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THE HIPPARIONINE HORSES (PERISSODACTYLA: MAMMALIA) FROM THE LATE MIOCENE OF TIZI N'TADDERHT (SOUTHERN OUARZAZATE BASIN; CENTRAL HIGH ATLAS; MOROCCO)

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Abstract. The fossiliferous locality of Tizi N'Tadderht, already known in the literature , has yielded a significant vertebrate fossil association as it represents the first documentation of a Late Miocene vertebrate fauna in the western area of North Africa. The group of fossil Equidae here analyzed had been preliminarly studied by previous authors, who identified the following hipparionini species: aff. *Cremohipparion periafricanum*, Hippotheriini gen. et sp. indet., and cf. *Hippotherium primigenium*. The sample retrieved from the considered area has been revised through the description of the morphologies and the dimensional measurements analysis. Then, it has been compared with the collection of fossil Equidae of the Libyan fossil site of As Sahabi, where the following species of Equidae hipparionini are represented: *Sivalhippus* sp., *Eurygnathohippus feibeli* and *Cremohipparion mattewi*. The revision of the Tizi N'Tadderht association led to the identification of the following species: *Hippotherium* sp. (characterized by large size); *Eurygnathohippus* cf. *feibeli* (a medium-sized Equidae; for the first time recognized in the Tizi N'Tadderht site); aff. *Cremohipparion periafricanum* (distinguished for its small size, as previously hypothesized in literature). The discovery of *Eurygnathohippus* cf. *feibeli* at Tizi N'Tadderht is of particular importance as it extends the paleogeographic record of this *Hipparion* species present in other African sites, showing that it is well represented in the fossil record of the Late Miocene.

Introduction

Tizi N'Tadderht, located in the southern Ouarzazate basin, Central High Atlas of Morocco, is a Late Miocene fossil vertebrate bearing area first reported by Zouhri et al. (2012). The Tizi N'Tadderht assemblage includes, in addition to an ostrich (cf. *Struthio* sp.) and two reptiles (the turtle cf. *Centrochelys* sp., and the crocodilian *Crocodylus* cf. *niloticus*), a number of large mammals (Zouhri et al. 2012; Geraads et al. 2012) among which three hipparionine horse species (object of the present study), two species of rhinoceros (cf. *Ceratotherium* sp., and aff. *Chilotherium* sp.), a proboscidean (cf. *Tetralophodon* sp.), a large giraffe (Giraffidae gen. et sp. indet.) and two bovids (cf. *Prostrepsiceros* sp., and *Skouraia helicoides* Geraads et al. 2012, a medium-sized Caprinae antelope with spiral horns).

Albeit representing a small faunal sample, the Tizi N'Tadderht assemblage represents the

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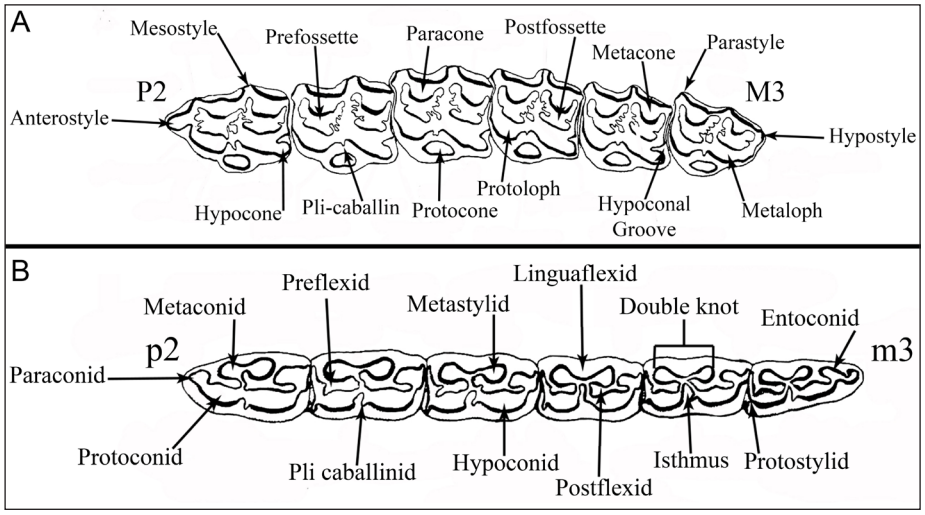

Fig. 1 - Anatomical nomenclature of upper and lower dentitions in the genus *Hipparion*.

westernmost Late Miocene large mammal fossil fauna of North Africa. This Moroccan mammal assemblage enriches our knowledge of the latest Miocene faunal dynamics in north Africa and provide us data for a better understanding of the zoogeographic patterns of large mammal faunas within the frame of the latest Miocene palaeobiogeographic history of the circum-Mediterranean (Bernor & Rook 2008; Marra et al. 2017; Pandolfi et al. 2019).

Materials and Methods

The material studied here includes the horse collection from the Late Miocene of Tizi N'Tadderht (southern Ouarzazate basin; Central High Atlas; Morocco) kept in the collections of the Faculty of Sciences "Ain Chock" of the Hassan II University (Casablanca) and the Tahiri Museum (Erfoud). The comparative sample used herein includes specimens from As Sahabi (Libya; Bernor et al. 2008, 2012), and other Old World samples. Measurement standards used for these statistical analyses follow Eisenmann et al. (1988) and Bernor et al. (1997). We undertook measurements with a digital caliper recording data to the nearest 0.1 that is the standard recognized for equid research (all measured elements are reported in Tables 1-3). We have used the Höwenegg *Hippotherium primigenium* sample (Bernor et al. 1997) as standard comparison for Log10 Ratio diagrams with selected and directly relevant species of Late Miocene-Pliocene hipparions, in order to show size and morphology of the postcranial bones analized. Fig. 1 provides the anatomical nomenclature for upper and lower dentition in the genus *Hipparion*.

Systematic Conventions. Hipparionine horses have an isolated protocone on maxillary premolar and molar teeth and tridactyl feet, including species of the following Old World genera: *Cormohipparion, Hippotherium, Cremohipparion, Hipparion, Sivalhippus, Eurygnathohippus* (= senior synonym of "*Stylohipparion*"), *Proboscidipparion, Plesiohipparion.* Characterizations of these taxa have most recently been made by Bernor & Harris (2003), Zouhri & Bensalmia (2005), Bernor & Kaiser (2006), Eisenmann & Geraads (2007), Woodburne (2007), Bernor & White (2009), Bernor et al. (2010, 2011, 2012), Rook et al. (2017), and references cited therein.

Institutional Abbreviations. Fsac: Faculty of Sciences "Ain Chock", Hassan II University, Casablanca (Morocco); MTE: Tahiri Museum, Erfoud (Morocco).

Anatomical Abbreviations. P^2: second upper premolar (txP2); P^3: third upper premolar (txP3); P^4: fourth upper premolar (txP4); M^1: first upper molar (txM1); M^2: second upper molar (txM2); M^3: third upper molar (txM3); P_2: second lower premolar (tmp2); P_3: third lower premolar (tmp3); P_4: fourth lower premolar (tmp4); M_1: first lower molar (tmm1); M_2: second lower molar (tmm2); M_3: third lower molar (tmm3); TX: upper tooth; Tm: lower tooth; MCIII: metacarpal of the third (central) digit; MTIII: metatarsal of the third (central) digit; AST: astragalus; CALC: calcaneum; 1PHIII: 1st phalanx of the third (central) digit; 2PHIII: 2nd phalanx of the third (central) digit; 3PHIII: 3rd phalanx of the third (central) digit. M1-M14: refer to measurements as prescribed by Eisenmann et al. (1988) and Bernor et al. (1997).

Geological Framework

The fossil vertebrate site of Tizi N'Tadderht is located in the Ouarzazate Basin about 12 km south-east of Toundoute (Fig. 2). The basin represents the southern foreland of the Central High Atlas (CHA) being in turn confined to the south by the Anti Atlas range. The basin formed as a flexural depression consequently to the Early Cenozoic tectonic inversion, of the Mesozoic CHA rifted basins related to the Africa-Europe plates collision (Frizon de Lamotte et al. 2008). The basin fill includes a relatively thick succession of alluvial and lacustrine deposits dating back to the late Eocene and referred to as the Imerhane Group (IG, El Harfi et al. 2001). The latter is considered to record the main stage of the CHA build up as suggested by its unconformable relations with the Mesozoic-Early Cenozoic syn- and post-rift successions (Frizon de Lamotte et al. 2008 for a review). The syn-tectonic

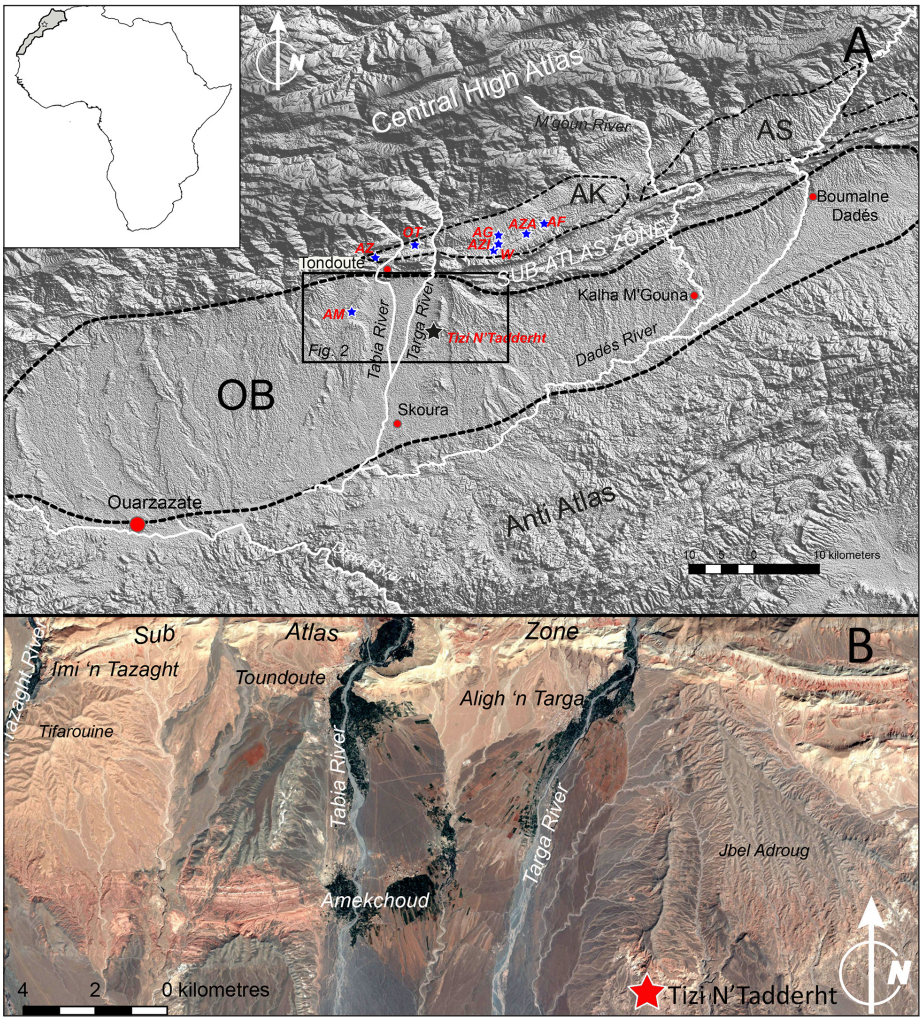

Fig. 2 - Locator map of the Tizi'N Tadderht area, modified from Benvenuti et al. 2019.

character of the IG is clearly proven by its progressive deformation related to the southward propagation of crustal shortening causing the development of the two adjacent Ait Kandoula and Ait Seddrat satellite depocentres facing the wider Ouarzazate basin. In all these areas the late Paleogene-Quaternary interval is recorded by the stacking of clastic formations, the lowermost being the Hadida-Ait Arbi formations. These respectively consist of reddish-greenish mudstone and evaporites and an alternation of sandstone and mudstone referred to the late Eocene (El Harfi et al 2001), recording the development of fluvial fans (Ait Arbi) prograding in a muddy playa lake (Hadida). The overlying, presumably Upper Oligocene, Ait Ouglif Fm. (Görler et al. 1988), is made of alluvial conglomerates and is followed by the Middle Miocene-Pliocene Ait Kandoula Fm., consisting of lacustrine sandstone, mudstone and limestone (Ait Ibrirene member in Teson et al. 2010). The latter is overlain by alluvial conglomerates and sandstones (Ait Seddrat member in Teson et al. 2010). Quaternary terraced clastic deposits, related to the fluvial entrenchment forced by the continued deformation and uplift of the CHA (Pastor et al. 2012), rest on top of the succession. The lacustrine mudstone of the Ait Kandoula Fm exposed in the homonym sub-basin, yielded associations of microvertebrates (Benammi et al. 1996; Benammi & Jaeger 2001; Benanmi 2006) attesting to the MN6-MN14 zones of the European Mammal Biochronology. Recently, a micromammal fauna hinting to the MN11 zone, has been reported also from the lower portion of the Ait Kandoula Fm cropping out in the Ouarzazate Basin not far from the Tizi N'Tadderht site (Teson et al. 2010). The integration of magnetostratigraphic data allowed to establish a chronostratigraphic framework for these faunas which are bracketed between the Middle Miocene and the Early Pliocene.

Stratigraphic and depositional setting of the Tizi N'Tadderht site

The vertebrate association including the discussed hipparionine horses is contained in strata

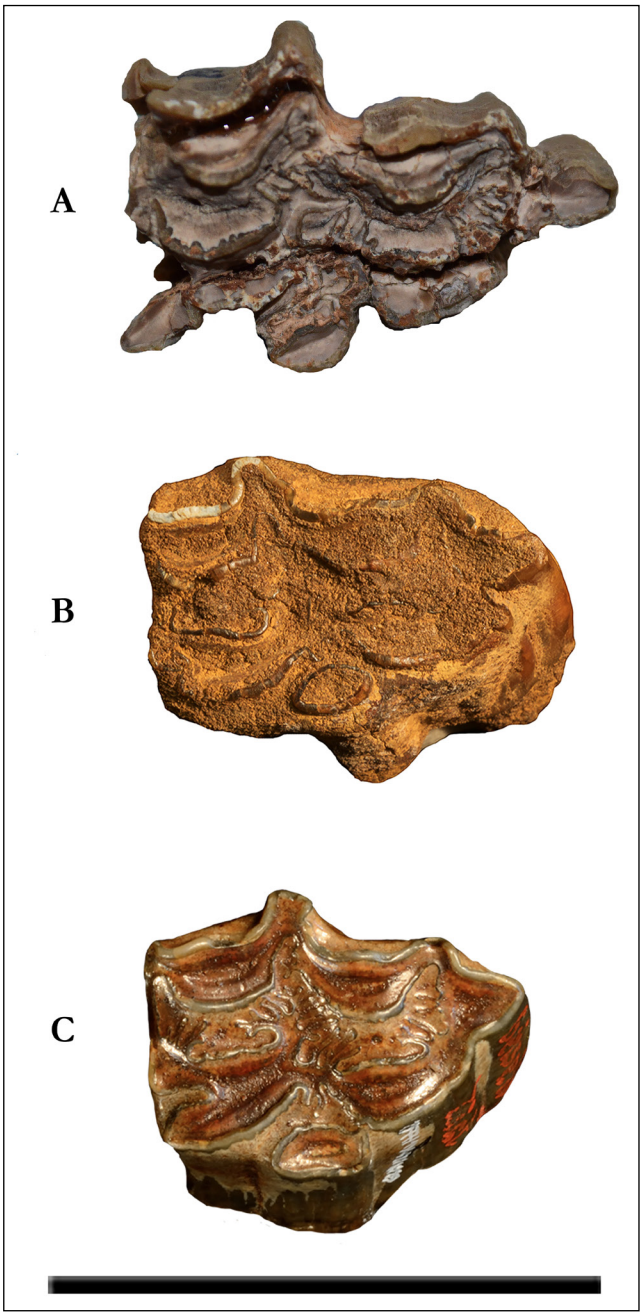

Fig. 3 - Occlusal view of *Hippotherium* sp. from Tizi N'Tadderht, Fsac-SK-03 (A), *Sivalhippus* sp. from As Sahabi, ISP164P65 (B) and "Pannonian C-E Hipparion" from Mariathal and Gaiselberg, M3540/8 (C). Scale bar 5 cm.

referred to the Ait Kandoula Formation (Zouhri et al. 2012). In the present study we refer to a revised subdivision of this formation (Benvenuti et al. 2019), exposed on the slopes flanking the Tabia River between Toundoute and Tizi N'Tadderht (Figs. 1 and 2 in Benvenuti et al. 2019) and undifferentiated in previous studies (Görler & Zucht 1986; Görler et al. 1988; Benammi et al. 1996; Benammi & Jaeger 2001; El Harfi et al. 2001; Teson et al. 2010). On the base of this revision four distinct unconformity-bounded sub-units, AK1-4, are established with the vertebrate-bearing strata ascribed to the AK3 sub-unit. AK3 overlies the previous deposits through an angular truncation being relatively exposed on the left of the Tabia River at the Tizi N'Tadderht site. Here, the related deposits are sub-horizontal and include from the base an alternation of channelized fine conglomerates and sandstones with a massive or through-cross stratified structure, outlining sediment transport from the ESE, and banded pale reddish/whitish mudstone. Fossil vertebrate remains are mostly dispersed in the sandstones. Upward, the succession becomes muddier culminating into a white marlstone, easily traceable also on the covered slopes on the right of the Tabia River. These deposits are sharply but conformably overlain by the AK4 sub-unit consisting of tabular reddish conglomerates and sandstones alternated to mudstones. Form a depositional point of view the AK3 sub-unit records the infill of a depocentre in the western portion of the Ouarzazate basin generated by a pulse of deformation as documented by the angular unconformity separating these deposits from the underlying AK1-2 sub-units. The depocentre was initially filled by fluvial deposits bearing the macro-vertebrate remains and carried by a channel network flowing to the WSW, that is sub-axially to the basin trend. The successive return to lacustrine condition recorded on top of this sub-unit hints to increase of accommodation leading to clastic sediment starving and chemical deposition. The overlying AK4 sub-unit documents a defective filling of the basin related to terminal fan systems advancing from the north in the basin.

Systematic Paleontology

Order **Perissodactyla** Owen, 1848
Suborder **Hippomorpha** Wood, 1937
Superfamily Equoidea Hay, 1902
Family Equidae Gray, 1821
Subfamily Equinae Steinmann & Doderlein, 1890
Genus *Hippotherium* Kaup, 1832

Hippotherium sp.

2012 cf. *Hippotherium primigenium* (Von Mayer, 1829) – Zouhri et al.

SPEC_ID	SPEC	BONE	SIDE	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
MTE_01	*Hippotherium* sp.	1ph3	rt.	64,8	58,6	34,7	47,7	33,0	46,2	38,5			44,4	44,4	16,1	16,7	
MTE_10	*Hippotherium* sp.	2ph3	lt.	40,7	25,5	36,1	44,0	25,0	37,1								
Fsac-SK-31	*Hippotherium* sp.	3ph3	lt.	56,3	52,3	67,3	59,9	29,3	44,5								
Fsac-SK-25	*Hippotherium* sp.	ast	rt.	58,8	55,6	26,5	60,9	47,8	31,2	67,3							
Fsac-SK-26	*Hippotherium* sp.	ast	rt.	60,1	55,2	29,5	66,1	51,8	34,9	63,3							
Fsac-SK-28	*Hippotherium* sp.	humerus	lt.	302,7	291,4	30,6	50,4	-	131,7	70,0	82,9	52,6	38,3	45,5			
Fsac-SK-02	*Hippotherium* sp.	mandible	rt.					85,3					106,8				
Fsac-SK-24	*Hippotherium* sp.	mcIII	rt.					45,1	27,7	35,3	11,7	12,3					
Fsac-SK-23	*Hippotherium* sp.	mcIII	rt.										38,7	36,9	30,2	25,9	27,6
Fsac-SK-02	*Hippotherium* sp.	tmm1	rt.	28,5	20,5	14,5	10,3	11,8	13,9	13,8	10,3	9,4	50,8				
Fsac-SK-02	*Hippotherium* sp.	tmm2	rt.	29,2		13,0	9,5	10,7	10,3		8,9	9,6	45,5				
Fsac-SK-02	*Hippotherium* sp.	tmm3	rt.	10,9		10,1	9,3	10,1	8,2		7,8	6,9	29,1				
Fsac-SK-18	*Hippotherium* sp.	tmp3	rt.	23,4	23,1	14,4	9,5	10,8	14,3	14,6	13,8	12,3	21,5				
Fsac-SK-19	*Hippotherium* sp.	tmp4	rt.	30,0	28,9	11,0	11,2	10,4	12,1	8,7	11,4	10,8	44,2				
Fsac-SK-09	*Hippotherium* sp.	txM1	rt.	30,7	23,5	27,3	25,9	47,3		5,0	4,0		7,7	4,3			
Fsac-SK-10	*Hippotherium* sp.	txM1	lt.	27,8	23,4	22,1	22,6	51,6	3,0	5,0	5,0	2,0	9,4	3,6			
Fsac-SK-11	*Hippotherium* sp.	txM2	lt.	31,5	26,3	26,3	24,3	47,1	3,0	5,0	6,0	3,0	7,1	4,2			
Fsac-SK-12	*Hippotherium* sp.	txM2	rt.	27,9	25,3	24,6	20,6	49,1	4,0	5,0	6,0	2,0	9,3	4,1			
Fsac-SK-15	*Hippotherium* sp.	txM3	rt.	20,9	25,1	14,7	15,1	46,4									
Fsac-SK-17	*Hippotherium* sp.	txM3	lt.	21,7	23,5	18,2	21,2	49,5									
Fsac-SK-03	*Hippotherium* sp.	txP2	rt.	35,7	33,6	24,9	23,7	38,6	4,0	5,0	4,0		6,7	4,0			
Fsac-SK-04	*Hippotherium* sp.	txP2	lt.	36,5	32,6	24,1	21,4	37,8	6,0	4,0	4,0	2,0	5,9	3,6			
Fsac-SK-05	*Hippotherium* sp.	txP3	rt.	27,7	22,3	24,7	23,6	48,1	5,0	6,0	5,0		6,8	4,3			
Fsac-SK-06	*Hippotherium* sp.	txP3	rt.	27,0	22,4	21,9	22,4	50,6		4,0	3,0	5,0	9,4	4,0			
Fsac-SK-07	*Hippotherium* sp.	txP4	rt.	29,8	27,0	24,6	25,4	50,7		4,0	5,0	4,0	9,3	4,0			
Fsac-SK-08	*Hippotherium* sp.	txP4	lt.	28,0	24,0	22,5	22,1	46,5	5,0		4,0						

Tab. 1 - Measurement of the *Hippotherium* sp. sample from Tizi N'Tadderht. Measurements are referred to Bernor et al. 1997 and Eisenmann et al. 1988.

Referred Specimens: Fsac-sk-03, right P^2; Fsac-SK-04, left P^2; Fsac-SK-05, right P^3; Fsac-SK-06, rigth P^3; Fsac-SK-07, right P^4; Fasc-SK-08, left P^4; Fsac-SK-09 right M^1; Fsac-SK-10, left M^1; Fsac-SK-11, left M^2; Fsac-SK-12, right M^2; Fsac-SK-15 right M^3; Fsac-SK-17, left M^3; Fsac-SK-02, right mandible with M_1-M_3; Fsac-SK-18, right P_3; Fsac-SK-19, right P_4; Fsac-SK-28, left humerus; Fsac-SK-23, right MCIII; Fsac-SK-24, right MCIII; Fsac-SK-25 right AST; Fsac-SK-26, right AST; MTE01, right 1PHIII; MTE10, left 2PHIII; Fsac-SK-31, left 3PHIII.

Description. This group of specimens has a common trait in the overall large dimensions and robustness, representing the largest horse occurring within the Tizi N'Tadderht collection. Zouhri et al. (2012) recognised this sample as belonging to a large and heavy built species with brachydont teeth and determined it as cf. *Hippotherium primigenium* (Von Mayer 1829).

In studying this sample, in addition to comparisons with other *Hippotherium* spp. (Bernor et al. 2017), we included in our comparative sample the largest hipparionine horse from the coeval North African site of As Sahabi (Lybia), i.e. *Sivalhippus* sp. (Bernor et al. 2008, 2012).

Although Tizi N'Tadderht largest specimens are comparable in size with *Sivalhippus* sp. from As Sahabi (Table 1), on the basis of upper and lower dentition occlusal morphology these largest specimens among Tizi N'Tadderht horses collection most resembles the overall morphology of the so called "Pannonian C-E Hipparions" (among the most primitive Old World hipparions), as defined in the Vienna basin record (Bernor et al. 2017).

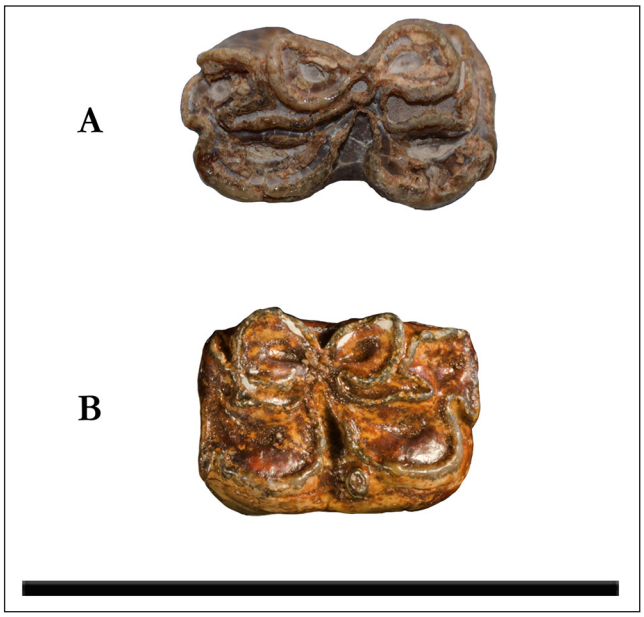

Fig. 4 - Occlusal view of *Hippotherium* sp. from Tizi N'Tadderht, Fsac-SK-18 (A) and "Pannonian C-E Hipparion" from Mariathal and Gaiselberg, M3540/206 (B). Scale bar 5 cm.

Figure 3 contrasts P^2 occlusal morphology of Fsac-SK-03 (Tizi N'Tadderht), with ISP164P65 (*Sivalhippus* sp. from Sahabi), M3540/8 ("Pannonian C Hipparion" from Mariathal and Gaiselberg). It appears evident that Fsac-SK-03 differs from *Sivalhippus* sp. having all tooth elements isolated and not

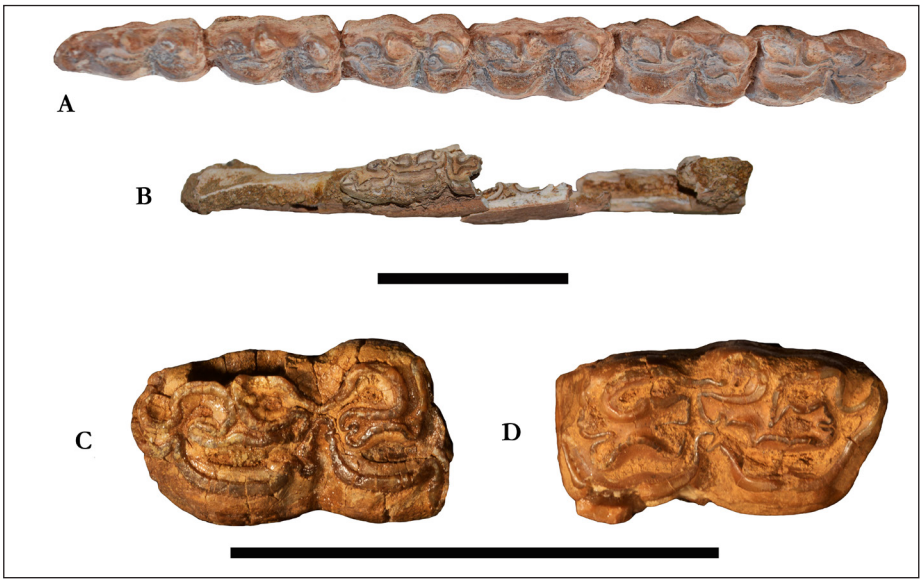

Fig. 5 - Occlusal view of *Eurygnathohippus* cf. *feibeli* from Tizi N'Tadderht, MTE12 (A) and Fsac-O-01(B) and *Eurygnathohippus feibeli* from As Sahabi, ISP3P34A (C) and ISP65P103 (D). Scale bar 5 cm.

included in the cementum; a well developed mesostyle, complex plications of the pre- and post-fossettes, an anterostyle more developed and isolated. The protocone is flat and convex. In general Fsac-SK-03 has higher resemblance with "Pannonian C-E Hipparion", although differing in protocone shape and in the amount of cementum characterising the tooth. Same overall similarities/differences are detectable in all available upper teeth.

Figure 4 contrasts lower premolar occlusal morphology of Fsac-SK-18 (Tizi N'Tadderht), with M3540/206, ("Pannonian C-E Hipparion" from Mariathal, Gaiselberg and Inzersdorf). Here a great similarity is evident between the Moroccan specimen and "Pannonian C-E Hipparion" from Vienna Basin. Albeit metastylid is not rounded in the Moroccan specimens, an elongated ectoflexid is a character in common particularly with the "Pannonian C–E Hipparion". Furthermore, the absences of ectostylid end of the pli caballinid are primitive traits typically found in genus *Hippotherium* sp. Postcranial elements of this sample are as large as the corresponding elements of *Sivalhippus* sp. from Sahabi albeit with stouter proportions, noticeably in MCIII, 1PHIII, 2PHIII and AST (Figure 6, 8, 9, 10, 11, 12).

Taking into account the morphodimensional comparisons, this Tizi N'Tadderht sample shows a higher overall similarity to Pannonian C-E Hipparions, attributable to genus *Hippotherium* more than to the Libyan *Sivalhippus*. Such conclusion allows us to partially confirm the preliminary determination to *Hippotherium* by Zouhri et al. (2012) although, we prefer avoiding a specific attribution (*Hippotherium primigenium*) and prudently leave the determination at generic level to *Hippotherium* sp., an Old World hipparionine genus with a wide zoogeographic range and known from the Late Miocene to the beginning of the Pliocene (Bernor et al. 2018).

Genus *Eurygnathohippus* Van Hoepen, 1930

Eurygnathohippus cf. ***feibeli*** Bernor & Harris, 2003

2012 Hippotheriini gen. et sp. indet. – Zouhri et al.

Referred Specimens: Fsac-SK-21, left mandible with M_1-M_3; MTE12, left mandible with P_2-M_3; Fsac-O-01, left P_2; FFsac-O-08, left M_3; Fsac-O-11, left M_1; Fsac-O-50, left M_1; Fsac-Sk-32, right TIBIA; Fsac-O-36, right AST; MTE11, right MTIII; MTE02, left 1PHIII; MTE03, right 1PHIII; MTE04, left 1PHIII; MTE05, left 1PHIII; MTE06, left 1PHIII; MTE07, right 1PHIII; Fsac-O-09, left 2PHIII; MTE08, left 2PHIII; MTE09, left 2PHIII.

Description. This group of fossils horses, smaller and more gracile in respect to the sample attributable to *Hippotherium* sp., was determined by Zouhri et al. (2012) as Hippotherini gen. et sp. indet. These authors considered the hypothesis of determining this sample as *Eurygnathohippus* but excluded the attribution because "*The typically hipparionine double knots and the absence of a developed ectostylid on the lower cheek teeth exclude the assignment of this form to the African genus Eurygnathohippus Van Hoepen 1930*" (Zouhri et al. 2012, p. 458).

SPEC_ID	SPEC	BONE	SIDE	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
MTE_02	*Eurygnathohippus* cf. *feibeli*	1ph3	lt.	59,5	52,1	30,2	41,2	29,4	34,3	24,8	20,1	16,1	45,8	45,4	11,0	11,7	
MTE_03	*Eurygnathohippus* cf. *feibeli*	1ph3	rt.	57,8	47,1	29,6	40,2	31,0	34,1	34,3	19,4	15,2	41,3	41,4	12,0	12,4	
MTE_04	*Eurygnathohippus* cf. *feibeli*	1ph3	lt.	59,4	50,6	29,8	41,4	30,4	33,5	33,8	18,7	15,9	41,1	44,0	13,0	12,6	
MTE_05	*Eurygnathohippus* cf. *feibeli*	1ph3	lt.	58,0	51,0	29,7	39,2	29,9	32,1	34,4	18,5	14,3	39,7	42,6	14,7	10,5	
MTE_06	*Eurygnathohippus* cf. *feibeli*	1ph3	lt.	57,4	50,2	28,2	39,2	28,0	32,3	31,3	17,2	15,9	41,2	44,1	12,6	11,5	
MTE_07	*Eurygnathohippus* cf. *feibeli*	1ph3	rt.	60,7	55,3	22,2		24,8	28,9	27,5	15,2			42,2	12,4	13,6	
Fsac-O-09	*Eurygnathohippus* cf. *feibeli*	2ph3	lt.	42,1	28,0	36,0	41,2	28,5	35,5								
MTE_08	*Eurygnathohippus* cf. *feibeli*	2ph3	lt.	38,2	28,7	34,8	40,9	26,1	38,0								
MTE_09	*Eurygnathohippus* cf. *feibeli*	2ph3	lt.	39,6	28,4	30,9	38,5	25,2	35,6								
Fsac-SK-21	*Eurygnathohippus* cf. *feibeli*	mandible	lt.					68,5									
MTE_12	*Eurygnathohippus* cf. *feibeli*	mandible	lt.		73,0	65,9	145,1	95,0		169,5	161,3	86,6	58,3	38,1			
MTE_11	*Eurygnathohippus* cf. *feibeli*	mtIII	rt.	257,2	251,2	27,8	24,7	39,6	31,4	10,4	7,4	6,7	34,6	33,0	23,6	24,7	18,9
Fsac-SK-32	*Eurygnathohippus* cf. *feibeli*	tibia	rt.	261,0		39,1	26,8			61,5	32,6	36,8					
Fsac-SK-21	*Eurygnathohippus* cf. *feibeli*	tmm1	lt.					7,7	7,5				34,5				
Fsac-O-11	*Eurygnathohippus* cf. *feibeli*	tmm1	lt.	24,9	19,7	12,1	7,2	10,0	9,5	8,9	9,0	8,2	40,3				
Fsac-O-50	*Eurygnathohippus* cf. *feibeli*	tmm1	lt.	26,4	25,7	11,1	7,5	9,6	9,8	11,8	8,0	7,8	15,8				
MTE_12_d	*Eurygnathohippus* cf. *feibeli*	tmm1	lt.	21,5		14,2	8,5	10,2	12,4		11,3	10,6					
Fsac-SK-21	*Eurygnathohippus* cf. *feibeli*	tmm2	lt.	22,8	20,9	12,5	9,4	10,6	11,4		11,0	10,7	34,4				
MTE_12_e	*Eurygnathohippus* cf. *feibeli*	tmm2	lt.	21,9		12,7	8,7	10,7	11,4		10,7	9,2					
Fsac-O-08	*Eurygnathohippus* cf. *feibeli*	tmm3	lt.	22,5	25,9	10,6	6,4	8,1	8,2	10,5	7,6	8,0	45,8				
Fsac-SK-21	*Eurygnathohippus* cf. *feibeli*	tmm3	lt.		27,4	7,3	6,8	8,8	9,5		9,8	9,3	38,6				
MTE_12_f	*Eurygnathohippus* cf. *feibeli*	tmm3	lt.	23,8		9,9	7,4	8,6	8,5		8,3	7,5					
Fsac-O-01	*Eurygnathohippus* cf. *feibeli*	tmp2	lt.	25,3		11,2	9,3	10,0	10,1		7,8	8,3	11,3				
MTE_12_a	*Eurygnathohippus* cf. *feibeli*	tmp2	lt.	25,5		12,1	9,4	12,4	13,0		10,3	13,0					
MTE_12_b	*Eurygnathohippus* cf. *feibeli*	tmp3	lt.	23,4		14,0	10,4	12,1	15,3		13,2	13,3					
MTE_12_c	*Eurygnathohippus* cf. *feibeli*	tmp4	lt.	22,8		13,2	10,1	11,4	14,3		12,3	13,0					

Tab. 2 - Measurement of the *Eurygnathohippus* cf. *feibeli* sample from Tizi N'Tadderht. Measurements are referred to Bernor et al. 1997 and Eisenmann et al. 1988.

Our comparative study has permitted us to revise the taxonomy of this taxon. The extensive comparison of Tizi N'Tadderht sample with the Sahabi collection temporarily housed at the Laboratory of Evolutionary Biology, Howard University, Washington D.C. revealed that either in size/proportions of postcranial skeleton, and in occlusal morphology both in upper and lower dentition this sample shows specific characteristics typical of the species *Eurygnathohippus feibeli*.

The mandibular dentition exhibits morphological consistent with referral to *Eurygnathohippus feibeli* (Fig. 5) where two mandibles from Tizi N'Tadderht (the adult individual MTE12, and the juvenile one Fsac-O-01) are comparted with two *Eurygnathohippus feibeli* specimens from Sahabi ISP3P34A (Fig. 5C) and ISP65P103 (Fig. 5D). All teeth exhibit a metastylid angled on the lingual side, and the occurrence of a pli caballinid adjacent to the hypoconid; the latter being as diagnostic feature, together with presence of ectostylid on an adult mandibular cheek tooth for *Eurygnathohippus feibeli*. In all premolars, the ectoflexid is shallow, while in molars is elongated. The preflexid exhibits a central introflexion in all specimens. The juvenile individual Fsac-O-01 dentition has a pli caballinid and an ectostylid on the labial side; such an element is commonly found in juvenile individuals, albeit it can be maintained in adults (as it is the case in MTE12 M_2). It is not unusual for different *Hipparion* lineages to show an ectostylid on the occlusal surface of the juvenile mandibular dentition; however, *Eurygnathohippus* and Pannonian C –E Hipparions have ectostylid on the adult dentitions.

Among the postcranial material, most significant are the third metatarsal, first phalanges of central digit and astragalus (as shown in figure 7, 8, 9 to 12), where Log 10 ratio diagrams of MTIII, 1PHI-II, 2PHIII and AST are included. Tizi N'Tadderht specimens are remarkably similar in dimensions and proportions to *Eurygnathohippus feibeli* from As Sahabi.

The direct comparison of Tizi N'Tadderht sample, previously identified by Zouhri et al. (2012) as Hippotheriini gen. et sp. indet., with the hipparionine horses collection from As Sahabi allows us to refer the Moroccan sample to *Eurygnathohippus* cf. *feibeli*, thus enlarging the zoogeographic range of this distinct clade of latest Miocene African hipparions including the westernmost part of North Africa.

Genus *Cremohipparion* Bernor & Tobien, 1989

Cremohipparion aff. ***periafricanum***

2012 *Cremohipparion* aff. *periafricanum* – Zouhri et al.

Referred Specimens: Fsac-SK-64, mandibular symphysis; Fsac-SK-22, left MCIII; Fsac-O-20, right MCIII; Fsac-O-29, right MCIII; Fsac-SK-27 left CALC; Fsac-SK-30, right 1PHIII.

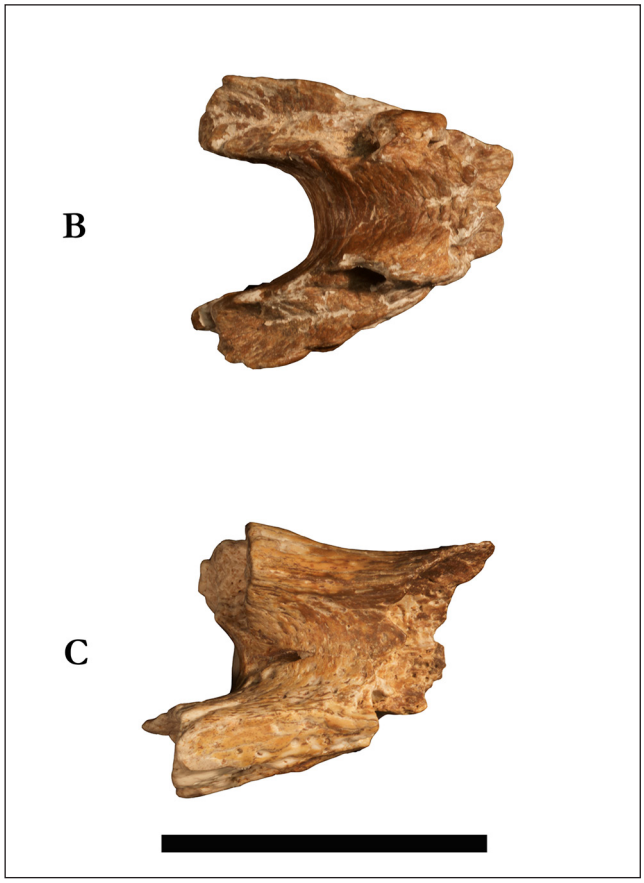

Fig. 6 - Mandibular symphysis of *Cremohipparion* aff. *periafricanum* from Tizi N'Tadderht, Fsac-SK-64 (A) and *Cremohipparion matthewi* from As Sahabi ISP28P25A (B) and ISP52P16A (C). Scale bar 5 cm.

Fig. 7 - Cranial view of the metacarpal of the third (central) digit; *Cremohipparion* aff. *periafricanum* from Tizi N'Tadderht, Fsac-SK-22 (A) and *Cremohipparion matthewi* from As Sahabi, ISP27P25B (B). Scale bar 5 cm.

Description. A few of a horse from Tizi N'Tadderht where identified by Zouhri et al. (2012) as *Cremohipparion* aff. *periafricanum*. These specimens are the smallest specimens of hipparionine horse found in the basin exhibiting extreme size reduction.

Since dental remains are not represented in the sample of this small taxon, our comparisons are thus based on the mandibular symphysis, and on the few postcranial remains. Also in this case we found a number of similarities with the smallest hipparionine species occurring in the Late Miocene site of Sahabi, *Cremohipparion matthewi* (Bernor et al. 2008).

Mandibular symphysis Fsac-SK-64, contrasts with same elements from As Sahabi (Fig. 6) is smaller (as already evidenced by Zouhri et al. 2012). If we consider postcranial elements, MTIII Fsac-SK-22 is remarkably similar in dimensions and proportions to ISP27P25B from Sahabi (Fig. 7). Both MTIIIs show a narrow diaphysis, with proximal and distal epiphysis proportionally larger. Comparing the sample using Log 10 ratio diagrams (Figs. 6–8 and 10) we report a slightly more robust aspect (measures 5 and 7) in the MCIII for the Moroccan sample,

SPEC_ID	SPEC	BONE	SIDE	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Fsac-SK-30	*Cremohipparion* aff. *periafricanum*	1ph3	rt.	47,8	43,3	26,3	33,3	24,1	29,2	29,1	14,7	11,5	34,6	37,3	12,9	11,4	
Fsac-O-36	*Cremohipparion* aff. *periafricanum*	ast	rt.	54,1	47,9	25,4	49,4	39,0	27,3	38,5							
Fsac-SK-27	*Cremohipparion* aff. *periafricanum*	calc	lt.	47,8	43,3	26,3	33,3	24,1	29,2	29,1	14,7	11,5	34,6	37,3	12,9	11,4	
Fsac-SK-64	*Cremohipparion* aff. *periafricanum*	mandible								25,6					37,3	45,6	16,5
Fsac-SK-22	*Cremohipparion* aff. *periafricanum*	mcIII	lt.	190,3	182,9	25,1	18,3	39,9		34,9	10,3			30,7			
Fsac-O-20	*Cremohipparion* aff. *periafricanum*	mcIII	rt.										32,4	31,2	26,1	21,4	22,4
Fsac-O-29	*Cremohipparion* aff. *periafricanum*	mcIII	rt.											30,7	24,2	21,1	23,7

Tab. 3 - Measurement of the *Cremohipparion* aff. *periafricanum* sample from Tizi N'Tadderht. Measurements are referred to Bernor et al. 1997 and Eisenmann et al. 1988.

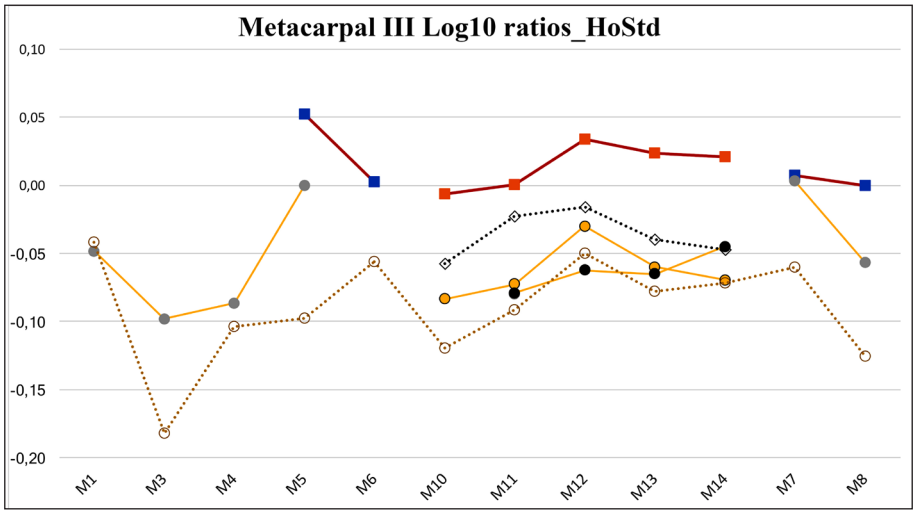

Fig. 8 - Log10 Ratio diagram of the metacarpal of the third (central) digit from Tizi N'Tadderht (solid lines) compared to As Sahabi (dots lines, MEAN). The specimens are analysed on the Hoewenegg *Hippotherium primigenium* sample. Red solid lines, *Hippotherium* sp. (Tizi N'Tadderht); yellow solid lines, *Cremohipparion* aff. *periafricanum* (Tizi N'Tadderht); grey dots lines, *Eurygnathohippus feibeli* (As Sahabi); brown dots lines, *Cremohipparion mattewi* (As Sahabi).

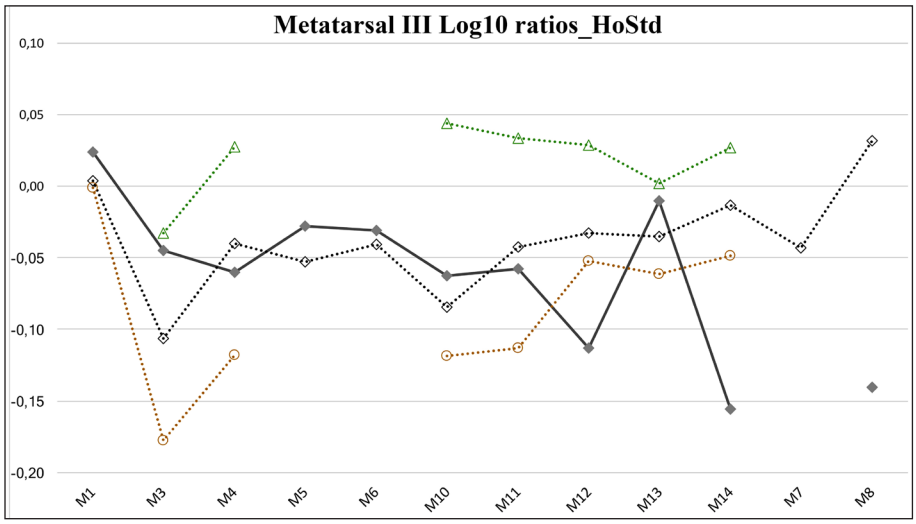

Fig. 9 - Log10 Ratio diagram of metatarsal of the third (central) digit from Tizi N'Tadderht (solid lines) compared to Sahabi (dots lines, MEAN). The specimens are analysed on the Hoewenegg *Hippotherium primigenium* sample. Grey solid lines, *Eurygnathohippus* cf. *feibeli* (Tizi N'Tadderht); green dots lines, *Sivalhippus* sp. (As Sahabi); grey dots lines, *Eurygnathohippus feibeli* (As Sahabi); brown dots lines, *Cremohipparion mattewi* (As Sahabi).

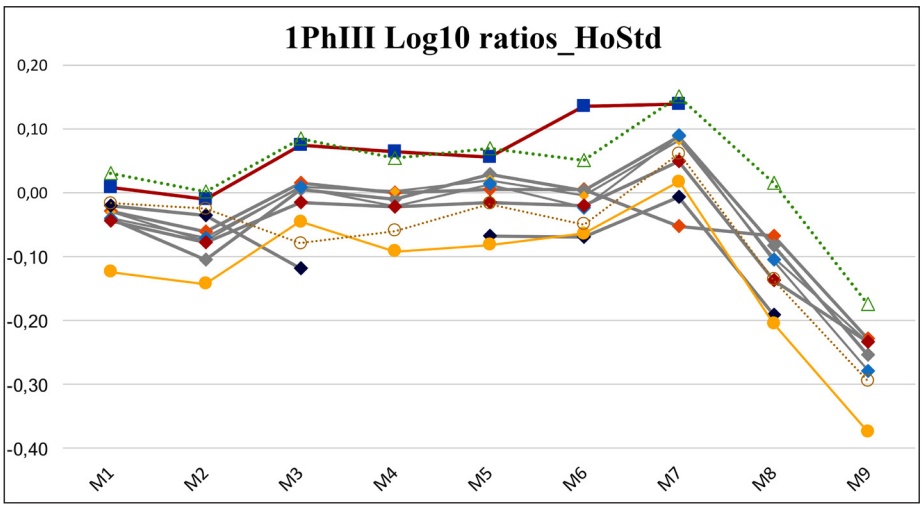

Fig. 10 - Log10 Ratio diagram of anterior first phanlanx of the third (central) digit from Tizi N'Tadderht (solid lines) compared to Sahabi (dots lines, MEAN). The specimens are analysed on the Hoewenegg *Hippotherium primigenium* sample. Red solid lines, *Hippotherium* sp. (Tizi N'Tadderht); grey solid lines, *Eurygnathohippus* cf. *feibeli* (Tizi N'Tadderht); yellow solid lines, *Cremohipparion* aff. *periafricanum* (Tizi'n Tadderht); green dots lines, *Sivalhippus* sp. (As Sahabi); brown dots lines, *Cremohipparion mattewi* (As Sahabi).

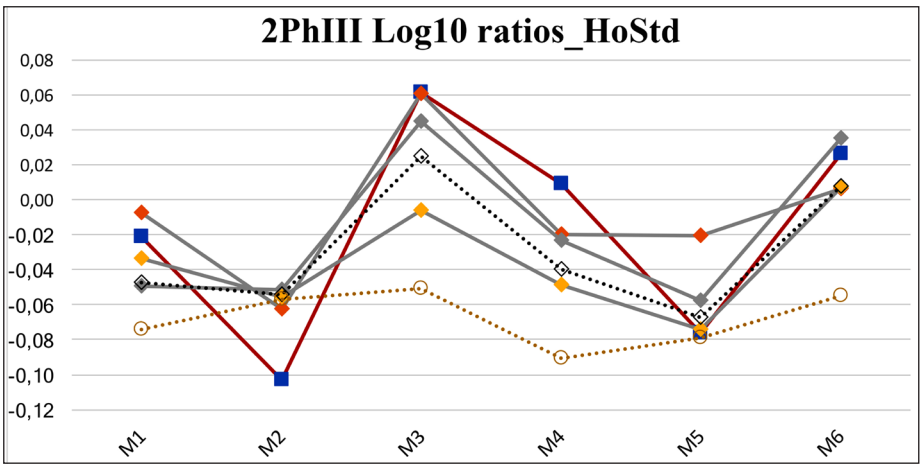

Fig. 11 - Log10 Ratio diagram of anterior second phalanx of the third (central) digit from Tizi N'Tadderht (solid lines) compared to As Sahabi (dots lines, MEAN). The specimens are analysed on the Hoewenegg *Hippotherium primigenium* sample. Red solid lines, *Hippotherium* sp. (Tizi N'Tadderht); grey solid lines, *Eurygnathohippus* cf. *feibeli* (Tizi N'Tadderht); grey dots lines, *Eurygnathohippus feibeli* (As Sahabi); brown dots lines, *Cremohipparion mattewi* (As Sahabi).

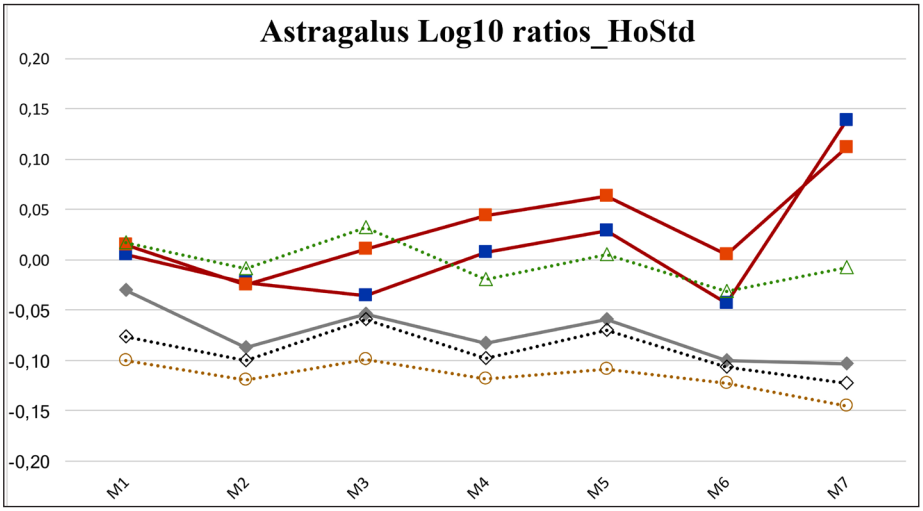

Fig. 12 - Log10 Ratio diagram of astragalus from Tizi N'Tadderht (solid lines) compared to As Sahabi (dots lines, MEAN). The specimens are analysed on the Hoewenegg *Hippotherium primigenium* sample. Red solid lines, *Hippotherium* sp. (Tizi N'Tadderht); grey solid lines, *Eurygnathohippus* cf. *feibeli* (Tizi N'Tadderht); green dots lines, *Sivalhippus* sp. (As Sahabi); grey dots lines, *Eurygnathohippus feibeli* (As Sahabi); brown dots lines, *Cremohipparion mattewi* (As Sahabi).

or slightly smaller (1PHIII, Fsac-SK-30; calcaneus, Fsac-SK-27).

Our comparisons confirm the attribution of this small sample to the genus *Cremohipparion*. Taking into account the differences with the Sahabi sample we maintain the attribution originally formulated by Zouhri et al. (2012) as *Cremohipparion* aff. *periafricanum*.

Discussion and Conclusion

The revision of the entire hipparionine horse collection from Tizi N'Tadderht (Ouarzazate basin, Morocco) allowed us to better define the equid component within the faunal assemblage from this important north African site (Geraads et al. 2012; Zouhri et al. 2012).

As suggested in a preliminary report on the Tizi N'Tadderht Equidae (Cirilli and Zouhri 2018), the hipparionine Equidae are represented at this Late Miocene site with three different species, one large and robust, *Hippotherium* sp., a middle sized and gracile form, *Eurygnathohippus* cf. *feibeli*, and a very small species, *Cremohipparion* aff. *periafricanum*.

While the occurrence of *Hippotherium* and *Cremohipparion* was already reported by previous authors (Zouhri et al. 2012), the identification of *Eurygnathohippus* within the faunal assemblage is recognized here for the first time.

Noteworthy the diverse horse fauna, with three different sympatric species, includes taxa with European affinities, and a taxon belonging to a distinct clade of Mio-Pliocene African hipparions recently also identified in the Pliocene of the Indian Subcontinent (Jukar et al. 2019).

The largest and smallest Tizi N'Tadderht hipparions reveal European affinities, *Hippotherium* sp. being most comparable with the morphotypes of the so called "Pannonian C-E Hipparion" group from Vienna Basin, and *Cremohipparion periafricanum* with the Late Miocene fossil record from Spain

(Zouhri & Bensalmia 2005; Zouhri et al. 2012). In the North Africa, the genus *Cremohipparion* was only known from the Late Miocene locality of As Sahabi, (Lybia), with the species *Cremohipparion matthewi* (Bernor et al. 2008). The identification of *Cremohipparion periafricanum* in the Tizi N'Tadderht site allows us to expand the biogeographic area of this genus during the Late Miocene, testifying the fauna exhange between Africa and Europe. The morphological comparison with the other *Cremohipparion* species from As Sahabi supports the presence of this genus during the Late Miocene in North Africa, suggesting a different geographical distribution of these two species: *Cremohipparion periafricanum* in the westpart of the Circum-Mediterraneum area (Spain and Morocco) and *Cremohipparion matthewi* in the central and eastward region (Lybia and Greece) (Zouhri et al 2005).

In addition, the occurrence of the genus *Eurygnathohippus* (*Eurygnathohippus* cf. *feibeli*) in the Late Miocene of Morocco extends westwards the zoogeographic range of this distinct clade of latest Miocene African hipparions, previously known from South Africa (Langebaanweg; Bernor & Kaiser 2006), Ethiopia (Aramis, Hadar; Bernor et al. 2010, 2013), Kenya (Lothagam and Ekora; Bernor & Harris 2003; Bernor et al. 2010) and Lybia (Sahabi; Bernor et al. 2012). The continental-scale wide extension of this *Eurygnathohippus* clade coincides with the time of open country woodlands expansion across Eurasia and Africa in the Late Miocene (Bernor et al. 1996; Eronen et al. 2009).

The hipparionine horse component within the land mammal assemblage of Tizi N'Tadderht confirms the occurrence, during the Late Miocene, of a biogeographic crossroads between western Eurasia and sub-Saharan Africa faunas (Bernor & Rook 2008; Marra et al. 2017) with a certain degree of biotic continuity between Eurasia and Africa in the Late Miocene.

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