenozoic carnivora of the southwestern Cape Province, South Africa. Ann. S. Afr. Mus. 63, 1–369.
Kovatchev, D., 2001. Description d'un squelette complet de *Metailurus* (Felidae, Carnivora, Mammalia) du Miocène supérieur de Bulgarie. Geol. Balk. 31, 71–88.
Kurtén, B., 1973. The genus *Dinofelis* (carnivora, mammalia) in the Blancan of North America. Pearce-Sellards Ser. 19, 1–7.
Lacruz, R., Turner, A., Berger, L.R., 2006. New *Dinofelis* (carnivora: Machairodontinae) remains from Sterkfontein valley sites and a taxonomic revision of the genus in southern Africa. Ann. Transvaal Mus. 43, 89–106.
Li, Y., 2014. Restudy of *Metailurus major* from Yushe Basin, Shanxi Province reported by teilhard de Chardin and Leroy. Vert. PalAs. 52, 467–485.
Li, Y., Spassov, N., 2017. A new species of *Paramachaerodus* (mammalia, carnivora, Felidae) from the Late Miocene of China and Bulgaria, and revision of *Promegantereon* kretzoi, 1938 and *Paramachaerodus* Pilgrim, 1913. PalZ 91, 409–426.
Petter, G., 1973. Carnivores pléistocènes du Ravin d'Olduvai (tanzanie). In: Leakey, L.S.B., Savage, R., Coryndon, S. (Eds.), Fossil Vertebrates in Africa, vol. 3, pp. 43–100.
Piñero, P., Agustí, J., Haddoumi, H., El Hammouti, K., Chacón, M.G., Sala-Ramos, R., 2019. *Golunda aouraghei*, sp. nov., the last representative of the genus Golunda in Africa. J. Vertebr. Paleontol. 39, e1742726.
Roussiakis, S.J., Theodorou, G.E., Iliopoulos, G., 2006. An almost complete skeleton of *Metailurus parvulus* (carnivora, Felidae) from the late Miocene of Kerassia (northern euboea, Greece). Geobios 39, 563–584.
Sahnouni, M., Parés, J.M., Duval, M., Cáceres, I., Harichane, Z., van der Made, J., Pérez-González, A., Abdessadok, S., Kandi, N., Derradji, A., Medig, M., Boulaghraif, K., Semaw, S., 2018. 1.9-million- and 2.4-million-year-old artifacts and stone toole cutmarked bones from Ain Boucherit, Algeria. Science 362, 1297e1301.
Salesa, M.J., Anton, M., Turner, A., Alcala, L., Montoya, P., Morales, J., 2010. Systematic revision of the Late Miocene sabre-toothed felid *Paramachaerodus* in Spain. Palaeontology 5, 1369–1391.
Spassov, N., Geraads, D., 2015. A new felid from the Late Miocene of the balkans and the contents of the genus *Metailurus* Zdansky, 1924 (Carnivora, Felidae). J. Mamm. Evol. 22, 45–56.
Spassov, N., Geraads, D., Hristova, L., Markov, G., Garevska, B., Garevski, R., 2018. The late Miocene mammal faunas of the Republic of Macedonia. Palaeontogr. Am. 311, 1–85.
Stoetzel, E., 2013. Late Cenozoic micromammal biochronology of northwestern Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 392, 359–381.
Turner, A., 1997. The Big Cats and Their Fossil Relatives: an Illustrated Guide to Their Evolution and Natural History. Columbia University Press.
Wallace, S.C., Hulbert Jr., R.C., 2013. A new machairodont from the palmetto fauna (early Pliocene) of Florida, with comments on the origin of the Smilodontini (Mammalia, Carnivora, Felidae). PloS One 8, e56173.
Werdelin, L., 2003a. Carnivora from the Kanapoi hominid site, turkana basin, northern Kenya. Contrib. Sci. (Los Angel.) 498, 116–134.
Werdelin, L., 2003b. Mio-pliocene carnivora from lothagam, Kenya. In: Leakey, M.G., Harris, J.H. (Eds.), Lothagam: the Dawn of Humanity in Eastern Africa. Columbia University Press, New York, pp. 261–330.
Werdelin, L., Lewis, M.E., 2001. A revision of the genus *Dinofelis* (mammalia, Felidae). Zool. J. Linn. Soc. 132, 147–258.
Werdelin, L., Peigné, S., 2010. Carnivora. In: Werdelin, L., Sanders, W. (Eds.), Cenozoic Mammals of Africa. University of California Press, San Francisco.
Werdelin, L., Yamaguchi, N., Johnson, W.E., O'Brien, S.J., 2010. Phylogeny and evolution of cats (Felidae). In: Macdonald, D.M., Loveridge, A. (Eds.), Biology and Conservation of Wild Felids. Oxford University Press, Oxford, pp. 59–82.
Werdelin, L., Lewis, M.E., 2013. Koobi Fora Research Project, vol. 7. California Academy of Sciences, San Francisco, p. 333. The Carnivora, Koobi Fora Research Project, vol. 7.
Werdelin, L., Flink, T., 2018. The phylogenetic context of *Smilodon*. In: Werdelin, L., McDonald, H.G., Shaw, C.A. (Eds.), *Smilodon*: the Iconic Sabertooth. Johns Hopkins University Press, Baltimore, pp. 14–29.
Zdansky, O., 1924. Jungtertiare carnivoren chinas. Palaeontol. Sin. Ser. C 1–149.