THE TUROLIAN HIPPARIONS FROM CIOBURCIU SITE (REPUBLIC OF MOLDOVA): SYSTEMATICS AND PALEODIET

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Abstract. The Cioburciu hipparions, Republic of Moldova, are included in a Turolian assemblage, approximately dated between 9 and 7 million years. We assess herein their taxonomic position, systematics, biogeography and paleodietary habits. We have undertaken standard equid measurements as well as accessing the Vera Eisenmann website for measurements and images and analysed craniodental and postcranial elements. This assemblage has been determined to be of a medium-sized hipparion with an elongated muzzle, well developed preorbital fossa that is dorsoventrally extensive and placed close to the orbit, lacking a caninus fossa and having a prominent and deep buccinator fossa. As such, this assemblage is referable to *Cremohipparion moldavicum* Gromova, 1952 common to the Western Ukraine, Balkans, Romania, Republic of Georgia, Turkey and Iran. We have employed a combination of gross cheek tooth wear morphology utilizing the mesowear method and a microscopic analysis of occlusal enamel scars utilizing the light microscope microwear technique. These complementary paleodietary methods indicate that these hipparions engaged in a mixed feeding dietary behavior and that the Cioburciu sample of *C. moldavicum* likely alternated its diet between browsing and grazing seasonally and/or regionally. A hierarchical cluster analysis based on average scratch and pit numbers positions this taxon among extant mixed feeding ungulates. Large pitting and gouging assessed through the microwear technique indicates occasional consumption of relatively coarser foods than typical mixed feeders or grazers or grit-laden food just prior to death while mesowear indicates that this was not a lifetime habit.

INTRODUCTION

We review here the Turolian hipparions from the Cioburciu site of the Republic of Moldova. The geologic deposits of the Cioburciu site are included in the Balta Formation (Hubca 1969; Fig. 1). According to Mathosko et al. (2016), these deposits are part of an Upper Miocene fluvio-deltaic system in the Eastern Carpathians Foreland. The paleontological collections for this site can be found at the paleontological museums of the Iasi, Odessa, and Moscow Universities. The Hipparion materials studied in this paper are from the Upper bed of the Cioburciu site.

The *Hipparion* sample studied herein was collected by Macarovici in 1929 during the fieldwork for his Ph.D. dissertation (Macarovici 1936; Macarovici 1940). Later, Macarovici (1967) reviewed all the Hipparion fossil material from the Meotian of

Romania and the Republic of Moldova and concluded that for this age, only four species should be considered: *Hipparion moldavicum*, *Hipparion verae* (previously known as, *Hipparion gromovae*), *Hipparion tudorovense* (small-sized) and *Hipparion platygenys*. Lungu et al. (1993) interpreted that for the Meotian deposits from the Republic of Moldova only these species should be considered: *H. moldavicum*, *H. verae*, *H. pregiganteum*, *H. platygenys* and *H.matthewi*. Krakhmalnaya (1996) reviewed all the Neogene Hipparions of the North of Black Sea and concluded that for the Turolian only the following species occurred: *H. moldavicum*, *H. giganteum*, *H. aff. praegiganteum*, *H. tudorovense*, *H. platygenys*, *Hipparion* sp. I, *Hipparion* sp. III and related forms.

The following mammalian species, have been found at the Cioburciu site (Lungu & Rzebik-Kowalska 2011): *Orycteropus gaudryi*, *Ictitherium viverinum*, *Adcrocuta exima*, *Machairodus schloseri*, *Machairodus cultridens*, *Mustela palaeatica*, *Simocyon primigenius*, *Choerolophodon pentelici*, *Deinotherium gigantissimum*, *Hipparion verae*, *Hipparion moldavicum*, *Aceratherium incissivum*, *Dicerorhinus schleiermacheri*, *Cervavitus varibilis*, *Palaeotragus rouenyi*, *Helladotherium duvernoyi*, *Tragoportax frolovi*, *Palaeoryx studzeri*, and *Gazella deperdita*. The microvertebrate fauna following the same authors is represented by: *Mioprotheus* cf. *caucasicus*, *Rana* sp., *Testudo bessarabica*, *Chelidropsis* sp., *Melanochelys* sp. , *Sakya* sp., *Lacerta* sp., *Ophizaurus* sp., *Natrix* sp., *Vipera* sp., *Struthio* sp., *Anas* sp., *Amphechinus* sp., *Shizogalerix* cf. *aticus*, *Desmana* sp., *Crusafontina* cf. *kormosi*, *Paenelimnoecus* cf. *repenningi*, *Prochotona* sp. nov., *Alilepus lascarevi*, *Spermophilinus* cf. *bredai*, *Vasseuromys theni*, *Hansdebruijnia neutrum*, *Castromys* sp., *Kowalskia lavocati*.

A systematic evaluation of the Cioburciu site Hipparions entailed measurement in millimeters rounded to (0.1 mm) cranial, dental and postcranial elements: premolars and molar teeth as well as metacarpals, metatarsals, astragali, and calcanea. Herein we describe skull, maxillary and mandibular morphology and analyze the third metacarpal (henceforth MCIII) and third metatarsal (MTIII) by Log10 ratio diagram comparisons.

We employed two different tooth wear proxies (mesowear and microwear) to reconstruct the probable diet of the hipparion(s) from Cioburciu. Mesowear analysis (Fortelius & Solounias 2000) has been used extensively to interpret paleodiet (e.g., Kaiser et al. 2000; Kaiser & Fortelius 2003;

Kaiser & Solounias 2003; Franz-Odendaal & Kaiser 2003; Semprebon et al. 2004a; Mihlbachler & Solounias 2006; Rivals & Semprebon 2006; Semprebon & Rivals 2007; Mihlbachler et al. 2011, Ackermans et al. 2020). Two variables are assessed using the mesowear technique: molar cusp shape and occlusal relief (the relative difference in height between cusp apices and intercusp valleys) in lateral (buccal) view. The technique examines attritional (tooth-on-tooth) versus abrasive (food-on-tooth) wear on tooth surfaces. Differences in the shape of cusps and in the level of occlusal relief are due to the relative levels of attritive wear (e.g., sharp cusps with high relief) and abrasive wear (more rounded or blunted cusps often with lower relief). Mesowear represents cumulative wear imposed on molars throughout the lifetime of an individual animal.

Microwear has also been used extensively to examine paleodiet (e.g., Rensberger 1978; Walker et al. 1978; Scott et al. 2005, 2006; Ungar et al. 2008, 2010; Semprebon 2002; Solounias & Semprebon 2002; Merceron et al. 2004, 2005; Semprebon et al. 2004). Microwear consists of examining microscopic wear that is etched into dental enamel (and sometimes dentine) via the last meals that were consumed by animals (Grine 1986). Microwear turns over more rapidly than mesowear, and thus it is sensitive to local, seasonal, and individual dietary variations. Microwear allows for changes in dietary behavior to be discovered before changes in gross craniodental morphology (including mesowear) can be seen.

The purpose of this study is to determine the systematic affinities of the assemblage and to reconstruct the dietary behavior of the Turolian equids from the Cioburciu site of the Moldavian Republic.

MATERIAL AND METHODS

Measurements

Measurements are all given in millimeters and rounded to 0.1 mm. Measurement numbers (M1, M2, M3, etc.) refer to those published by Eisenmann et al. (1988) and Bernor et al. (1997) for cranial and postcranial elements. Tooth measurement numbers refer to those published by Bernor et al. (1997) and Bernor and Harris (2003). M1-M38 refers to cranial measurements as described by Eisenmann et al. (1988) and Bernor et al. (1997).

Element abbreviations: POF = preorbital fossa; POB = preorbital bar; IOF = infraorbital foramen I3 = third upper incisor; P2 = second upper premolar; P3 = third upper premolar; P4 = fourth upper premolar; M1 = first upper molar; M2 = second upper molar; M3 = third upper molar; p2 = second lower premolar; m3 = third lower molar, MCII = metacarpal II; MCIII = metacarpal III; MCIV = metacarpal IV; MTII = metatarsal II; MTIII = metatarsal III; MTIV = metatarsal IV; 3PHIII = 3rd phalanx of the third (central) digit; CALC = calcaneum; AST = astragalus.

We sampled the following museum and institutional vertebrate collections for this study:

AICUPM – Alexandru Ioan Cuza University Paleontological Museum
LPB (FGGUB) – Laboratory of Paleontology of the Faculty of Geology and Geophysics, University of Bucharest
ONHM – Odessa National History Museum
MGRI – Moscow Vernadsky Geological State Museum.

We have used herein measurements and images of the Cioburciu hipparions from the Vera Eisenmann website (https://vera-eisenmann.com/chobruchi-data-and-photos) for our morphological observations and systematic determinations.

We follow Bernor et al. (1997, 2016) in describing and diagnosing the cranial and dental measurements herein. In various studies, Eisenmann, (see Eisenmann 1995 for a comprehensive summary), has used Log10 ratio diagrams to evaluate differences in hipparion metapodial proportions as a basis for recognizing taxa and their evolutionary relationships. Recently, Bernor et al. (2016) used Log10 ratio diagrams, to evaluate and resolve the alpha systematics of Maragheh hipparionine horses which includes *Cremohipparion* cf. *moldavicum*. We incorporate these previously used methodologies in this work. Our statistical analysis uses the skeletal population from Höwenegg (Hegau, southern Germany, 10.3 Ma; Bernor et al. 1997) as a mean log standard for calculating metacarpal III and metatarsal III Log10 ratio diagrams herein (MCIII and MTIII respectively).

Tooth wear Sample
Samples were acquired from the Alexandru Ioan Cuza University Paleontological Museum. All original specimens are housed in the collections of this institution. The specimens were screened for potential taphonomic alteration of enamel surfaces (after King et al. 1999) under a stereomicroscope by GMS (Gina M. Semprebon). Eleven specimens were determined to be suitable for analysis and subjected to microwear analysis.

Microwear technique
Eleven tooth surfaces were cleansed, molded, and casted (after Solounias & Semprebon 2002). All molar casts were examined at 35 times magnification using a Zeiss Stemi-2000C stereomicroscope. Microwear was scored by GMS to exclude potential interobserver error. Microwear scars were visualized on the second enamel band of the paracone of the upper M2 or the protoconid of the m2 of adult individuals (young and old adults were discarded) using external oblique illumination (An M1-150 high intensity Dolan-Jenner fiber optic light source) directed across the surface of casts at a 45-degree angle to the occlusal surface. The average number of pits (rounded features) and the average number of scratches (elongated features) were assessed within a 0.4 mm square area (0.16 mm²) using an ocular reticle. Also, it was also noted if more than four large pits were present or absent per within the 0.4 mm square area and whether gouges were present or absent (after Solounias & Semprebon 2002 and Semprebon et al. 2004). Results were then compared to an extant ungulate average scratch and pit database (data from Semprebon 2002) to determine the dietary categories of browser versus grazer. Scratch textures were also scored as being either fine (i.e., narrow with low refractivity and dull in appearance), coarse (i.e., wider with a higher refractivity and bright white in appearance) and hypercoarse (i.e., very wide and/or deep and non-refractile or dark in appearance), a mixture of fine and coarse, or a mixture of coarse and hypercoarse scratch types per tooth surface. A scratch width score (SWS) was ascribed to a sample as follows: a score of 0 was given to teeth with predominantly fine scratches; a score of 1 was given to those with a mixture of fine and coarse types of textures; a score of 2 was given to those with predominantly coarse scratches; and a score of 3 was given to those with a mixture of coarse and hypercoarse types of scratches. An average of individual scores for a sample produced an average scratch width score for that taxon. Lastly, because extant seasonal or regional mixed feeders alternately feed on both browse and grass and may overlap the browsing or grazing average scratch/pit ecospaces, raw scratch distributions per taxon were constructed. Grazers have unimodal, high scratch distributions, browsers have unimodal,

low raw scratch distributions, and mixed feeders show a bimodal split of both high scratch individuals and low scratch individuals. We also calculated the percentage of raw scratches in each taxon that fell into the low scratch range (0-17 scratches) and compared them to an extant ungulate database (data from Semprebon 2002).

Mesowear Technique

Mesowear was scored by a single investigator (GMS) to exclude potential interobserver error. We used only those specimens in which the last molar was in occlusion and the first molar retained an occlusal shape similar to that of the second to minimize potential age effects although Rivals et al. (2007) demonstrated that the mesowear signal is known to be relatively stable throughout much of the adult lifespan of hypsodont taxa such as the fossil hipparion analyzed here.

Mesowear was assessed macroscopically from the buccal side of the paracone of the second upper molars two different ways. First, molars were scored as in Fortelius and Solounias (2000) whereby cusp shape in buccal view was scored as sharp, round, or blunt and occlusal relief was scored as high or low. The percentages of sharp, round, and blunt cusps as well as the percentages of high and low relief were calculated. Secondly, we employed the more standardized mesowear "ruler" method (Mihlbachler et al. 2011) whereby samples are compared to a standard template with seven qualitative wear stages (0-6). The ruler is comprised of extant horse cusps which represent a gradient of cusp wear from high relief and sharp cusp shape (assigned a score of 0) to completely blunt cusp shape with no relief (assigned a score of 6). The ruler is used as a reference for cusp shape and occlusal relief which are combined into one score as others have pointed out (e.g., Mihlbachler et al. 2011) that the variables used in the mesowear method are not strictly independent. We slightly modified this methodology by also recognizing intermediate scores in 0.5 increments assigned if the observed cusp shape could not be definitively assigned to one of the seven original wear stages but fell in between two steps (i.e., 0.5, 1.5, 2.5, 3.5, 4.5, 5.5). An average mesowear score was calculated. Finally, we employed a hierarchical cluster analysis (using PAST 3.25 – Hammer et al.

2001) to compare the fossil hipparion mesowear scores to those of extant ungulates with known diets.

GEOLOGICAL SETTING

The material of *Cremohipparion moldavicum* originates from the Upper Miocene locality of Cioburciu (Ciobruciu, Chiobruciu), Republic of Moldova (Fig. 1). Lungu and Rzebik-Kowalska (2011) have presented the detailed overview on Cioburciu geology, taphonomy, and chronology. Cioburciu village is situated in the eastern part of Dragos –Voda District, approximately 100 km southeast of Khisinev Town.

The Upper Miocene section of Cioburciu is exposed in the lower part yellowish – greenish clay rich in shells of Khersonian mollusks (*Mactra caspia*). In the upper part of the geological section, there are two fossiliferous layers: the first one is composed of white-yellowish sands with a large concentration of well-preserved remains of fossil mammals. The second part is composed of gray-greenish sandy clays. Vangengeim and Tesakov (2013) considered that the lower bed of Cioburciu 1 should be assigned to MN10 and the upper bed of Cioburciu 2 to MN12. This assignment, however, does not agree with data from Vasiliev et al. (2011), who provided a radioisotopic age suggesting that the Khersonian (an equivalent of middle Tortonian) most likely correlates to the younger Chron C4An and later part of Chron C4Ar, and therefore, the Kherosnian–Meotian boundary is probably drawn within Chron C4Ar which is 8.5 Ma. This means that the "Vallesian" localities in Moldova are significantly younger than 11.2 Ma and correlative with the lower part of the Turolian (MN11).

The radioisotopic data by Vasiliev et al. (2011) for the Khersonian–Meotian boundary indicates a correlation of the normal polarity interval of the Khersonian to the younger chron C4An (8.6 – 8.2 Ma). The reversed intervals with the Bessarabian–Khersonian boundary may consequently correspond to C4Ar. Thus, the Hipparion localities in Moldova may be significantly younger than suggested (8.0 Ma) by Vangengeim et al. (2006) and Vangengeim and Tesakov (2013), probably 7.5 – 7.0 Ma (MN12).

Fig. 1 - Geographical and Geological map showing the deposits of the Cioburciu fossil site within the Balta Formation of the Republic of Moldova.
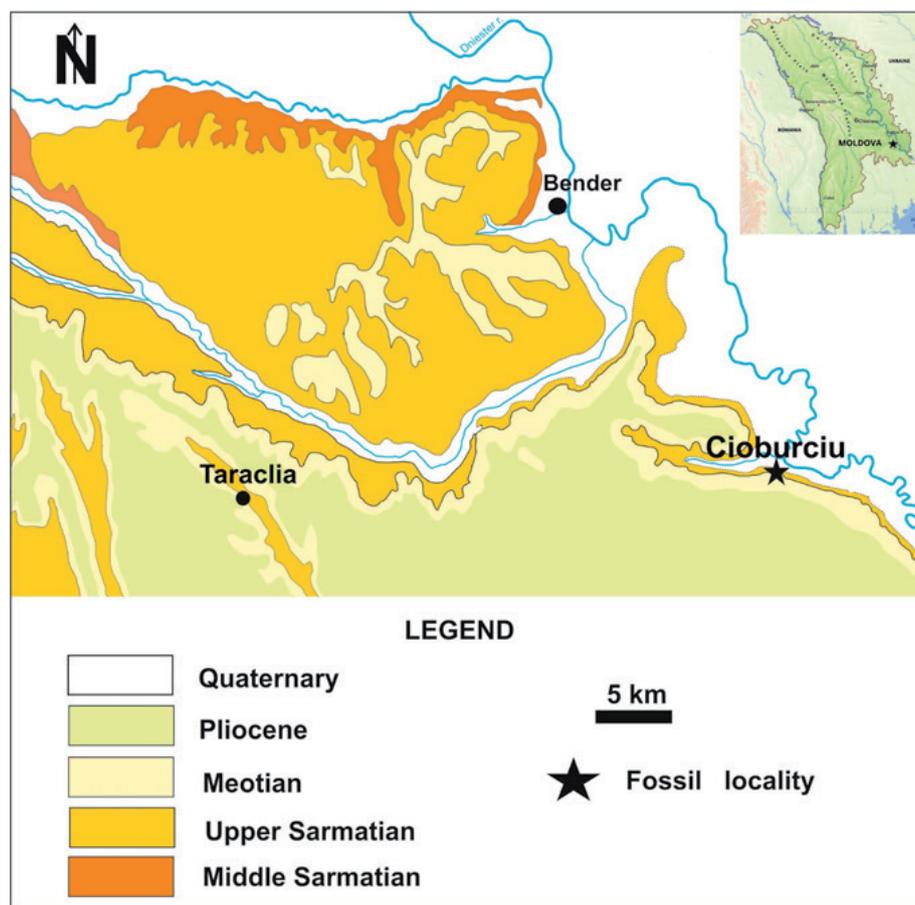
SYSTEMATIC PALEONTOLOGY

Order **Perissodactyla** Owen, 1848
Family Equidae Gray, 1821
Subfamily Equinae Equinae Gray, 1821
Tribe Hipparionini Quinn, 1955
Genus *Cremohipparion* Qiu, Huang & Guo, 1988

Cremohippparion moldavicum Gromova, 1952

Holotype of *Cremohipparion moldavicum* (Gromova, 1952): P.I.N. 1256-3639, Academy of Sciences Paleontological Institute of the U.S.S.R., figured by Gromova, 1952, Figures 1-3

Type Locality: Taraklia, Republic of Moldova, District of Benderi.

Age: Meotian (= Medial Turolian, MN 12)

Geographic Range: Western Ukraine, Romania, Balkans, Republic of Georgia, Republic of Moldova, Turkey and Iran.

Diagnosis (Translated from Gromova 1952: 154-155): Medium size hipparion, basal length of cranium = 271-273 mm.; length of cheek teeth (P2-M3) = 121-141 mm.; muzzle elongate; index of orbital-facial length = 67; index of anatomical axes = 214.6. Frontals narrow, width index = about 38.2; frontal-basal index = 261.4 mm. Dental series short; index of length to basal width = 33.5 mm; to the premolars, 41.2-46.8 mm; diastemato-dentary index = 66.1-28.9 mm. Upper molars large relative to premolars; molar-premolar index = 82.4-91 mm. A single POF, very long and elevated, index of position relative to orbit = 26.6-37.8 mm; relative to the facial crest, 16.7-64.3 mm. Nasal notch moderately deep, its posterior border is at the level of, or slightly anterior to the anterior border of P2. The diastema is well developed; its index is 60.4-77 mm. Protocone is short and wide, length index of P3-M2 in little or moderately worn individuals is 20.7-37.5 mm, in very worn teeth, 25-43.3 mm; index of form in the same conditions 42.8-78.3 and 57.1-92.3 mm. Enamel plication is moderate in upper cheek teeth, on the posterior wall of the prefossette and anterior wall of the postfossette; when P3, P4, M1 and M2 are very worn or moderately worn, they have 3.5-6.5 to 9.5 plis. Cheek teeth have a height-length index on P3, P4 of 156-195.5 mm; on M1-M3, 204.3 – 232.5 mm; on p3, p4, m1 and m2, 159-200 mm. A double knot (metaconid-metastylid) of *Hipparion* type (rounded with intervening V-shaped linguaflexid). External depression in low-

Fig. 2 - The nearly complete cranium LPB(FGGUB) 522 within the original plaster collection jacket with the mandible associated. Scale bar: 15 cm.

er cheek teeth deep, complementary elements little developed. The islette occupies the anterior portion of the I3 crown. The postcranials are gracile and elongate; index of width in the lower articulation relative to the width of MCIII, 14.5-16.3 mm; to the length of MT III, 12.4-14.2 mm. Metapodial length relative to width: MT/T = 74.4 mm. Lateral digits are moderately developed; moderate indices of lower extremities diameters MC II and IV to MC III, 75.8 mm – MT II and IV to MT III, 66.8 mm; moderate indices of length of the first phalanges of the lateral digits to those of the anterior median digits, 58.2 mm; posterior 53.8 mm. Extremities recurved to the level of articulations; moderate index of the pisiform bone 114.3 mm; anterior 3PHIII narrow; length-width index of posterior 3PHIII 71.4-86.6 mm.

Emended diagnosis (after Bernor et al. 2016): A medium-sized hipparionine with an elongate snout. The POF is single, subtriangular shaped, anteroposteriorly oriented and elongate, dorsoventrally and medially deep, with slight posterior pocketing, a distinct anterior rim, and strongly expressed peripheral outline. Lacking a caninus (= intermediate) facial fossa. The POB is short with the lacrimal bone invading the posterior aspect of the POF. The nasal notch is incised at a level either just above the mesial border of P2, or slightly mesial to it. Middle wear adult cheek teeth have moderately complex plications of the pre- and postfossettes; protocones are round to oval and show lingual flattening in some individuals. The P2 anterostyle is usually elongate but can be short and rounded in some individuals. MCIIIs and MTIIIs are elongate and slender. P2-M3 length ranges from 120.0-145.2 mm.

Description

The most complete material includes 4 crania from Cioburciu, Odessa 3801, Odessa 2064 Odessa 2067 (or alternatively Odessa 2078). Of these the best preserved is Odessa 3801 (Supplementary Fig. 1; https://vera-eisenmann.com/chobruchi-data-and-photos). There is also a nearly complete cranium, LPB(FGGUB) 522 lacking the snout with a mandible in occlusion (Fig. 2). There are a number of maxillary cheek tooth series that are diagnostic of the *Hipparion* species (Fig. 3 A-D): AICUPM4003 (P2-M3), AICUPM4004 (P2-M3), AICUPM4006 (P2-M3), AICUPM4010 (P2-M3). Eisenmann (https://vera-eisenmann.com/chobruchi-data-and-photos) has further provided excellent images of 5 left maxillary cheek tooth series (Odessa 2064, 2067or2061, 2085, 3078-1, 3078-2 and 3801) which augment the basis for our amended diagnosis of the species (Supplementary Fig. 2).

Odessa 3801 (Supplementary material – Supplementary Fig. 1) is a complete, well preserved cranium characterized by the following features: a very large, subtriangular shaped preorbital fossa (POF) placed close to the orbit (with a short POB) that is dorsoventrally and medially deep and distinctly invaded by the lacrimal bone; caninus fossa is lacking; buccinator fossa is large and deep; infraorbital foramen (IOF) is placed near the anterior-most limit of

the POF; there is no intermediate (= caninus) fossa; buccinator fossa is distinct and deeply excavated; nasal notch is shallowly incised extending anterior to P2. The canine is large indicative of a male individual; cheek teeth have M3 in full occlusion and P2 is very worn indicative of a fully adult individual; cheek teeth have oval protocones; pre- and postfossettes are moderately complex; pli caballins appear single or double; hypoglyphs are moderately deeply incised. P2-M3 length is 136 mm in length.

Odessa 2064 is a moderately crushed skull and lacks the posterior cranium and snout. POF is as in Odessa 3801. Odessa 2067 (or 2061) is dorsoventrally crushed and preserves little anatomical detail. Odessa 2078 is a mandible viewed labially with no extraordinary features. (Length p2-m3 – 149 mm). Both Odessa 3801 and BPU clearly have a large preorbital fossa, subtriangular shaped, medially very deep, with a distinct anterior rim and placed very close to the orbit with a short preorbital bar. There is no apparent intermediate (= caninus fossa) diagnostic of *Cremohipparion moldavicum* and not the closely related species *C. mediterraneum*. While Odessa 2064 (Supplementary Fig. 1) is more fragmentary it displays all the facial characters of the other two crania.

LPB(FGGUB) 522 (Fig. 2) is a skull with mandible in occlusion retained within the original plaster collection jacket. The skull lacks the snout and the mandible is lacking the symphysis. In occlusion one can see the same essential salient features of the face: POB is short; POF is subtriangular shaped, medially deep and has a distinctly well-developed peripheral rim with IOF at the anterior limit of the POF. Occlusal details of either the skull or mandibular cheek teeth are not visible. P2-M3 is 125 mm in length and p2-m3 is 130 mm in length.

Figure 3 (A-D) includes occlusal views of AICUPM4003 (Fig. 3A), 4004 (Fig. 3B), 4006 (Fig. 3C), and 4010 (Fig. 3D) P2-M3. AICUPM4003 (Fig. 3A) has protocones rounded to oval; P2 has a short anterostyle; pli caballin is double to complex on P2-M2 on all cheek teeth; fossette are complex on all cheek teeth. AICUPM4004 (Fig. 3B) is similar to AICUPM4003 but not as in advanced wear. P2 also has a short anterostyle; protocones are oval; pli caballin is single to double on the cheek teeth; P2 has pre- and postfossettes linked which is a primitive feature for Old World hipparions. AICUPM4006 (Fig. 3C) is a young adult with P4 and M3 just
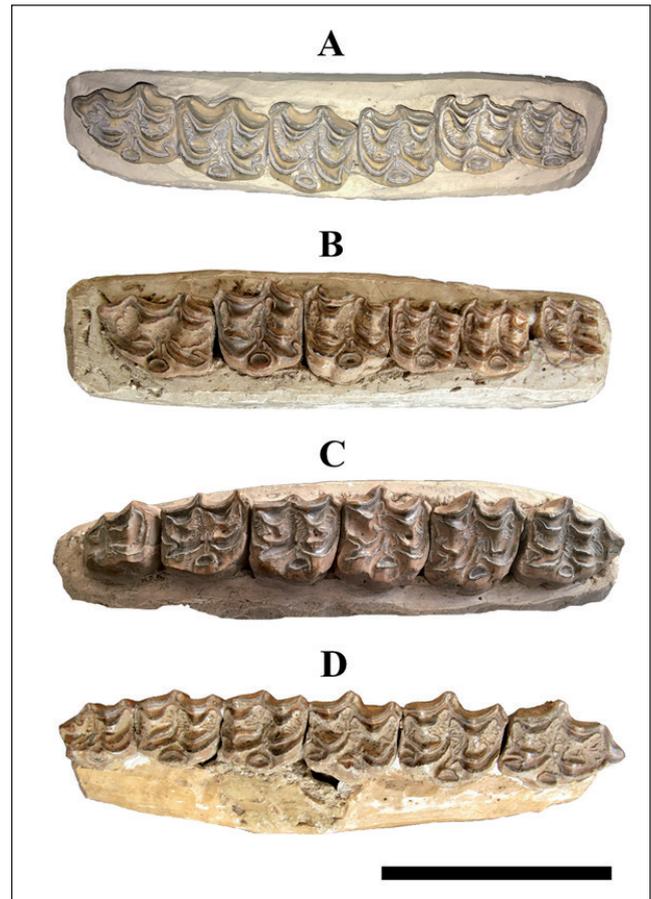

Fig. 3 - Occlusal views of: A) AICUPM4003 (P2-M3), B) AICUPM4004 (P2-M3), C) AICUPM4006 (P2-M3), and D) AICUPM4010 (P2-M3). Scale bar : 6 cm.

coming into occlusion. P2 has a very short anterostyle; protocone is small and round in P2; P3 – M2 protocones are lingually flattened and otherwise short-oval shape due to their early wear; pre- and postfossettes of M1 and M2 are in wear and are very complexly plicated; all cheek teeth have poorly developed pli caballin due to relatively early wear and the protocones are lingually flattened on P3-M2. P2-M3 length = 141 mm. AICUPM4010 (Fig. 3D) is another young adult P2-M3. The cheek teeth are in too early stage of wear to characterize (P2-M3 - 137 mm**).**

Eisenmann (https://vera-eisenmann.com/chobruchi-data-and-photos) figured 6 maxillary cheek tooth series from Odessa (2064, 2067 or 2061, 2085, 3078-1. 3078-2 and 3801, with associated skull, Supplementary Fig. 1 and Supplementary Fig. 2). These series have the following salient features: protocones short, oval to rounded; P2 anterostyles mostly short, but some extended; pli caballins vary from double to single; pre- and postfossettes
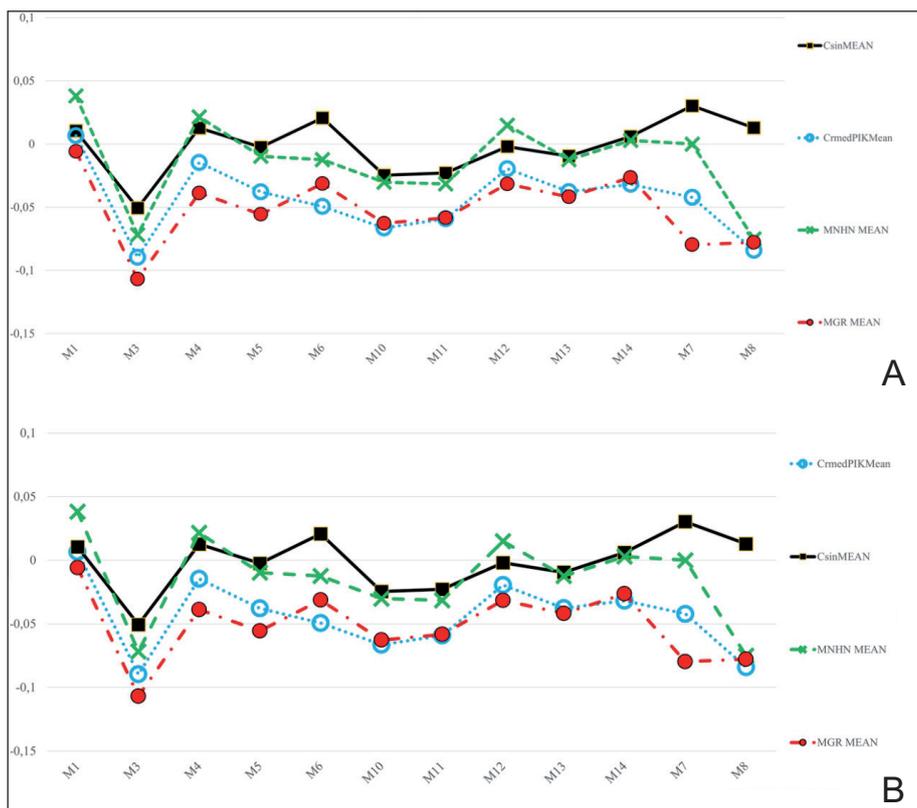
Fig. 4 - A) Depiction of the Log10 ratio analysis of MCIII comparing Sinap *Cormohipparion sinapensis* (Csin MEAN; Bernor et al. 2003), Pikermi *Cremohipparion mediterraneum* (CmedPIK MEAN; Koufos 1987a, b; Bernor et al. 2003), Maragheh *Cremohipparion* cf. *moldavicum* (MNHN MEAN; Bernor et al. 2016) and Cioburciu *Cremohipparion moldavicum* (MGR Mean) to the Hoewenegg *Hippotherium* mean Log10 standard (Bernor et al. 1997). B) Moldova, Maragheh and Pikermi *Cremohipparion* MTIII Compared to Sinap *Cormohipparion sinapensis* Log 10 Ratio, Ho Std.

are complexly plicated; linking of P2 pre- and postfossettes occurs on Odessa 3078-2 and 3801 (a primitive feature; Bernor et al. 2017).

Eisenmann (https://vera-eisenmann.com/chobruchi-data-and-photos) has figure 7 mandibular cheek tooth series (Odessa 3077, 3078-2, 3078-3, 3078-4, 3078-5, no number and 2078) (Supplementary material - Fig. 3). The most salient features of these cheek teeth are that metaconid and metastylid are mostly rounded, pli caballinids and protostylids are lacking and, primitively, ectoflexid of p2 and p4 can sometimes extend in between metaconid and metastylid (also a primitive feature; Bernor et al. 2017).

Figure 4A is a Log10 ratio analysis of MCIII comparing Sinap *Cormohipparion sinapensis* (Csin MEAN; Bernor et al. 2003), Pikermi *Cremohipparion mediterraneum* (CmedPIK MEAN; Koufos 1987a, b; Bernor et al. 2003), Maragheh *Cremohipparion* cf. *moldavicum* (MNHN MEAN; Bernor et al. 2016) and Cioburciu *Cremohipparion moldavicum* (MGR Mean) to the Hoewenegg *Hippotherium primigenium* mean Log10 standard (Bernor et al. 1997). The results show that the total MCIII sample has strikingly narrow mid-shaft dimensions (M3) contrasting with relatively deeper midshaft depths (M4); Bernor et al. (2003) termed this the "Esme-Acakoy" effect

and heralded this as an adaptation to open country running. Of the entire sample, the Maragheh form, ca. 8 Ma (Bernor et al. 2016), has a markedly longer maximum length (M1). All MCIIIs illustrated in Fig. 4a have similar Log10 trajectories and in most dimensions are more slightly built than the Hoewenegg population of *Hippotherium primigenium.*

Figure 4B shows very much the same results as Fig. 4A. Maragheh maximum length (M1) is greater than the rest of the sample. *Cormohipparion sinapensis* again exhibits the "Esme Acakoy" effect whereby midshaft width (M3) is much more slender than the Hoewenegg standard but midshaft depth (M4) is about the same. The contrast in M3 and M4 measurements is further accentuated in Maragheh, Pikermi and the Cioburciu hipparions and the latter two, Pikermi and Cioburciu are virtually identical.

Remarks

The genus *Cremohipparion* was originally recognized at the subgenus rank (*Hipparion* (*Cremohipparion*) by Qiu et al. (1987) for the Chinese species *Hipparion* (*Cremohipparion*) *forstenae* and *licenti*. Bernor and Tobien (1989) recognized *Cremohipparion* as being a distinct lineage warranting its generic rank for the small Samos Hipparion *C. nikosi*. Bernor et al. (1996; 2021) later recognized a number of species

Tab. 1 - Microwear and mesowear results for fossil horses. Abbreviations: P = average number of pits; S = average number of scratches; SWS = average scratch width score; LP, average number of large pits; ST = scratch texture; G = presence or absence of gouges; MWS = mesowear score.

Specimen #	P	S	LP	SWS	ST	G	Cusp Shape	Relief	MWS
AICUPM4000	28	20.5	7	1	mixed	absent	blunt	low	6
AICUPM4001	24	21.5	5	2	coarse	present	blunt	low	6
AICUPM4002	19	25.5	5	2	coarse	absent	sharp	high	0
AICUPM4003	20.5	21.5	4.5	2	coarse	absent	round	high	1.5
AICUPM4004	26	16.5	6.5	1	mixed	absent	round	low	1.5
AICUPM4005	30.5	20	10.5	1	mixed	present	-	-	-
AICUPM4006	-	-	-	-	-	-	blunt	low	6.0
AICUPM4007	35.5	21.5	4	2	coarse	present	sharp	high	1.0
AICUPM4008	19.5	21.5	3.5	2	coarse	absent	round	high	2.0
AICUPM4009	25	11	9.5	2	coarse	absent	round	high	1.5
AICUPM4010	30.5	20	10.5	1	mixed	present	round	high	1.0
AICUPM4011	-	-	-	-	-	-	round	high	2.0
AICUPM4012	36	17	13.5	2	coarse	present	round	high	2.0

of *Cremohipparion* and currently these include: *C. mediterraneum, C. proboscideum, C. forstenae, C. licenti, C. moldavicum, C. macedonicum, C. matthewi, C. nikosi, C. periafricanum* and *C. antelopinum*. According to Zouhri and Bensalmia (2005), the Spanish species *"H." concudense* and *"H." gromovae* are also referable to *Cremohipparion*. All *Cremohipparion* taxa are characterized by having a short POB and the more primitive forms have dorsoventrally and medially deep POF that are also subtriangular shaped. *Cremohipparion mediterraneum, C. proboscideum* and *C. licenti* all have an intermediate (= caninus) fossa and Chinese *C. licenti*, the youngest *Cremohipparion* (= 4 Ma, China) had an additional malar fossa and posteriorly deeply pocketed buccinator fossa. *Cremohipparion licenti* has an enhanced development of its facial fossae, accompanied by a strong, deep nasal notch incision to P4, were likely in support of a highly mobile snout for feeding. *Cremohipparion* species never achieved a maximum crown height greater than 55-60 mm.

The Cioburciu sample of *Cremohipparion moldavicum* exhibits primitive characters including: skull, with very large, medially deep and dorsoventral-

ly deep preorbital fossa placed close to the orbit; nasal notch short, incised anterior to P2; cranium lacking caninus fossa; maxillary cheek teeth with P2 having a short anterostyle and rounded protocone, pli caballins varying from single to complex; pre- and postfossettes complexly plicated with opposing borders that occasionally link together; mandibular cheek teeth mostly with rounded metaconids and metastylids; MCIIIs and MTIIIs that are elongate and slender and exhibit sharply contrasting midshaft width (M3) and depth (M4) dimensions. These characters support the hypothesis that *Cremohipparion* was most likely derived from a form like Sinap *Cormohipparion sinapensis,* but without excluding the possibility that *Cremohipparion* was derived from a more primitive member of the *Cormohipparion* clade (sensu Woodburne 2007).

Microwear and Mesowear

Microwear. Raw fossil hipparion microwear is shown in Tab. 1 and summary statistics are summarized in Tab. 2. Figure 5A shows the average scratch and pit results for the fossil hipparion plotted in

Taxon	P	SP	S	SS	LP	F	M	C	SWS	G	SC	RC	BC	H	MWS
Ciuburciu Hippparion	26.8	6.0	19.6	3.8	7.1	0	36.4	63.6	1.6	45.6	16.7	58.3	25.0	66.7	2.5

Tab. 2 - Mesowear and microwear summary statistics for Ciuburciu hipparion. P = average pits, SP = standard deviation of pits, S = average scratches, SS = standard deviation scratches, LP = average number large pits, F = percentage of finely textured scratches, M = percentage of mixed finely and coarsely textured scratches, C = percentage of coarsely textured scratches, SWS = scratch width score, G = percentage of gouges, SC = percentage of teeth with sharp cusp shapes, RC = percentage of teeth with rounded cusp shapes, BC = percentage of teeth with blunt cusp shapes, H = percentage of teeth with high occlusal relief, MWS = average mesowear score.
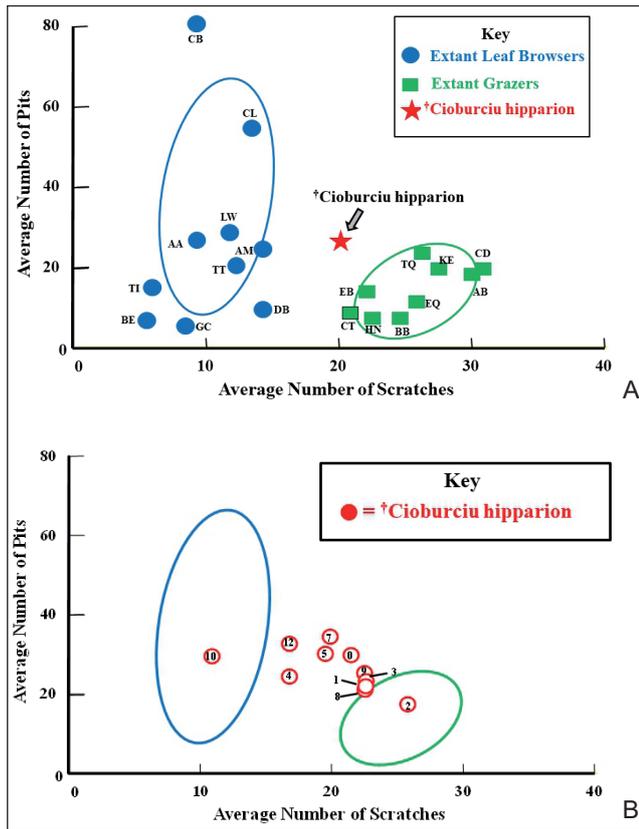
Fig. 5 - Scratch and pit results for the fossil hipparion from the Cioburciu deposits plotted in reference to Gaussian confidence ellipses (*p=0.95*) on the centroid for extant browser (B) and grazer (G) data adjusted by sample size (Semprebon, 2002; Solounias & Semprebon 2002). A) The placement of the Cioburciu hipparion in the gap between the extant browsing and extant grazing ecospace (average scratch and pit data). B) Raw scratch and pit results for the Cioburciu hipparion plotted in reference to Gaussian confidence ellipses (*p=0.95*) on the centroid for extant browser and grazer data adjusted by sample size (Semprebon 2002; Solounias & Semprebon 2002).
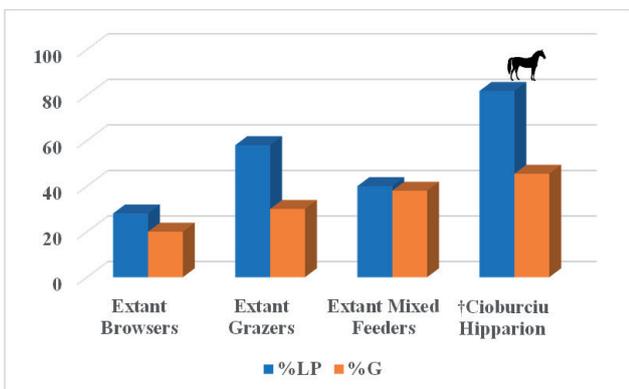

Fig. 6 - Bar graph showing the percentages of finding more than 4 large pits and the percentages of gouges found within the optical reticle imposed on the microscopic field of view for both extant ungulates with different known diets (data from Semprebon 2002) and the Cioburciu fossil hipparion examined in this study.

reference to Gaussian confidence ellipses (*p=0.95*) on the centroid for extant browser (B) and grazer (G) data adjusted by sample size (from Semprebon 2002 and Solounias and Semprebon 2002). Figure 5A shows that the fossil hipparion has an average scratch and pit count that falls in the gap between the extant browsing and extant grazing ecospace. Figure 5B displays raw scratch and pit results for the fossil hipparion plotted in reference to Gaussian confidence ellipses (*p=0.95*) on the centroid for extant browser and grazer data adjusted by sample size (from Semprebon 2002 and Solounias and Semprebon 2002). Figure 5B shows that the fossil hipparion has scratch and pit results that overlaps the browsing and grazing ecospaces but most samples fall in the gap between them.

Figure 6 shows the percentages of finding more than 4 large pits and the percentages of gouges found within the optical reticle imposed on the microscopic field of view for both extant ungulates with different known diets (data from Semprebon 2002) and the fossil hipparion examined in this study. What is clearly shown, is that the fossil hipparion has more large pits and gouging than is typical of the extant ungulates studied via microwear.

Interestingly, Fig. 7A shows that the fossil hipparion has a percentage of low scratches that falls within the extant mixed feeder range even though its scratch width score (Fig. 7B - differences in the range of scratch textures) is more similar to that of extant grazing ungulates (data from Semprebon 2002).

Figure 8 shows the percentages of sharp, round, and blunt cusps as well as the percentages of teeth that showed high and low occlusal relief for the fossil hipparion. It is clear that the fossil hipparion has relatively few sharp cusps (17%) typical of most extant browsers. The majority of cusps are rounded (58%) followed next by some blunt cusps (25%).

Figure 9 shows the results of the hierarchical cluster analysis. The Cioburciu hipparion clusters with a group of extant mixed feeding ungulates (i.e., those that alternate regionally or seasonally between browsing and grazing) and away from a cluster of extant browsers and grazers. This designation matches the scratch/pit results obtained through microwear.

Fig. 7 - A) Box plots of the percentage of scratches per taxon that fall within the low scratch range (i.e., between 0 and 17) for the Cioburciu fossil hipparion compared to results for extant ungulates (extant data from Semprebon 2002). B) Box plots of the scratch width score of the Cioburciu fossil hipparion compared to results for extant ungulates (extant data from Semprebon 2002).
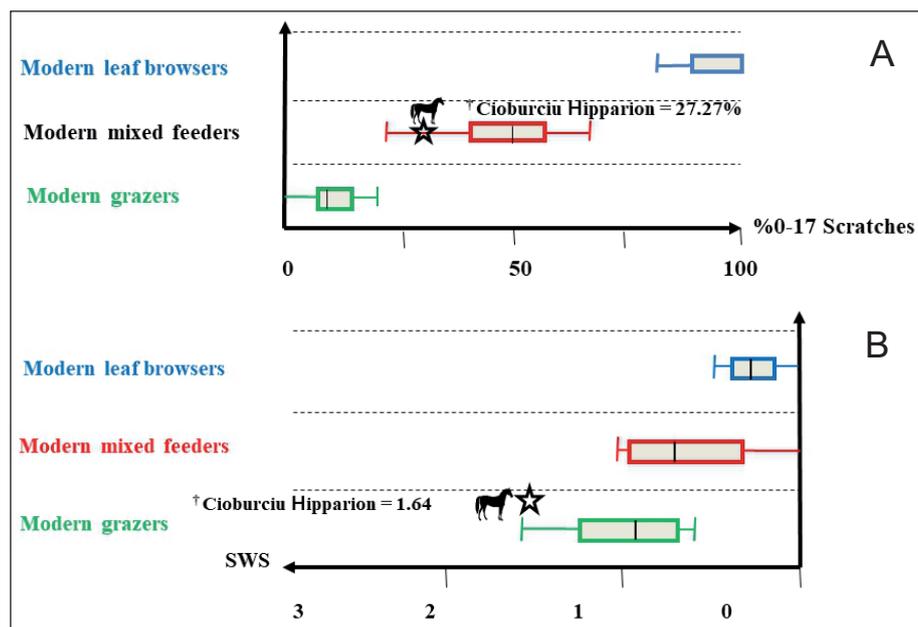
Discussion

Cremohipparion moldavicum first appeared in the Ukraine and Balkans during MN 10 (Gromova 1952; Bernor et al. 1996), while the somewhat smaller species *C. macedonicum* appeared at this time in Greece (Koufos 2016). *Cremohipparion moldavicum* occurred in the Ukraine, Balkans, Romania, Georgia and Iran during MN11 to 13. The dwarf form *Cremohipparion matthewi* overlapped its stratigraphic range with *C. moldavicum* in the Maragheh section (Bernor et al. 2016). *Cremohipparion mediterraneum* and *C. proboscideum* occurred in Greece also in MN12 and 13, *C. antelopinum* in the Siwaliks in MN10-13, *C. forstenae* in China in MN13 and 14, *C. nikosi* in Greece in MN13 and *C. periafricanum* in southern Europe and North Africa in MN13 and 14. *Cremohipparion licenti* is the latest occurring member of the genus and was restricted to China in MN 15 (ca. 4.0 Ma). The genus *Cremohipparion* was one of the chronologically and geographically longest Old World hipparion lineages extending its chronologic range from MN10-MN15 (9.7-4.0 Ma), from Spain to China and the Indian Subcontinent and North Africa (Bernor et al. 2021). Most species were medium sized to very small. *Cremohipparion proboscideum* was the largest member of the clade and distinguished by having very retracted nasals (Bernor et al. 2018).

The evolutionary origins of *Cremohipparion* are a matter for debate. Bernor et al. (1996) suggested that *Cremohipparion* was derived from *Hippotherium primigenium*. Another suggestion is that the Turk-
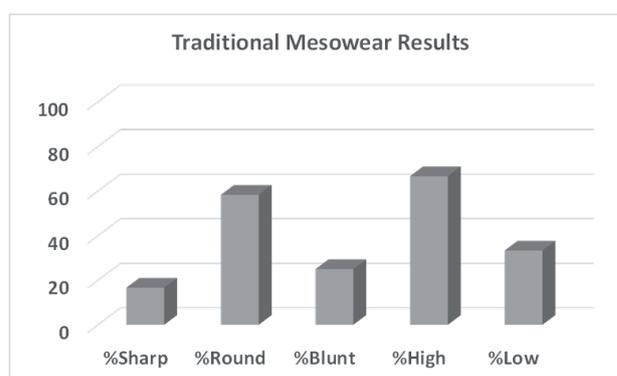

Fig. 8 - Bar chart of the percentages of sharp, round, and blunt cusps as well as the percentages of teeth that showed high and low occlusal relief for the Cioburciu fossil hipparion.

ish early Vallesian species *Cormohipparion sinapensis* could be a likely ancestral stock for *Cremohipparion*. For this to be supported, we would have to accept the hypothesis that the preorbital bar reduced secondarily in length after increasing in length for both *Hippotherium primigenium* and *Cormohipparion sinapensis* which in turn was derived from a member of the *Cormohipparion occidentale* Complex of Woodburne (2007). Another possibility is that the somewhat more primitive North American *Cormohipparion, C. quinni* with a shorter POB and large POF, could be the genetic source for *Cremohipparion. Cremohipparion moldavicum* would appear to be the most primitive member of the *Cremohipparion* clade and the size, great medial depth, distinct peripheral rim and subtriangular shape is shared with *Hippotherium primigenium* and *Hippotherium weihoense* (Sun et al. 2019). *Cre-*
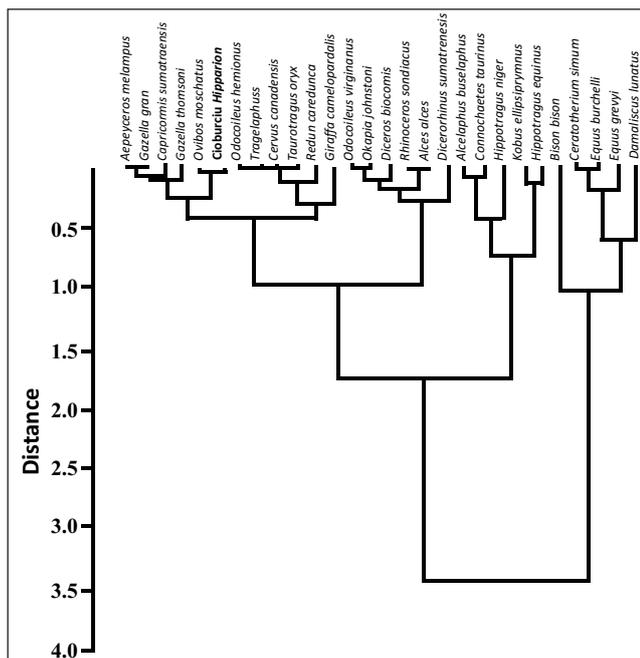
Fig. 9 - Results of a hierarchical cluster analysis of extant ungulate browsers, grazers and mixed feeders and the Cioburciu hipparion. The present analysis depicts the fossil hipparion clusters within a group of extant mixed feeding ungulates.

mohipparion moldavicum has MCIII and MTIII log10 ratio trajectories that are elongate and slender, albeit more elongate than *Cormohipparion sinapensis.* Bernor et al. (2020) noted that both *Cremohipparion* and African *Eurygnathohippus feibeli* has elongate-slender metapodial IIIs which were similar but longer, and potentially derived from, Sinap *Cormohipparion sinapensis.*

There is no current radioisotopic data, or for that matter well corroborated magnetostratigraphic data, that supports the occurrence of *Cremohipparion moldavicum*, or for that matter any member of the *Cremohipparion* clade occurring as early as the *Cormohipparion* Datum in Central Europe at 11.4-11.0 (Bernor et al. 2017), or the first occurrence of *Cormohipparion sinapensis* in Turkey, 10.8 Ma., or *Cormohipparion* sp. in the Potwar Plateau, Pakistan at 10.8 Ma. (Bernor et al. 2021). Nevertheless, *Cremohipparion* has primitive features of the POF, dentition and postcranial morphology that on morphological bases cannot deny the possibility that it represents a primitive morphology of Old World hipparion.

The Cioburciu hipparion is referred herein to *Cremohipparion moldavicum,* a medium sized, primitive hipparion common to Moldova, Ukraine, Turkey, Iran and likely the Democratic Republic of Geor-

gia. *Cremohipparion moldavicum* was likely adapted for cursorial locomotion in Eurasian "Pikermian" open county woodlands (Eronen et al. 2009; Kaya et al. 2018). Our results show that both dietary proxies employed here (i.e., microwear and mesowear) point to a mixed feeding dietary behavior in the fossil hipparion studied. As shown in Fig. 5A, average scratch and pit results place the fossil hipparion clearly in the gap between extant browsers and grazers and individual raw scratch/pit results cluster mainly in the gap between extant browsers and grazers but also overlap both browsing and grazing ecospaces (Fig. 5B). These results indicate that the fossil hipparion from Cioburciu most likely alternated between browsing and grazing regionally or seasonally. Figures 5A and 7 corroborate this conclusion by showing that the fossil hipparion has a percentage of low scratches that falls within the extant mixed feeder range and clusters on a hierarchical cluster analysis with extant mixed feeders. However, microwear also revealed that the fossil hipparion from Cioburciu had more large pits and gouges in its dental enamel than is typically seen in the extant ungulates studied by GMS (Semprebon 2002 & Solounias and Semprebon 2002) as well as scratch textures more typical of grazing ungulates than mixed feeders. Since microwear captures only a snapshot of dietary behavior (i.e., short-term) just before death, these results indicate that the fossil hipparion, though typically engaging in a mixed feeding diet, consumed relatively coarser foods (i.e., coarser grasses or browse) and/or grit-laden food just prior to death but most likely not typically (i.e., mesowear results are not coarse enough to indicate a lifetime habit of consuming highly coarse or grit-laden foods).

Conclusions

The Turolian Cioburciu hipparions from the Republic of Moldova were investigated for both their likely paleodietary behavior and systematic position. Regarding systematics and alpha taxonomy, both craniodental and postcranial measurements and observations have allowed us to refer this assemblage as *Cremohipparion moldavicum* Gromova 1952 – a medium-sized, primitive hipparion with an elongated muzzle and well-developed and dorsoventrally extensive preorbital fossa which is sit-

uated close to the orbit. *Cremohipparion moldavicum* has been shown here to be closely related to Pikermi *Cremohipparion mediterraneum* in cranial, dental and postcranial anatomy, and both of these taxa are Turolian age. We concur with previous studies (Bernor et al. 2003, 2017, 2020, 2021; Woodburne 2007) that *Cremohipparion* was most likely derived from a species close to *Cormohipparion sinapensis* from the Vallesian of Sinap, Turkey. Two paleodietary proxies – microwear and mesowear indicate that the Cioburciu hipparions engaged in seasonal or regional mixed feeding and thus alternated between browsing and grazing. Microwear reveals the occasional consumption of relative coarser foods or foods laden with grit. The systematic and paleodiet results are consistent with previous attributions that *Cremohipparion moldavicum* inhabited Western Eurasian Pikermian mixed woodland-grassland biomes (Bernor et al. 2021).

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