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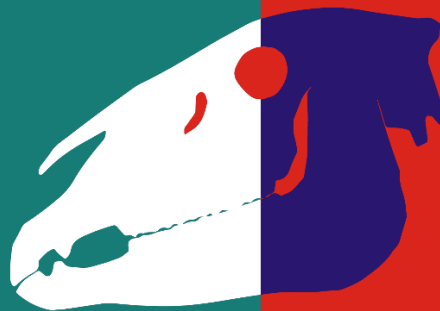


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**STUDY OF THE HIPPARIONINE HORSE CRANIAL MATERIAL  
FROM THE NEW EXCAVATIONS IN PIKERMI (ATTICA,  
GREECE)**

MASTER THESIS

*DIRECTION: Macropalaeontology  
Directed by: Aristotle University of Thessaloniki*



ATHENS  
2022



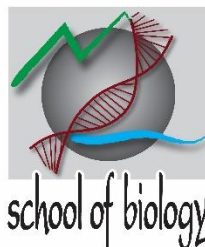


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STUDY OF THE HIPPARIONINE HORSE CRANIAL MATERIAL  
FROM THE NEW EXCAVATIONS IN PIKERMI (ATTICA, GREECE)

ΜΕΛΕΤΗ ΤΟΥ ΚΡΑΝΙΑΚΟΥ ΥΛΙΚΟΥ ΙΠΠΑΡΙΩΝ ΑΠΟ ΤΙΣ ΝΕΕΣ ΑΝΑΣΚΑΦΕΣ  
ΣΤΟ ΠΙΚΕΡΜΙ (ΑΤΤΙΚΗ, ΕΛΛΑΔΑ)

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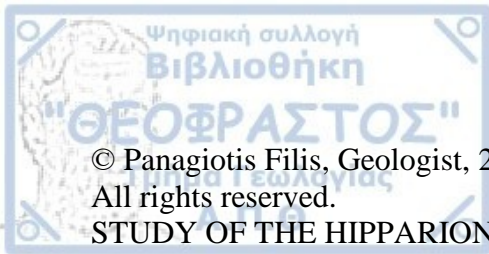
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STUDY OF THE HIPPARIONINE HORSE CRANIAL MATERIAL FROM THE NEW  
EXCAVATIONS IN PIKERMI (ATTICA, GREECE) – *Master Thesis*

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Με επιφύλαξη παντός δικαιώματος.

ΜΕΛΕΤΗ ΤΟΥ ΚΡΑΝΙΑΚΟΥ ΥΛΙΚΟΥ ΙΠΠΑΡΙΩΝ ΑΠΟ ΤΙΣ ΝΕΕΣ ΑΝΑΣΚΑΦΕΣ  
ΣΤΟ ΠΙΚΕΡΜΙ (ΑΤΤΙΚΗ, ΕΛΛΑΔΑ) – *Μεταπτυχιακή Διπλωματική Εργασία*

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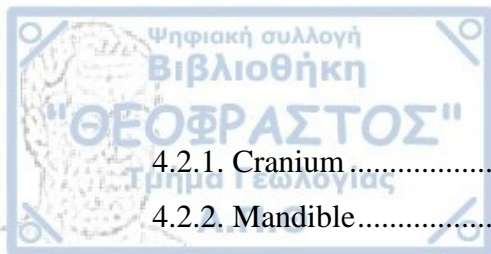
## **To my father (1954-2020)**



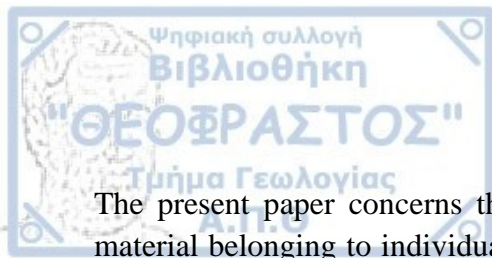
## Table of Contents

<b>ABSTRACT</b> .....	<b>1</b>
<b>ΠΕΡΙΛΗΨΗ</b> .....	<b>2</b>
<b>ACKNOWLEDGEMENTS</b> .....	<b>3</b>
<b>1. INTRODUCTION</b> .....	<b>4</b>
1.1. The Pikermi excavation sites.....	4
1.2. Geology of the Mesogeia basin .....	5
1.3. Old-world hipparionine horses .....	7
1.3.1. Issues with Pikermian hipparionine horse systematics .....	8
1.3.2. The genus <i>Cremohipparion</i> .....	9
1.3.3. The genus (or superspecific group) <i>Hippotherium</i> .....	9
1.4. Abbreviations .....	10
<b>2. MATERIAL AND METHODOLOGY</b> .....	<b>11</b>
2.1. Material .....	11
2.2. Measurements.....	11
2.2.1. Cranium .....	12
2.2.2. Mandible.....	14
2.2.3. Upper dentition .....	15
2.2.4. Lower dentition .....	16
2.2.5. Hypsodonty index.....	17
2.2.6. Protocone index .....	17
<b>3. SYSTEMATICS</b> .....	<b>18</b>
<b>Order Perissodactyla</b> .....	18
<b>Family Equidae</b> .....	18
<b>Genus <i>Hippotherium</i></b> .....	18
<i>Hippotherium brachypus</i> .....	18
<b>Genus <i>Cremohipparion</i></b> .....	21
<i>Cremohipparion mediterraneum</i> .....	21
<b>4. COMPARATIVE ANALYSIS</b> .....	<b>24</b>
4.1. Descriptive characters .....	24
4.2. Metric characters .....	25





4.2.1. Cranium .....	26
4.2.2. Mandible .....	32
4.2.3. Dentition .....	36
4.2.3.1. Upper dentition .....	36
4.2.3.2. Lower dentition .....	48
<b>5. DISCUSSION .....</b>	<b>60</b>
5.1. Potential locality-specific features .....	60
5.2. Inter-site sample comparisons .....	60
5.3. Paleoecological remarks .....	61
5.4. The elusive “third species” .....	62
<b>6. CONCLUSIONS .....</b>	<b>65</b>
<b>LITERATURE .....</b>	<b>67</b>
<b>APPENDIX A: Measurement tables.....</b>	<b>73</b>
<b>APPENDIX B: Plates .....</b>	<b>90</b>
<b>APPENDIX C: List of prepared material for the NKUA/AMPG .....</b>	<b>108</b>



## ABSTRACT

The present paper concerns the study and taxonomical determination of cranio-dental material belonging to individuals of the tribe Hipparionini, from the PV1, PV3 and PV4 excavation sites in Pikermi, Attica. The sites are situated in East Attica, along the bank of the Megalo Rema stream and are the target of annual excavations by the National and Kapodistrian University of Athens since 2008. Pikermi is one of the most important fossiliferous localities in Europe, with the numerous excavations being conducted from the middle of the 19th century until now, unveiling a rich and diverse mammal fauna of Turolian age. Along with bovids, hipparionine horses are the most common representatives of the Pikermian fauna and account for the vast majority of remains found. The typical Pikermian species *C. mediterraneum* and *H. brachypus* account for the hipparionine cranio-dental material found in the newer sites. The studied specimens, composed of crania, mandibles and solitary buccal teeth are described and compared with material from homologous localities. Furthermore, remarks on inter-site and inter-locality relations, as well as comments on the paleoecology of the Pikermian biome are provided. Finally, the possibility of an -as of yet- not fully identified additional hipparionine group, present in the locality, is discussed.

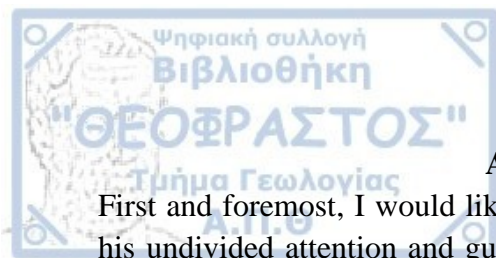
**KEYWORDS:** Hipparionini, Systematics, Paleoecology, Osteometry, Pikermi, Turolian, Cranial, Dental



## ΠΕΡΙΛΗΨΗ

Η παρούσα εργασία αφορά στη μελέτη και τον ταξινομικό προσδιορισμό κρανιο-οδοντικού υλικού απόμων της φυλής Hipparionini από τις θέσεις PV1, PV3 και PV4 του Πικερμίου Αττικής. Η θέσεις απαντώνται στην Ανατολική Αττική, σε εγγύτητα με το Μεγάλο Ρέμα Πικερμίου και αποτελούν -από το 2008 έως σήμερα- χώρο τακτικής διεξαγωγής ανασκαφών, υπό τον έλεγχο του Εθνικού και Καποδιστριακού Πανεπιστημίου Αθηνών. Το Πικέρμι αποτελεί μία εκ των σημαντικότερων απολιθωματοφόρων τοποθεσιών στην Ευρώπη. Ο μεγάλος αριθμός ανασκαφών που πραγματοποιούνται από τον 19ο αιώνα έως σήμερα έχει αποκαλύψει εκτεταμένη πανίδα θηλαστικών Τουρόλιας ηλικίας. Τα ιπάρια (Tribe: Hipparionini), μαζί με τα βοοειδή, συγκαταλέγονται στους πλέον κοινούς και πολυάριθμους εκπροσώπους της Πικερμικής πανίδας. Το κρανιο-οδοντικό υλικό που περιγράφεται στην παρούσα εργασία αντιστοιχεί στα τυπικά Πικερμικά ιπάρια *C. mediterraneum* και *H. brachyrus*. Τα υπό μελέτη ευρήματα, αποτελούμενα από κρανία, κάτω γνάθους και μεμονωμένους οδόντες περιγράφονται εκτενώς και συγκρίνονται με δείγματα από παρεμφερείς θέσεις. Επιπλέον, παρέχονται παρατηρήσεις στους συσχετισμούς μεταξύ ανασκαφικών θέσεων και ευρύτερων εντοπιότητων, όπως και στο γενικότερο παλαιοοικολογικό πλαίσιο. Τέλος, συζητάται η πιθανότητα ύπαρξης μίας επιπλέον ομάδας ιπαρίων στο Πικέρμι, η οποία στερείται ακόμη πλήρους διάγνωσης.

**ΛΕΞΕΙΣ ΚΛΕΙΔΙΑ:** Ιπάρια, Συστηματική, Παλαιοοικολογία, Οστεομετρία, Πικέρμι, Τουρόλιο, Κρανιακό, Οδοντικό



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The excavations in the PV1-4 sites of Pikermi, Attica were conducted under contract between the municipality of Rafina-Pikermi and the National and Kapodistrian University of Athens, titled "Location and rescue-oriented collection of fossilized Upper-Miocene mammals and other fossils from the wider designated area of the Municipality of Rafina - Pikermi" (KA 70/3/12977). The position of scientific supervisor was filled by prof. em. Dr. G. Theodorou and complemented by ass. prof. Dr. S. Roussiakis as assistant scientific supervisor.



## 1. INTRODUCTION

### 1.1. The Pikermi excavation sites

Pikermi has been hailed as one of the most important fossiliferous localities of Europe. The fossil bearing sediments can be found along the bed of the Valanaris stream, which is a tributary of the “Megalo Rema” river. The first fossils to ever be discovered in the locality were found in 1836 by the Scottish historian G. Finlay. Finlay was followed by a series of natural scientists and paleontologists from Greece and abroad, such as A. Linder Mayer in 1843, J. Roth in 1852, H. Mitzopoulos in 1853 and later in 1860 to 1861, A. Gaudry in 1855 to 1856 and in 1860, W. Dames in 1882, M. Neumayer and L. V. Tausch in 1885, A. S. Woodward and Th. Skoufos in 1901, O. Abel in 1912 (Roth & Wagner, 1854; Gaudry, 1862-1867; Dames, 1883; Weithofer, 1888; Woodward, 1901; Abel, 1922). Excavations also took place in the neighbouring site of “Chomateri” by N. Symeonidis, F. Bachmayer and H. Zapfe in the years 1972 to 1980 (Symeonidis *et al.*, 1973; Bachmayer *et al.*, 1982). These series of excavation campaigns led to the amassing of rich paleontological collections by all of the major European museums of natural history. The material collected has served as a reference for the completion of a large number of comparative studies and has been used as the source material for a number of publications that played a major role in shaping early mammal paleontology (e.g., Wagner, 1839, 1840; Roth & Wagner, 1854; Gaudry, 1862-1867).

Since 2008 -almost two centuries after the first excavations by Finlay-, the NKUA has begun a new cycle of fieldwork in the area, with the initiation of annual excavations under the supervision of prof. em. G. Theodorou (Theodorou *et al.*, 2010, 2013). Prospecting and preliminary studies in the area uncovered three new sites, dubbed PV1, PV3 and PV4. PV3 and PV4 (which is mere meters away from PV3) are considered to be coeval and in very close proximity to the classical site (Roussiakis *et al.*, 2014), while PV1 -in which the bulk of the excavation activity has taken place- is situated 500 m to the East of the former and is somewhat younger in age (Böhme *et al.*, 2017). The existence of a PV2 site is briefly mentioned in Roussiakis *et al.* (2014), but no further details are given and no specimens, -apart from a sole bovid maxilla (specimen number PV2/1), exhibited in the EPTP- have been found by the author to correspond to it, in either the NKUA or the EPTP collections. Systematic excavations have taken place in PV1, for durations of up to three months each year. Up until 2020, over 50 students of the NKUA and other institutions have participated and over 2000 specimens have been extracted (Roussiakis *et al.*, 2019).

Study of the collected material reveals a rich and diverse mammal fauna, which includes representatives of most of the major groups of macromammals in the Turolian of Greece. The PV1 site is dated at 7.27 Mya, while PV3 is dated at 7.29 to 7.33 Mya (Böhme *et al.*, 2017). Among the most common representatives of the fauna are hipparionine horses and bovids. The faunal list includes the two equid species studied herein, as well as numerous bovid species, giraffids, suids, rhinocerotids, proboscideans, mustelids, rodents,

felids, hyaenids and primates, complemented by a relatively small number of birds and reptiles (Table 1; Theodorou *et al.*, 2010, 2013; Roussiakis *et al.*, 2014, Filis *et al.*, 2019; Roussiakis *et al.*, 2019). The most recent paleoecological studies place the above fauna in a mixed woodland to open grassland biome, forming a savanna-type ecosystem (Böhme *et al.*, 2017), thus validating the earliest hypothesis put forward by A. Gaudry (1862-67).

**Table 1.** Faunal diversity of the Pikermi locality (Roussiakis *et al.*, 2019).

Reptilia	Mammalia	Bovidae	Carnivora
Chelonia	Primates	<i>Tragoportax amalthea</i>	Felidae
Testudinidae	Cercopithecidae	<i>Miotragocerus gaudryi</i>	<i>Metailurus major</i>
<i>Testudo marmorum</i>	<i>Mesopithecus pentelicus</i>	<i>Palaeoryx pallasi</i>	<i>Metailurus parvulus</i>
<i>Titanochelon</i> sp	Hyracoidae	<i>Protoryx carolinae</i>	<i>Amphimachairodus giganteus</i>
Squamata	Phoiyracidae	<i>Prostrepsiceros rotundicornis</i>	<i>Paramachairodus orientalis</i>
Varanidae	<i>Phoiyrax graecus</i>	<i>Pseudotragus parvidens</i>	<i>Pristifelis attica</i>
<i>Varanus marathonensis</i>	Perissodactyla	<i>Palaeoreas lindermayeri</i>	Hyaenidae
	Equidae	<i>Protragelaphus skouzei</i>	<i>Acerocuta eximia</i>
	<i>Creomhipparion mediterraneum</i>	<i>Oioceros rothi</i>	<i>Hyaenictis graeca</i>
	<i>Hippotherium brachypus</i>	<i>Gazella capricornis</i>	<i>Lycæna chaeritis</i>
<b>Aves</b>	Rhinocerotidae	Suidae	<i>Ichitherium viverrinum</i>
Struthioniformes	<i>Dihoplus pikermiensis</i>	<i>Microstonyx major</i>	<i>Hyaenictitherium wongii</i>
<i>Struthio karatheodoris</i>	<i>Diceros neumayri</i>	Proboscidea	<i>Plioviverrops orbigny</i>
Falconiformes	<i>Acerorhinus neleus</i>	<i>Deinotherium proavum</i>	Ursidae
<i>Gyps</i> sp.	Chalicotheriidae	<i>Choerolophodon pentelici</i>	<i>Indarctos atticus</i>
Gruiformes	<i>Ancylotherium pentelicum</i>	<i>Konobelodon atticus</i>	Mustelidae
<i>Grus pentelici</i>	<i>Chalicotherium goldfussi</i>	<i>Mammut</i> sp.	<i>Enhydriodon (?) latipes</i>
Ciconiiformes	Artiodactyla	Rodentia	<i>Promeles palaeatticus</i>
<i>Ciconia gaudryi</i>	Giraffidae	Muridae	<i>Martes woodwardi</i>
Galliformes	<i>Bohlinia attica</i>	<i>Parapodemus gaudryi</i>	<i>Promephitis larteti</i>
<i>Pavo archiaci</i>	<i>Ielladotherium duvernoyi</i>	Hystriidae	<i>Sinictis (?) pentelici</i>
Phoenicopteriformes	<i>Palaeotragus rouenii</i>	<i>Hystrix primigenia</i>	Ailuridae
<i>Phoenicopterus</i> sp.	Cervidae	Insectivora	<i>Simocyon primigenius</i>
	<i>Phiocervus pentelici</i>	Erinacidae	
	<i>Lucentia</i> sp.	<i>Schizogalerix moedling</i>	

## 1.2. Geology of the Mesogeia basin

The excavation sites of Pikermi are located in the Mesogeia basin, which is surrounded by the mountains Penteli and Hymettus in the North and West respectively, the hills of Koropi and Markopoulo in the South and the Euboic bay in the East. The hydrographic network of the basin is composed of mostly seasonal streams, that originate from Penteli and Hymettus, with a N-S orientation in higher altitudes and an Easternly one in lower elevations. These streams converge into the Megalo Rema river, which flows out into the Euboic bay. One of the larger streams is Valanaris, on the banks and bed of which the fossiliferous sites of Pikermi can be found (Roussiakis, 1996).

The upper-Miocene sediments of the Megogeia Basin can be divided into the terrestrial and fluvial Pikermi formation and the palustrine to lacustrine Rafina formation (Fig. 1). The up to 30 m thick Pikermi formation is mainly composed of reddish silts, which are penetrated by conglomerate channels and contains the terrestrial fossiliferous sites discussed. This formation is laid discordantly above a lower carbonate formation, composed of palustrine to lacustrine marls and lignites. The Rafina formation, which contains clays, lignites and platy limestones lays concordantly above the Pikermi formation (Böhme *et al.*, 2017).

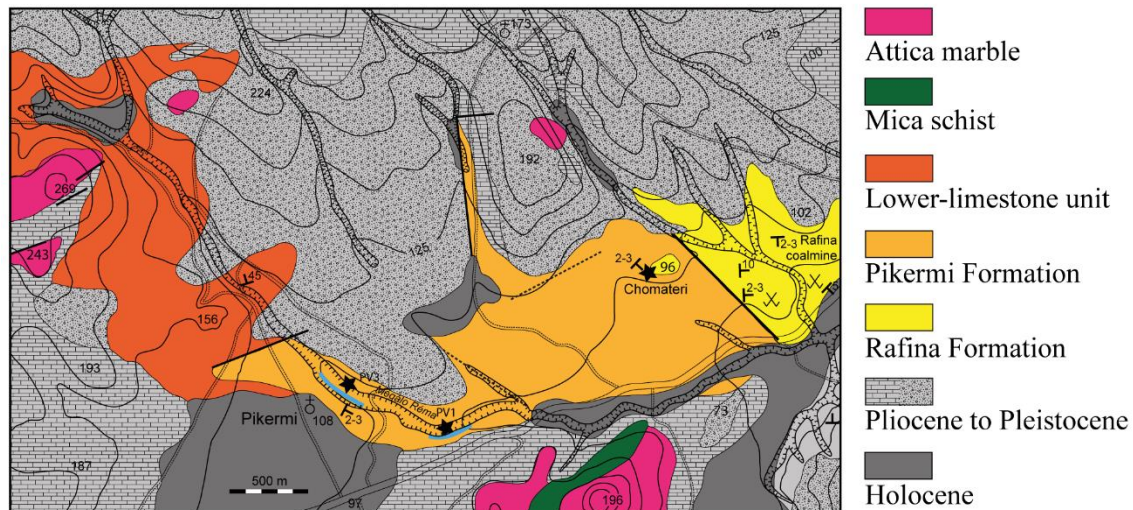
The Pikermi formation itself can be divided firstly into a lower “Red Conglomeratic Member” (Böhme *et al.*, 2017), characterized by reddish silts with a weak pedogenetic footprint and debris flows and secondly into an upper “Chomateri member” which is

composed of fluvio-alluvial sediments. The existence of a pronounced relief in the area can be inferred by the existence of conglomeratic material originating from mt. Penteli inside the debris flows. Both PV1 and PV3 fossil accumulations can be found within this lower silt member (Fig. 1; Theodorou *et al.*, 2010; Böhme *et al.*, 2017).

The upper “Chomateri member” is composed of alternating beds of reddish to yellow silts, with intertwined fluvial channels and channel-fill deposits. The “Chomateri” fossil site is found inside a carbonate paleosol, contained within the member (Symeonidis *et al.*, 1973). The uppermost Rafina formation can be divided into a lower lacustrine and an upper palustrine member (Böhme *et al.*, 2017).

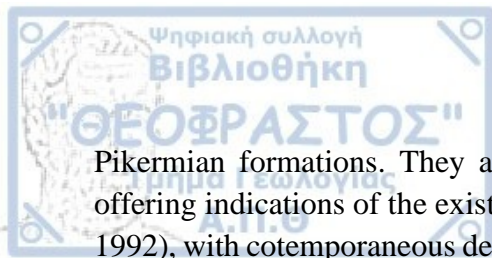
The two Miocene-dated formations lay discordantly -as it has already been stated- upon a system of lacustrine marls and lignites of Neogene age. This system is laid, in turn upon the crystalline Alpine bedrock, which is composed of marbles and mica schists (Fig. 1). This formation regularly emerges through the Neogene-Quaternary beds and appears as individual stratigraphic “islands” within it (Roussiakis, 1996).

Above the two previously mentioned formations lies a concordant series of lacustrine beds of platy limestones, marls and conglomerates, where accumulations of *Melanopsis cf. anceps*, *Melanopsis cf. costata* and *Planorbis sp.* can be found. The Neogene beds are overlaid by a thick series of Quaternary conglomerates and sandy clays (Marinos & Symeonidis, 1973).



**Figure 1.** Geological map of the Mesogeia basin, with excavation sites denoted by black stars (Böhme *et al.*, 2017).

To the East lie the marine deposits of Rafina, which are of early-Pliocene age according to Mitsopoulos (1949), or early-middle Pliocene according to Constandinides *et al.* (1992) and carry within them a rich assemblage of marine fossils. These sediments shift laterally into fluvial-terrestrial deposits, which lay discordantly upon the upper-Miocene



Pikermian formations. They are found on an elevation of 40 m above sea level, thus offering indications of the existence of a slightly more recessed ancient shoreline (Mettos, 1992), with cotemporaneous deposition of marine sediments on the edge of it and terrestrial depositions on the inner part.

The deposit gradients are generally gentle in the central parts of the basin and reach inclinations of 35°-40° in the vicinity of Rafina. The Pikermi deposits in particular display a dip direction towards the S-SE (Mposkos *et al.*, 2007). The upper Miocene deposits are affected by two fault systems with W-NW and N-NE orientations (Roussiakis, 1996).

The combination of the fault system's dip extent, the overlaid deposits and the observed discordant contact of the Pikermi formation with the "Lower Limestone Unit" make it hard to gauge the former's true thickness. Mposkos *et al.* (2007) report a thickness of up to 15 m, while Böhme *et al.* (2017) raise it to 30 m.

Despite the lack of information regarding the exact geometry of the formation, a useful inference from the known geology of the basin is that one can follow lines of roughly W-SW to E-NE orientation, passing over the three progressively younger sites of PV3, PV1 and Chomateri to find coeval sediments. This being said, the observable stratigraphy may allow for potentially younger fossiliferous sediments to be found to the SE, while older ones could only be surveyed for in the thin strip of Pikermian sediments up the small valley, North of the main formation (Fig. 1). In any case PV3 seems to be close to, or at the local basement of the formation.

### 1.3. Old-world hipparionine horses

The tribe Hipparionini of the subfamily Equinae is composed of tridactyl horse species belonging to the genus *Hipparion* and various similar forms. Hipparionine horses originate from the middle Miocene of North America. They are considered to be among the descendants of the group known as Merrychippines (Alberdi, 1989), which are recognized as the first grazing horses.

A migratory wave from the Bering Strait -taking place during the Late Miocene-lead to the outspread of *Hipparion s.l.* in Eurasia and Africa up until the early Pleistocene (Athanassiou, 2018; Koufos *et al.*, 2021). The systematic collection and study of hipparionine remains, from South Asia to the extreme West of Europe, documents their very rapid (almost instantaneous, in geologic terms) spread and diversification (MacFadden, 1992, Bernor & Hussain, 1985, Agusti *et al.*, 1997). This event (thought to have taken place between 11.9 to 11.2 Mya) marks the beginning of the Vallesian period and is known as the "*Hipparion Datum*" (Koufos *et al.*, 2021).

The particulars of this migration event remain unclear, with researchers such as MacFadden & Skinner (1977) claiming the reported *Hipparion (s.l.)* to be an amalgam of two separate genera, tied to equally separate migration events within the Late Miocene. MacFadden (1980) recognized a *Hipparion s.s.* genus in Europe, which corresponds to N. American species such as *Hipparion tehonense* and *H. forcei*. This position was supported



by Woodburne (1989), who assigned the first migratory wave to *Cormohipparion* and the second one to *Hipparion* (s.s.). Zhegallo (1978) added a third event in the Later Miocene, which carried the genus *Neohipparion* into Asia (Zhegallo, 1978; Forstén, 1984; Qiu *et al.*, 1987). Eisenmann and Sondaar (1998) disagreed with the latter, instead attributing the similarities of certain Asian hipparionine species to the N. American *Neohipparion*, to parallel evolution.

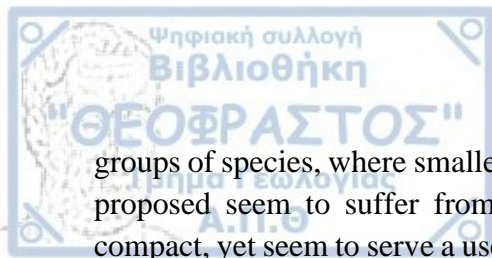
Greece is home to a large number of mammal localities from the late Miocene. These almost exclusively correlate with either the Vallesian (MN9-MN10) and Turolian (MN11-MN12) periods. Hipparionine remains are overly abundant in these localities, usually constituting more than 50% of the material collected. Their abundance has led to them being used as useful proxies for the extraction of biostratigraphical, paleoecological, and paleobiogeographical conclusions. Among the Greek localities, Pikermi stands out as being the one to offer the first-ever described specimens of hipparionine horses (Wagner, 1840; Gaudry, 1862-1867) for the country and also for the large number of specimens extracted, both from the classical sites, as well as the active newer ones (Roussiakis *et al.*, 2019; Koufos *et al.*, 2021).

### 1.3.1. Issues with Pikermian hipparionine horse systematics

The question of whether Pikermian hipparionines can be ascribed to a single *Hipparion* genus, or divided into the *Cremohipparion* and *Hippotherium* lineages is the subject of an ongoing discussion amongst mammal paleontologists. The resolution of this debate is beyond the scope of this thesis and the specific names of *C. mediterraneum* and *H. brachypus* are used in a provisional -albeit informed- manner.

The rationale for this choice over *Hipparion* stems from the fact that, at least *Cremohipparion* -if not both of the groups mentioned (see 1.3.2. The genus *Hippotherium*)- fall well within the rank of genus, when defined simply as a monophyletic grouping of species, nested with certainty within a previously determined categorical rank greater than itself (Giribet *et al.*, 2016). The implied monophyly of these groups has been investigated by various authors (Bernor *et al.*, 1988; 1996; 1999; Bernor & Lipscomb, 1995; Bernor & Franzen, 1997; Zouhri & Belsanmia, 2005; Hristova, 2012) and the apparent shared paleoecological, biogeographical and morphological traits between members of each group can only serve to reinforce this idea.

Furthermore -if the issue of monophyly is acknowledged as in need of further investigation and set aside-, there really is no other obstacle in accepting the validity of these generic designations. A detrimental trend in hipparionine horse systematics (or the systematics of any group of living organisms for that matter) would be the tendency of either classifying numerous small to monotypic genera with no functional taxonomic purpose (although certain authors -e.g. Sigwart *et al.*, 2017- argue that extensive monotypicity on the genus level is no artifact but a direct consequence of taxonomies reflecting real evolutionary processes) or, conversely, creating needlessly expansive



groups of species, where smaller-scale phylogenetic associations might be lost. The groups proposed seem to suffer from none of the above shortcomings. They are sufficiently compact, yet seem to serve a useful classification purpose without requiring any significant restructuring of hipparionine systematics.

### **1.3.2. The genus *Cremohipparion***

Members of the *Cremohipparion* group are characterized by their short preorbital bar and the position of the anterior part of the lacrimal bone within the border of the preorbital fossa (Bernor & Tobien, 1989). The temporal range of the genus spans the late Vallesian to the middle Pliocene of Eurasia. Species ascribed to the genus include *C. moldavicum*, *C. mediterraneum*, *C. proboscideum*, *C. matthewi*, *C. nikosi*, *C. periafricanum*, *C. forstenae* and *C. licenti* (Bernor *et al.*, 1999).

While the shortening of the preorbital bar is a common trait of all *Cremohipparion* members, two separate evolutionary radiations can be traced within the genus. The first of the two includes those species which attain increasingly retracted nasals and enlarged preorbital fossa, while the second is characterized by little -if any- retraction of the nasals, decreasing size, loss of the preorbital fossa and extreme elongation of the metapodials (Bernor *et al.*, 1999). Of the two, the former group is of the most interest within the context of this thesis, since the species *C. mediterraneum* is the sole member of the *Cremohipparion* group that can be found in the studied locality.

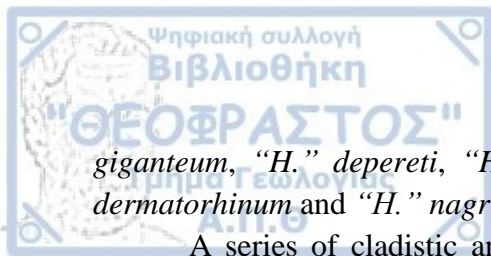
Members of the first subgroup are further characterized by dietary adaptations towards foraging and browsing. The crown height of the buccal teeth never exceeds 50 mm. Furthermore, the enlarged preorbital fossa and in some cases additional facial fossae serve as anchor points for muscles controlling an enlarged upper lip or even a small proboscis (Bernor *et al.*, 1999).

At least one member of these larger sized *Cremohipparion* species (Bernor *et al.*, 1989; Bernor & Armour-Chelu, 1999; Hayek *et al.*, 1991), as well as all members of the second, smaller-sized subgroup (Bernor & Armour-Chelu, 1999) are found to have developed adaptations to grazing, but the particulars of these adaptations are irrelevant to the subject of this thesis.

In general, members of the *Cremohipparion* group can be described as medium to small sized hipparionine horses with mainly browser-oriented dietary habits (though obligate grazers are also found within the group), sharing the common traits of a short to very short preorbital bar, shortened muzzle and relatively low-crowned teeth.

### **1.3.3. The genus (or superspecific group) *Hippotherium***

Members of the *Hippotherium* group are characterized by their relatively large size, well developed preorbital fossa and robust metapodials (Bernor *et al.*, 1999). The temporal range of the group spans the Vallesian to the Turolian of Eurasia and Africa. Species ascribed to the group include *H. primigenium*, "*H.*" *catalaunicum*, "*H.*" *brachypus*, "*H.*"



*giganteum*, “*H.*” *depereti*, “*H.*” *citifense*, “*H.*” *koengswaldi*, “*H.*” *weihoense*, “*H.*” *dermatorhinum* and “*H.*” *nagriensis* (Bernor *et al.*, 1996; 1999).

A series of cladistic analyses (Bernor *et al.*, 1988; Bernor & Lipscomb, 1995; Bernor & Franzen, 1997) have provided evidence for five stages of evolution in the *H. primigenium* of Central Europe and led to the inclusion of species such as “*H.*” *catalaunicum*, “*H.*” *brachypus* and “*H.*” *giganteum* to the group.

*Hippotherium primigenium* is close or equal in size to a Burchell's zebra and while it is considered more robust than members of the *Cremohipparion* group, it is still gracile in its build and is adapted for leaping and springing rather than sustained running. Members of the *Hippotherium* group are found in sub-tropical to warm-temperate woodland environments. While they aren't considered to have been obligate browsers, they are thought to have incorporated a large percentage of browse in their diet (Bernor *et al.*, 1999).

It should be noted that the *Hippotherium* designation is the more tentative of the two used in the present thesis, as its exact phylogeny and affinities remain unresolved by admission of the authors who have reinstated it as a generic name in recent literature (Bernor *et al.*, 1996; 1999). While some workers argue for the use of the name in the context of “subgenus” within *Hipparion* (Qiu *et al.*, 1987) and others reject its validity altogether (Koufos, 1987; Koufos & Vlachou, 2005; Vlachou & Koufos, 2009), the author of the present work chooses to utilize Hristova's (2009) naming scheme of *Hippotherium brachypus* without quotation marks in the generic name.

#### 1.4. Abbreviations

- Institution names:

AMPG – Museum of Paleontology and Geology of the National and Kapodistrian University of Athens.

EPTP – Exhibition of Paleontological Treasures of Pikermi.

MNHN – Muséum national d'Histoire naturelle, Paris

NHML – Natural History Museum of London

NHMW – Museum of Natural History of Vienna.

NKUA – National and Kapodistrian University of Athens.

PMA – Paleontology Museum of Assenovgrad.

RCC – Rafina Cultural Center.

UNIVIE – University of Vienna.

- Anatomical nomenclature:

m1-m3 – 1<sup>st</sup> to 3<sup>rd</sup> lower molar

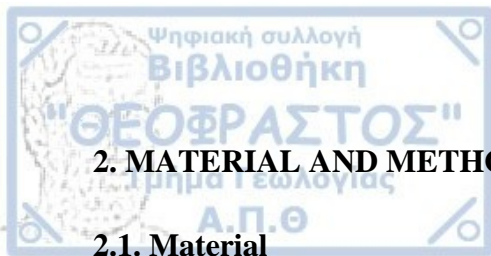
M1-M3 – 1<sup>st</sup> to 3<sup>rd</sup> upper molar

p1-p4 – 1<sup>st</sup> to 4<sup>th</sup> lower premolar

P1-P4 – 1<sup>st</sup> to 4<sup>th</sup> upper premolar

POB – Preorbital bar

POF – Preorbital fossa



## 2. MATERIAL AND METHODOLOGY

### 2.1. Material

Specimens from the PV1 site numbered PV1/200, PV1/204, PV1/219, PV1/221, PV1/232, PV1/233, PV1/276, as well as PV1/672 to PV1/1230 and PV1/1790 to PV1/2634 belong to the collection of -and are currently stored in- the EPTP, in Pikermi, Attica. Material on display at the RCC is part of the EPTP collection, so no distinction is made throughout the text, except in Appendix A. The rest of the PV1 material (PV1/18 to PV1/650 -barring the individual specimens mentioned above- and PV1/1282 to PV1/1298), along with all the specimens from PV3 (PV3/12 to PV3/2048) and PV4 (PV4/7 to PV4/9) are part of the collection of the AMPG. It should be noted that the ranges provided do not necessarily contain full series of consecutive numbers, but merely non-overlapping groups of specimens numbered between and containing the minimum and maximum of the values given. An expansive list of the material can be found in Appendix A and photographs of selected specimens in Appendix B.

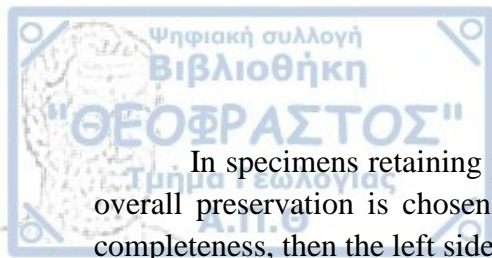
The criteria for selecting suitable material for the present work include it belonging to the cranial skeleton (crania, mandibles and isolated teeth and tooth rows) of both adult and juvenile individuals and being complete and well-preserved enough to retain identifying morphological features. In particular, due to the remarkable similarity between the 2<sup>nd</sup> premolars to the 2<sup>nd</sup> molars of both the maxilla and the mandible, identification of individual teeth falling into to the above range and not associated to any other cranial remains, was deemed too unreliable and such material was excluded from the present work.

All specimens, apart from the series PV1/18-PV1-650, were prepared and documented with the collaborative effort of the author with fellow geologists and preparators S. Sklavounou and S. Kirdis. A list of the complete material prepared in the AMPG (including other taxa, identified by Sklavounou, in prep.), can be found in Appendix C. This appendix was prepared for the sake of preservation, since no unified database exists for the documentation of the museum's material, as of yet.

Material from Samos -Greece and Maragheh -Iran (Bernor *et al.*, 1980, 1985; Woodburne & Bernor, 1980; Bernor & Hussain, 1985; Watabe & Nakaya, 1991; Forstén, 1999) used for comparisons, belongs to the collections of the NHMW and UNIVIE and was remeasured and evaluated by the author, while material from Hadjidimovo -Bulgaria (Hristova, 2003, 2009; Hristova *et al.*, 2003) is part of the collection of the PMA and measurements were kindly provided by L. Hristova.

### 2.2. Measurements

All measurements are given in mm and are rounded-off to the first decimal place. A 150 mm digital caliper with a resolution of 0.01 mm was used for most of the measurements, apart from the few that surpassed the calipers maximum extension and required the use of a 300 mm analog caliper with a resolution of 0.1 mm.

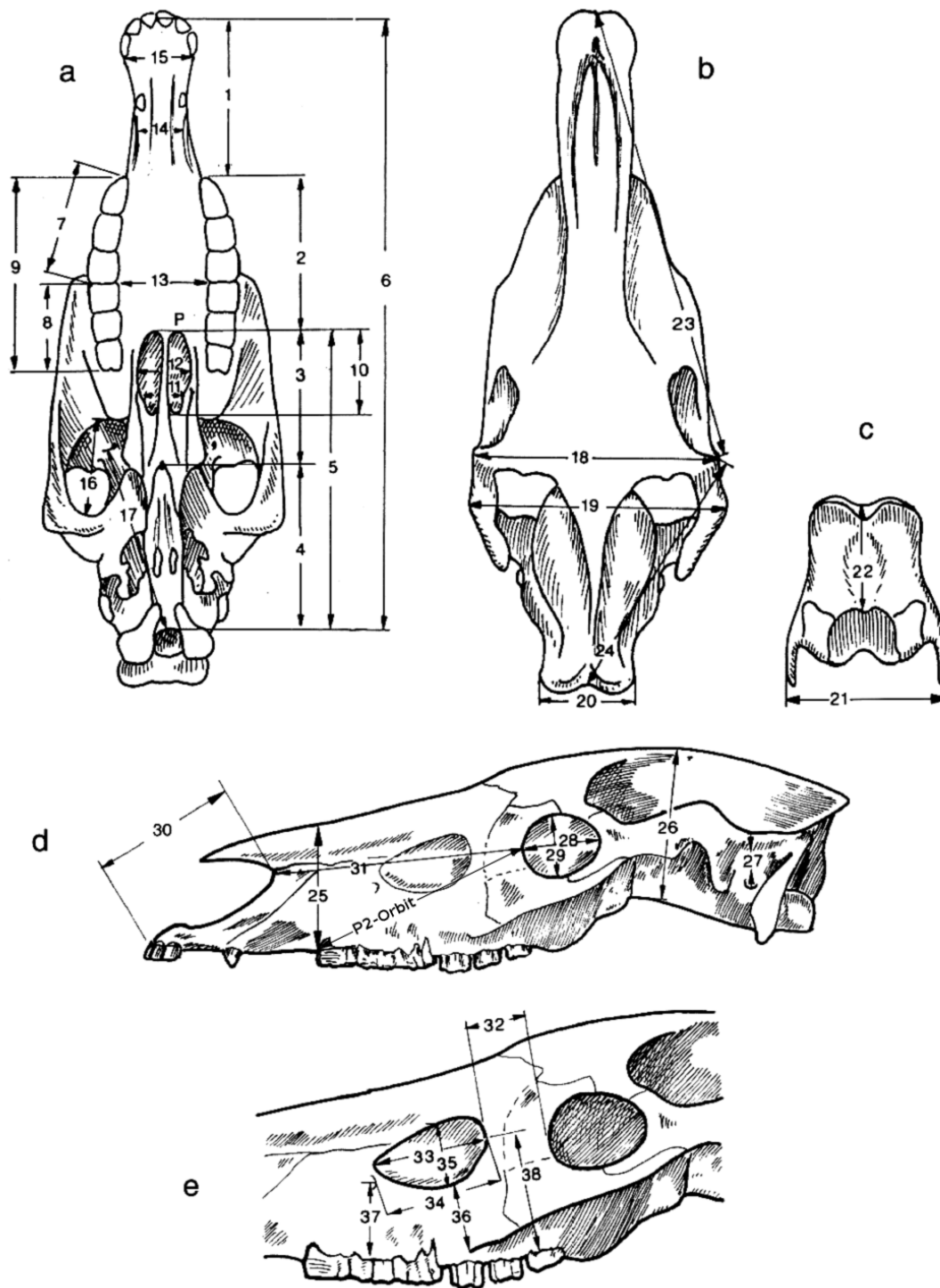


In specimens retaining pairs of conjugal features, the side which exhibits the best overall preservation is chosen. If both sides are in a similar state of preservation and completeness, then the left side is chosen.

### 2.2.1. Cranium

The measurements used for craniometry on the studied specimens are based upon the -by now- rather standardized template (Fig. 2) offered by Eisenmann *et al.* (1988) and utilized prominently by Bernor *et al.* (1997). To these measurements, the additional measure of the linear distance between the front edge of the orbit and the anterior-most part of the alveolar level of the P2 (Forstén, 1999; Watabe, 2011) is included. The measurements are as follows:

1. Length from the prosthion to the middle of the line connecting the anterior borders of the P2.
2. Minimal length between the middle of the line connecting the anterior borders of the P2 and the line denoted as “P”, which is situated at the base of the palatal spur.
3. Length from “P” to the middle of the vomerine notch.
4. Length from the middle of the vomerine notch to the basion.
5. Length from “P” to the basion.
6. Length from prosthion to basion.
7. Length of the premolar series (dP1 excluded if present), alveolar and on the vestibular side.
8. Length of the molar series (dP1 excluded if present), alveolar and on the vestibular side.
9. Buccal teeth series overall length (dP1 excluded if present), alveolar.
10. Approximative length from “P” to the point where the guttural and caudal parts of the vomer meet.
11. Minimal breadth of the choanae.
12. Maximal breadth of the choanae.
13. Palatal breadth at the level of P4-M1.
14. Minimal muzzle breadth at the level of the premaxillary ridges.
15. Muzzle breadth between the posterior borders of the I3.
16. Maximal length of the fossa temporalis.
17. Length between the basion and the foramen ethmoidalis.
18. Maximal breadth between the orbital processes.
19. Maximal breadth between the outer-most points of the zygomatic arches.
20. Maximal breadth of the supra-occipital crest.
21. Maximal breadth at the base of the paroccipital process.
22. Height from the middle of the dorsal border of the foramen magnum to the middle of the supra-occipital crest.
23. Length from prosthion to the exterior-most point of the orbital process.

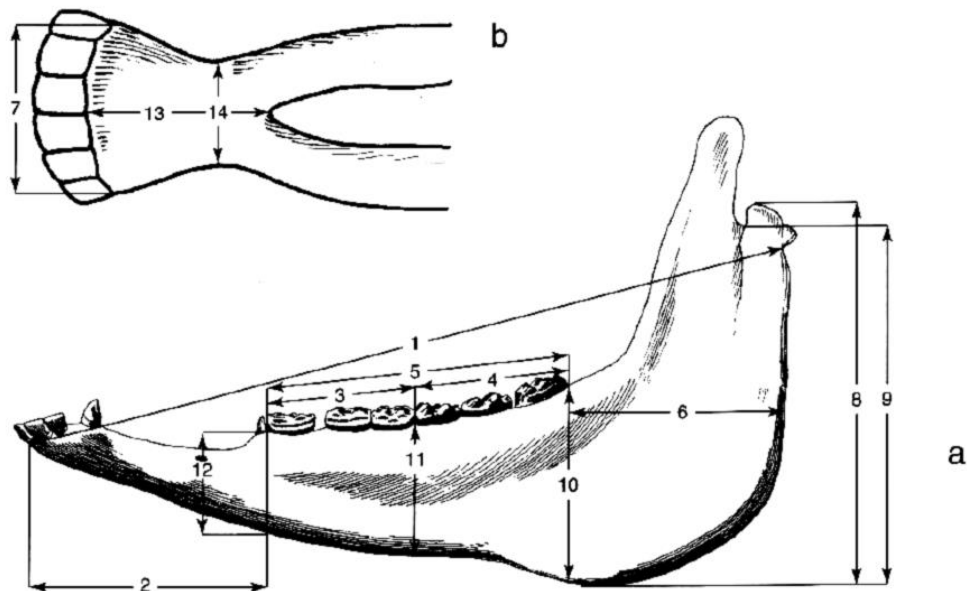


**Figure 2.** Cranial measurements (modified from Bernor *et al.*, 1997). a) Inferior aspect. b) Superior aspect. c) Posterior aspect. d) Lateral aspect. e) Detail of the lateral aspect.

24. Length from the outer-most point of the orbital process to the middle of the supra-occipital crest.
25. Facial height at the point at the level of P2.
26. Cranial height at the level of the posterior margin of the orbital process.
27. Height of the meatus auditivus externus.
28. Antero-posterior diameter of the orbit.
29. Dorso-ventral diameter of the orbit (perpendicular to the above).
30. Length from prosthion to the back of the narial opening.
31. Length from the back of the narial opening to the anterior-most point of the orbit.
32. Length between the orbit and the preorbital fossa.
- P2-Orbit. Length between the front edge of the Orbit and the anterior-most part of the alveolar level of the P2.
33. Maximal length of the preorbital fossa.
34. Length between the back of the preorbital fossa and the foramen infra-orbitale.
35. Height of the preorbital fossa (perpendicular to 33).
36. Length between the preorbital fossa and facial crest.
37. Height of the back of the foramen-infraorbitale above the alveolar border.
38. Height of the back of the preorbital fossa above the alveolar border.

### 2.2.2. Mandible

The measurements used on the mandibles studied are also based upon the Eisenmann template (Fig. 3; Eisenmann *et al.*, 1988; Bernor *et al.*, 1997). They are as follows:

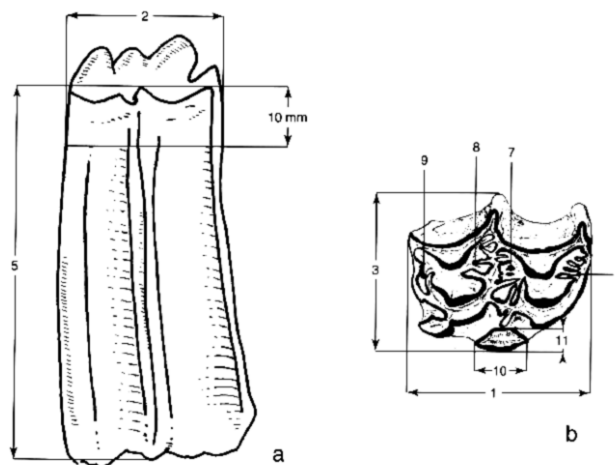


**Figure 3.** Mandibular measurements (modified from Bernor *et al.*, 1997). a) Buccal aspect. b) Inferior-anterior aspect.

1. Length from the point between the alveoles of the i1 to the back of the condyle.
2. Length from the point between the alveoles of the i1 to the middle of the line connecting the anterior borders of the p2.
3. Length of the premolar series, alveolar and on the vestibular side.
4. Length of the molar series, alveolar and on the vestibular side.
5. Buccal teeth series overall length, alveolar.
6. Length between the back of the alveole of m3 and the posterior edge of the ascending ramus.
7. Breadth between the posterior alveolar borders of the i3.
8. Height from the top of the condyle to the plane tangent to the horizontal ramus.
9. Height from
10. Height of the mandible, posterior to the m3.
11. Height of the mandible, between p4 and m1.
12. Height of the mandible, in front of p2.
13. Length of the symphysis from the point between the alveoles of the i1 to the posterior-most part.
14. Minimal breadth of the symphysis.

### 2.2.3. Upper dentition

The measurements used on the upper buccal teeth (Fig. 4) studied are based upon the template given by Bernor *et al.* (1997). Enamel plications are counted as invaginations inside the fossettes and evaginations out towards the protocone (Eisenmann *et al.*, 1988). In order for a single plication to be counted, it has to have a length at least equal or larger than the thickness of the enamel in the immediate area. The measurements are as follows:



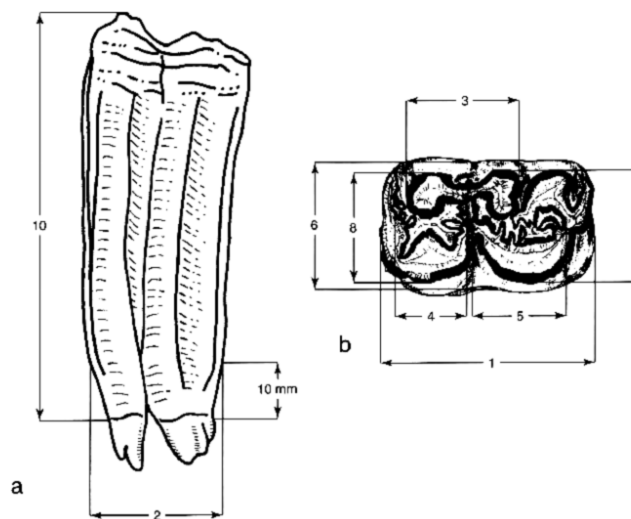
**Figure 4.** Upper buccal tooth measurements (modified from Bernor *et al.*, 1997). a) Buccal aspect. b) Occlusal aspect.



1. Length of the tooth at the occlusal level.
2. Length of the tooth at 10 mm above the base of the root.
3. Breadth of the tooth at the occlusal level, taken from the protocone to the mesostyle.
4. Breadth of the tooth at 10 mm above the base of the root.
5. Height of the tooth from the base of the root to the edge of the mesostyle.
6. Number of plications on the anterior part of the prefossette.
7. Number of plications on the posterior part of the prefossette.
8. Number of plications on the anterior part of the postfossette.
9. Number of plications on the posterior part of the postfossette.
10. Length of the protocone at the occlusal level
11. Breadth of the protocone at the occlusal level.

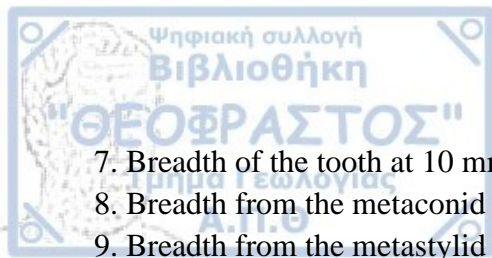
#### 2.2.4. Lower dentition

The measurements used on the lower buccal teeth (Fig. 5) studied are also based upon the template given by Bernor *et al.* (1997). They are as follows:



**Figure 5.** Lower buccal tooth measurements (modified from Bernor *et al.*, 1997). a) Buccal aspect. b) Occlusal aspect.

1. Length of the tooth at the occlusal level.
2. Length of the tooth at 10 mm above the base of the root.
3. Length of the metaconid-metastylid complex at the occlusal level.
4. Length of the prefossette.
5. Length of the postfossette
6. Breadth of the tooth at the occlusal level, along the line connecting the ectoflexid to the linguaflexid.



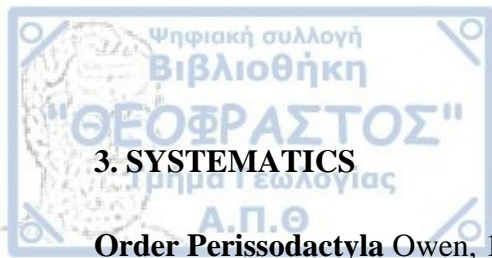
7. Breadth of the tooth at 10 mm above the base of the root.
8. Breadth from the metaconid to the enamel band labial to the protoconid.
9. Breadth from the metastylid to the enamel band labial to the hypoconid.
10. Height from the base of the root to the upper-most part of the mesial face of the tooth.

#### **2.2.5. Hypsodonty index**

The hypsodonty index (Eisenmann *et al.*, 1988) is used as an estimate of the animal's adaptation to a coarse-grained diet. It is expressed as  $HI=100I^t/h$ , where  $I^t$  is the length of the tooth at 10 mm above the base of the root (see 2.2.3. Upper dentition, measurement 2 and 2.2.4. Lower dentition, measurement 2) and  $h$  is the overall height of the tooth (see 2.2.3. Upper dentition, measurement 5 and 2.2.4. Lower dentition, measurement 10). It should be calculated on unworn or very little worn teeth (Eisenmann *et al.*, 1988).

#### **2.2.6. Protocone index**

The protocone index carries diagnostic value for interspecific discrimination (Eisenmann *et al.*, 1988) and is expressed as  $PI=100I^p/I^o$ , where  $I^p$  is the length of the protocone on the occlusal level (see 2.2.3. Upper dentition, measurement 10) and  $I^o$  is the overall length of the tooth at the occlusal level (see 2.2.3. Upper dentition, measurement 1).



### 3. SYSTEMATICS

Order *Perissodactyla* Owen, 1848

Family *Equidae* Gray, 1821

Genus *Hippotherium* Kaup, 1833

*Hippotherium brachypus* (Hensel, 1862)

#### Synonyms:

*Equus primigenius* Wagner, 1848 (in part), *Hipparion gracile* var. *mediterraneum* Roth and Wagner, 1854 (in part), *Hipparion brachypus* Hensel, 1862.

#### Type:

The original syntypes (Hensel, 1862) have been lost (Koufos *et al.*, 2021). Koufos (1987) has proposed the metacarpal NHML-PIK-M.11240, housed in the NHML, as a neotype and the metatarsal NHML-PIK-M.11265 and metapodials MNHNP-PIK-42, 46, 48, 52, 54, 59 & 104, housed in the MNHN as topotypes of the species (Koufos *et al.*, 2021).

#### Material:

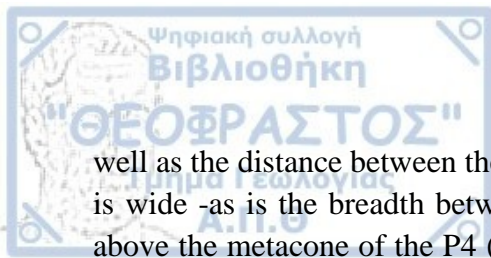
Adult: Crania (PV1/233, PV1/689, PV1/1067, PV1/1298, PV1/2634), upper buccal tooth rows (PV1/672, PV1/768, PV1/1214, PV1/2115, PV1/2282, PV1/2285, PV1/2337, PV1/2570, PV1/2576, PV1/2578, PV1/2622, PV3/12, PV3/96, PV3/138, PV3/2012), isolated second upper premolars (PV1/650, PV1/857, PV1/877, PV1/906, PV1/1230, PV1/1799, PV1/1800, PV1/1939, PV1/2075, PV1/2286, PV1/2327, PV3/134), mandibles (PV1/221, PV1/1090, PV1/2153, PV1/2469, PV3/2037), lower buccal tooth rows (PV1/1284, PV1/2030, PV3/2005, PV3/2007, PV3/2008, PV3/2035, PV3/2036), isolated second lower premolar (PV1/566), isolated third lower molars (PV1/534, PV1/2335, PV1/2533, PV3/128). Juvenile: Crania (PV1/2008, PV3/115), upper buccal tooth rows (PV1/1286, PV1/2580, PV3/2011), isolated second upper deciduous premolars (PV1/752, PV1/876), lower buccal tooth rows (PV1/196, PV1/333, PV1/832, PV1/1198A, PV1/1215, PV3/2043, PV3/2045), isolated third lower deciduous premolars (PV1/899-A, PV1/1187), isolated fourth lower deciduous premolars (PV1/718, PV3/2009).

#### Description:

##### Cranium:

The cranium is characterized by its large size and elongated facial area (Koufos, 1987; Mirzaie *et al.*, 2011; Lazaridis, 2015; Koufos *et al.*, 2021). The narial opening length, as

18



well as the distance between the naso-incisival notch and the orbit are large. The diastema is wide -as is the breadth between the orbital processes. The crista facialis usually ends above the metacone of the P4 (Koufos, 1987). The choanae are narrow and their anterior border is at the level of M1 and M2. The palate is large in both breadth and length (Koufos, 1987).

The POF is oval to sub-triangular in shape (Hristova, 2009) and well-defined at the posterior border. It is oriented horizontally along the long axis of the skull. There is a posterior pocket present in the POF, that may be slightly (e.g., PV1/1298; Appx. B, Plate 2, A-B) to moderately (e.g., PV1/689; Appx. B, Plate 1, A-B) pronounced in different specimens (Bernor *et al.*, 1997). While the inferior and posterior borders of the POF are usually well-delineated, the superior and anterior ones are sometimes weakly defined (Hristova, 2009). The distance between the POF and the orbit is large (Bernor *et al.*, 1996) and the lacrimal bone extends for more than half the distance between the orbit and the POF (Bernor *et al.*, 1997). The infra-orbital foramen is situated at the antero-inferior corner of the POF (Bernor *et al.*, 1997).

#### **Mandible:**

The mandible is similarly large in both the anteroposterior and dorsoventral axis, with an elongated symphysis. Its breadth is relatively small, giving the mandible a long and narrow appearance (Koufos, 1987; Lazaridis, 2015).

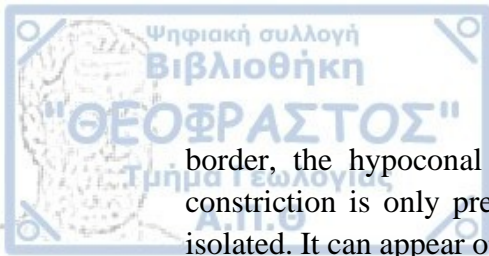
#### **Upper dentition:**

##### **Deciduous:**

The upper deciduous buccal teeth are large and elongated. The fossettes appear closed in fairly worn teeth, but they can be found to be posteriorly open when relatively unworn. The hypocone has a rounded border, the hypoconal groove is deep and a small hypoconal constriction is present (Koufos, 1987). The protocone is elliptical to oval and typically isolated. It can appear open only in advanced stages of wear. The plication count is high (Koufos, 1987; Koufos & Vlachou, 2005; Vlachou & Koufos, 2009), but can similarly appear as reduced in extreme stages of wear, as well as in unworn teeth (e.g., PV1/2008; Appx. B, Plate 7, C). The plis caballin count is variable [1 to 4 plis generally, although the maximum number of plis found in the -rather small- studied sample (n=7) is 3 (PV1/1286)], but usually two well-developed plis are present (Koufos, 1987). A dP1 may be present (Koufos, 1987) and may be retained into adulthood in some cases (PV3/2011).

##### **Permanent:**

The upper permanent buccal teeth are characteristically large and the fossettes are closed (with the exception of P2 in some cases). The hypocone has a rounded



border, the hypoconal groove is shallow and narrow and a small hypoconal constriction is only present in the M3. The protocone is generally elliptical and isolated. It can appear open only in advanced stages of wear. The plication count is high -with deep and narrow individual plis-, but can appear as reduced in extreme stages of wear, as well as in unworn teeth (e.g., PV1/1067; Appx. A, Upper Teeth Measurements). The plis caballin have 1-4 plications (Koufos, 1987; Koufos *et al.*, 2021), although the maximum number of plis found in the studied sample (Appx. A, Upper Teeth Measurements) is 3.

### **Lower Dentition:**

#### **Deciduous:**

The lower deciduous buccal teeth are large with elongated hypoconulids. The metaconid is elliptical to sub-triangular, the metastylid is oval to sub-triangular and the entoconid is rounded. The ectoflexid is deep, extending as much as to the level of the preflexid and may even invade well within the isthmus in dp3-dp4. The parastylid is well-developed, as is the ectostylid and a protostylid is usually present in dp3-dp4. The flexids appear plicated and a single pli caballinid is usually present (PV1/196, PV3/2043). A dp1 may be present (Koufos, 1987) and it may be retained into adulthood in some cases (none of the studied specimens exhibit this feature).

#### **Permanent:**

The lower permanent buccal teeth are large and elongated. The metaconid is elliptical to oval, the metastylid is oval to sub-triangular and the entoconid is rounded or sub-rectangular. The ectoflexid is deep and narrow, extending as much as to the level of the preflexid and may even invade well within the isthmus in m1-m3. The parastylid is less developed than in the deciduous teeth and the ectostylid is absent, as is the protostylid. The flexids appear plicated and a single (PV1/566, PV1/1284, PV1/2030, PV1/2153) or double (none of the studied specimens exhibit this feature) pli caballinid is sometimes present (Koufos, 1987).



Genus *Cremohipparion* Qiu, Weilong & Zhihui, 1987

*Cremohipparion mediterraneum* (Roth & Wagner, 1854)

**Synonyms:**

*Equus primigenius* Wagner, 1848 (in part), *Hipparion gracile* var. *mediterraneum* Roth and Wagner, 1854 (in part), *Hipparion mediterraneum* Hensel, 1862.

**Type:**

The holotype is unknown. Various neotypes and lectotypes have been proposed (Forstén, 1968; Bernor, 1985; Koufos, 1987). As it stands today, the skull and associated mandible MNHNP-PIK-259, housed in the MNHN, are considered as the neotypes of *C. mediterraneum* (Koufos *et al.*, 2021).

**Material:**

Adult: Crania (PV1/1794, PV1/1850, PV1/1874, PV1/1988, PV1/2205, PV1/2631, PV3/2041, PV3/2048), upper buccal tooth rows (PV1/837, PV1/901, PV1/1295, PV1/2259, PV1/2451, PV1/2527, PV1/2589, PV3/2042), isolated second upper premolars (PV1/585, PV1/730, PV1/845, PV1/1285, PV1/2171, PV1/2206, PV1/2222, PV3/2038), isolated third upper molars (PV1/64, PV1/724, PV1/1921), mandibles (PV1/219, PV1/232, PV1/430, PV1/458, PV1/758, PV1/766, PV1/785, PV1/1296, PV1/1924 $\alpha$ , PV1/1960, PV1/2138, PV1/2151, PV1/2308, PV1/2417, PV1/2575, PV3/68, PV4/7+PV4/8, PV4/9), lower buccal tooth rows (PV1/200, PV1/276, PV1/699, PV1/840, PV1/993, PV1/1068, PV1/1125, PV1/1282, PV1/1287, PV1/1913, PV1/2060, PV1/2202, PV1/2454, PV1/2577, PV3/47, PV3/60, PV3/2000, PV3/2004, PV3/2006, PV3/2046), isolated second lower premolars (PV1/87, PV1/1283, PV1/1883, PV1/2058 $\alpha$ , PV1/2058 $\beta$ , PV1/2082), isolated third lower molars (PV1/430B, PV3/2002). Juvenile: Crania (PV1/1896, PV3/2013), upper buccal tooth rows (PV1/275, PV1/315, PV1/335, PV1/431, PV1/784, PV1/920, PV1/1987, PV1/2125), isolated second upper deciduous premolars (PV1/751, PV1/875), isolated third upper deciduous premolars (PV1/66, PV1/344, PV1/492, PV1/493), mandibles (PV1/804, PV1/1790), lower buccal tooth rows (PV1/18, PV1/204, PV1/432, PV1/433, PV1/917, PV1/1058 $\alpha$ , PV1/1820, PV1/1993, PV1/2194, PV1/2264, PV1/2316, PV1/2383, PV1/2596), isolated second lower deciduous premolars (PV1/317, PV1/584, PV1/899-B), isolated third lower deciduous premolars (PV1/865, PV1/1130, PV1/1860), isolated fourth lower deciduous premolars (PV1/65, PV1/567).



### **Description:**

#### **Cranium:**

The cranium is characterized by its relatively short facial area (Koufos, 1987, 1988). The nasal opening length, as well as the distance between the naso-incisival notch and the orbit are short (Koufos, 1987; Koufos *et al.*, 2021). The diastema is relatively short as well. The crista facialis usually ends above the border of the P4 and M1. The choanae are very wide and their anterior border is at the middle of M2 (Koufos, 1987, 1988). The palate is elliptical in shape, with its minor axis situated at the border of P4 and M1. (Koufos, 1987).

The POF is oval to sub-triangular in shape (Koufos, 1987, 1988; Bernor *et al.*, 1997) and well-defined at all borders, apart from the superior (Hristova, 2009). It is oriented at an approximately 45° angle to the long axis of the skull (Koufos, 1987). The posterior pocket present in the POF, that may be more or less pronounced in different specimens [PV3/2041 (Appx. B, Plate 10, A-B) is the only specimen with a somewhat pocketed POF], but tends to be reduced in adult specimens (Hristova, 2009). The distance between the POF and the orbit is short and the lacrimal bone may invade the posterior border of the POF (Koufos, 1987, Bernor *et al.*, 1997). The infra-orbital foramen is situated at the antero-inferior corner of the POF (Bernor *et al.*, 1997). A caninus fossa with a well-defined posterior border may be present, anterior to the POF, in certain specimens (Bernor *et al.*, 1997), although the incompleteness of the studied specimens prevented the identification of such a feature in the present work.

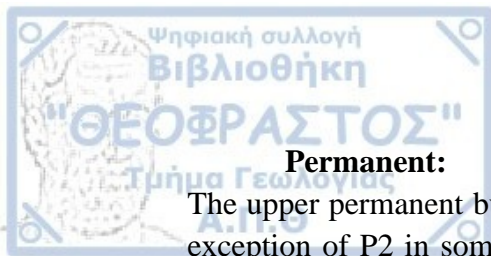
#### **Mandible:**

The mandible is short in both the anteroposterior and dorsoventral axis, as is the symphysis. Its breadth is also relatively small (Koufos, 1987, 1988).

#### **Upper dentition:**

##### **Deciduous:**

The upper deciduous buccal teeth are small. The fossettes appear closed in fairly worn teeth, but they can be found to be posteriorly open when relatively unworn. The hypocone has a rounded -or angular in less worn teeth- border, the hypoconal groove is deep and the hypoconal constriction is very small to absent. The protocone is elliptical to oval and isolated. It can appear open only in advanced stages of wear. The plication count is moderate to small, and can appear as further reduced in extreme stages of wear, as well as in unworn teeth. The plis caballin count is variable (1 to 4 plis), but usually one or two small plis are present (Koufos, 1987, 1988). A dP1 may be present (Koufos, 1987) and may be retained into adulthood in some cases (PV1/1988; Appx. B, Plate 6, B).



#### **Permanent:**

The upper permanent buccal teeth are small and the fossettes are closed (with the exception of P2 in some cases). The hypocone has a rounded -or angular in less worn teeth- border, the hypoconal groove is deep and the hypoconal constriction is very small to absent. The protocone is elliptical to sub-triangular and isolated. It can appear open only in advanced stages of wear. The plication count is moderate to small, and the plis are usually shallow. The plis caballin are small and usually one or two are found in each tooth (Koufos, 1987, 1988). Two of the more senile specimens studied (PV1/585 & PV1/2259) have none.

#### **Lower Dentition:**

##### **Deciduous:**

The lower deciduous buccal teeth are small. The metaconid is elliptical, the metastylid is elliptical to oval and the entoconid is rounded. The ectoflexid (labial depression) is shallow, barely extending to the level of the preflexid. The parastylid and protostylid are moderately developed and the ectostylid is small -when present. The flexids don't exhibit significant plication and a single pli caballinid (PV1/2383) is sometimes present (Koufos, 1987, 1988). A dp1 may be present (Koufos, 1987), though none of the studied specimens exhibit this feature.

##### **Permanent:**

The lower permanent buccal teeth are small. The metaconid is oval, the metastylid is elliptical to sub-triangular and the entoconid is rounded or sub-rectangular. The ectoflexid is shallow in the premolars and deep in the molars. The ectostylid is absent, as is the protostylid. The flexids don't exhibit significant plication and a single pli caballinid (PV1/87, PV1/766, PV1/1125, PV1/1883, PV1/1924α, PV1,1960, PV1/2082, PV1/2202, PV1/2308, PV1/2454, PV1/2577, PV3/47, PV4/9) is sometimes present (Koufos, 1987, 1988).



#### 4. COMPARATIVE ANALYSIS

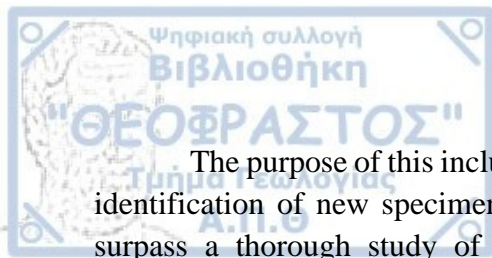
For the identification and taxonomic determination of the studied material, measurements were taken in accordance with the prevailing literature. Those were then put up against the given comparative material and similarities, as well as differences were discussed. This was complemented by the statistical analysis of a few suitably large sets of data. Additionally, remarks made on certain descriptive morphological characters were also compared with the literature and the given identified examined by the author.

##### 4.1. Descriptive characters

The following characters (Table 2) represent first and foremost features of the skull and dentition that cannot adequately and completely be described by spatial measurements, but carry diagnostic significance nonetheless. These include general shape and texture, including size ratios that serve more purpose when expressed descriptively (e.g., long, short, narrow, wide etc.), as well as the presence or absence of certain morphological elements. Added to the above are the descriptive expressions of most of the metric characters analyzed in the following section.

**Table 2.** Table of the main distinguishing craniodental features of *H. brachypus* and *C. mediterraneum*. The features presented are a combination of what is discussed in the relevant literature, with minor amendments stemming from the author's own observations.

Features	<i>C. mediterraneum</i>	<i>H. brachypus</i>
Snout length	short	long
Palate shape	elliptical with wide choanae	straight, with narrow choanae
POF shape	oval to sub-triangular, placed at an angle to the skull	oval to sub-triangular, placed horizontally
POF-orbit distance	very short	long
Lacrimal position	at the border or invading the POF	at the border of the POF to more than half the POF-Orbit distance
Caninus fossa presence	present	absent
Mandible shape	short and low	narrow and long
Buccal teeth size	small	large
Protocone shape	elliptical to subtriangular	elliptical, sometimes subtriangular
Hypoconal groove	shallow	shallow to deep
Plication count	small to moderate	moderate to large
Metastylid & metaconid shape	circular to subtriangular	subtriangular to irregular



The purpose of this inclusion is the creation of a usable reference table for the quick identification of new specimens collected from the locality. This, of course, can never surpass a thorough study of the material, but can nevertheless serve to facilitate a preliminary identification on the field.

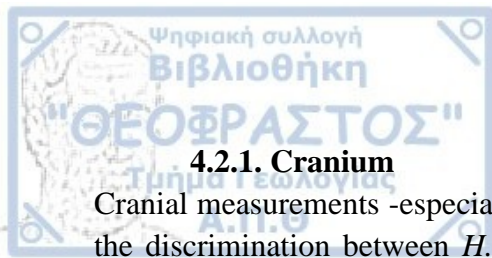
Beginning with the general shape of the facial skull, the studied material agrees with the descriptions provided by the relevant literature (Koufos, 1987, 1988; Bernor *et al.*, 1996, 1997; Hristova, 2009; Atabaadi *et al.*, 2011; Lazaridis, 2015; Koufos *et al.*, 2021) - with *C. mediterraneum* appearing to possess a short and blunt snout and *H. brachypus* a relatively thinner and more elongated one. The mandible follows the shape of the skull and as such, appears shorter in *C. mediterraneum* (Appx. B, Plates 11, 13, 14) and larger and longer in *H. brachypus* (Appx. B, Plates 12, 15). The position of the POF in relation to the orbit also follows the standard. The distance between it and the orbit is characteristically short *C. mediterraneum* (Appx. B, Plates 3-6, 8, 10) and longer in *H. brachypus* (Appx. B, Plates 1, 2, 7). The lacrimal conforms to the space it is given in each case and thus touches or invades into the POF in *C. mediterraneum* and is generally situated outside it in *H. brachypus*. The buccal tooth row is short in *C. mediterraneum* and longer in *H. brachypus*, whose individual teeth are also generally larger in size and height.

Dental characters have proven to be less reliable and with more overlap between species than cranial ones. Nevertheless, they have served their purpose -when falling into morphological extremes, unique to each species- in the identification of specimens where poor preservation and incompleteness hindered the examination of other features. As an example to the first statement, the shape of the protocone can take on either an elliptical or subtriangular shape in both species and the only observation that can be made a posteriori is that subtriangular protocones appear with a greater frequency in *C. mediterraneum* individuals (50% of studied specimens, as opposed to 35.7% for *H. brachypus*). Similarly, the hypoconal groove may be especially deep in members of *H. brachypus* but can also appear as shallow, as does in *C. mediterraneum*. Lastly, no discernible difference was observed in the depth of the ectoflexid for the mandibular teeth studied. In both species the ectoflexids seem to start as somewhat shallow in the P2 and progressively deepen along the premolar row in moderately worn teeth. Any other form of variability in ectoflexid depth is shared between both species.

The presence of a caninus fossa (Bernor *et al.*, 1997) for *C. mediterraneum* is only mentioned for its general diagnostic importance and could not be found in any of the studied specimens due to their state of preservation.

#### 4.2. Metric characters

Metric character measurements follow the numbering scheme outlined in Section 2.2 (Measurements). In the diagrams, they are denoted either as "Measurement x", or as "(x)" for brevity, where x is the corresponding measurement number for each cranial element.



#### 4.2.1. Cranium

Cranial measurements -especially in the facial region- have proven to be very reliable for the discrimination between *H. brachypus* and *C. mediterraneum*. Unfortunately, crania with adequate preservation were relatively few (e.g., Appx. B, Plates 1-10). Nevertheless, they have proven useful in their completeness and served as a fairly rigid template for the identification of partial specimens, in combination with the comparative material.

The length between the orbit and the preorbital fossa (measurement 32) in particular, shows a clear separation of the two groups, as does the length between the preorbital fossa and facial crest (measurement 36; Fig. 6). The same can be said about the solitary juvenile specimen belonging to *H. brachypus* (PV1/2008; Appx. B, Plate 7), which falls neatly within the area demarcated by its peers from Bulgaria (Fig 7). *H. brachypus* is shown to have a POF placed further away from the orbit and high in the face, while *C. mediterraneum* has lower POF, which is situated very near the orbit.

Measurements linked to the shape of the POF, such as the maximal length (measurement 33) or height of the preorbital fossa (measurement 35) could have also served a similar function but -again, the number of specimens preserving these features in a measurable state was inadequately low. Consequently, the author was limited to a descriptive evaluation of the shape and size of the fossae.

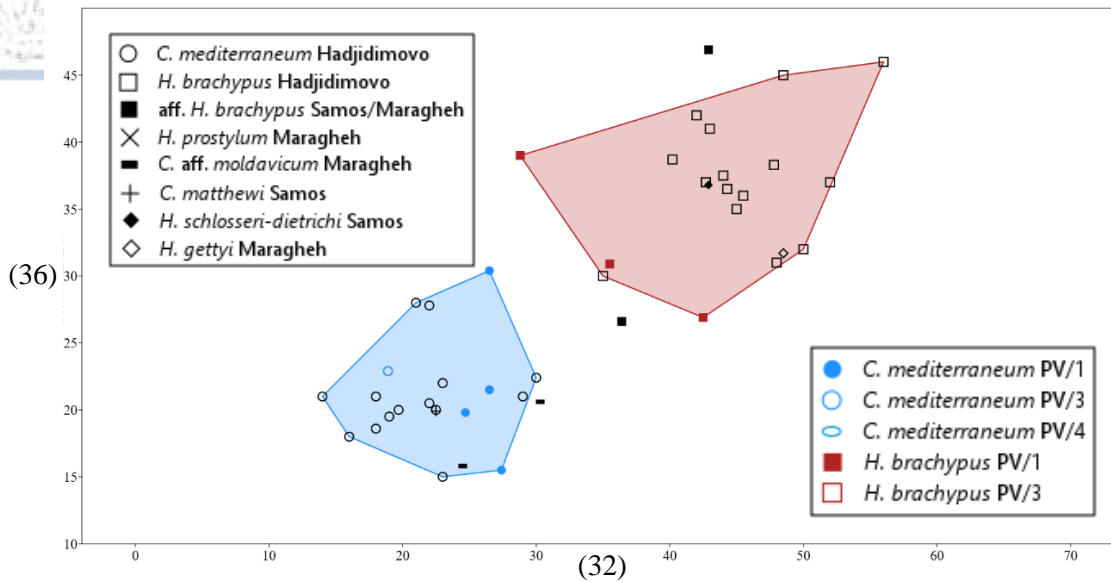
The length from the back of the narial opening to the anterior-most point of the orbit (measurement 31) can be a great indicator for the length of the face, but specimens in the studied material tended to have their naso-incisival notch missing. Fortunately, the length of the anterior border of the orbit to the anterior-most part of the alveolar level of the P2 (P2-Orbit) came to the rescue, providing an alternative approximation.

Even so, the difference between the two species was barely noticeable, but present nonetheless. As can be seen in Fig. 8, members of *H. brachypus* tend to have a slightly longer facial area than *C. mediterraneum*, but the overlap is almost total, when taking the comparative material into account.

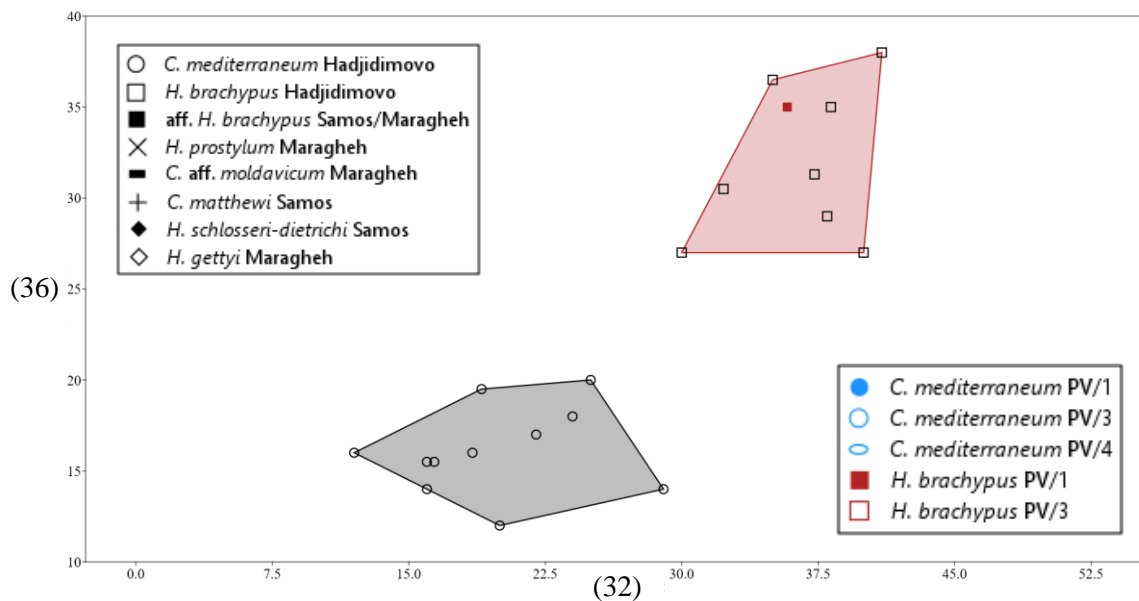
Fig. 9 was constructed with the purpose of expressing the relation of the premolar row length to the total length of the buccal tooth row. As can be witnessed, *H. brachypus* tends to have a longer tooth row, as well as a longer premolar row. Again, a certain degree of overlap is observed, which is mitigated -rather than amplified- by disregarding the comparative material [only one studied specimen (PV1/1988; Appx. B, Plate 6) is found in said area].

The tooth row length measurements -seen individually, offer a clearer picture of the distinction between the two identified species. Both the premolar (Fig. 10) and molar (Fig 11) row lengths share little overlap and appear greater in *H. brachypus*. Peculiarly, the distinction is hazier for the comparative material in the case of the premolar row.

As expected from the above, the whole tooth row measurements (Fig. 12) follow the same rule, with greater overall lengths attributed to *H. brachypus* than in *C. mediterraneum* and again, the difference is less distinct for the comparative material.



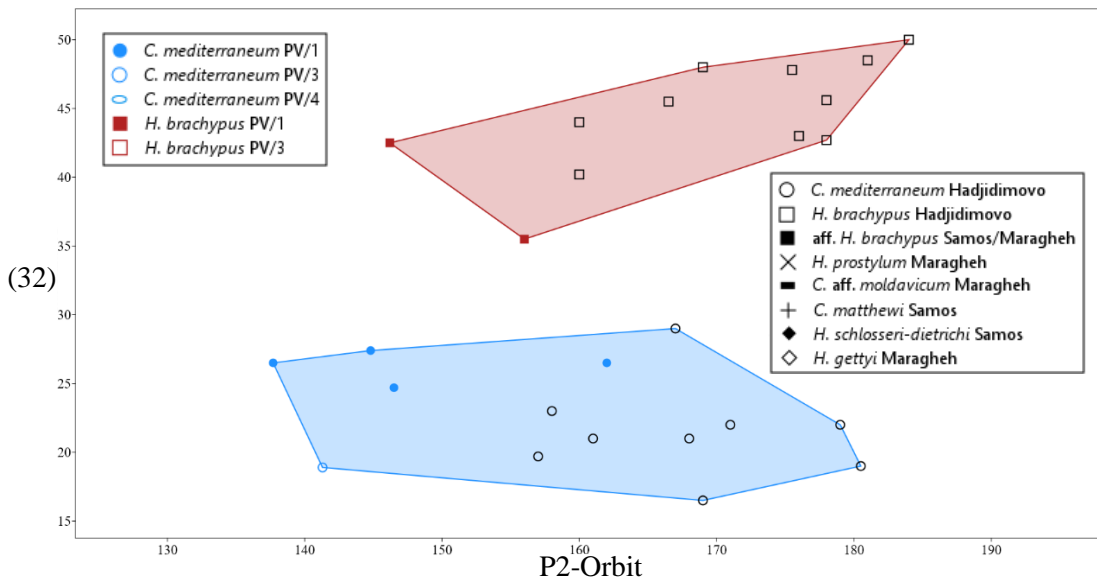
**Figure 6.** Scatter plot of cranial measurements 32 and 36 (Eisenmann *et al.*, 1988) for adult specimens and associated comparative material.



**Figure 7.** Scatter plot of cranial measurements 32 and 36 (Eisenmann *et al.*, 1988) for juvenile specimens and associated comparative material.

The above observations are reiterated in the deciduous premolar row length comparisons (Fig. 13). In this case the comparative material is shown, not only as overlapping, but actually as the reverse of what should be expected. This could be attributed to a small sample size, containing mainly outliers by pure chance.

Finally, all cranial measurements with a sample population of  $n \geq 3$  are presented in the logarithmic diagram of Fig. 14. Among the most pronounced differences are the length between the orbit and the preorbital fossa (measurement 32) and the length between the preorbital fossa and facial crest (measurement 36), which are significantly greater in *H. brachypus* than in *C. mediterraneum*. Greater also, but to a lesser degree, are the minimal



**Figure 8.** Scatter plot of the P2-Orbit length and cranial measurement 32 (Eisenmann *et al.*, 1988) for adult specimens and associated comparative material.

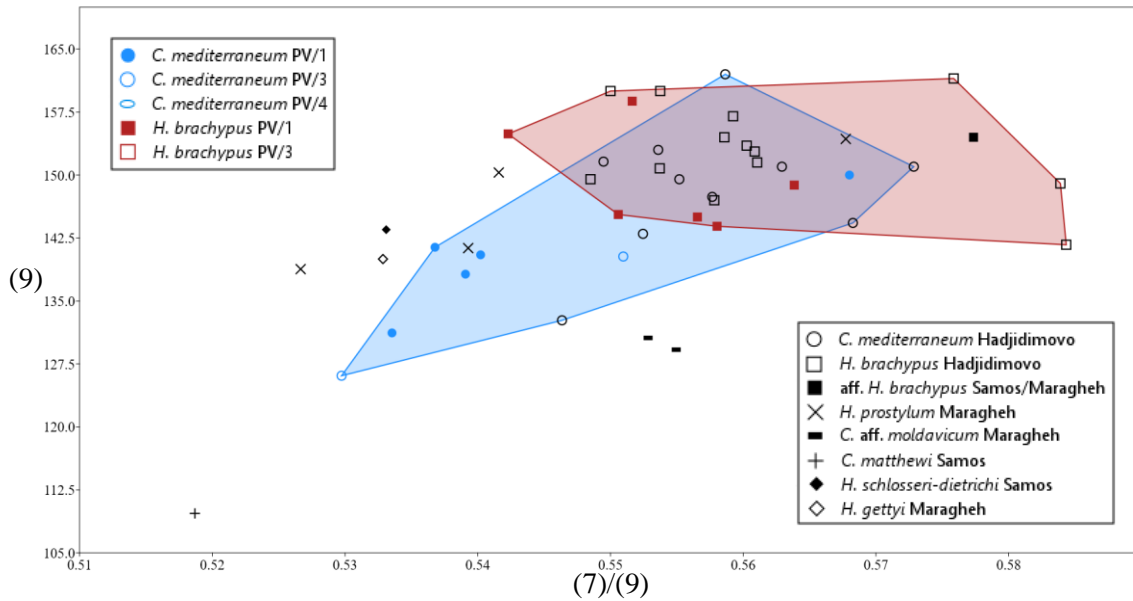
length between the middle of the line connecting the anterior borders of the P2 and the base of the palatal spur (measurement 2), the length of the molar and premolar series (measurements 7, 8 & 9) and the length of the fossa temporalis (measurement 16).

Few measurements appear smaller for *H. brachypus*. Among them are the height (measurement 35) and length (measurement 33) of the preorbital fossa, as well as the breadth of the choanae (measurement 12) and the palate (measurement 13).

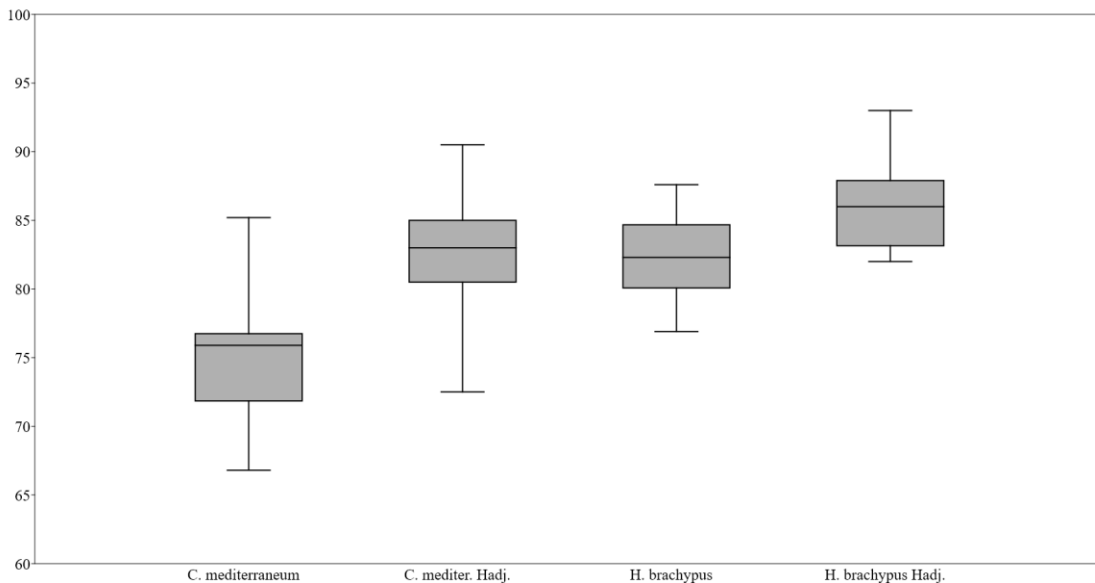
Complementarily to comparisons with identified members the two prevailing species of the locality, the studied specimens' cranial measurements were further compared to material belonging to other hipparionines from the similarly dated localities of Samos - Greece and Maragheh - Iran, with the purpose of highlighting similarities or differences between the former and the latter.

*C. matthewi* is the most distinct of the species compared, displaying a very small overall tooth row size (Fig. 9), while its POF position is similar to that of *C. mediterraneum* (Fig. 6). *H. schlosseri-dietrichi* and *H. gettyi* fall within the region of *H. brachypus* for the

immediately preceding measurements (Fig. 6), but then switch their allegiance to *C. mediterraneum* for the length of their tooth rows (Fig. 9). *H. gettyi* is also close to *C.*

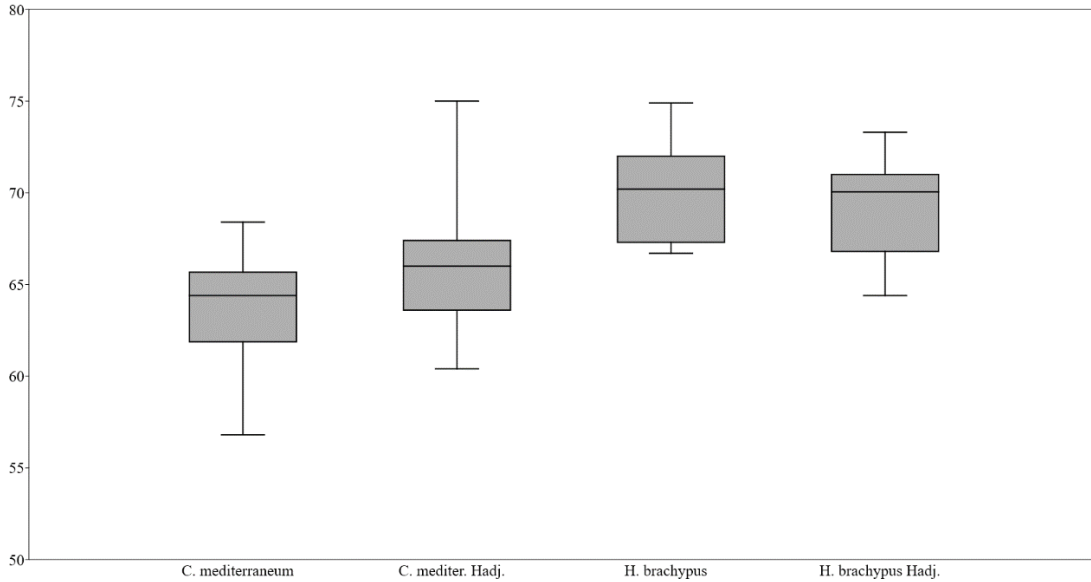


**Figure 9.** Scatter plot of the ratio of the length of the premolars to the overall buccal tooth row length (7/9) and the latter (measurement 9; Eisenmann *et al.*, 1988) by itself, for adult specimens and associated comparative material.

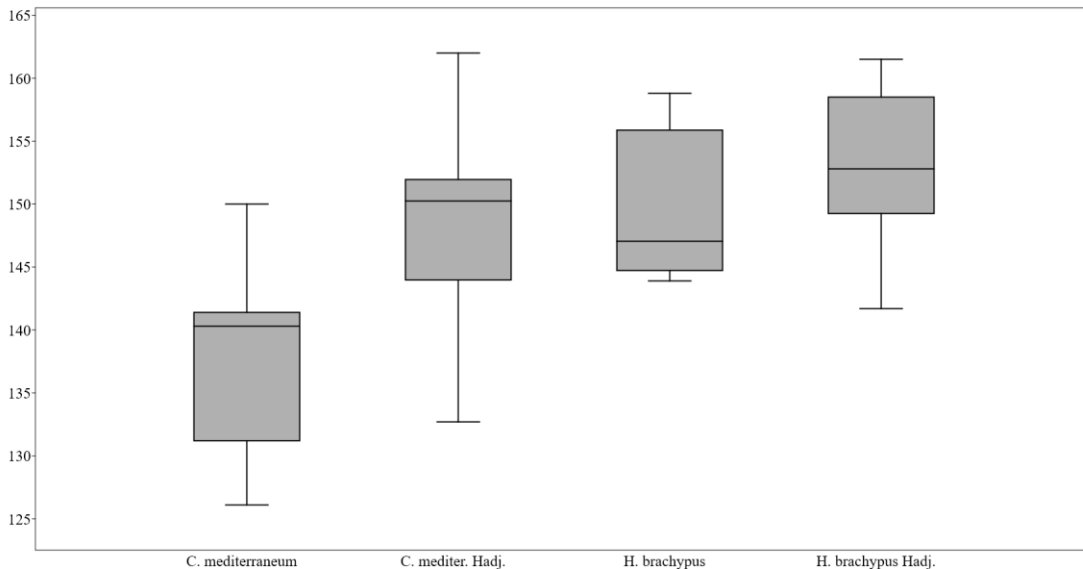


**Figure 10.** Box plot of the premolar row lengths (measurement 7; Eisenmann *et al.*, 1988) of adult specimens and associated comparative material.

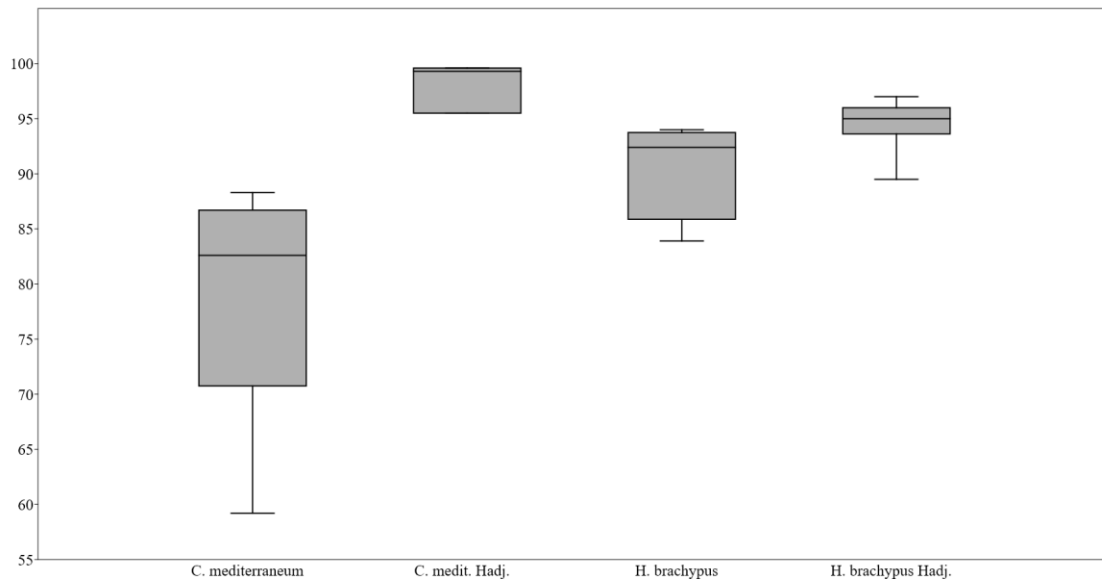
*mediterraneum* -POF position and tooth row length-wise. Lastly, *H. prostylum* presents with a buccal tooth row length which is intermediate to both of the identified species. The



**Figure 11.** Box plot of the molar row lengths (measurement 8; Eisenmann *et al.*, 1988) of adult specimens and associated comparative material.

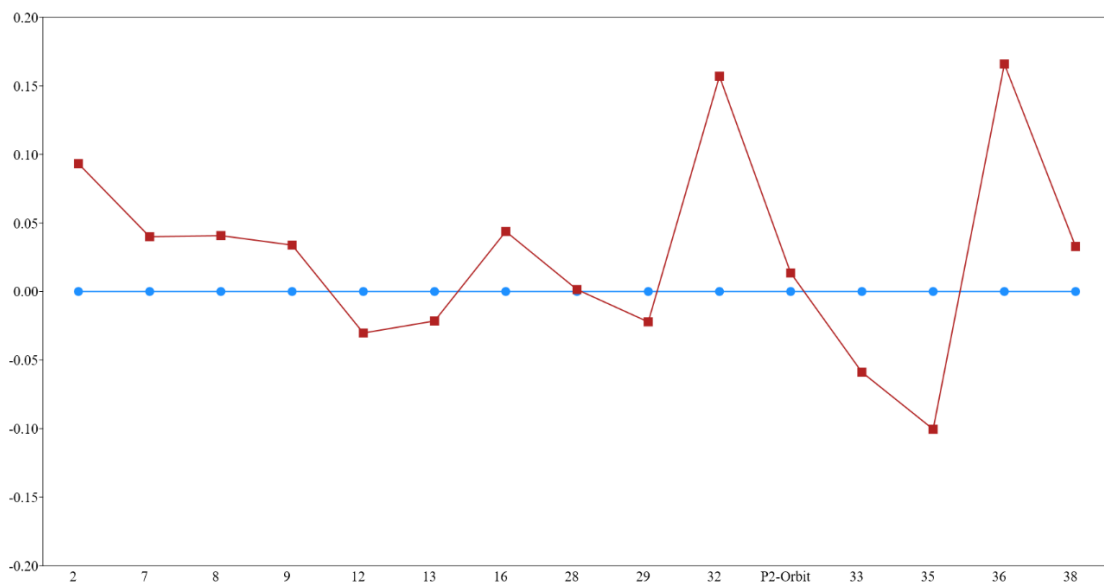


**Figure 12.** Box plot of the buccal tooth row lengths (measurement 9; Eisenmann *et al.*, 1988) of adult specimens and associated comparative material.



**Figure 13.** Box plot of the deciduous premolar row lengths (measurement 9; Eisenmann *et al.*, 1988) of adult specimens and associated comparative material.

ratio of the length of the premolars to the complete row length is in the region of *C. mediterraneum* for all measured crania of *H. prostylum*, with the exception of one specimen, which is still nested within the area of overlap between *C. mediterraneum* and *H. brachypus*.



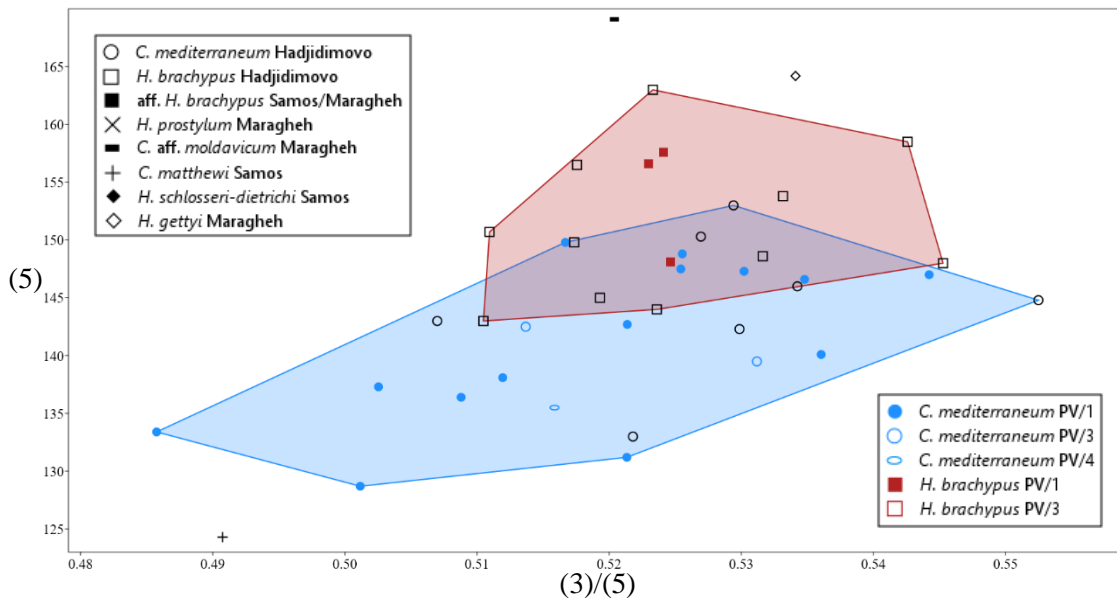
**Figure 14.** Decimal logarithm diagram of the ratios of *H. brachypus* cranial measurements (red) to those of *C. mediterraneum* (blue), which is plotted as the baseline.



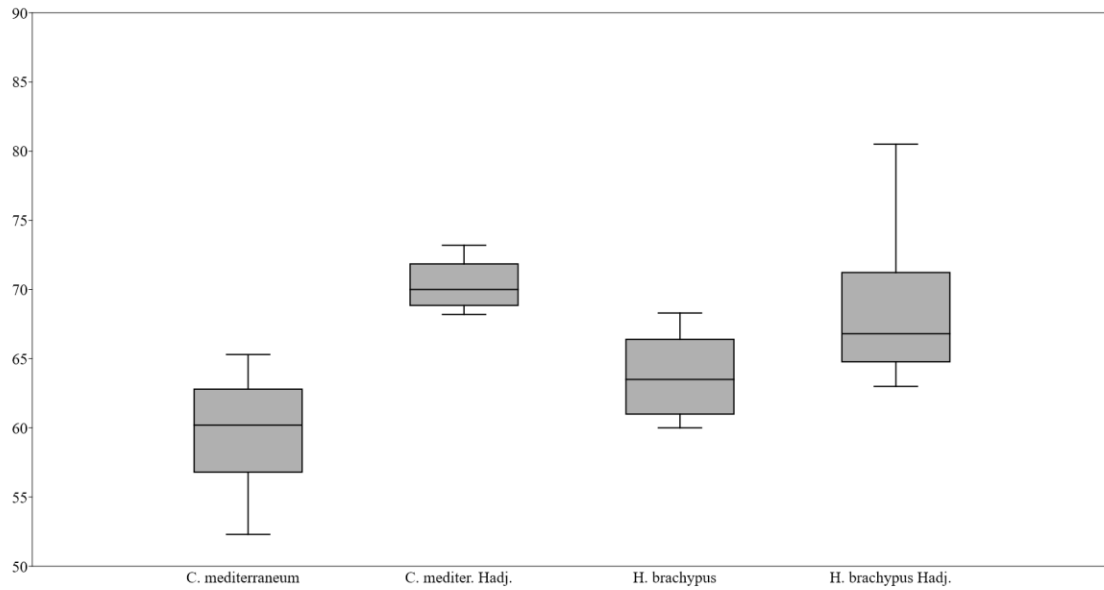
#### 4.2.2. Mandible

Hipparionine mandibles are generally poorer in defining features, when compared to the skulls. Still, a number of differences were found and described. Fig. 15 was constructed with a similar mindset as Fig. 9 -only for the lower dentition- and unsurprisingly, displays a similar pattern with the latter. Specifically, *C. mediterraneum* seem to possess a shorter buccal tooth row, while *H. brachypus* have a longer one [PV1/1090 (Appx. B, Plate 12) is the sole exception among the studied material], where the length of the premolar row tends to be more dominant. A certain degree of overlap exists, especially for the ratio of the premolar row length to the overall tooth row length, for which *C. mediterraneum* exhibits a great degree of variability.

Several measurements exist (namely measurements 9, 10, 11 & 12), pertaining to the height of the mandible, but the one producing the most distinct apparent difference among the described species is the height between p4 and m1 (measurement 11). This can be seen in Fig. 16, where the bulk of the measurements for *H. brachypus*, of both the studied and comparative specimens appear greater than for the studied *C. mediterraneum*. Meanwhile, the comparative material for *C. mediterraneum* presents with an anomaly in this particular case (appearing greater than both of the studied species' measurements) but this too can be attributed to a small and uncharacteristic sample.

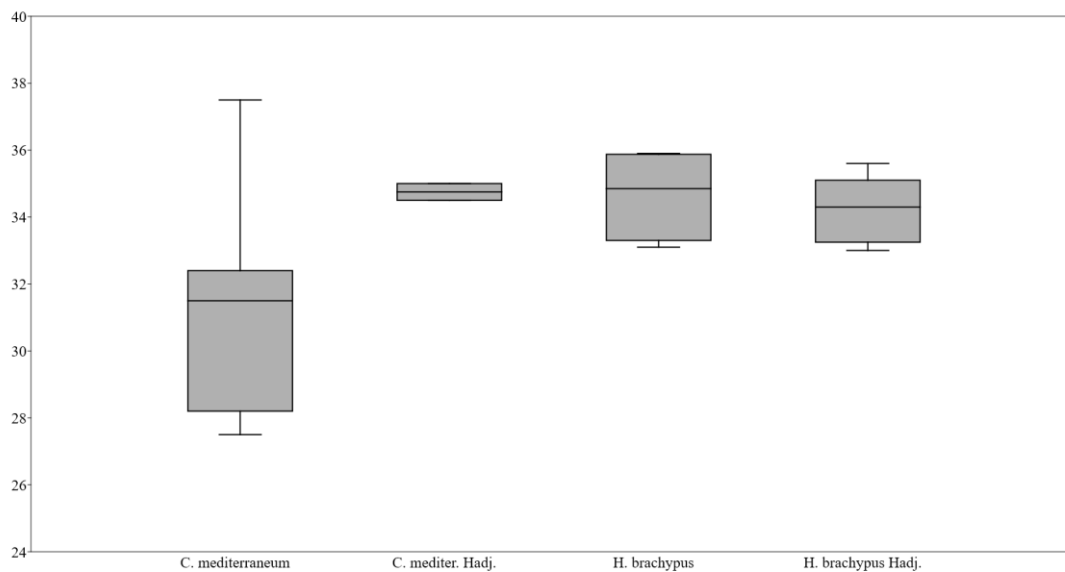


**Figure 15.** Scatter plot of the ratio of the length of the lower premolars to the overall buccal tooth row length  $(3/5)$  and the latter (measurement 5; Eisenmann *et al.*, 1988) by itself, for adult specimens and associated comparative material.



**Figure 16.** Box plot of mandibular measurement 11 (Eisenmann *et al.*, 1988) of adult specimens and associated comparative material.

A similar pattern is observed in the minimal breadth of the symphysis (measurement 14). *C. mediterraneum* present with a markedly smaller value [with the exception of a single, older individual with highly worn teeth (PV3/68; Appx. B, Plate 16)], while *H. brachypus* form a well-defined sample of distinctly higher values (Fig. 17).

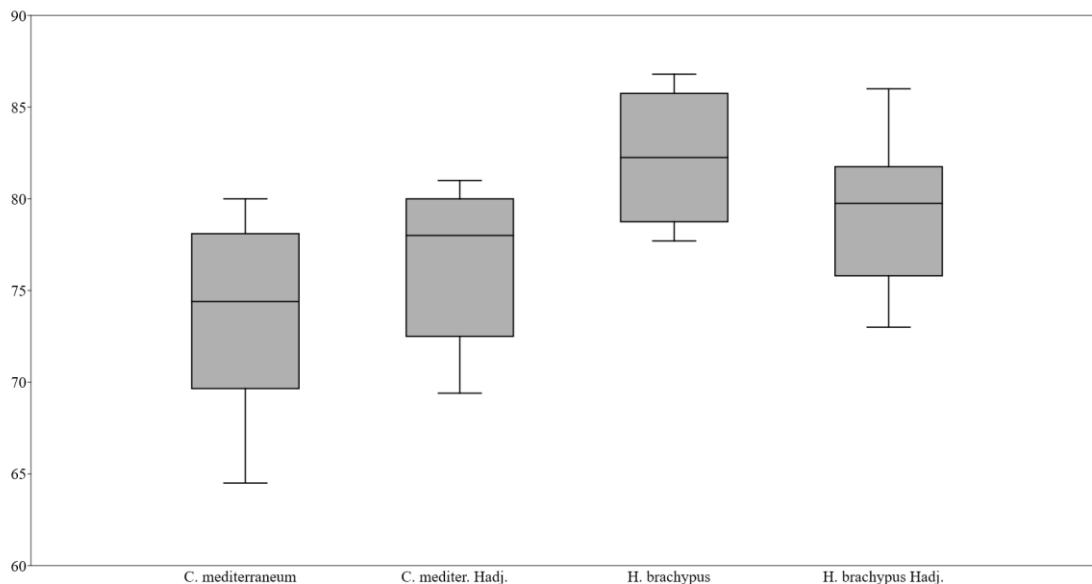


**Figure 17.** Box plot of mandibular measurement 14 (Eisenmann *et al.*, 1988) of adult specimens and associated comparative material.

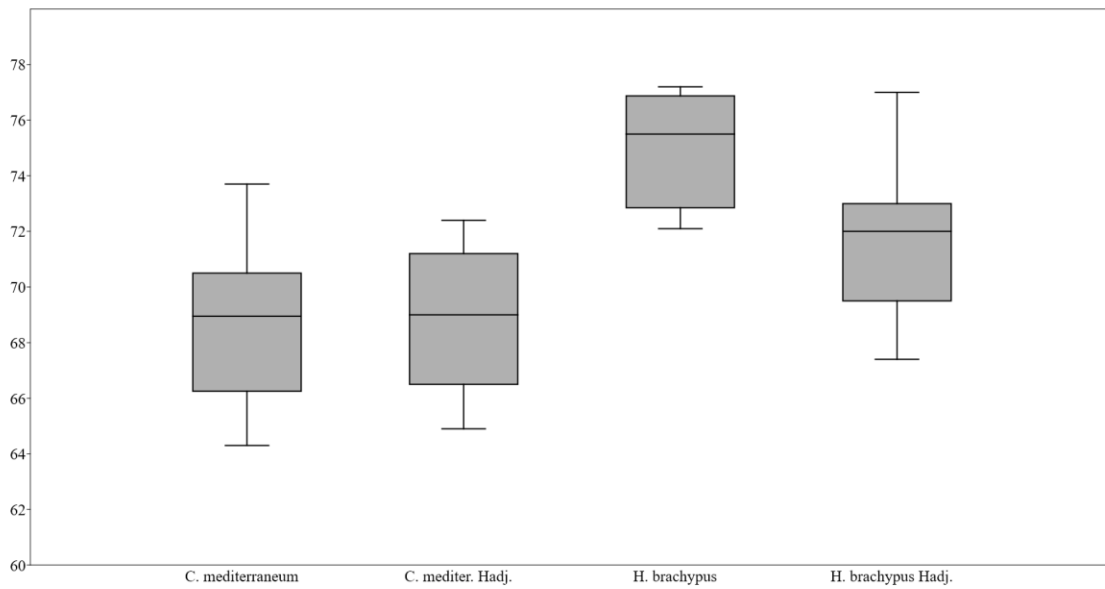
The individual lower buccal dentition measurements continue to mirror the values of the upper dentition. Fig. 18 displays the collected lower premolar row lengths (measurement 3) for the studied and comparative material, while Fig. 19 shows the lower molar lengths (measurement 4) and Fig. 20 the total tooth row lengths (measurement 5). In each case, generally larger values for *H. brachypus* can be observed, perhaps with even greater clarity than in the upper teeth. The comparative material is also more complete and better-behaved in this measurement set.

As with the cranial ones, all mandibular measurements with a sample population of  $n \geq 3$  are presented in a logarithmic ratio diagram (Fig. 21). With the exception of the length between the back of the alveole of m3 and the posterior edge of the ascending ramus (measurement 6), all other measurements appear invariably greater in *H. brachypus*, denoting a definite distinction between the two species. Among the most pronounced differences are the length from the point between the alveoles of the i1 to the middle of the line connecting the anterior borders of the p2 (measurement 2), the length of the premolar series (measurement 3), the length of the molar series (measurement 4) -and consequently, the buccal teeth series overall length (measurement 5), the breadth between the posterior alveolar borders of the i3 (measurement 7), the length of the symphysis (measurement 13) and the minimal breadth of the symphysis (measurement 14).

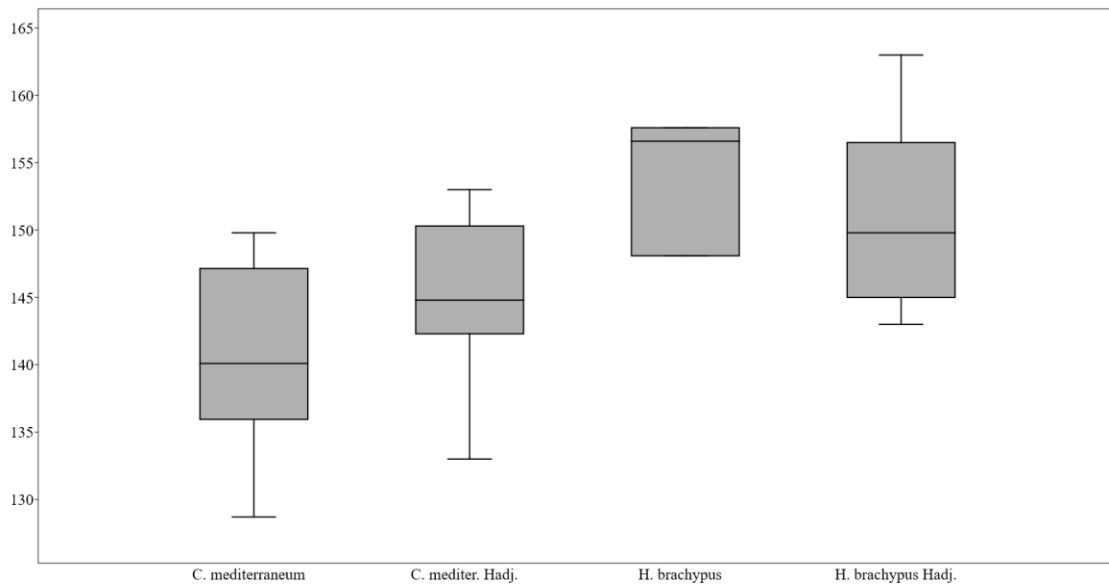
The one measurement which appears smaller (and significantly so) in *H. brachypus* is measurement 6, which points to a narrower ramus and a fuller -more round cheek region for *C. mediterraneum*.



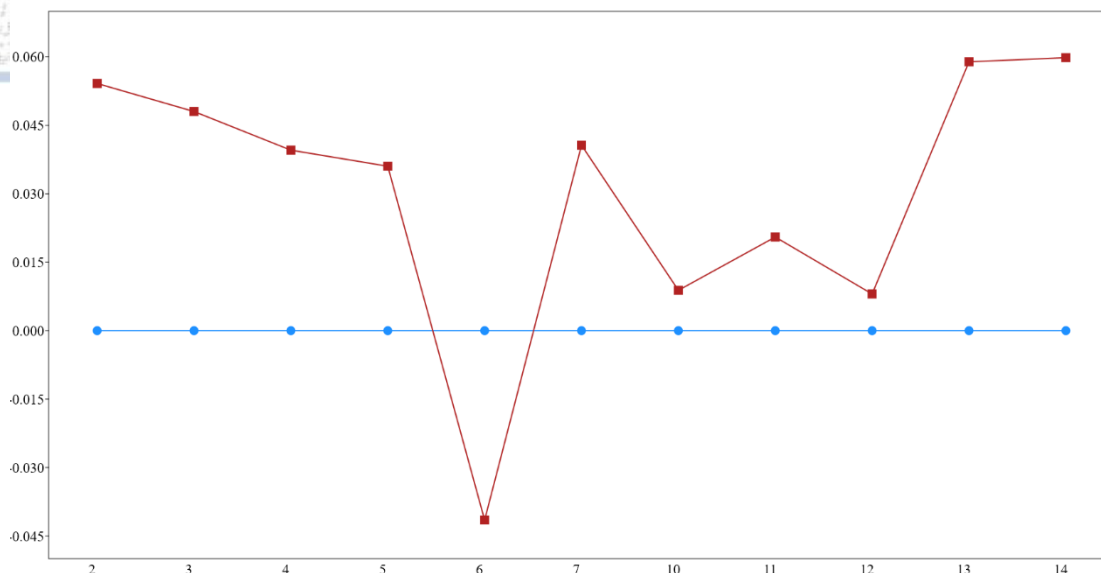
**Figure 18.** Box plot of the lower premolar row lengths (measurement 3; Eisenmann *et al.*, 1988) of adult specimens and associated comparative material.



**Figure 19.** Box plot of the lower molar row lengths (measurement 4; Eisenmann *et al.*, 1988) of adult specimens and associated comparative material.



**Figure 20.** Box plot of the lower buccal tooth row lengths (measurement 5; Eisenmann *et al.*, 1988) of adult specimens and associated comparative material.



**Figure 21.** Decimal logarithm diagram of the ratios of *H. brachypus* mandibular measurements (red) to those of *C. mediterraneum* (blue), which is plotted as the baseline.

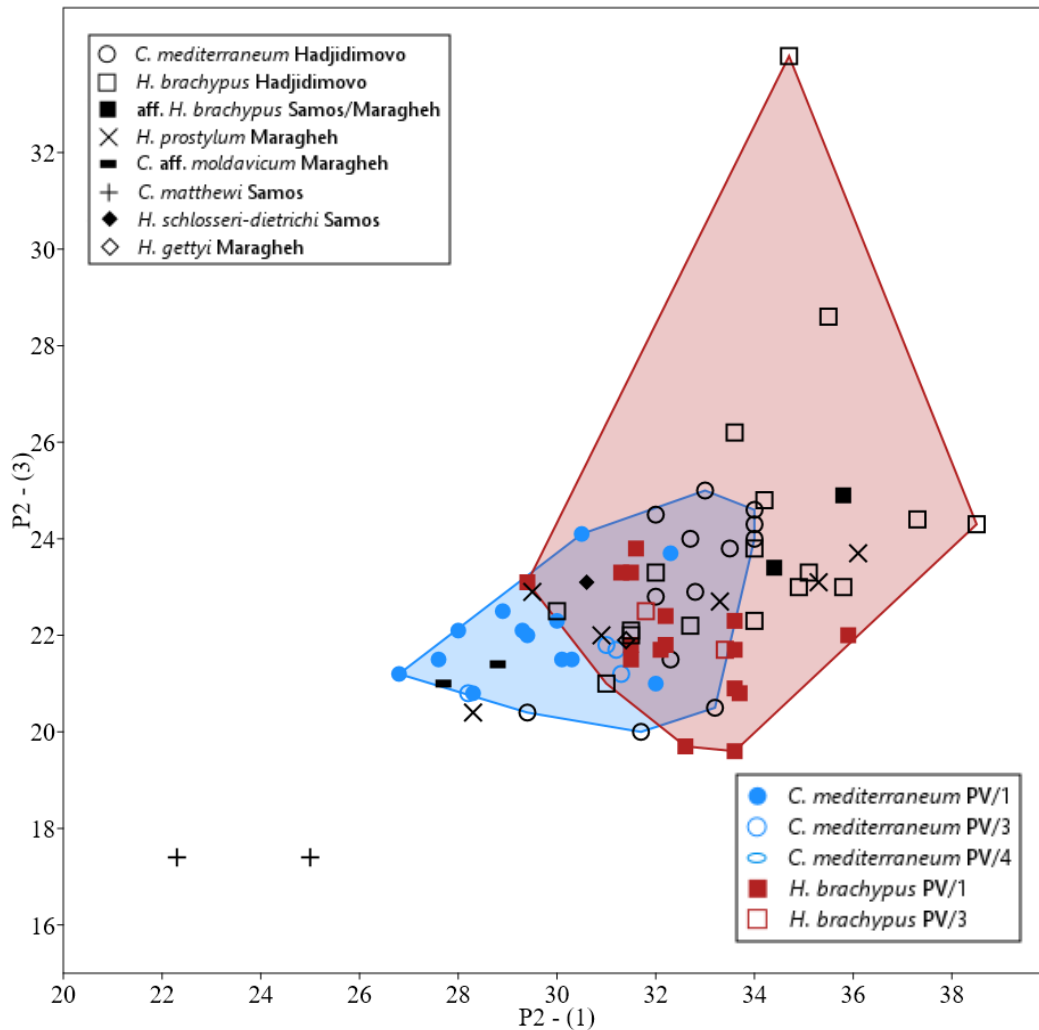
As for complementary comparisons with material belonging to other hipparionine horse species (solely from Maragheh – Iran this time), only two suitable specimens were examined, one belonging to *C. aff moldavicum* and one belonging to *H. gettyi*. The comparison was made for the ratio of the length of the premolar row by the overall buccal tooth row length to the latter by itself (Fig. 15). Both identified specimens fall outside the areas occupied by the measurements of samples from both the studied material and the comparative sample from Hadjidimovo and present with larger tooth row lengths and intermediate premolar row lengths.

### 4.2.3. Dentition

The comparison of individual teeth may serve to partition the sample in more or less distinct morphologies -especially when assisted in its identification by cranial measurements- but as it will become apparent, they often share significant overlap, making the identification of isolated teeth and partial tooth rows rather difficult.

#### 4.2.3.1. Upper dentition:

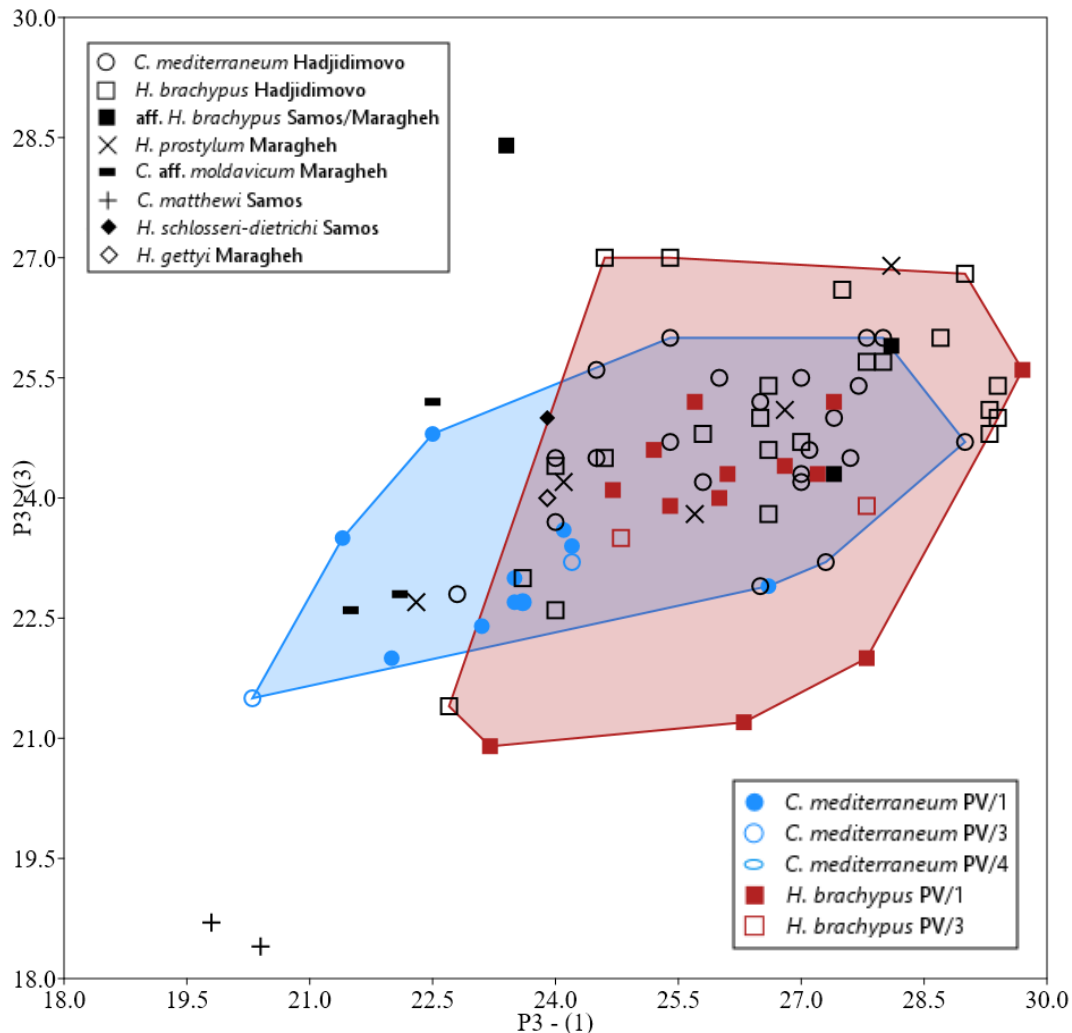
A great place to begin when attempting to untangle the slight mess that is individual teeth measurements, is P2 dimensions on the occlusal level (Fig. 22). The comparative material is of not much help in this case, as it appears shifted up in size as a whole and for both measurements (tooth length and breadth) and presents with a considerable amount of overlap. When left with the studied material, the situation becomes somewhat better-defined, but still the degree of overlap is great.



**Figure 22.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and width (measurement 3; Eisenmann *et al.*, 1988) of the P2 for adult specimens and associated comparative material.

Nevertheless, a tendency for the first premolars of *H. brachypus* to be larger, mainly in their length can be observed.

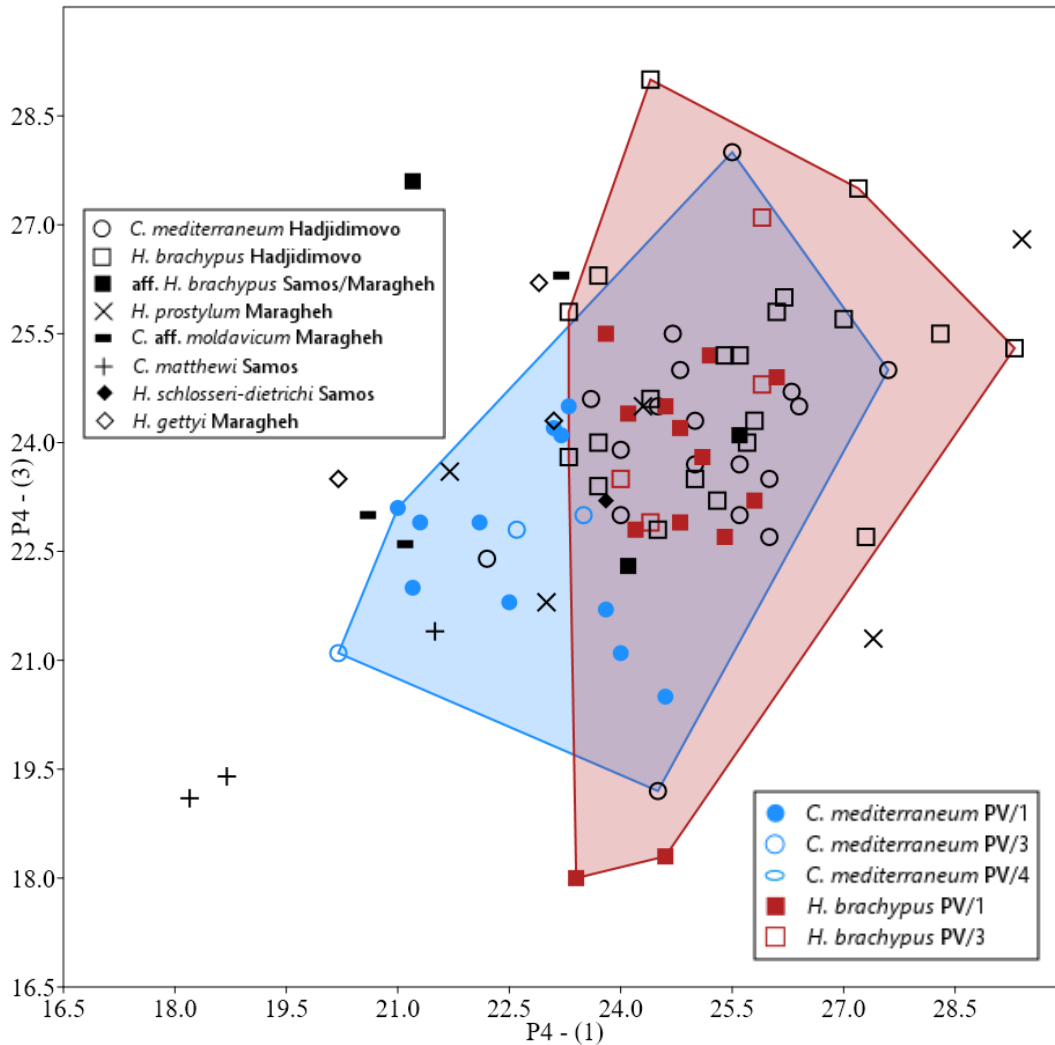
As one continues to move along the tooth row, the picture becomes progressively more muddled. So, for the case of the third premolars (Fig. 23), the comparative material from Hadjidimovo can be disregarded altogether, as the two species demonstrate no distinct clustering. Within the studied material though, the tendency of *H. brachypus* to possess longer teeth is still apparent, while the tooth-width variability is somewhat smaller for *C. mediterraneum* but still within an overlapping interval with *H. brachypus*.



**Figure 23.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and width (measurement 3; Eisenmann *et al.*, 1988) of the P3 for adult specimens and associated comparative material.

The fourth premolar (Fig. 24) still manages to offer some useful degree of distinction between the two species. This time, *H. brachypus* specimens appear to possess both longer and wider teeth as far as the studied material is concerned. The comparative material from Hadjidimovo, on the other hand, is completely intertwined in both axes.

The first two molars offer a recapitulation of what has already been discussed for the premolar series (Fig. 25, Fig. 26). The teeth belonging to the studied sample, which correspond to *H. brachypus* are generally larger and the two species are almost indistinct from one another in the comparative material.

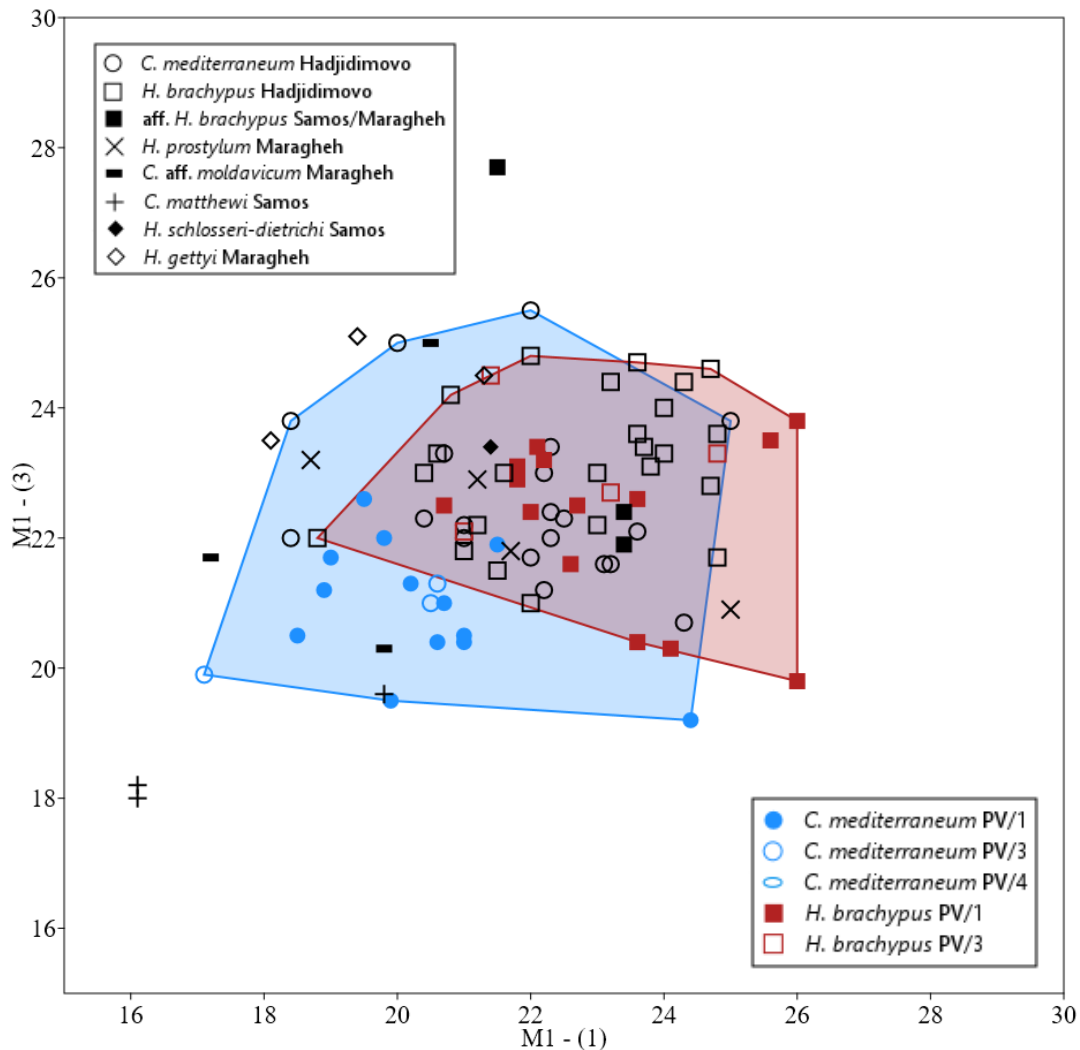


**Figure 24.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and width (measurement 3; Eisenmann *et al.*, 1988) of the P4 for adult specimens and associated comparative material.

The only somewhat noteworthy case, is that of the third molars (Fig. 27), which still tend to be longer for *H. brachypus*, but also seem to trend towards being slightly less wide than in *C. mediterraneum*. The overlap is at its greatest for this tooth though and the difference is barely noticeable.

The deciduous tooth row, on the other hand, offers much clearer results. The second deciduous premolars of the two species form distinguishable clusters (Fig. 28). In general, the dP2 of *H. brachypus* tend to be longer and slightly wider than those of *C. mediterraneum*. The comparative material also tends to be more cooperative in creating a cohesive overall picture this time -with the exception of a

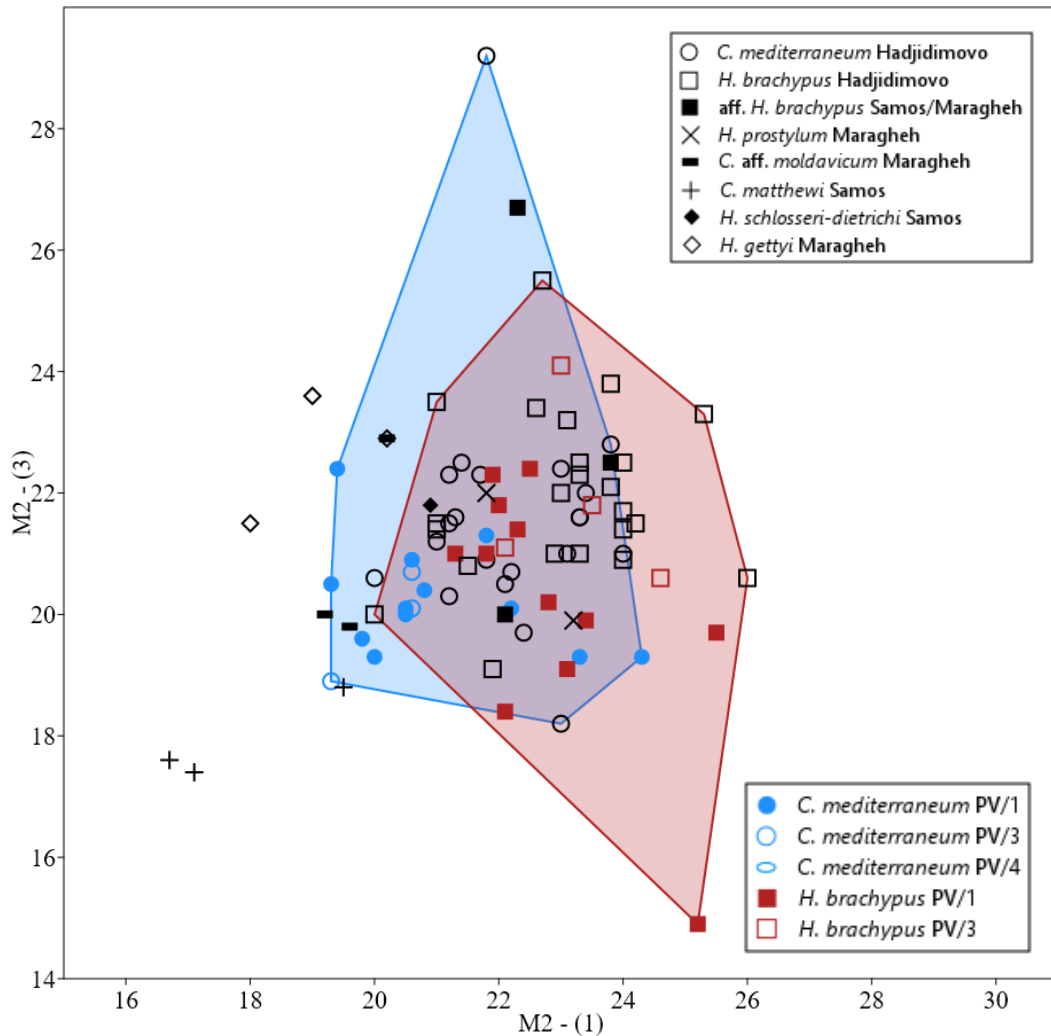




**Figure 25.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and width (measurement 3; Eisenmann *et al.*, 1988) of the M1 for adult specimens and associated comparative material.

pair of teeth, belonging to each of the two species, which seem to occupy the exact same point on the graph. The author has reviewed the sample multiple times and what can be inferred is that duplication of data can be ruled out, as the two specimens have slight differences in their other measurements. What's left, is the possibility the specimens showing actual complete overlap. The specimens in question are PMA 10059 & 10015.

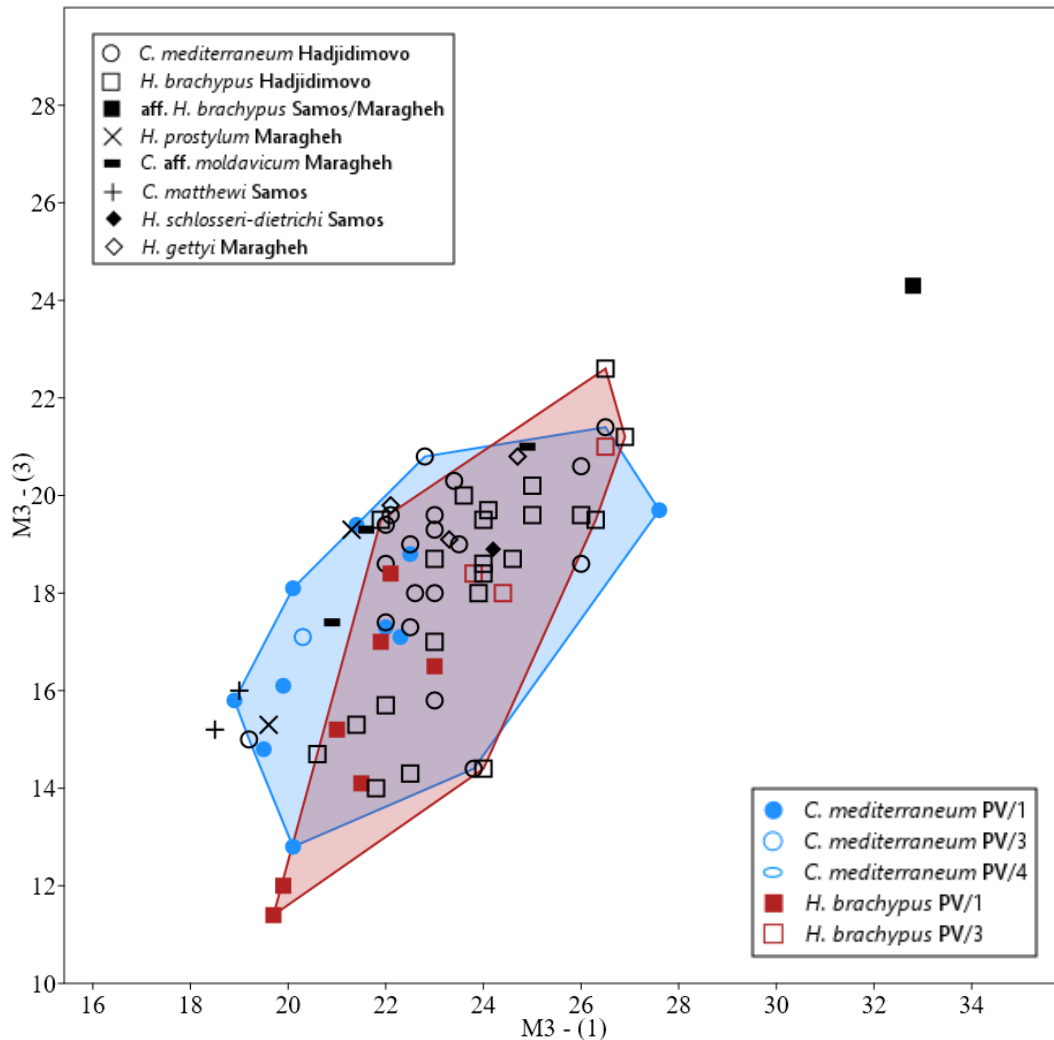
Moving on to the third deciduous premolars (Fig. 29), the *H. brachypus* sample is at its smallest -counting just four specimens-, but the comparative material comes to its support. The same general trend as with the dP2 can be



**Figure 26.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and width (measurement 3; Eisenmann *et al.*, 1988) of the M2 for adult specimens and associated comparative material.

observed, only amplified for the axis of width, rather than for the length of the tooth. This translates to the teeth of *H. brachypus* being generally wider -all the more so than being longer, compared to those of *C. mediterraneum*.

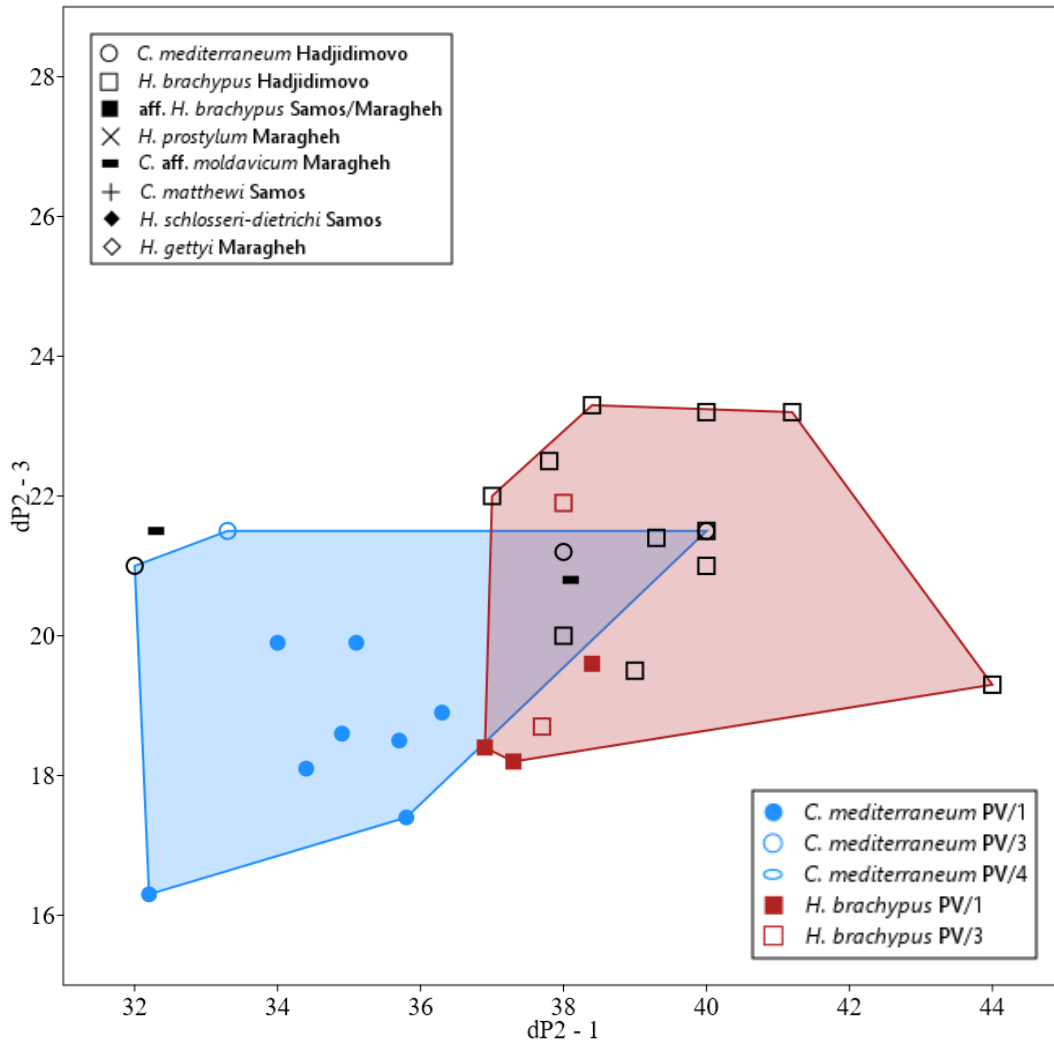
The fourth deciduous premolars are a more extreme example of the above case (Fig. 30). The overlap is extensive but the tendency of the dP4 of *H. brachypus* to be wider than those of *C. mediterraneum* is apparent, while both of the species' dP4 lengths vary to a similar degree and around a similar mean value.



**Figure 27.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and width (measurement 3; Eisenmann *et al.*, 1988) of the M3 for adult specimens and associated comparative material.

A relatively safer dental indicator for the distinction between the two studied species is the plication count of the buccal teeth. As is demonstrated by the diagram in Fig. 31, the plication count is consistently higher for the upper buccal dentition of *H. brachypus*. The difference peaks at P2 and M1, while it is at its lowest -to the point of the two groups being virtually indistinguishable from one another- for M3 (less than one single pli).

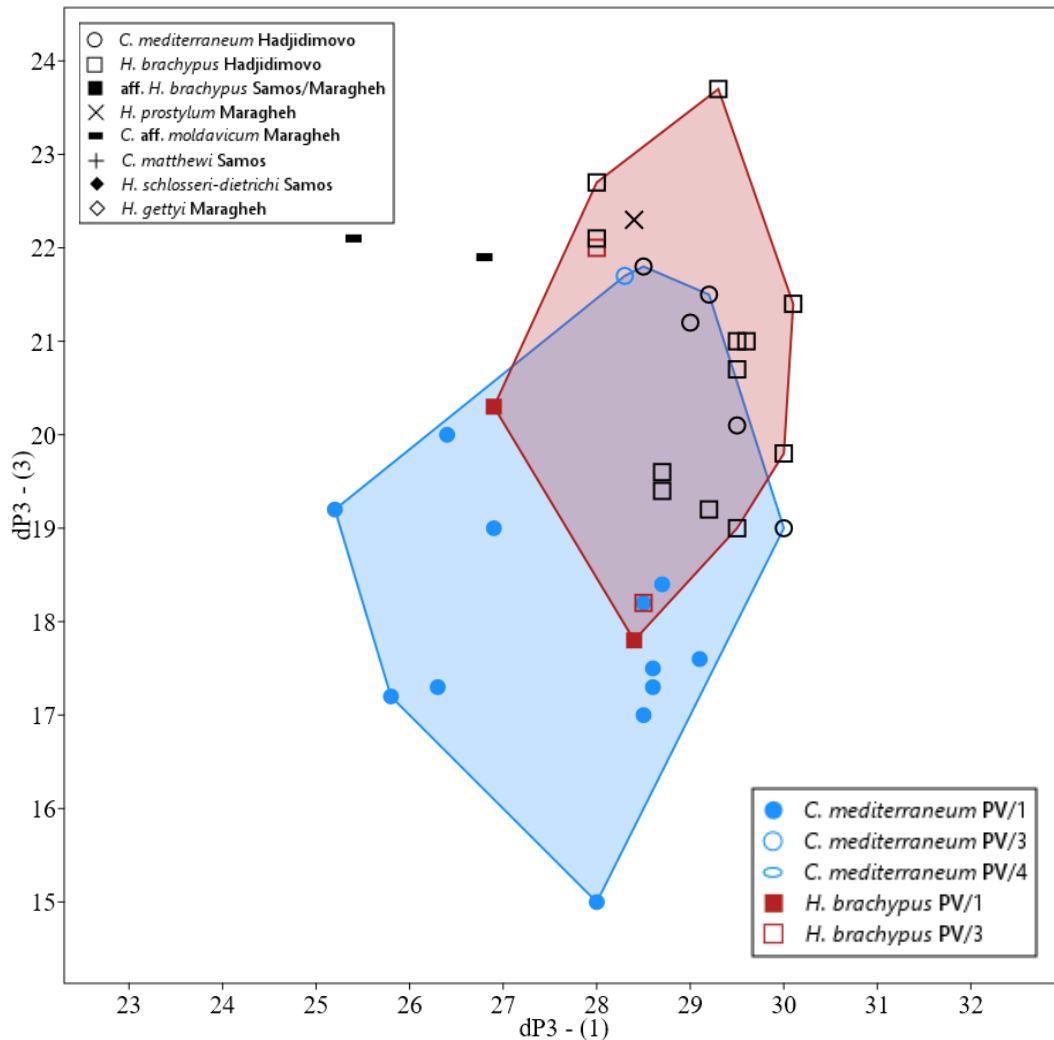
It should be noted at this point that even this feature is not free of overlap and specimens attributed to both species can be said to possess a “moderate” plication



**Figure 28.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and width (measurement 3; Eisenmann *et al.*, 1988) of the dP2 for juvenile specimens and associated comparative material.

count, falling in between the extremes present in the sample. This observation holds ground even if older or younger age groups are done away with.

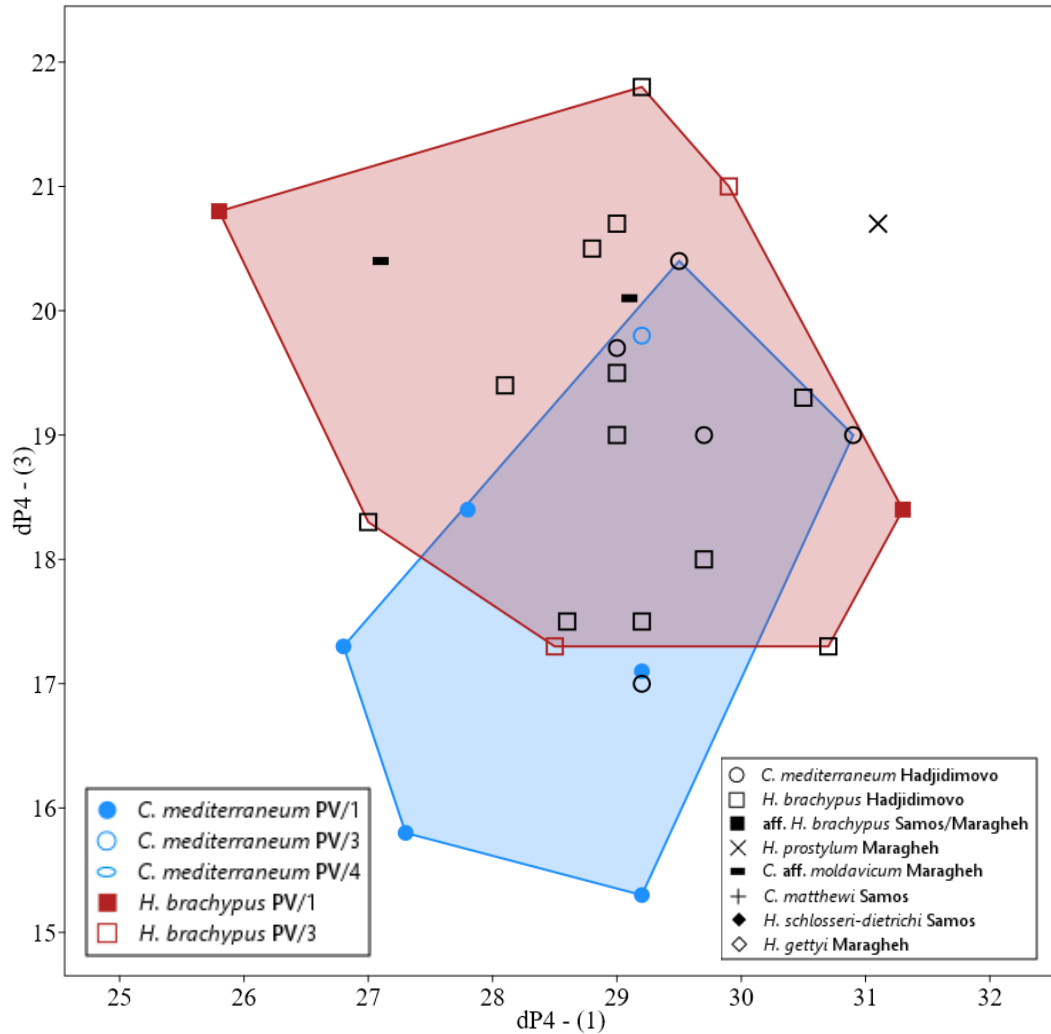
Overall, dental measurements at the occlusal level and plication counts are a rather unreliable means of identification for the species studied, but since isolated teeth or partial tooth rows with no other distinguishing or measurable cranial feature are frequently found in the locality, they cannot be overlooked. The identifications can be considered as accurate only if singular and bound feature (such as the length/width ratio or protocone index) measurements fall into an interval of non-



**Figure 29.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and width (measurement 3; Eisenmann *et al.*, 1988) of the dP3 for juvenile specimens and associated comparative material.

overlap -as mentioned before-, or if multiple independent measurable features are present and their correlation leans unambiguously towards one or the other species.

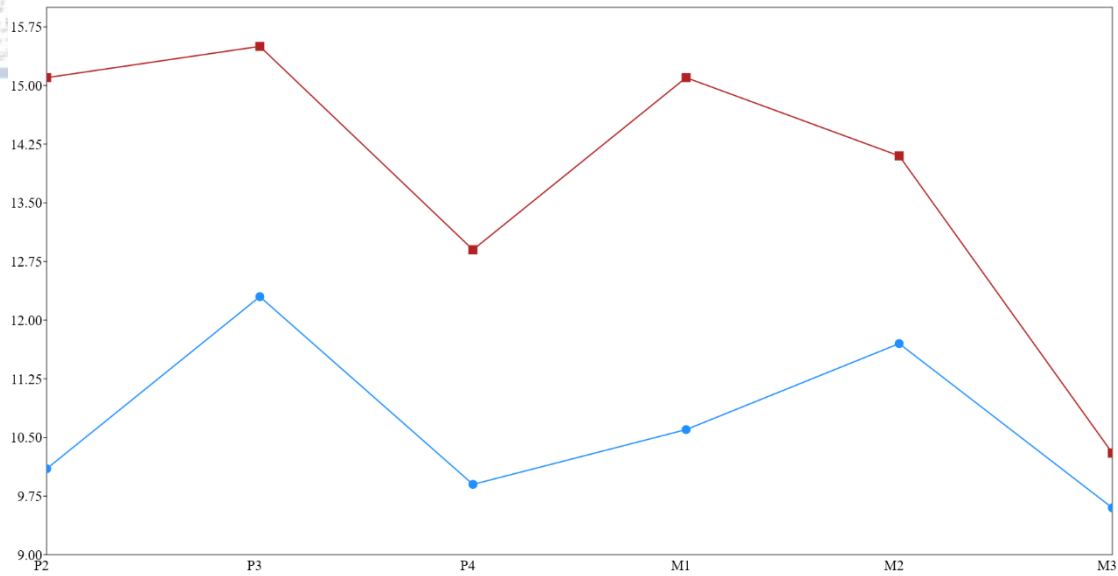
The protocone index expresses the percentage of the tooth's overall length the protocone covers. A comparison of the collected mean indices of all buccal teeth for the two species can be found in Fig. 32. The indices for *H. brachypus* appear lower than those of *C. mediterraneum*, indicating a smaller protocone in relation to the length of the tooth for the former. The familiar phrase of "significant overlap" echoes through this dataset as well, with only a handful of outliers steering the resulting means towards their respective values for each tooth.



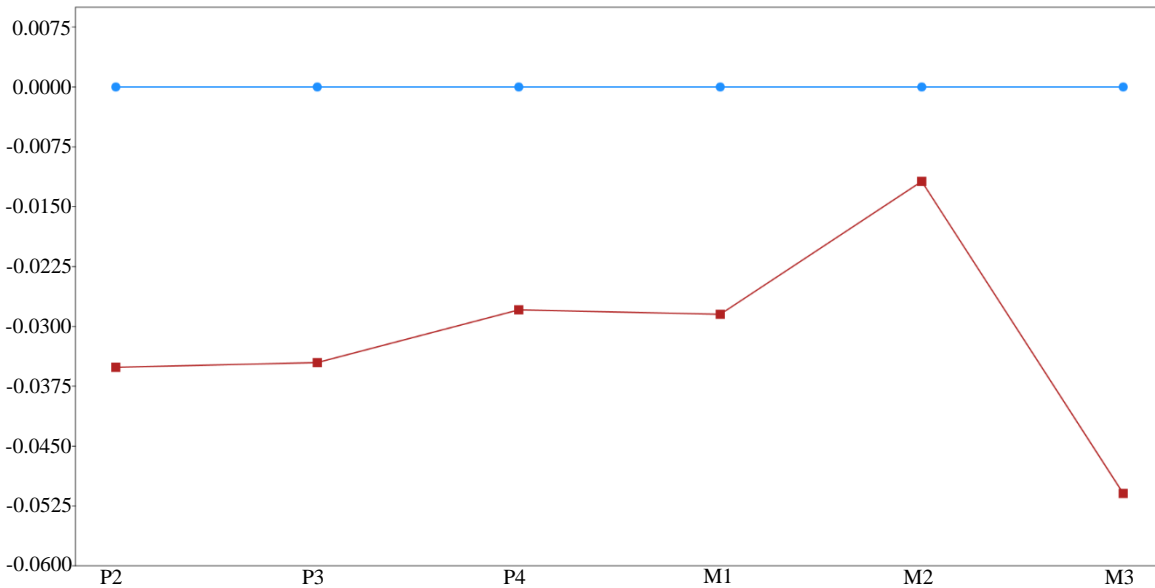
**Figure 30.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and width (measurement 3; Eisenmann *et al.*, 1988) of the dP4 for juvenile specimens and associated comparative material.

Finally, the hypsodonty index can be a useful taxonomic identifier, as well as a paleoecological proxy (Valen, 1960), but can only be implemented on unworn teeth, where their full length, all the way to the root, is exposed. As such, only intact and fully exposed teeth can be used for the extraction of the index. The most suitable candidate for this operation is isolated P2 specimens, with their distinct shape allowing for secure identification.

The results can be seen in Fig. 33, where the *C. mediterraneum* sample exhibits a higher index (which translates to less hypsodontic teeth) with a rather



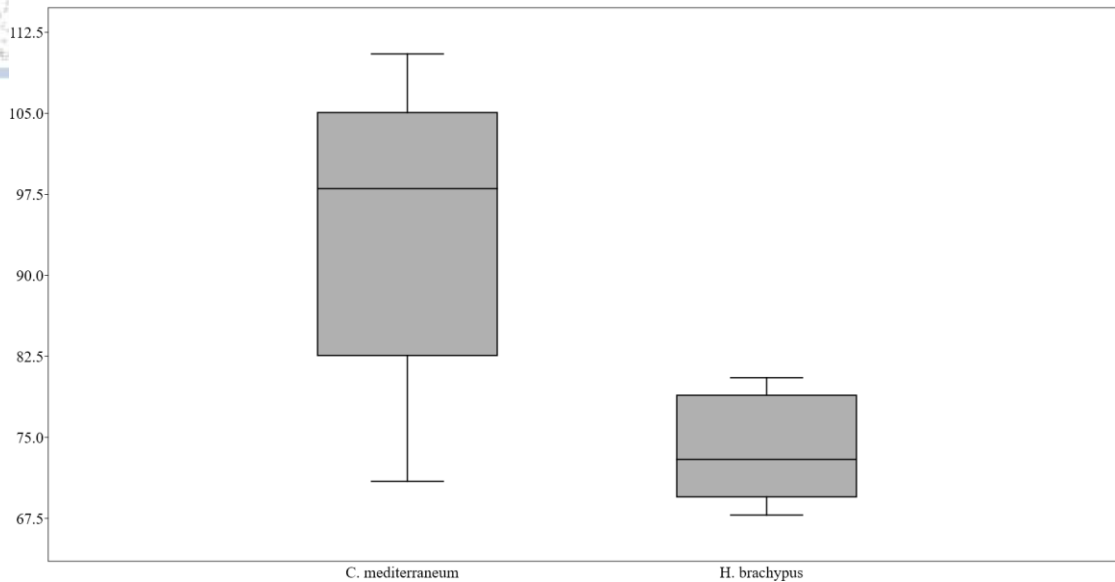
**Figure 31.** Diagram of the mean plication counts of *H. brachypus* (red) and *C. mediterraneum* (blue).



**Figure 32.** Decimal logarithm diagram of the ratios of the protocone indices of *H. brachypus* (red) to those of *C. mediterraneum* (blue), which is plotted as the baseline.

extended variability of values, while the *H. brachypus* one is more conservatively hypsodont.

As for the comparisons with material attributed to other species and localities (apart from Hadjidimovo), the first and easiest remark to make is about



**Figure 33.** Box plot of the hypsodonty indices of adult specimens.

*C. matthewi*. The two measured specimens of this species take their place consistently outside the point clouds of both of the described species, with their distinctively small values in all available measurements. What can be said with a certain degree of confidence at this point, is that if a specimen of the size class of *C. matthewi* existed in the studied sample, it would not be hard to identify.

The remaining comparative specimens, on the other hand, fall very near or within the areas occupied by *H. brachypus* and *C. mediterraneum*. *C. aff. moldavicum* specimens for example, tend to side with the most distinct of the *C. mediterraneum* specimens, while *H. prostylum* has a laxer behavior, occupying points in both of the species areas of congregation. Furthermore, *H. schlosseri-dietrichi* specimens tend to occupy points that lie almost exclusively within the intersections of both *H. brachypus* and *C. mediterraneum* groupings. This holds true for all of the plotted lengths to widths provided (Figures 22-30), for both adult and juvenile specimens.

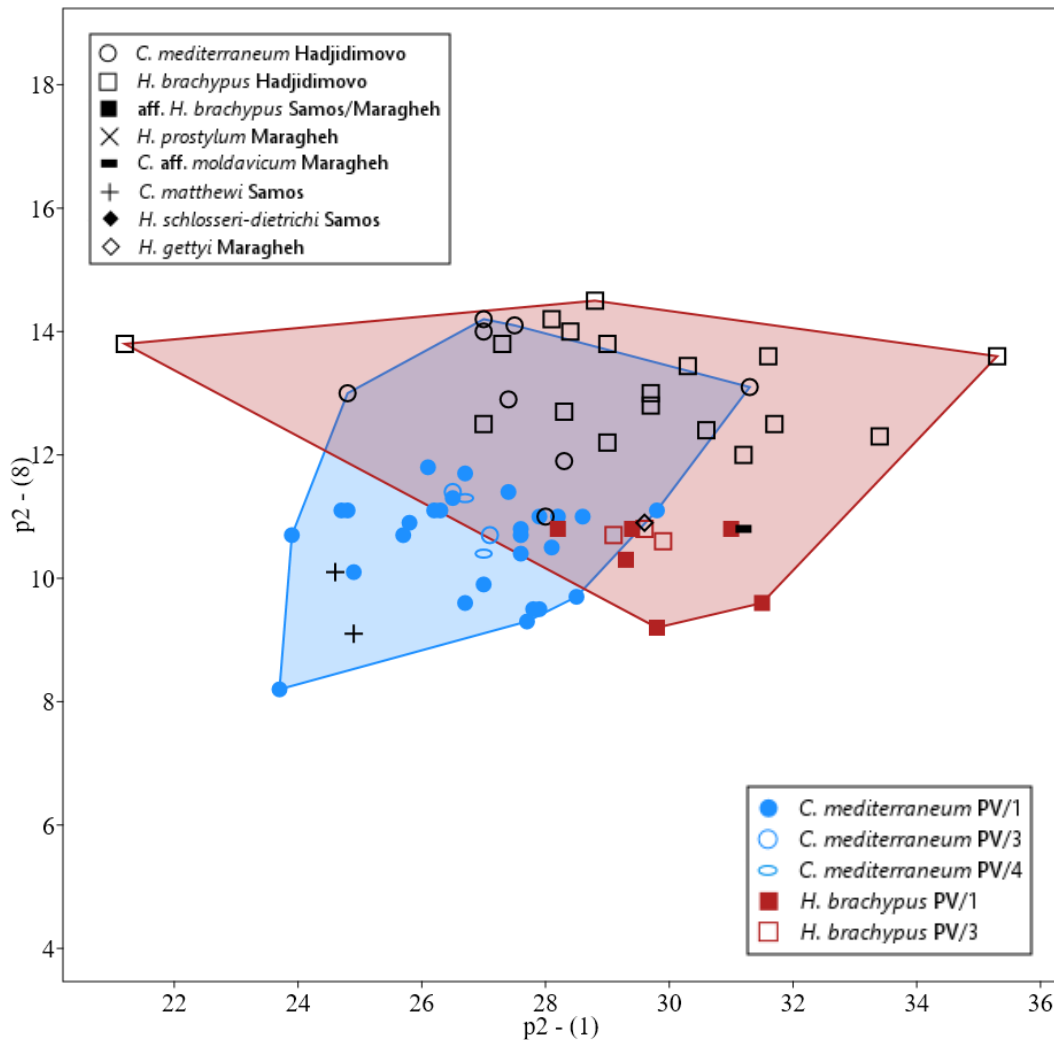
One noteworthy anomaly is this of specimen 1911/0005/118 (A4740) from Samos, attributed to aff. *H. brachypus* by Woodburne & Bernor (1980) and Forstén (1999), which -as distinctly small as *C. matthewi* appears- takes its respective place as perceptibly large in tooth dimensions (Figures 23-27) and especially in the width of its buccal teeth. It should be noted that examination of said specimen revealed it to be of a rather old individual (and this could be a contributing factor to the perceived anomaly). It should also be said that the studied sample itself contains older individuals as well, which tend to drag the plotted hulls towards larger values



(PV1/2622 is the sole example for *H. brachypus*), but not to the degree observed in the aforementioned specimen.

#### 4.2.3.2. Lower dentition:

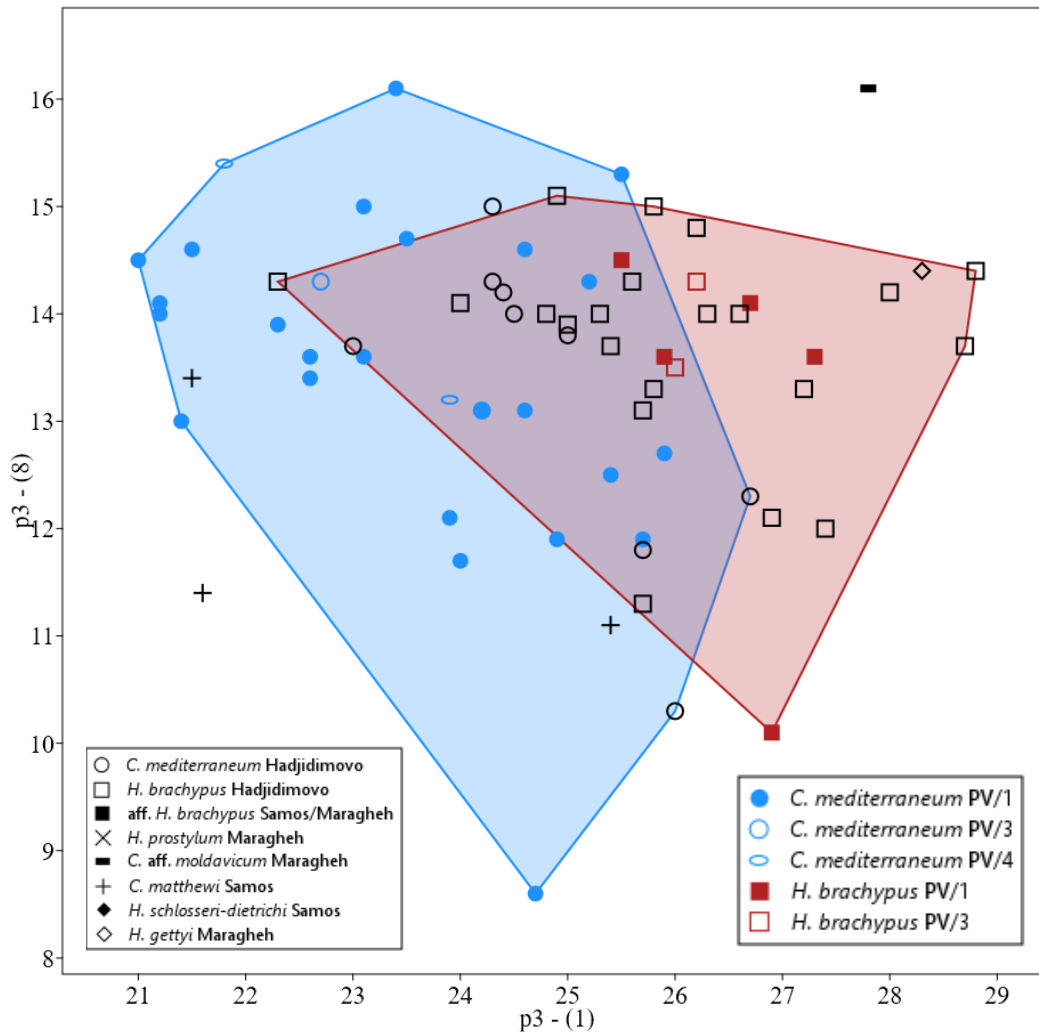
The lower dentition carries the distinction of being feature-full and feature-lacking at the same time, in the sense that -while it comes packed with various measurements, outlined for it in the given literature-, it is generally poor in measurable features that truly stand out, as is the case with the upper dentition.



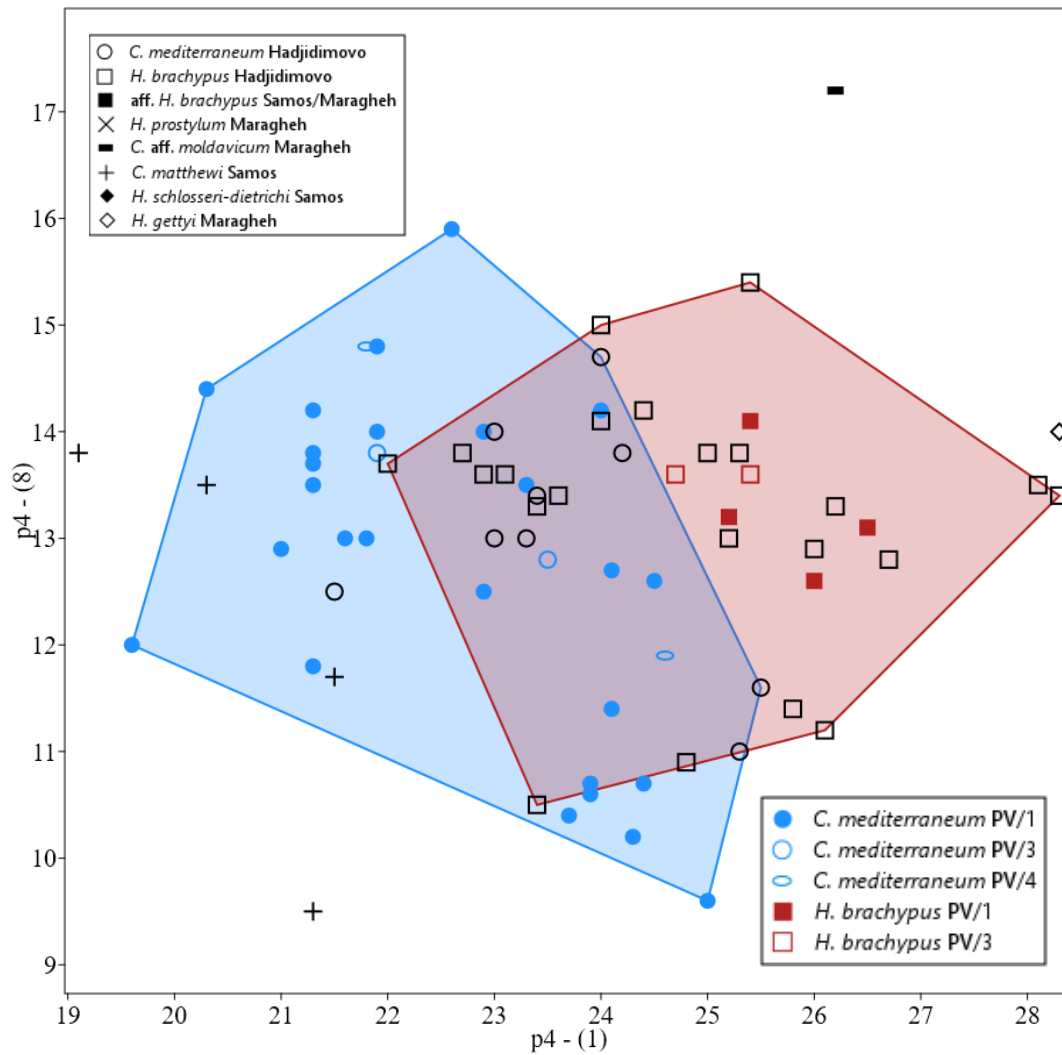
**Figure 34.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and the breadth from the metaconid to the enamel band labial to the protoconid (measurement 8; Bernor *et al.*, 1997) of the p2 for adult specimens and associated comparative material.

Plications (apart for the plis caballinid) and crenulations can only be qualitatively described and measurements for the anterior half of the tooth tend to closely follow the corresponding ones for the posterior half (e.g. measurements 4 & 5, or 8 & 9). Again, only their combined utilization has the capacity to produce relatively secure identifications.

The second lower premolar (Fig. 34) is yet another example of a slightly unhelpful comparative sample. Both of the species' measurements cluster together at larger tooth breadths. The studied sample, on the other hand, clusters quite neatly



**Figure 35.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and the breadth from the metaconid to the enamel band labial to the protoconid (measurement 8; Bernor *et al.*, 1997) of the p3 for adult specimens and associated comparative material.

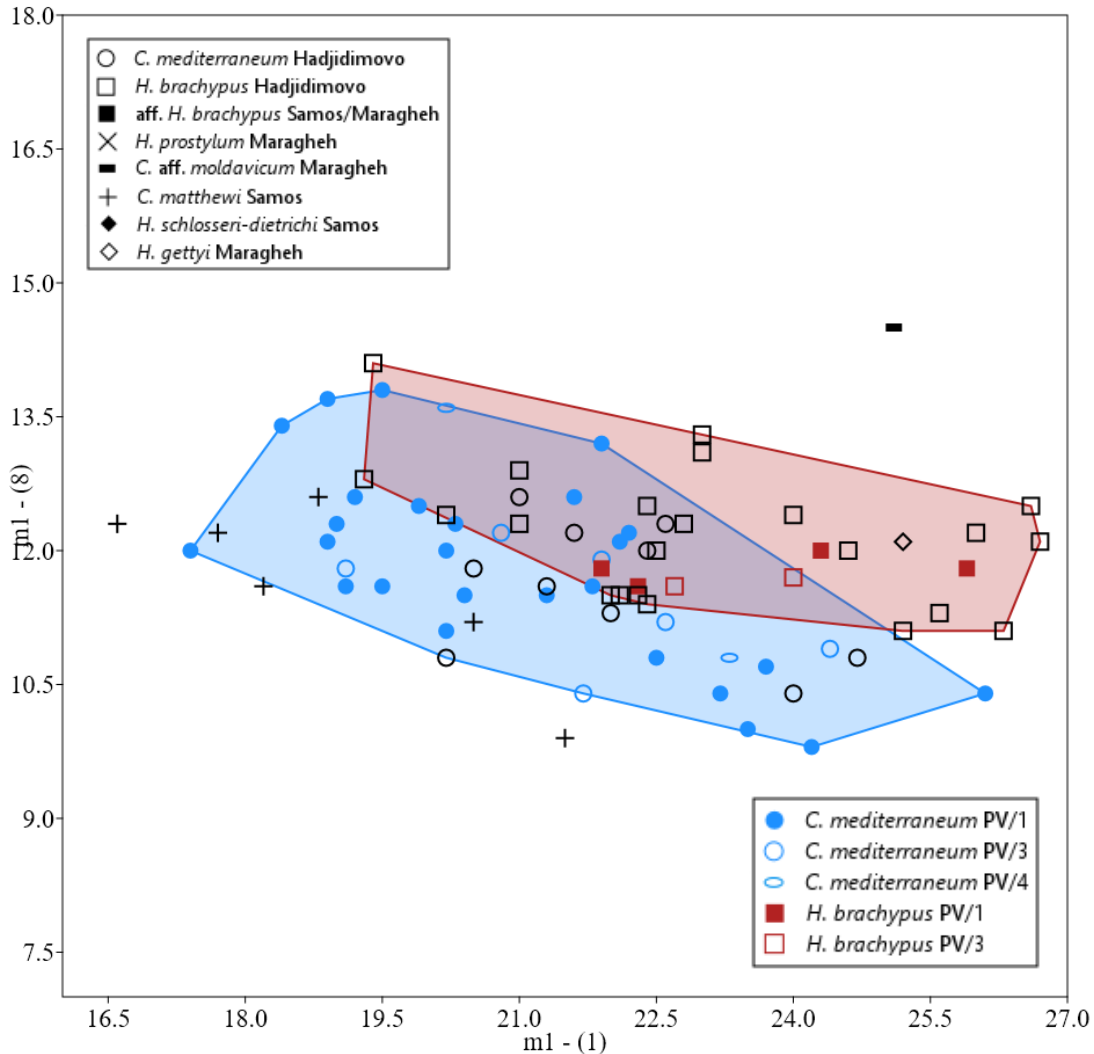


**Figure 36.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and the breadth from the metaconid to the enamel band labial to the protoconid (measurement 8; Bernor *et al.*, 1997) of the p4 for adult specimens and associated comparative material.

into two distinct groupings (Fig. 34) of equal breadth ranges, with *C. mediterraneum* exhibiting smaller lengths and *H. brachypus* larger ones.

This picture loses definition for the third and fourth premolars (Fig. 35 & Fig. 36), with the comparative sample occupying the center of the plot, along with *H. brachypus* and *C. mediterraneum* specimens of the studied sample. Even so, the studied material itself maintains the same behavior as with the p2, with *H. brachypus* grouped quite cleanly to the right (larger lengths) and *C. mediterraneum* to the left (smaller lengths).

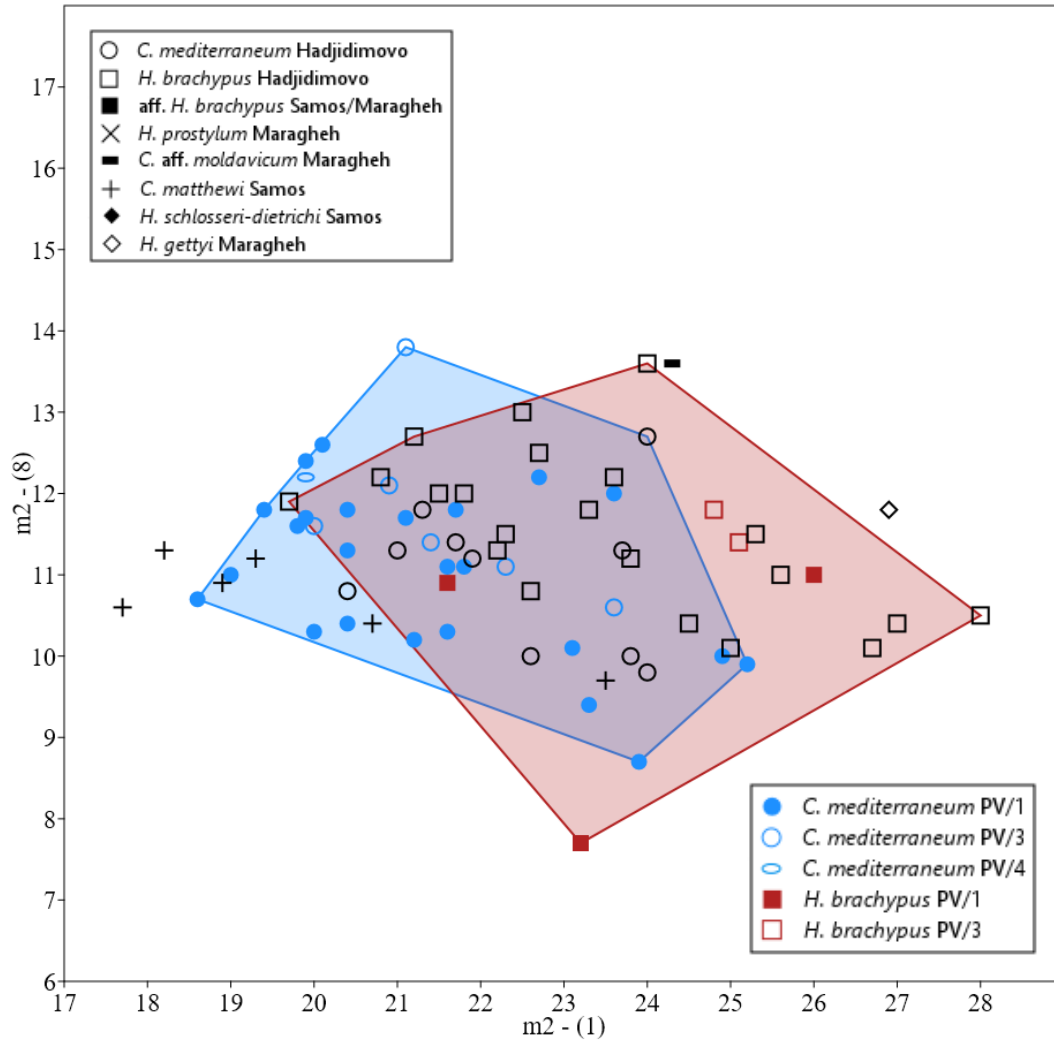
This horizontal arrangement takes up a meager vertical component in the case of the m1 (Fig. 37), where the measured *H. brachypus* specimens seem to tend towards longer and somewhat wider fourth premolars. An extended area of overlap is present for both the studied and the comparative material this time.



**Figure 37.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and the breadth from the metaconid to the enamel band labial to the protoconid (measurement 8; Bernor *et al.*, 1997) of the m1 for adult specimens and associated comparative material.

Even so, any meaningful signal of distinctness among the two species seems to deteriorate quickly along the molar row, so the m2 (Fig 38) carries all but the slightest horizontal component of differentiation, with even more extended overlap. A rather quirky aspect of the comparisons attempted in the present work is the fact

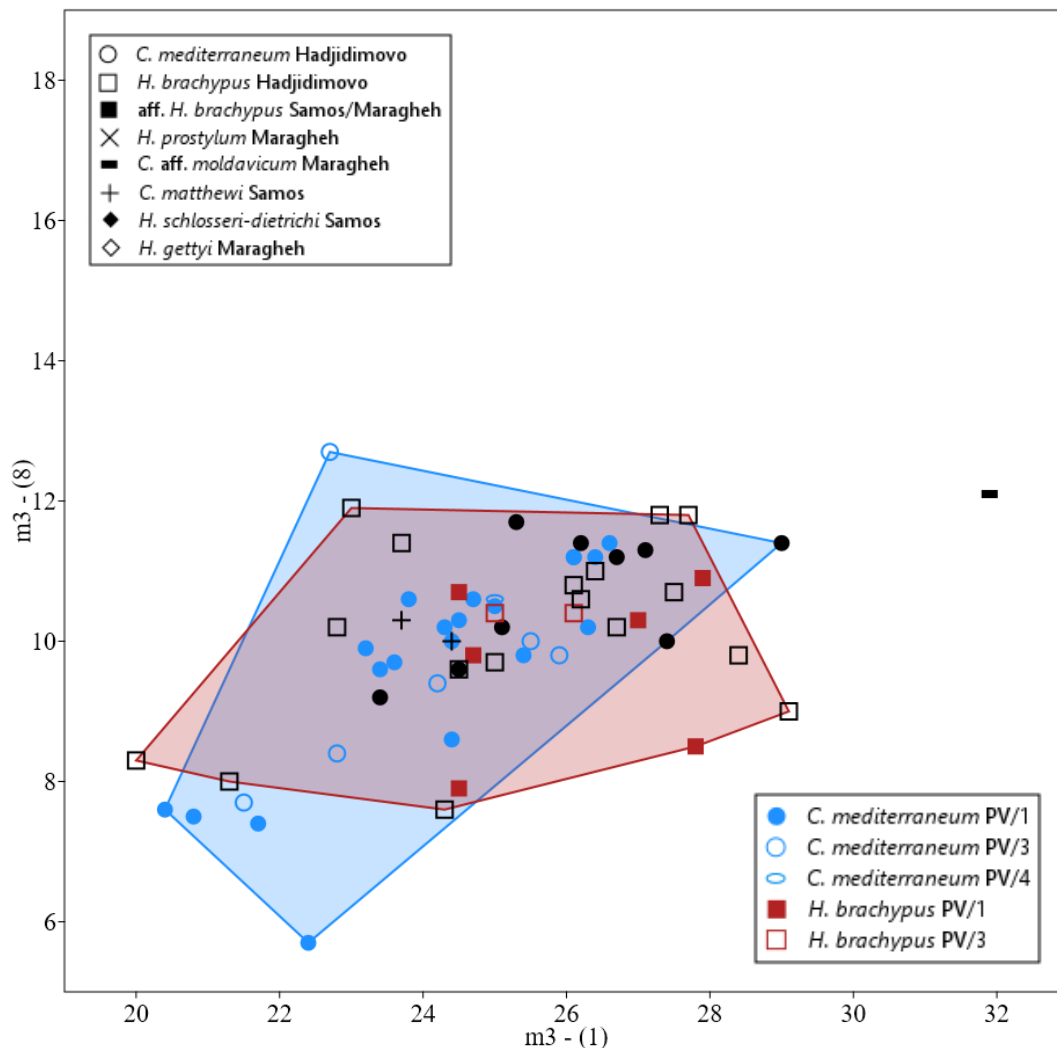
that -as far as dental measurements are concerned- the comparative data seems to be in agreement with the studied material mostly in cases -such as in this particular



**Figure 38.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and the breadth from the metaconid to the enamel band labial to the protoconid (measurement 8; Bernor *et al.*, 1997) of the m2 for adult specimens and associated comparative material.

one- where no strong conclusions can be drawn about the distinctness of the two species.

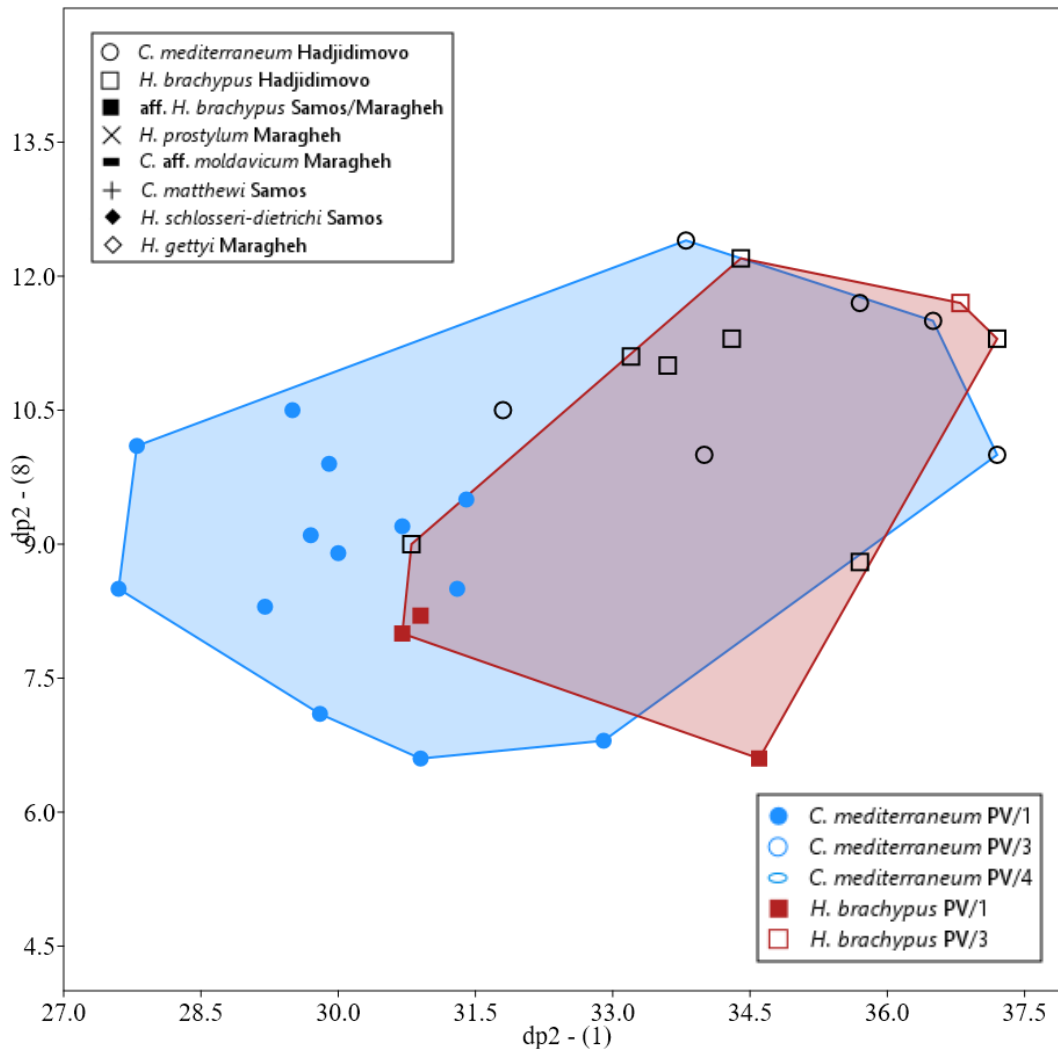
The m3 is where the overlap becomes total (Fig 39). The comparative material, not only offers no hinderance in making this situation obvious, but also helps in the identification of a possible -but very minor- trend towards smaller lengths for *C. mediterraneum* and larger ones for *H. brachypus*. This can be made



**Figure 39.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and the breadth from the metaconid to the enamel band labial to the protoconid (measurement 8; Bernor *et al.*, 1997) of the m3 for adult specimens and associated comparative material.

apparent if one is to eliminate the outliers from both the studied and the comparative material, and leave behind a visibly tighter clustering of points belonging to specimens of both species at the center of the graph.

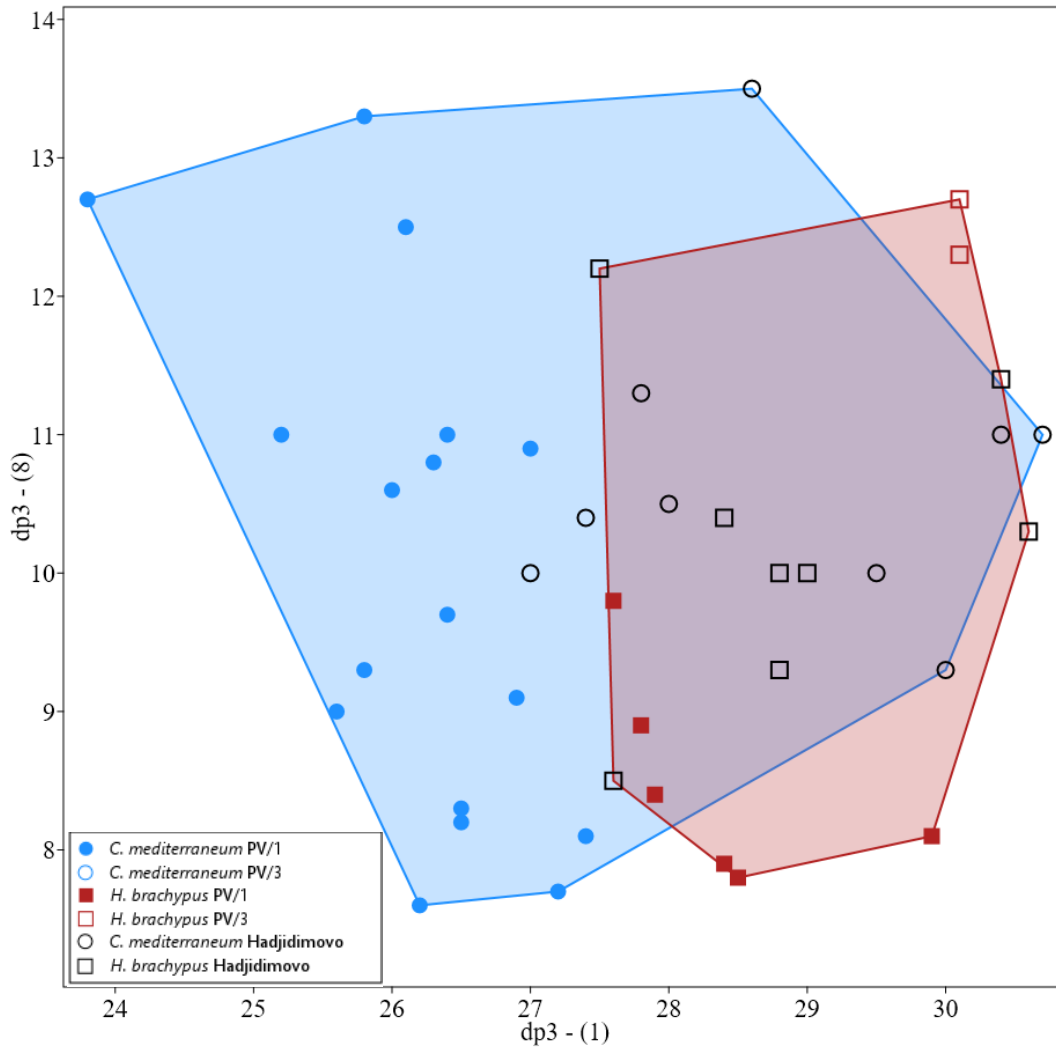
The tendency to differentiate length-wise and not so in breadth, is carried on to the deciduous teeth. The second deciduous premolars (Fig. 40) demonstrate this rather weakly, as the overlap is once again great. Secondly, the specimens



**Figure 40.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and the breadth from the metaconid to the enamel band labial to the protoconid (measurement 8; Bernor *et al.*, 1997) of the dp2 for juvenile specimens and associated comparative material.

of both species from PV1 seem to cluster together towards the smaller lengths (as well as somewhat smaller breadths), while the comparative material -accompanied by the sole measured specimen from PV3 occupy the antipodal area, towards larger lengths and slightly larger breadths.

This is carried over to the third deciduous premolars (Fig. 41), only now the vertical differentiation is once again lost. The aboved mentioned tendency

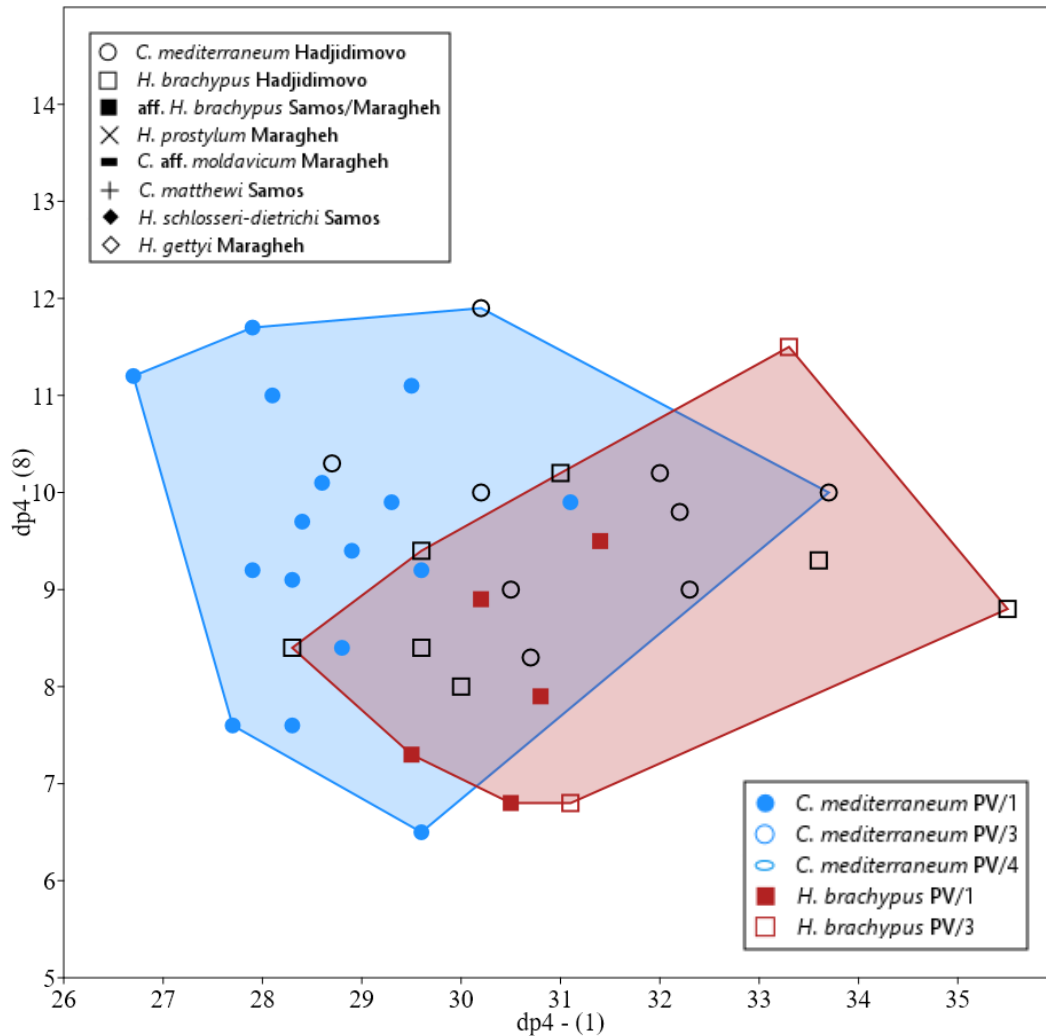


**Figure 41.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and the breadth from the metaconid to the enamel band labial to the protoconid (measurement 8; Bernor *et al.*, 1997) of the dp3 for juvenile specimens and associated comparative material.

of the material from PV1 to cluster towards smaller lengths is retained though, and the comparative material is now accompanied by two specimens from PV3 at the opposite side.

The Hadjidimovo material finally gives up the race for the fourth deciduous premolars, by moving closer to the PV1 material (Fig 42). The two measured PV3 specimens still maintain their place towards larger sizes though, alongside a few

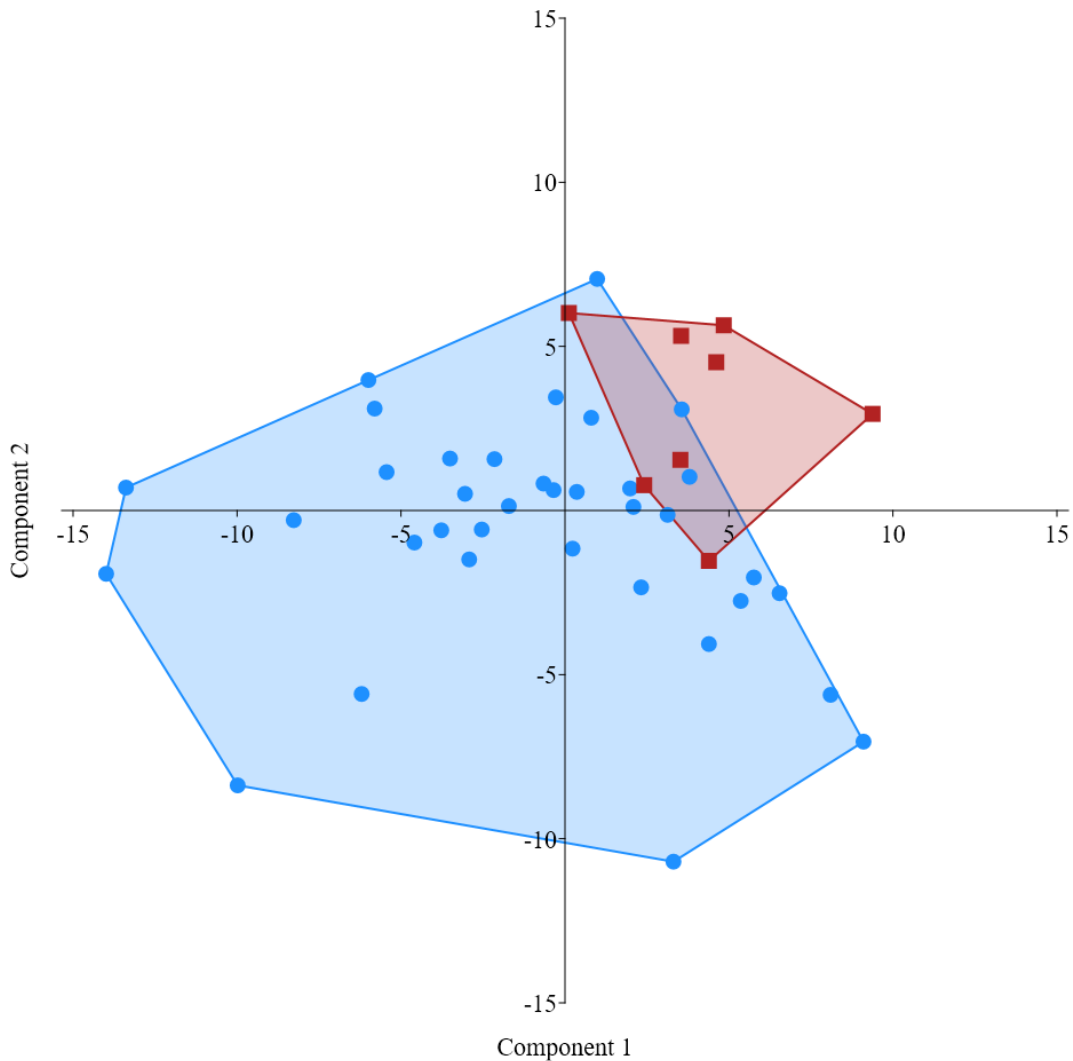




**Figure 42.** Scatter plot of the length (measurement 1; Eisenmann *et al.*, 1988) and the breadth from the metaconid to the enamel band labial to the protoconid (measurement 8; Bernor *et al.*, 1997) of the dp4 for juvenile specimens and associated comparative material.

specimens of the comparative sample. A slight reversal of the observed trend is witnessed on the breadth axis, with *C. mediterraneum* specimens clustering around higher values than *H. brachypus*.

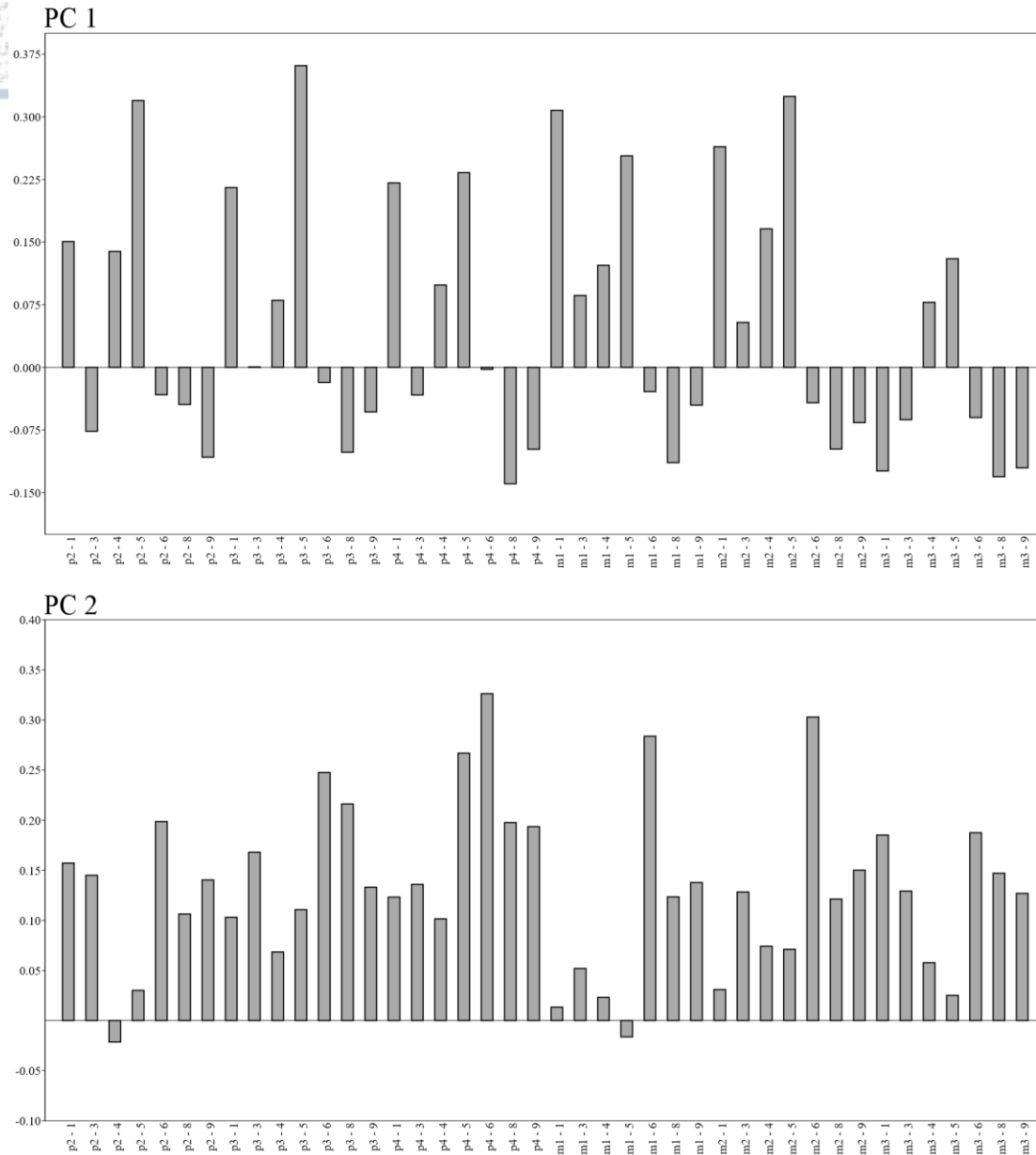
As far as the remaining comparative material is concerned, the usual suspect, *C. matthewi* is not as conspicuous as the upper dentition measurements let it on to be. They are still found at the lowest length and breadth areas for every



**Figure 43.** Principal component analysis of the combined mandibular tooth measurements of adult specimens. *H. brachypus* is represented by red squares and *C. mediterraneum* by blue circles. The loadings plots can be found in Fig. 44.

buccal tooth (Figures 34-39), only now in close proximity to smaller examples of *C. mediterraneum*. On the other hand, *C. aff. moldavicum* and *H. gettyi* from Maragheh take their place in the regions occupied by *H. brachypus*, towards larger lengths and breadths.

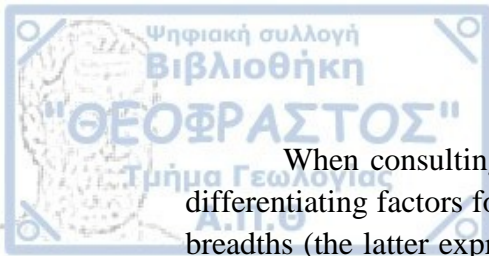
The remaining measurements for the lower dentition offered no particularly interesting plotting possibilities, either due to small sample sizes, or due to reduced



**Figure 44.** Loadings plots for the mandibular measurements of Principal Component 1 (top) and Principal Component 2 (bottom) used in the PCA analysis of Fig 45.

visual distinctiveness among species when plotted in pairs. Thus, the decision was made to not let them go to waste, but rather include them all -together with measurements 1 and 8, already outlined in Figures 34-39- in a Principal Component Analysis Plot (Fig. 43).

The analysis was performed for adult specimens, belonging to the studied material. Through it, two visible clusters of points emerged for the two studied species, with a minor degree of overlap.



When consulting the Loadings plots (Fig. 44), one can see that the main differentiating factors for the observed groupings -other than the tooth lengths and breadths (the latter expressed as the breadth from the metaconid to the innermost enamel band of the protoconid – or measurement 8), are the lengths of the postfovettes (measurement 5) and the breadth of the tooth, this time expressed as the width along the line connecting the ectoflexid to the linguaflexid (measurement 6).

One inference that can be made from the above is that the hypoconid is the element of the tooth that contributes the most to the increased overall length of the lower teeth of *H. brachypus*. Apart from this, the fact that another measurement expressing the general breadth of the teeth (measurement 6) has equal footing with the one (measurement 8) already having been observed to vary between the studied species is rather unsurprising and warrants no further examination.

## 5. DISCUSSION

### 5.1. Potential locality-specific features

No strong conclusions pointing to the studied hipparionine morphologies being temporally or geographically bound in relation to the comparative sample could be drawn. On that note, the Hipparionie-bearing site from Hadjidimovo is reportedly somewhat older than both PV1 and PV3 (Spasov 2002; Hristova, 2009).

That is not to say that differences were not observed. A noteworthy example is the tendency for *H. brachypus* specimens (Fig. 6) to cluster at lower values for the POB length (measurement 32) and the height of the POF (measurement 36) than their counterparts from Hadjidimovo. The same is true for the P2-Orbit distance (Fig. 8) along with a similar tendency for *C. mediterraneum* specimens. The studied sample is small in both cases.

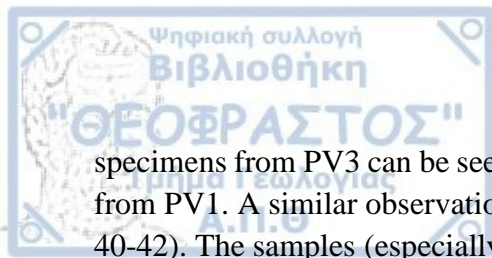
Another striking difference is in the total upper tooth row lengths (Fig. 12) for *C. mediterraneum* specimens. The Hadjidimovo sample could be said to be more akin to the given *H. brachypus* ranges, with its standard deviation interval sharing no values with that of the *C. mediterraneum* from Pikermi. This is reflected in the lower buccal tooth row as well (Fig. 20), but not to such a great degree.

In the case of the individual tooth measurements, the tendency for Hadjidimovo specimens to take on larger size values is continued to varying degrees -from barely visible to readily apparent. An example of the latter is the length and breadth values of the lower second premolars (Fig. 34), where the entire Hadjidimovo material is shifted upwards towards larger breadths. An overall remark -and one that warrants further study- is that distinct morphotypes for both of the studied species, may possibly exist at least at the two discussed localities. Whether these types bear a geographic or temporal component (or both) is an added unknown.

### 5.2. Inter-site comparisons

Inter-site similarities and differences are a tougher issue to tackle, mainly because the sample for PV3-PV4 is somewhat lacking in usable material. This is due to the smaller span of time for which said site remained active. Furthermore, the contemporaneity and faunal homogeneity along the various fossiliferous beds (Abel, 1912) of the classical site has been put into question in the past (e.g., Dermitzakis, 1976; Theodorou & Nicolaidis, 1988). This serves in making comparisons of its collective faunal content, with that of the newer sites (PV1-PV4), precarious at best.

From the very few samples retaining cranial features (Fig. 8, 9) no observable differentiation is apparent. This is also true for the mandibles examined (Fig. 15). Conversely, a slight grouping of PV3 *H. brachypus* specimens towards higher values can be seen in the length and breadth measurements of the M2 (Fig. 26), but the corresponding sample is small (only four molars from PV3). This can also be observed in the M3 (Fig. 27), where -if one is to remove the totally overlapping *C. mediterraneum* sample- the M3



specimens from PV3 can be seen to be drawn towards larger overall dimensions than those from PV1. A similar observation can be made for the lower deciduous premolars (Figures 40-42). The samples (especially for PV3) are, again, woefully small.

Even if the results presented herein are somewhat weak, the question of whether the (probably older than PV1, acc. to Böhme *et al.*, 2017) PV3 site has any correlation to Hadjidimovo (and other related Upper Miocene sites, such as in Northern Greece, Turkey and Iran), or even whether it stands as intermediate between it and PV1, is one deserving further examination -especially in the wake of continued excavation efforts, uncovering more and more material for study.

On that note, Pikermi is home to numerous excavation sites, of which PV1 is the only one to see persistent field activity, up until the present day. It would be a shame if the relation between the geographically neighboring, but temporally disparate sites of PV1, PV3 and Chomateri remained unexploited. For this reason, the need for the distribution of excavation campaigns out towards previously inactive and possibly new sites within the Mesogeia basin is much needed.

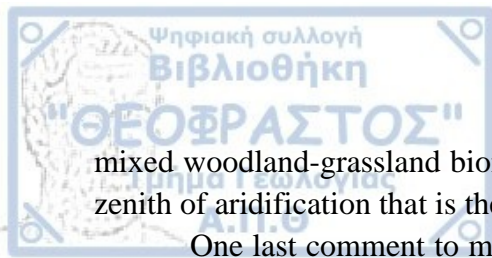
### 5.3. Paleocological remarks

The greater paleocological context in which the studied material can be accommodated is that of the gradually aridified Mediterranean region during the Turolian. It is marked by a drop in both temperature and humidity and extensive turnovers in vegetation and faunas. The vegetational transition from the expansive woodlands of the Vallesian to grasslands is well-documented (Quade *et al.*, 1989; Cerling, 1992; Morgan *et al.*, 1994; Suc *et al.*, 1999), as is the subsequent replacement of closed environment-adapted animals by open-adapted ones (Fortelius *et al.*, 2006). The studied locality of Pikermi finds itself in the middle of the Turolian and its documented faunal content is indicative of the aforementioned transition (Agustí & Antón, 2002).

As far as the present work is concerned, the only part of the implemented methodology that leaves room for paleocological interpretation is the measured hypsodonty indices (Fig. 33). Through them, the relative high degree of hypsodonty in *H. brachypus* is clearly demonstrated. As is known, the more hypsodont an animal is, the more well adapted to a coarse-grained diet it succeeds in being (Valen, 1960).

Both of the described species have equal footing in the faunal context of the locality, so there's a niche available for a more consistent grazer, which is filled by *H. brachypus*, as well as one for more generalist tendencies, which is in turn filled by *C. mediterraneum*. No readily apparent "tipping of the scale" towards one dietary habit or the other is observed, a fact consistent with what is already known about the locality (Roussiakis *et al.*, 2017).

So, in a sense, much of what is there to report about the material studied in the present paper, serves to reinforce known and agreed-upon concepts pertaining to the local paleoecology. Those can be summed up as the notion of the mid-Turolian Pikermi as a



mixed woodland-grassland biome -on some million years long steady course towards the zenith of aridification that is the Messinian Salinity Crisis (Hsü *et al.*, 1973).

One last comment to make though, is that one should not get too carried away by the “woodland receding into grassland” trope. Or -rather- by the notion that hipparionines are the perfect model animals to verify this transition. Bernor *et al.* (1999) remind us that while being more heavily built and hypsodont than previous forms, even members of the heavily-built *Hippotherium* complex are still far more gracile than modern equids -and much more inclined to browse at that.

This is something that should be kept in mind when attempts are made at adjusting reconstructions of the Pikermian paleoenvironment. The C3/C4-ratio proxies measured at the locality (Böhme *et al.*, 2017) are hard to overlook, but perhaps a mere shift in vegetation types, with the retention of a rather dense, but open-canopy woodland environment should not be out of the question. Perhaps, Solounias *et al.* (1999) and their “savanna myth” need a revisiting -with all the required modifications stemming from more recent studies.

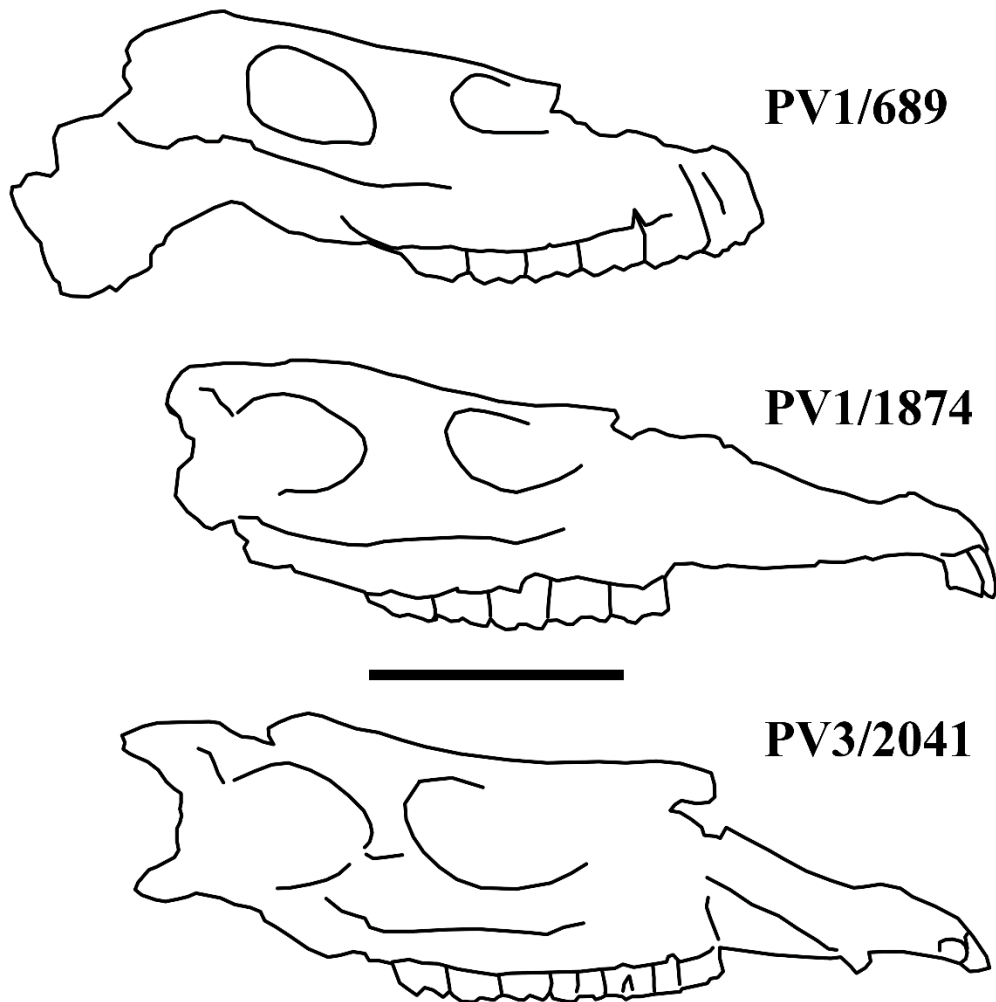
#### 5.4. The elusive “third species”

Among the modern literature describing the equids of Pikermi, Woodburne & Bernor (1980) and Bernor *et al.*, (1980, 1989) stand out for recognizing three hipparionine species in the locality. Of those species, the first two correspond to the unambiguously recognized and well-documented *H. brachypus* and *C. mediterraneum*. The third species was designated as *H. cf. prostylum* and was primarily based on a single specimen from Pikermi (NHML M42603). The specimen is described as having a longer preorbital bar and a narrower snout than *H. mediterraneum* (Bernor *et al.*, 1996). Bernor *et al.* (1996) note the difficulty in distinguishing the latter species due to its similarities with *H. mediterraneum* and its apparent rarity in the locality of Pikermi. *H. cf. prostylum* in relation to Pikermi resurfaces in Bernor *et al.* (2016), where the presence of a single calcaneus, attributed to either *C. mediterraneum* or the former is briefly mentioned and plotted.

Woodburne & Bernor (1980) and Bernor *et al.*, (1980) also refer to a specimen attributed to *H. cf. prostylum* from the NHMW, numbered A4673 and tentatively to a fourth possible species with an affinity towards *H. proboscideum* (NHMW A4668). This is partially amended though, in a later work by Bernor *et al.* (1996), which only recognizes three hipparionine species at Pikermi (*H. brachypus*, *C. mediterraneum* and *H. cf. prostylum*). On a similar note, Theodorou (1997) tentatively recognizes more than two morphotypes in Pikermi, based on the dimensions of postcranial elements.

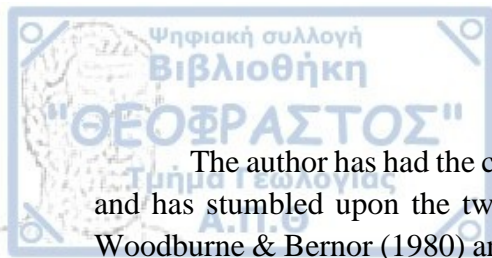
The reason for referring to the above remarks is that all specimens studied in the present work but one, fall very well within the osteometric and descriptive confines of *H. brachypus* and *C. mediterraneum*. The one exception (PV1/1874; Appx. B, Plate 4), may be have been provisionally attributed to *C. mediterraneum* by the author -as it lies neatly within the measured ranges of the species’ cranial morphology- but some aspects of the facial area stand out. For one, the POB is rather oval and elongated and it’s distinctly

antero-posteriorly aligned, rather than in an angle as is typical for *C. mediterraneum* (Fig. 45). The preorbital bar seems slightly elongated -again in visual comparison with definite *C. mediterraneum* specimens (Fig. 45)- even though it doesn't veer wildly off typical measurements. Secondly, the snout appears narrow, having a breadth at the posterior borders of the I3 which is the smallest measured and almost a centimeter narrower than the other two measured specimens. Other than the above, the rest of the cranial measurements, as well as the dental morphology and morphometrics correspond to the studied and comparative material attributed to *H. mediterraneum*.



**Figure 45.** Skull outline of PV1/1874 (Appendix B – Plate 4) in lateral aspect, compared to those of PV1/689 (*H. brachypus*; Appendix B – Plate 1) and PV3/2041 (*C. mediterraneum*; Appendix B – Plate 10). Scale bar is 10 cm.





The author has had the chance to review the hipparionine material from the NHMW and has stumbled upon the two previously mentioned problematic skulls referenced by Woodburne & Bernor (1980) and Bernor *et al.*, (1980). The one attributed tentatively to *H. proboscideum* (MNHW A4668) is of no particular interest as pertaining to the subject discussed and the author has to agree with Koufos (1987) that it closely resembles *C. mediterraneum*, especially as far as the short length of its POB goes.

The remaining one (NHMW A4673) proved impossible to get a full set of measurements from, as it is still attached to its mandible by a mass of the original matrix. The length of the partially destroyed POB could be gauged, at least. It provided with a POB length of 35,9 mm, which falls in between those of referenced and studied specimens of *H. brachypus* and *C. mediterraneum*. The measured POB length of PV1/1874 is somewhat smaller, but still closer to the former than any other specimen, attributed to *C. mediterraneum*. The shape of the POF is reminiscent of *H. brachypus*. It's short, oval or tear-shaped and positioned parallel to the antero-posterior axis of the skull. Further preparation of specimen NHMW A4673 is recommended, as the separation of the mandible from the skull could provide access to further measurements and observations.

Other than the above-mentioned comparisons, an affinity to *C. matthewi* can be quickly ruled out, since most of its cranial measurements present with characteristically lower values than any of the reviewed samples. The other species composing the extended comparative material (*C. moldavicum*, *H. "schlosseri-dietrichi"* acc. to Forsten, 1999, *H. gettyi*) do not fit the bill either, as they have been shown to approach or surpass *H. brachypus* in cranial and dental measurements. Finally, the recently discovered *H. phlegrae* from the Turolian locality of Kryopygi (Lazaridis & Tsoukala, 2014) also does not fit the description, as the snout dimensions differ significantly.

As it seems, the implications of specimen PV1/1874's peculiar morphology will remain unresolved for the time being. Additionally, the discussion may have resumed, but the wider issue is no nearer to being settled. Once more the "suspect sample" is a mere single specimen. A point can be made here about the perils of provisional diagnoses, based on incomplete datasets. Bernor *et al.* (1996) for example, argue that this third species exists but is exceedingly rare, compared to the ubiquitous *H. brachypus* and *C. mediterraneum*. Could it be that this third representative is not really as rare as purported, but has rather been erroneously absorbed by either or both of the two remaining species in following works, due to misattribution of relatively incomplete specimens?

For the resolution of this matter, it is the author's opinion that, even minor divergences from the expected variability in the hipparionine horse sample from Pikermi should be evaluated meticulously, when studying new material -or revising existing data- from the type or related localities. Then perhaps, after a sufficient dataset has been built, a definite answer may be given as to the presence of additional forms, their taxonomic identity and their share in the faunal content of the locality.

## 6. CONCLUSIONS

Despite the difficulties the two studied species (*H. brachypus* and *C. mediterraneum*) pose in their distinction and identification, the extraction of definite diagnoses has proven attainable for the whole of the studied material. One conclusion arose with certainty during the process: The range of measured values for nearly all metric characters share at least some degree of overlap between the two identified species. This, coupled with the added commonality of possible descriptive character states leads to two groups that -if examined in a comparative material-free vacuum- may become undoubtedly distinct from each other, only through the examination of their POB and POF.

Put simply, if an imaginary Pikermian hipparionine head (Fig. 46) was to be constructed, by selecting particular existing values from the provided measurement ranges and a drape was thrown over its facial region -covering the POB and leaving the overall dimensions of the skull and features of the complete dentition open to examination-, one would definitely fail to identify whether the hipparionine horse in question was either *H. brachypus* or *C. mediterraneum*.



**Figure 46.** Pikermian hipparion in the face of existential dread.

This, of course, is not a conclusion aiming to assist in the dissolution of the known systematics of the species in question. Quite the contrary. The picture never be complete without the comparative examination of more related forms in order to reconstruct a complete evolutionary history.

A possible anagenetic (real or hypothetical) series of genera, along with their closest branching relatives, may differ from other representatives of their collective higher taxonomic rank solely on the length of the little toe for example -but still, if that little toe bears clear signs of certain evolutionary trends along said series, this is a fact that cannot

be overlooked when constructing the systematics of the groups in question. The resolution of these issues is beyond the scope of this thesis, but the contributions of other workers (Bernor *et al.*, 1988; 1996; 1999; Bernor & Lipscomb, 1995; Bernor & Franzen, 1997; Hristova, 2012), detailing the possible phylogenetic groupings of Old-World hipparionines were taken into consideration and have already been discussed.

Leaving ties to higher systematics behind and moving on to the species level *per se*, no doubt whatsoever emerges for the ubiquitous presence of both *H. brachypus* and *C. mediterraneum* in the studied sites. The combined evaluation of all cranial, mandibular and dental features conforms to the descriptions provided by the relevant literature. Therefore, a blunt-snouted (Koufos, 1987, 1988; Koufos *et al.*, 2021) *C. mediterraneum*, with a wide, elliptical palate (Koufos, 1987) and a large -mainly subtriangular POF, positioned close to the orbit (Koufos, 1987, 1988; Bernor *et al.*, 1997; Hristova, 2009), was found to stand alongside a more long and narrow-snouted *H. brachypus* (Koufos, 1987; Atabaadi *et al.*, 2011; Lazaridis, 2015; Koufos *et al.*, 2021), with generally highly plicated upper buccal teeth (Koufos, 1987; Koufos & Vlachou, 2005; Vlachou & Koufos, 2009; Koufos *et al.*, 2021) and bearing a smaller, more oval POF, which sits further away from the orbit (Bernor *et al.*, 1996; Koufos, 1987; Hristova, 2009; Koufos *et al.*, 2021).

The paleobiogeographic and paleoecological analysis performed in the present work is confined to comparisons with a limited dataset, from the single other locality of Hadjidimovo - Bulgaria (Hristova, 2003, 2009; Hristova *et al.*, 2003). It is incomplete at best, but serves to indicate possible threads of further study that can be carried through with the enrichment of the local sample and the continued examination of all available comparative material.

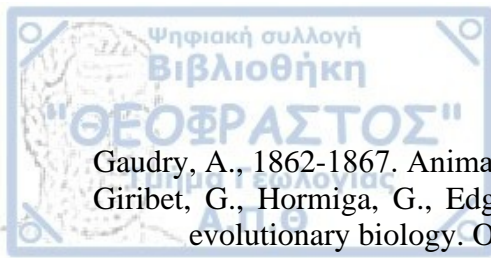
All of the above, coupled with the ever-present suspicion (further incited by the problematic PV1/1874 specimen) of one or more, as-of-yet unidentified hipparionine species native to the locality (Woodburne & Bernor, 1980; Bernor *et al.*, 1980, 1989, 1996, 2016), serve to prove that Pikermi -even after nearly two centuries of excavations- still seems to withhold new and significant insights into the zoographic, biogeographic and ecological past of Greece and beyond.



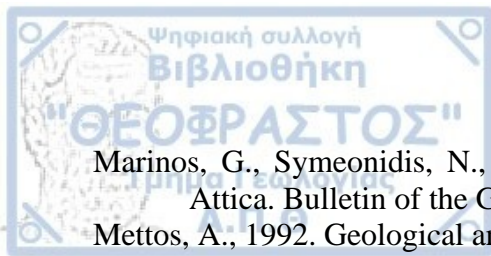
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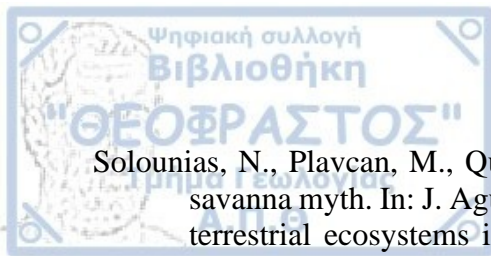
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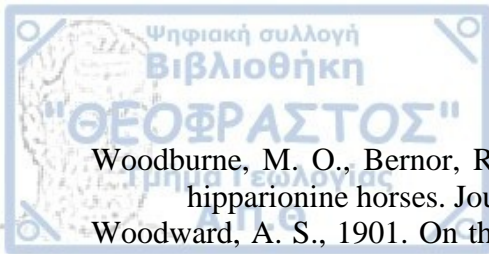


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## APPENDIX A: Measurement tables

Specimen #	Cranial Measurements (mm)																			
<b>C. mediterraneum</b>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Adult																				
n	3	3	1				9	10	7	1	3	2	5	2	3	2				1
Average	100.6	90.33	102.2				75.06	63.86	138.2	65	33.67	39.1	63.08	36.65	50.93	65				155
Minimum	87.6	74	102.2				66.8	56.8	126.1	65	31.3	38.3	61.7	35.8	45.5	58				155
Maximum	108.2	107	102.2				85.2	68.4	150	65	38.1	39.9	67.2	37.5	54.8	72				155
Std. deviation	9.236	13.47	0				4.791	3.171	7.117	0	3.137	0.8	2.078	0.85	3.955	7				0
Coef. of variation	0.092	0.149	0				0.064	0.05	0.051	0	0.093	0.02	0.033	0.023	0.078	0.108				0
Juvenile																				
n							5													
Average							78.73													
Minimum							59.2													
Maximum							88.3													
Std. deviation							11.47													
Coef. of variation							0.146													
<b>H. brachypus</b>																				
Adult																				
n		3	2	2	2		8	11	6	1	1	3	3			2	1			
Average		112	96.15	86	173.9		82.29	70.15	149.5	67.9	32.4	36.47	60.03			71.9	142.7			
Minimum		108.2	87.6	73.8	148.2		80	66.7	143.9	67.9	32.4	35.7	53.4			64.6	142.7			
Maximum		118.2	104.7	98.2	199.6		87.6	74.9	158.8	67.9	32.4	38	66.9			79.2	142.7			
Std. deviation		4.439	8.55	12.2	25.7		3.188	2.606	5.558	0	0	1.084	5.514			7.3	0			
Coef. of variation		0.04	0.089	0.142	0.148		0.039	0.037	0.037	0	0	0.03	0.092			0.102	0			
Juvenile																				
n	1	1	1				4				1	1	1	1	1	1			1	
Average	96.9	102.3	91.8				89.57				32.2	37.4	55	36.4	59.7	58.4			164.5	
Minimum	96.9	102.3	91.8				83.9				32.2	37.4	55	36.4	59.7	58.4			164.5	
Maximum	96.9	102.3	91.8				93				32.2	37.4	55	36.4	59.7	58.4			164.5	
Std. deviation	0	0	0				4.037				0	0	0	0	0	0			0	
Coef. of variation	0	0	0				0.045				0	0	0	0	0	0			0	
Specimen #	Cranial Measurements (mm)																			
<b>C. mediterraneum</b>	21	22	23	24	25	26	27	28	29	30	31	32	P2-Orbit	33	34	35	36	37	38	
Adult																				
n					1	1		2	3	2	4	5		5	5		5	5	1	5
Average					75.5	95.5		61.2	41.2	134.9	129.8	24.8	146.46	62.24			41.4	22.02	49.2	58.66
Minimum					75.5	95.5		58.1	35.2	125.5	121.4	18.9	137.7	54			28.9	15.5	49.2	41.5
Maximum					75.5	95.5		64.3	48.4	144.3	134	27.4	162	67.3			58.5	30.4	49.2	83
Std. deviation					0	0		3.1	5.455	9.4	4.936	3.078	8.338009	4.444			9.602	4.873	0	14.05
Coef. of variation					0	0		0.051	0.132	0.07	0.038	0.124	0.05693	0.071			0.232	0.221	0	0.239
Juvenile																				
n																				
Average																				
Minimum																				
Maximum																				
Std. deviation																				
Coef. of variation																				
<b>H. brachypus</b>																				
Adult																				
n						2		2	2				3	2	2		2	3		3
Average						72.05		61.4	39.15				35.6	151.1	54.35		32.85	32.27		63.27
Minimum						68		55.7	38.1				28.8	146.2	49.5		28.8	26.9		58.8
Maximum						76.1		67.1	40.2				42.5	156	59.2		36.9	39		67.6
Std. deviation						4.05		5.7	1.05				5.593	4.9	4.85		4.05	5.033		3.594
Coef. of variation						0.056		0.093	0.027				0.157	0.032429	0.089		0.123	0.156		0.057
Juvenile																				
n				1					1					1		1				1
Average				295					59					35.8		51.6				57
Minimum				295					59					35.8		51.6				57
Maximum				295					59					35.8		51.6				57
Std. deviation				0					0					0		0				0
Coef. of variation				0					0					0		0				0

Ψηφιακή συλλογή

Specimen #	Mandible Measurements (mm)													
<b>C. mediterraneum</b>	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Adult														
n		8	24	25	16	4	10	2	3	7	10	13	9	11
Average		97.1	73.74	68.54	140.7	107.3	48.81	175	155.1	77.11	59.78	45.97	74.89	30.21
Minimum		91.7	64.5	64.3	128.7	95.4	43.6	175	140.5	72.9	52.3	41.6	67.5	27.5
Maximum		110.7	80	73.1	149.8	117.2	53.5	175	165.1	85.3	65.3	52.2	82.6	32.4
Std. deviation		7.902	4.724	2.389	6.672	9.019	3.267	0	10.54	4.106	4.234	3.897	4.796	1.941
Coef. of variation		0.081	0.064	0.035	0.047	0.084	0.067	0	0.068	0.053	0.071	0.085	0.064	0.064
Juvenile														
n			11								5	6		1
Average			84.57								53.14	36.03		28
Minimum			81.2								47.2	30.5		28
Maximum			87.4								58.3	40.9		28
Std. deviation			1.916								3.576	3.392		0
Coef. of variation			0.023								0.067	0.094		0
<b>H. brachypus</b>														
Adult														
n		1	4	4	3	2	2			3	5	5	3	4
Average		110	82.37	75.08	152.9	97.55	53.6			78.7	62.67	46.83	85.77	34.68
Minimum		110	77.7	72.1	148.1	93.3	49.9			78.7	60	40.5	81.4	33.1
Maximum		110	86.8	77.2	157.6	101.8	57.3			78.7	64.5	53.4	89.9	35.9
Std. deviation		0	3.719	1.874	4.75	4.25	3.7			0	1.929	5.995	3.474	1.209
Coef. of variation		0	0.045	0.025	0.031	0.044	0.069			0	0.031	0.128	0.041	0.035
Juvenile														
n			4								1	3		
Average			93.5								51.2	41.65		
Minimum			90.1								51.2	35.3		
Maximum			99.3								51.2	48		
Std. deviation			4.121								0	6.35		
Coef. of variation			0.044								0	0.152		





Specimen #	Cranial Measurements (mm)																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<b>C. mediterraneum</b>																				
Adult																				
PV1/1794-A&B								63.6												
PV1/1850		[107]	[102,2]				74.5	64.9	138.2	[65]						72				
PV1/1874	87.6						75.9	68	141.4		[31,3]		62.4	[35,8]	45.5					
PV1/1988							85.2	68.4	150		31.6	38.3	61.8			58			[155]	
PV3/2041	108.2	90					66.8	56.8	126.1		38.1	39.9	62.3	[37,5]	54.8					
PV1/2205	106	74					70	61.2	131.2				61.7		52.5					
PV1/2631							75.9	64.7	140.5											
PV1/837							64.1													
PV1/901																				
PV1/2589							62.1													
PV1/730																				
PV1/845																				
PV1/1285																				
PV1/2171																				
PV1/64																				
PV1/724																				
PV1/1921																				
PV3/2048 (A+B)							77.3	64.8	140.3				67.2							
PV3/2042							76.2													
PV3/2038																				
PV1/1295																				
PV1/2259																				
PV1/2451							73.7													
PV1/2527																				
PV1/585																				
PV1/2206																				
PV1/2222																				
<b>H. brachypus</b>																				
Adult																				
PV1/1298		118.2	104.7	98.2	199.6		84	71.3	154.9	[67,9]		35.7	66.9		79.2	142.7				
PV1/233							87.6	[73,8]	[158,8]											
PV1/2115							69.1													
PV1/2285																				
PV1/2337																				
PV1/2576																				
PV1/2578							70.7													
PV1/672																				
PV1/768							80.7	70.2	145											
PV1/1214																				
PV1/857																				
PV1/906																				
PV1/1230																				
PV1/1939																				
PV1/2075																				
PV1/2286																				
PV1/2327																				
PV3/12							68.7													
PV3/96							84.9													
PV3/134																				
PV3/138							72													
PV3/2012							74.9													
PV1/689		[109,5]	[87,6]	[73,8]	[148,2]		80	67.3	145.3		[35,7]	[53,4]			64.6					
PV1/1067							83.9	[66,7]	[148,8]											
PV1/2634		108.2					80.3	66.9	143.9		32.4	38	59.8							
PV1/2282																				
PV1/2570																				
PV1/650																				
PV1/2622							76.9													
PV1/877																				
PV1/1799																				
PV1/1800																				

Specimen #	Cranial Measurements (mm)																		
	21	22	23	24	25	26	27	28	29	30	31	32	P2-Orbit	33	34	35	36	37	38
<b>C. mediterraneum</b>																			
Adult																			
PV1/1794-A&B																			
PV1/1850						95.5		58.1	48.4		132	26.5	162	64		40.7	[30,4]	49.2	83
PV1/1874									[40]		131.9	27.4	[144,8]	[62,2]		38	[15,5]		51.7
PV1/1988							64.3					26.5	137.7	[54]		[28,9]	21.5		63.6
PV3/2041					75.5					144.3	[121,4]	18.9	141.3	67.3		58.5	22.9		53.5
PV1/2205									[35,2]	[125,5]	134	24.7	146.5	[63,7]		40.9	[19,8]		41.5
PV1/2631																			
PV1/837																			
PV1/901																			
PV1/2589																			
PV1/730																			
PV1/845																			
PV1/1285																			
PV1/2171																			
PV1/64																			
PV1/724																			
PV1/1921																			
PV3/2048 (A+B)																			
PV3/2042																			
PV3/2038																			
PV1/1295																			
PV1/2259																			
PV1/2451																			
PV1/2527																			
PV1/585																			
PV1/2206																			
PV1/2222																			
<b>H. brachypus</b>																			
Adult																			
PV1/1298						[76,1]		67.1	[40,2]			42.5	146.2	[59,2]		36.9	[26,9]		67.6
PV1/233																			
PV1/2115																			
PV1/2285																			
PV1/2337																			
PV1/2576																			
PV1/2578																			
PV1/672																			
PV1/768																			
PV1/1214																			
PV1/857																			
PV1/906																			
PV1/1230																			
PV1/1939																			
PV1/2075																			
PV1/2286																			
PV1/2327																			
PV3/12																			
PV3/96																			
PV3/134																			
PV3/138																			
PV3/2012																			
PV1/689						[68]		55.7	38.1			35.5	156	[49,5]		28.8	30.9		63.4
PV1/1067																			
PV1/2634												[28,8]					[39]		[58,8]
PV1/2282																			
PV1/2570																			
PV1/650																			
PV1/2622																			
PV1/877																			
PV1/1799																			
PV1/1800																			

Specimen #	Cranial Measurements (mm)																			
<i>C. mediterraneum</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Juvenile																				
PV1/1896							59.2													
PV1/275																				
PV1/315							[82,6]													
PV1/335																				
PV1/431																				
PV1/784							82.3													
PV1/920																				
PV1/1987							88.3													
PV1/2125																				
PV1/751																				
PV1/875																				
PV1/66																				
PV1/344																				
PV1/492																				
PV1/493																				
PV3/2013							85.1													
<i>H. brachypus</i>																				
Juvenile																				
PV1/2008	96.9	102.3	91.8				83.9	[72,9]	[152,5]		32.2	37.4	55	36.4	59.7	58.4		164.5		
PV1/1286																				
PV1/2580							[94]													
PV1/752																				
PV1/876																				
PV3/115							91.8													
PV3/2011							93													

Specimen #	Cranial Measurements (mm)																			
<i>C. mediterraneum</i>	21	22	23	24	25	26	27	28	29	30	31	32	P2-Orbit	33	34	35	36	37	38	
Juvenile																				
PV1/1896																				
PV1/275																				
PV1/315																				
PV1/335																				
PV1/431																				
PV1/784																				
PV1/920																				
PV1/1987																				
PV1/2125																				
PV1/751																				
PV1/875																				
PV1/66																				
PV1/344																				
PV1/492																				
PV1/493																				
PV3/2013																				
<i>H. brachypus</i>																				
Juvenile																				
PV1/2008			295			[62,3]		59	[34,5]	92.6	[135]	35.8	134.3	51.6		[26,7]	[35]		57	
PV1/1286																				
PV1/2580																				
PV1/752																				
PV1/876																				
PV3/115																				
PV3/2011																				



Specimen #	Mandible Measurements (mm)													
<i>C. mediterraneum</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Adult														
PV1/430			76.4								62.8	41.9		[28,3]
PV1/232			74.4	69.9	142.7	[100]				74.9	60	43.4		
PV1/458			69.4	67.3	136.4					73	52.3	42.3		
PV1/766			78.1				49.1							
PV1/785							52.2						82.6	32.4
PV1/1296			64.5	66.3	128.7		43.6				[61]	52.2	71.2	29.9
PV1/1924α			77.5	71.5	147.5					85.3	56.8	44.2		
PV1/1960		92	80	67.1	147	95.4	50.3		140.5	77.2	63.5	47	67.5	27.5
PV1/2138	[360]	[97]	69	70.5	137.3	109.4		175	159.6	75.9	62	51.5		28
PV1/2151 (α+β)	[370]	[106,8]	68.4	64.3	131.2		46.3			72.9	55.3	44.3	73.6	31.5
PV1/2308		[101,5]	78.2	70	148.8		[48]				65.3	44.2	[73,8]	
PV1/2417	[390]	110.7	70.7	68.1	138.1	117.2	48.4	[140]				[39,4]	78.7	32.4
PV1/2575							53.5						72.4	[32,4]
PV1/200				67.3										
PV1/276			78.1	69.5	147.3					80.4	[60]	42.3		
PV1/699														
PV1/840				65.5		[99,3]			165.1					
PV1/993				67.8										
PV1/1068			74											
PV1/1125			78.4	69.5	146.6									
PV1/1282			73.2											
PV1/1287				[73,7]										
PV1/1913			77.4	73.1	149.8									
PV1/2060														
PV1/2202				71.3										
PV1/2454			75.1	65.2	140.1					75.1	60.2	41.6		
PV1/2577			75.7											
PV1/87														
PV1/1883														
PV1/2058α														
PV1/2058β														
PV1/2082														
PV1/1283														
PV1/430 B														
PV3/47			78.2											
PV3/60				65.5										
PV3/2000				72.6										
PV3/2004				68.6										
PV3/2006				70.5										
PV3/2002														
PV4/9			79											
PV1/219		91.7	66.9									51.9	78.2	28.2
PV1/758		94	64.8	69.5	133.4		44.4							31.8
PV3/68		[97,3]	73.2	69.3	142.5		51.5					48.2	[72,4]	[37,5]
PV3/2046			[74,1]	[65,8]	[139,5]									
PV4/7, PV4/8			69.9	66.1	135.5									
<i>H. brachypus</i>														
Adult														
PV1/221							49.9						89.9	33.1
PV1/1090			77.7	72.1	148.1	101.8				[81,5]	64.5	41.2		33.9
PV1/2153			[81,9]	75.1	[156,6]	93.3				78.7	63.5	40.5		
PV1/2469		110	82.6	75.9	157.6		57.3			[71]	[62]	[44,7]	81.4	35.9
PV1/2030			86.8								60			
PV1/1284														
PV1/534														
PV1/2533														
PV3/2005														
PV3/2007											[68,3]			
PV3/2008				77.2										
PV3/2035												53.4		
PV3/2036												52.2		
PV3/128														
PV1/566														
PV1/2335														
PV3/2037													86	35.8

Specimen #	Mandible Measurements (mm)													
<i>C. mediterraneum</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Juvenile														
PV1/804			83.8									34		28
PV1/1790			83.4								47.2	30.5		
PV1/18														
PV1/204			82.5								58.3			
PV1/432			84								53.3	38.2		
PV1/433			85.9											
PV1/917														
PV1/1058α			[85,5]											
PV1/1820														
PV1/1993			81.2								54.4	40.9		
PV1/2194			87.3									38		
PV1/2264														
PV1/2316			85.8											
PV1/2383			87.4								52.5	34.6		
PV1/2596			84.4											
PV1/317														
PV1/584														
PV1/899-B														
PV1/865														
PV1/1130														
PV1/1860														
PV1/65														
PV1/567														
<i>H. brachypus</i>														
Juvenile														
PV1/196			90.1											
PV1/333														
PV1/832			91.1								51.2	35.3		
PV1/1198A			[91,7]											
PV1/1215														
PV1/899-A														
PV1/1187														
PV1/718														
PV3/2043			99.3									48		
PV3/2045												[50]		
PV3/2009														

Specimen #	Upper Teeth Measurements (mm)																						
<i>C. mediterraneum</i>	P2-1	P2-2	P2-3	P2-4	P2-5	P2-6	P2-7	P2-8	P2-9	P2-10	P2-11	P3-1	P3-2	P3-3	P3-4	P3-5	P3-6	P3-7	P3-8	P3-9	P3-10	P3-11	
Adult																							
PV1/1794-A&B												23.5		23	26	20.7		2	5	7	1	7.1	5.4
PV1/1850	29.3		22.1			2	5	2	1	7.3	5.6	23.6		[22,7]			1	5	4	1	6.7	5.2	
PV1/1874	32.3		23.7			2	4	3	1	7.7	5.8	24.1		23.6			2	6	7	1	7	5.8	
PV1/1988	32		21			2	1	2	1	6.4	4.4	26.6		22.9			4	3	3	1	5.4	4.2	
PV3/2041	28.2		20.8			2	1	2	0	7.7	4.8	20.3		21.5			0	2	2	0	6.8	4.9	
PV1/2205	28		22.1			5	4	6	1	8.1	4.8	23.5		22.7			1	6	6	1	7.6	4.6	
PV1/2631	30.1		21.5			3	5	4	1	6.1	4.2	24.2		23.4			4	5	6	1	5.2	4	
PV1/837																							
PV1/901													[22]		22		30.9	2	4	5	1	5.9	4.7
PV1/2589																							
PV1/730	30.3	28.3	21.5	20.6	39.9	5	5	6	2	6.4	4.1												
PV1/845	28.9	28.4	22.5	21.8	25.7	4	4	5	2	7	4												
PV1/1285	30	29.9	22.3	22.2	30.5	3	5	4		6.9	4.5												
PV1/2171	29.4	27.2	22	21.6	27.3	3	0	1	1	6.4	4.3												
PV1/64																							
PV1/724																							
PV1/1921																							
PV3/2048 (A+B)	31.2		21.7			3	3	4	1	6.9	4.7	24.2		23.2			6	6	6	1	6.2	4.5	
PV3/2042	31.3		21.2			3	3	2	1	6.5	4.7	23.6		22.7			1	2	3	1	6.2	4.8	
PV3/2038	31	29.4	21.8	19.9	31.2	3	3	2	1	6.2	4.6												
PV1/1295												21.4		23.5		12.3	1	1	1	1	1	7.4	6
PV1/2259																							
PV1/2451	30.5		24.1		16.8	3	3	3	1	7.9	6.2	[22,5]		24.8		15.3	1	4	1	1	7.1	6.7	
PV1/2527												23.1		22.4			1	3	2	1	7.6	5.9	
PV1/585	26.8		21.2		9	2	1	1	0	6.7	5.2												
PV1/2206	27.6	26.4	21.5	21.8	17	2	3	6	1	7.6	4.7												
PV1/2222	28.3	28	20.8	20.2	13.2	4	2	3	0	7.4	4.8												
<i>H. brachypus</i>																							
Adult																							
PV1/1298	33.6		20.9			4	2	1	1	7	4.8	26.1		24.3			3				8.2	4	
PV1/233	35.9		22		39.3					6.9	4.8	29.7		25.6		43.7	5	7		0	8.9	4.2	
PV1/2115																							
PV1/2285												26		24	24.8	31.1	7	4	6	2	7.3	4.9	
PV1/2337												[25,7]		25.2			5	4	5	1	6.8	5	
PV1/2576												[23,2]	22.1	[20,9]	21.1	17.5	1	6	6	1	7.5	5.8	
PV1/2578																							
PV1/672	32.2		22.4		24.9	4	2	6	2	6.7	4.6	25.2		24.6		31.4	5	5	9	2	4.8	7.8	
PV1/768	32.1		21.7			6	2	5	3	6.5	5.2	25.4		23.9			6	4	8	1	6.5	5.1	
PV1/1214																							
PV1/857	33.6	30.1	21.7	22.3	44.4																		
PV1/906	33.6	32.2	22.3	23.1	41.1	2	2	4	0	6.4	5												
PV1/1230	31.5	29.2	21.8	20.9	35	6	5	5	3	6.6	4.1												
PV1/1939	31.6	30.9		22	42.9	2	3	2	1														
PV1/2075	31.5	29.8	21.5	21	34.1	6	4	7	1	6.6	3.9												
PV1/2286	31.3	30.4	23.3	22.7	25.6	6	8	7	1	8	4.6												
PV1/2327	33.7	29.7	20.8	21	42.4																		
PV3/12												24.8		23.5			1	4	5	0	6.5	5.2	
PV3/96	33.4		21.7			3	2	4	3	7.5	4.5	27.8		23.9			1	4	3	1	7.6	5	
PV3/134	31.8	28.4	22.5	22.7	29.6	3	2	3	1	7	4.3												
PV3/138			22.6			3	2	4	1	7	5.1	27.2		24.3			4	4	6	2	6.8	5.2	
PV3/2012																							
PV1/689	31.6		23.8			0	3	4	0	7.1	4.8	27.4		25.2			1	2	3	0	8.4	4.8	
PV1/1067	32.6	31	19.7	22.9	38.5	3	2	2	1	7.4	3.8	26.3		21.2			2	2	2	0	5.8	3.8	
PV1/2634	31.5		23.3		35.3	5	4	5	3	6.8	4.7	26.8		24.4			1	5	7	1	6.7	5.2	
PV1/2282												28.9			21	49							
PV1/2570												27.8		22								5.6	3.4
PV1/650	33.6	33.1	19.6	21.8	44.8																		
PV1/2622	29.4		23.1			6	3	6	1	8.2	5	24.7		24.1			2	3		1	8.4	5.1	
PV1/877	32.2	29.9	21.8	20.5	16	5	3	4	1	7.1	4.4												
PV1/1799			22.3	21.4	15.7	5	5	4	1	7.3	5												
PV1/1800	33.5	32.4				5	5	5	1	7	5												

Specimen #	Upper Teeth Measurements (mm)																						
	P4-1	P4-2	P4-3	P4-4	P4-5	P4-6	P4-7	P4-8	P4-9	P4-10	P4-11	M1-1	M1-2	M1-3	M1-4	M1-5	M1-6	M1-7	M1-8	M1-9	M1-10	M1-11	
<b>C. mediterraneum</b>																							
Adult																							
PV1/1794-A&B	23.2		24.1			3	4	5	1	7.9	5.7	21.5		21.9			3	3	5	2	8.4	5.1	
PV1/1850	22.1		22.9			1	3	4	1	6.3	4.6	20.2		21.3			1	6	4	1	6.3	6.3	
PV1/1874	23.1		24.2			1	5	6	2	6.9	5.4	19.8		22			1	5	4	2	7.3	5.3	
PV1/1988	24		21.1			1	2	0	0	5.8	3.5	24.4		19.2			6	3	3	3	5.6	4.1	
PV3/2041	20.2		21.1			0	1	6	1	7	4.9	17.1		19.9			0	4	3	1	6.6	4.6	
PV1/2205	21.2		22			1	6	6	1	7	4.3	19		21.7			1	5	7	1	7	4.7	
PV1/2631	23.8		21.7			3	3	1	1	5	3.7	20.6		20.4			1	5	5	2	5.4	3.9	
PV1/837	24.6		20.5			1	3	2	1	6.8	4.2	21		20.5			1	4	4	0	6.4	4	
PV1/901	22.5		21.8			1	4	4	1	5.6	4.7	20.7		21			1	5	3	1	6	4.6	
PV1/2589			[19,2]						2	1	5.9	4	19.9		19.5			1	4	3	2	6.2	3.8
PV1/730																							
PV1/845																							
PV1/1285																							
PV1/2171																							
PV1/64																							
PV1/724																							
PV1/1921																							
PV3/2048 (A+B)	23.5		23			4	5	3	1	6.4	4.4	20.5		21			3	3	3	1	6.3	4.1	
PV3/2042	22.6		22.8			1	2	2	1	6.3	5.6	20.6		21.3			1	3	3	1	6.1	4.4	
PV3/2038																							
PV1/1295	21.3		22.9			1	1	1	1	7.7	5.7	18.9		21.2			1	1	2	1	7.2	4.9	
PV1/2259												21		20.4			1	3	2	0	6.7	4.7	
PV1/2451	23.3		24.5			1	1	1	1	8.3	6	19.5		22.6			0	1	1	1	7.1	5.4	
PV1/2527	21		23.1			1	5	1	1	7.4	5.1	18.5		20.5			1	2	3	1	7.1	5.4	
PV1/585																							
PV1/2206																							
PV1/2222																							
<b>H. brachypus</b>																							
Adult																							
PV1/1298	24.8		22.9			1			1	9	4.1	23.6		22.6			5	3	4	1	7.9	4.1	
PV1/233	25.4		22.7				6	3	0	7.8	3.7	26		23.8			5	3	4	1	8.5	4.1	
PV1/2115	25.2	24.9	25.2	27.8	30.1	5	4	4	1	7.5	5.7	22.7		22.5		28	2	4	7	2	8.1	5.1	
PV1/2285	25.1		23.8		35.9	8	3	1	1	6.2	4.8												
PV1/2337	24.8	21.5	24.2		37.2	6	3	1	2	6.8	4.7	20.7		22.5			4	4	5	1	6.9	4.4	
PV1/2576	23.8	22.8	25.5	25.2	22.3	1	6	8	0	7.3	5.6	21.8		22.9	22.8	20.2	3	4	5	1	7.5	5.4	
PV1/2578												23.6		20.4			2	5	4	2	5.7	4.5	
PV1/672																							
PV1/768	24.6		24.5			7	6	8	2	6.6	4.8	22.2		23.2			5	5	11	5	6.1	4.6	
PV1/1214	25.8		23.2		48	3	4	3	1	5.6	4.3	22		22.4		39.9	2	4	4	4	6.2	4.3	
PV1/857																							
PV1/906																							
PV1/1230																							
PV1/1939																							
PV1/2075																							
PV1/2286																							
PV1/2327																							
PV3/12	24		23.5			2	4	4	2	6.5	5.1	21		22.1			1	4	4	1	6.5	4.7	
PV3/96	24.4		22.9			1	2	3	1	6.5	3	[24,8]		23.3			5	6	3	4	7	4.3	
PV3/134																							
PV3/138	25.9		24.8			3	7	8	2	6.5	5.2	23.2		[22,7]			6			1	6.5	[4,7]	
PV3/2012	25.9		27.1			1	6	7	1	8.6	6.1	21.4		24.5			3	4	6	1	8.5	5.9	
PV1/689	26.1		24.9			1	4	4	1	7.9	4.5	22.1		23.4			1	1	3	1	7.8	4.4	
PV1/1067	23.4		18			0	0	1	0	4.1	2.2	24.1		20.3			1	6	5	2	6	4	
PV1/2634	24.2		22.8			1	3	2	1	6.4	4.3	22.6		21.6			1	4	4	2	6.3	4.1	
PV1/2282												26		19.8			1	4	3	1	6.5	3.5	
PV1/2570	[24,6]		18.3									25.6		23.5			4	5			6.8	4.3	
PV1/650																							
PV1/2622	24.1		24.4			2	3	6	1	8.6	5.2	21.8		[23,1]							8.1	5.2	
PV1/877																							
PV1/1799																							
PV1/1800																							

Specimen #	Upper Teeth Measurements (mm)																						
<i>C. mediterraneum</i>	M2 - 1	M2 - 2	M2 - 3	M2 - 4	M2 - 5	M2 - 6	M2 - 7	M2 - 8	M2 - 9	M2 - 10	M2 - 11	M3 - 1	M3 - 2	M3 - 3	M3 - 4	M3 - 5	M3 - 6	M3 - 7	M3 - 8	M3 - 9	M3 - 10	M3 - 11	
<b>Adult</b>																							
PV1/1794-A&B	21.8		21.3			4	3	5	2	6.5	4.6	21.4		19.4			4	3	3	1	7.1	4.1	
PV1/1850	20.8		20.4			1	4	4	1	5.8	4.8	22.5		18.8			1	5	4	2	6	3.9	
PV1/1874	20.6		20.9			1	5	6	1	7.1	4.7	27.6		[19,7]			1	3	5	3	8.1	3.7	
PV1/1988	24.3		19.3			3	2	4	1	5.6	3.6	20.1		12.8			0	0	0	0	4.3	2.3	
PV3/2041	19.3		18.9			0	4	3	0	6.4	4.4	20.3					0	2	4	0	[6]		
PV1/2205	19.3		20.5			1	4	7	1	6.1	4.5	22.3		17.1			1	5	5	1	7.4	3.5	
PV1/2631	20.5		20			2	5	3	1	5.1	3.8	18.9		15.8			1	4	2	1	5.7	3	
PV1/837	22.2		20.1			4	3	3	1	6.6	4.2	19.5		14.8			1	1	3	0	6.8	3.5	
PV1/901	20.5		20.1			2	5	4	1	5.5	4.5												
PV1/2589	20		19.3			4	4	6	2	5.3	3.5	19.9		16.1			2	2	2	3	5.2	3.4	
PV1/730																							
PV1/845																							
PV1/1285																							
PV1/2171																							
PV1/64												22	18.4	17.3	23.6	29.9	1	1	1	1	7	3.4	
PV1/724													22.6	15.4	20	41.2					5.8	3.6	
PV1/1921												20.1	21.9	18.1	20.5	31.3	3	4	4	2	6.8	3.4	
PV3/2048 (A+B)	20.6		20.7			3	5	5	1	6.2	4.2	20.3		[17,1]			3	3	2	1	5.8	[3,7]	
PV3/2042	20.6		20.1			1	3	4	1	6.2	4.1												
PV3/2038																							
PV1/1295																							
PV1/2259	23.3		19.3			1	2	3	2	5.8	3.9												
PV1/2451	19.4		22.4			1	3	1	1	7	5.4												
PV1/2527	19.8		19.6			1	4	4	1	6.8	4.6												
PV1/585																							
PV1/2206																							
PV1/2222																							
<b>H. brachypus</b>																							
<b>Adult</b>																							
PV1/1298	23.4		19.9			3			0	6.7	3.7	21.5		14.1							6.1	2.6	
PV1/233	25.5		19.7			1	4	4	0	8.5	3.9												
PV1/2115	22.5		22.4		32.8	2	5	5	1	7.5	[4,7]	22.1		[18,4]		35	6	3	2	2	6.9		
PV1/2285																							
PV1/2337	22		21.8			1	4	4	1	6.2	4.4												
PV1/2576	21.9	21.4	22.3	22.8	20.2	1	6	6	2	6.7	5.4												
PV1/2578	23.1		19.1			2	5	3	1	5.7	4.1	19.7		11.4									
PV1/672																							
PV1/768	21.3		21			4	4	8	4	5.6	4.6	23		16.5			3	2	4	4	5.6	3.9	
PV1/1214	22.8	18.8	20.2	21.9	45.9	3	4	3	2	5.9	4.5												
PV1/857																							
PV1/906																							
PV1/1230																							
PV1/1939																							
PV1/2075																							
PV1/2286																							
PV1/2327																							
PV3/12	22.1		21.1			2	4	5	1	5.9	4.2	23.8		18.4			2	4	2	3	6	3.5	
PV3/96	24.6		20.6			5	3	5	1	7.1	3.5												
PV3/134																							
PV3/138	23.5		21.8			1	5	6	2	6.3	4.7	24.4		18			2	4	2	1	5.9	4.3	
PV3/2012	23		24.1			3	5	8	2	7.4	5.3	26.5		21			3		5	4	6.7	4.8	
PV1/689	22.3		21.4			1	3	3	2	7.2	4.5	21.9		17			1	3	1	1	6.8	4.2	
PV1/1067	22.1		18.4			2	5	3	1	5.8	3.8	19.9		12			0	0	0	0	3.9	2.5	
PV1/2634	21.8		21			1	4	3	2	6	4.3	21		15.2							6.3	3.6	
PV1/2282	25.2		14.9																				
PV1/2570																							
PV1/650																							
PV1/2622																							
PV1/877																							
PV1/1799																							
PV1/1800																							

Specimen #	Upper Teeth Measurements (mm)																						
<b>C. mediterraneum</b>	dP2 - 1	dP2 - 2	dP2 - 3	dP2 - 4	dP2 - 5	dP2 - 6	dP2 - 7	dP2 - 8	dP2 - 9	dP2 - 10	dP2 - 11	dP3 - 1	dP3 - 2	dP3 - 3	dP3 - 4	dP3 - 5	dP3 - 6	dP3 - 7	dP3 - 8	dP3 - 9	dP3 - 10	dP3 - 11	
Juvenile																							
PV1/1896	34.4		18.1			1	1	1	1	5.3	4.8	26.9		19			3	3	3	1	5.1	4.9	
PV1/275	34		19.9		15.8	2	3	3	0	5.8	4.7	27.3					3	3	2	0	5.7	4.6	
PV1/315	[32,2]		16.3		20.4							28	26.7	15		21.9							
PV1/335			19.6	19.8	19							28.7	27.5	18.4	21.6	21.3						4.7	
PV1/431			19.3			3	3	3	1	6.6	3.9	26.4		20			4	5	3	1	5.4	3.9	
PV1/784	[35,1]		[19,9]									25.8		[17,2]								5	3.2
PV1/920												29.1		17.6								4.2	2.8
PV1/1987	36.3	36.5	18.9	21.3	15.26	2	2	3	0	4.6	3.4	28.5		18.2	21.1	14.6	2	3	1	0	4.6	3.2	
PV1/2125	35.8		17.4	20.1	17.6					6.8	2.9	28.6	26.6	17.5	21.1	19.6						3.9	3.4
PV1/751	34.9	34.7	18.6	20	19.9																		
PV1/875	35.7	34.7	18.5	22.1	18.5					5.3	3.8												
PV1/66												25.2		19.2		16	1	2	3	1	4.6	3.4	
PV1/344												28.6	26.5	17.3	20	23.9						7.3	
PV1/492												26.3	26.3	17.3	19.9	19						4	2.4
PV1/493												28.5	26	17	19.6	22.9						5.6	1.9
PV3/2013	33.3		21.5			4	4	4	1	6.5	4.8	28.3		21.7			3	5	3	2	5.8	4.6	
<b>H. brachypus</b>																							
Juvenile																							
PV1/2008																							
PV1/1286			20.2			5	2	3	1	7.2	4.7	26.9		20.3		11.8	1	4	3	1	6.6	4.8	
PV1/2580	37.3		18.2		20.8					4.7	3	28.4		17.8		20.6						4.4	2.9
PV1/752	36.9	36.5	18.4	19.4	19.6																		
PV1/876	38.4	38.3	19.6	20	20.9																		
PV3/115	38		21.9			2	3	3	2	6.1	4.9	28		22			3	6	4	2	5.6	5.1	
PV3/2011	37.7		18.7									28.5		18.2									
Specimen #	Upper Teeth Measurements (mm)																						
<b>C. mediterraneum</b>	dP4 - 1	dP4 - 2	dP4 - 3	dP4 - 4	dP4 - 5	dP4 - 6	dP4 - 7	dP4 - 8	dP4 - 9	dP4 - 10	dP4 - 11	M1 - 1	M1 - 2	M1 - 3	M1 - 4	M1 - 5	M1 - 6	M1 - 7	M1 - 8	M1 - 9	M1 - 10	M1 - 11	
Juvenile																							
PV1/1896	27.8		[18,4]			3	3	1	0	5.3	[4]	25.3		18.3									
PV1/275																							
PV1/315	27.7	27.2			21.4																		
PV1/335																							
PV1/431	26.8		17.3			1	4	3		5.6	3.4	22.5		[16,7]									
PV1/784	27.3		15.8							5.5	2.9												
PV1/920	29.2		15.3							4.4	2.1												
PV1/1987	29.2	28.5	17.1	20.7	17.8	0	2	0	0	5.1	2.5												
PV1/2125																							
PV1/751																							
PV1/875																							
PV1/66																							
PV1/344																							
PV1/492																							
PV1/493																							
PV3/2013	29.2		19.8			3	4	4	0	6.4	4.1												
<b>H. brachypus</b>																							
Juvenile																							
PV1/2008												26.4		22.1			1	3	4	1	7.3	4.4	
PV1/1286																							
PV1/2580	[31,3]		[18,4]							5	2												
PV1/752																							
PV1/876																							
PV3/115	29.9		21			6	4	5	2	6.1	4.7												
PV3/2011	28.5		17.3																				
Specimen #	Upper Teeth Measurements (mm)																						
<b>C. mediterraneum</b>	M2 - 1	M2 - 2	M2 - 3	M2 - 4	M2 - 5	M2 - 6	M2 - 7	M2 - 8	M2 - 9	M2 - 10	M2 - 11	M3 - 1	M3 - 2	M3 - 3	M3 - 4	M3 - 5	M3 - 6	M3 - 7	M3 - 8	M3 - 9	M3 - 10	M3 - 11	
Juvenile																							
PV1/1896																							
PV1/275																							
PV1/315																							
PV1/335																							
PV1/431																							
PV1/784																							
PV1/920																							
PV1/1987																							
PV1/2125																							
PV1/751																							
PV1/875																							
PV1/66																							
PV1/344																							
PV1/492																							
PV1/493																							
PV3/2013																							
<b>H. brachypus</b>																							
Juvenile																							
PV1/2008	25.6		17.6			0	1	1	0	7.4	3.9												
PV1/1286																							
PV1/2580																							
PV1/752																							
PV1/876																							
PV3/115																							
PV3/2011																							

Specimen #	Lower Teeth Measurements (mm)																			
<i>C. mediterraneum</i>	p2-1	p2-2	p2-3	p2-4	p2-5	p2-6	p2-7	p2-8	p2-9	p2-10	p3-1	p3-2	p3-3	p3-4	p3-5	p3-6	p3-7	p3-8	p3-9	p3-10
<b>Adult</b>																				
PV1/430	27.9		12	7.4	11.5	12.7		11	12.8		25.5		16	8.9	10.4	15.7		15.3	[13,7]	
PV1/232	27.6		11.2	7.1	11.3	14		10.7	12.4		22.3		14.9	6.7	11.9	15.1		13.9	14.5	
PV1/458	25.7		12.6	3.8	2.5	10.9		10.7	14.4		23.1		14.3	6.1	3	13.6		13.6	14.6	
PV1/766	28.2		11.2	7.7	8.4	13.1		11	12.8		24.6		13.9	8.8	7.5	15.4		13.1	13.3	
PV1/785																				
PV1/1296	24.9		11.5	6.1	8.4	12.4		10.1	13.4		21.4		13.6	6	4.1	11.9		13	13	
PV1/1924α	28.5		10.7	7.9	13.2	11.1		9.7	10.8		23.9		12.7	8.3	12.6	12.2		12.1	12.6	
PV1/1960	28.1		10.9	8.2	11.7	12.2		10.5	12.4		25.9		14.5	8.2	11.3	14.5		12.7	13.7	
PV1/2138	24.8		11.4	7.2	7.2	11.5		11.1	13.2		21.5		13.4	7.6	7.3	14.9		14.6	13.9	
PV1/2151 (α+β)	23.9		10.3	7.4	9	13.1		10.7	13.2		21.2		13.9	8.9	10.6	15.4		14.1	14	
PV1/2308	27.9		9.1	8.9	11.2	11		9.5	11.6		25.7		12.5	8.3	11.5	13		11.9	12.8	
PV1/2417	26.2		11.4	6.7	11.5	13.4		11.1	13.1		23.5		14.2	8.2	11.7	15.3		14.7	13.9	
PV1/2575																				
PV1/200											23		14.7	7.2	10.3	14			13.3	
PV1/276	27.6		10.4	8	11.9	14.1		10.4	12.2		24.2		14.7	8.3	13.1	16.3		13.1	13.1	
PV1/699																				
PV1/840											21.2		14.1	8.4	10	14.9		14	14.4	
PV1/993																				
PV1/1068	28.6		12.2	8.2	10.3	14.2		11	12.9		23.1		13.9	8	10.2	15.5		15	13.3	
PV1/1125	27.6		11.1	8.6	9.4	11.7		10.8	11.9		25.4		15.4	8.7	11.8	15.1		12.5	12.9	
PV1/1282	26.7		12.3	6.7	6.6	12		11.7	13.4		23.4		15	8.6	7.4	15		16.1	15	
PV1/1287								14			24.6		15.2	8.3	11.9	15.2		14.6	13.9	
PV1/1913	29.8		12.6	7.6	9.1	12.6		11.1	14		25.2		15	9.3	7.9	14.8		14.3	14.2	
PV1/2060	25.8		12.7	6.4	9.4	13.1		10.9	12		22.6		14.5	6.8	10.5	16.2		13.4	13.3	
PV1/2202											24.9		14.2	8.8	9.8	13.5		11.9	12.4	
PV1/2454	23.7		9.7	8.4	8.9	8.3		8.2	9.6		24.7		11.7	8	10.4	10.7		8.6	10.3	
PV1/2577	27		10.9	7.9	12.2	12.4		9.9	12.2		24		14.2	7.5	12	14.7		11.7	12.6	
PV1/87	26.5	25.5	10.6	[6,5]	10.5	12.2	13.5	11.3	12.9	[31]										
PV1/1883	27.8	26.5	10.9	9.2	10.6	11.6	13.6	9.5	11.1	27.8										
PV1/2058α	26.3	25.3	13.4	8.2	11.9	13.2	14.9	11.1	13.3	19.1										
PV1/2058β	26.1	24.8	14.3	8.6	12.2	13.9	14.9	11.8	[13]	19.3										
PV1/2082	27.7	26	10.7	8.4	10.1	12.6	13.3	9.3	11.8	27.7										
PV1/1283	27.4	28	12.3	6.4	[13,8]	14.2	16.3	11.4	14.5	23.2										
PV1/430 B																				
PV3/47	27.1		11.7	7.3	12.3	11.7		10.7	12.1		24.2		15.6	9.4	13	12.9		13.1	13.5	
PV3/60																				
PV3/2000																				
PV3/2004																				
PV3/2006																				
PV3/2002																				
PV4/9	27		11.8	8.3	8.9	12.5		10.4	12.9		23.9		14.7	8.6	11.2	15.3		13.2	13.8	
PV1/219	26.7		10.2	5.5	7.7	10.3		9.6	12.7		22.6		13.4	7.6	7	12.1		13.6	12.8	
PV1/758	24.7		[13,7]		3.4	11.7		11.1	14.1		21		[14,9]		2.2	14.5		14.5	14.3	
PV3/68	26.5		10.6	7	8.3	12.6		11.4	13.5		22.7		14.1	7.9	12	13.9		14.3	13.6	
PV3/2046			14.6	5.1	5.6	[15,5]		12.1	15.8											
PV4/7, PV4/8	26.7		12.4	5.8	8.6	14		11.3	14.1		21.8		13.8	8.2	9.1	15.7		15.4	14	
<b><i>H. brachypus</i></b>																				
<b>Adult</b>																				
PV1/221																				
PV1/1090	28.2		13.4	7.6	10.7	14.9		10.8	13.3		26.7		16.1	8.7	7.1	17.5		14.1	14.4	
PV1/2153	29.4		11.8	9.1	11.7	11.2		10.8	12.3		27.3		14.6	8.6	12.6	14.6		13.6	13.9	
PV1/2469	29.3		12.1	7.9	13.9	13.1		10.3	12.9		25.5		16.3	9.1	12.2	13.9		14.5	13.6	
PV1/2030	31		14	7.9	10.3	11.3		10.8	12.8		25.9		15.1	9	8.4	14.2		13.6	14.1	
PV1/1284	29.8		10.2	10	14.2	12.2		9.2	11.7		26.9		12.6	9.7	13.6	12.6		10.1	12.4	
PV1/534																				
PV1/2533																				
PV3/2005	29.9		11.3	9.4	10.4	12.9		10.6	12.8		26		14.6	9.5	12.7	13.4		13.5	13.3	
PV3/2007											26.2		14.7	9.5	12.8	15.9		14.3	14.1	
PV3/2008																				
PV3/2035	29.1		13.3	8.8	8.9	13		10.7	13.5					10				14.1		
PV3/2036	29.6		12.2	9.3	9.6	13.3		10.8	13.2											
PV3/128																				
PV1/566	31.5		13.4	10.9	12.2	10.8		9.6	11.5	11.8										
PV1/2335																				
PV3/2037																				

Specimen #	Lower Teeth Measurements (mm)																			
<i>C. mediterraneum</i>	p4 - 1	p4 - 2	p4 - 3	p4 - 4	p4 - 5	p4 - 6	p4 - 7	p4 - 8	p4 - 9	p4 - 10	m1 - 1	m1 - 2	m1 - 3	m1 - 4	m1 - 5	m1 - 6	m1 - 7	m1 - 8	m1 - 9	m1 - 10
<b>Adult</b>																				
PV1/430	22.9		14.2	7.9	9.5	13.7		14	13		21.6		13.1	7.1	7.6	12.7		12.6	11.1	
PV1/232	21.3		14	7.2	8.5	14.5		14.2	12.7		20.2		12.4	6.9	6.9	13		12	10.6	
PV1/458	21.9		14.1	6.4	6.3	15.2		14.8	14.4		18.9		13	5.2	5.1	13.3		13.7	11.3	
PV1/766	24.1		13.3	6.5	6.6	15.1		12.7	12.3		22.2		12.7	7.5	8.6	13.5		12.2	11.2	
PV1/785																				
PV1/1296	19.6		14.6		2.8	10		12	[12]		17.4					9.4		12	11	
PV1/1924α	25		10.2	7.2	8.9	11.9		9.6	8.7		23.5		12.8	7.7	11.4	11.2		10	9	
PV1/1960	24.3		11.7	7.5	10.5	13.3		10.2	10.9		22.5		13.8	7.1	8.1	11.1		10.8	10.4	
PV1/2138	21.9		13.2	7.2	7.1	14.5		14	13.4		19.2		12.1	5.2	5.5	11.5		12.6	10.6	
PV1/2151 (α+β)	21.8		13.3	8.3	10.1	13.7		13	12.3		19.5		12.5	5.9	7.1	11.4		11.6	9.7	
PV1/2308	23.9		11.3	8.2	9.5	12.5		10.6	10		26.1		13.8	7.7	9.3	[8,9]		10.4	9.8	
PV1/2417	21.6		12.9	6.9	8	14.6		13	11.9		20.3		12.7	5.2	5.7	12		12.3	10.1	
PV1/2575																				
PV1/200	21.3		13.9	6.1	7.6	14.3		13.5	12.1		19.1		12.9	5.3	5.3	12.1		11.6	9.5	
PV1/276	24.5		13.9	8.5	11.7	15.7		12.6	12.3		21.8		13.1	7	7.3	13.1		11.6	10	
PV1/699	22.9		13.8	7.6	11.5	14.2		12.5	12	32.5	21.3		12.3	6.4	8.4	12.9		11.5	9.8	
PV1/840	21		13.5	7.6	8.2	13.4		12.9	13.3		19.9		12.3	5.5	6.5	11.7		12.5	10.9	
PV1/993											20.4		12.4	6.5	7.7	12.2		11.5	10	
PV1/1068	21.3		13.4	6.7	9.1	15.1		13.8	11.9		19		11.6	5.8	6.5	12.9		12.3	10.1	
PV1/1125	23.9		12.6	8.8	10.7	12.4		10.7	10.4		23.7		13.7	7.6	8.2	11.2		10.7	9.9	
PV1/1282	22.6		14.2	7.2	7.3	13.5		15.9	13.8		19.5		13.3	5.5	5.4	11.5		13.8	11.2	
PV1/1287	24		14.9	8.4	11	15.7		14.2	13.3		21.9		14.4	7.1	7.7	14.2		13.2	12.3	
PV1/1913	23.3		14.3	8.1	7.4	14.8		13.5	13.3		22.1		13.8	6.8	8.1	11.9		12.1	11	
PV1/2060	21.3		12.6	6.9	9.6	14		11.8	12		20.2		11.3	6.2	6.4	11.8		11.1	9.6	
PV1/2202	23.7		12.7	7.9	9.1	12.7		10.4	11.3		23.2		14.2	7.5	8.8	11.2		10.4	9.5	
PV1/2454	24.1		14.6	5.9	5.4	10.7		11.4	10.2		24.2		12.9	7.4	8.5	9.5		9.8	8.5	
PV1/2577	24.4		12.8	7.5	11.5	15		10.7	11.4											
PV1/87																				
PV1/1883																				
PV1/2058α																				
PV1/2058β																				
PV1/2082																				
PV1/1283																				
PV1/430 B																				
PV3/47	23.5		15.4	8.8	11.8	13.4		12.8	12.7		21.9		13.6	7.7	8.6	11.1		11.9	11.3	
PV3/60											19.1		12.2	6.1	6.6	12.9		11.8	10.2	
PV3/2000											24.4		13.7	8.3	10.5	10.3		10.9	10.2	
PV3/2004											21.7		12.9	7.7	7.8	10.8		10.4	9.3	
PV3/2006											22.6		14.1	7.2	8.3	13.2		11.2	10.1	
PV3/2002																				
PV4/9	24.6		13.3	8	10.2	13.8		11.9	11.9		23.3		13.9	7	8.3	13		10.8	10.1	
PV1/219	21.3		12.9	7.3	7	11.8		13.7	12		18.9		11.8	4	4.8	9.6		12.1	9.5	
PV1/758	20.3		13	4.5	4.3	13.8		14.4	13.3		18.4		11.2		3.2	12.9		13.4	10.8	
PV3/68	21.9		14	7	10.7	13.6		13.8	12.9		20.8		12.4	7	9.8	10.5		12.2	10.2	
PV3/2046																				12.8
PV4/7, PV4/8	21.8		14.2	8	8.8	15.5		14.8	[12,7]		20.2		12.7	7	5.2	13.5		13.6	11.3	
<b><i>H. brachypus</i></b>																				
<b>Adult</b>																				
PV1/221																				
PV1/1090	25.2		15	8.7	7.9	17.1		13.2	13.2		22.3		13.6	6.8	7.5	15		11.6	10.3	
PV1/2153	26		14	9	11.7	14		12.6	12.3		24.3		13.3	8.3	10.4	12.4		12	10.8	
PV1/2469	25.4		15.8	8.9	10.5	14.4		14.1	12.8		21.9		14.1	7.6	8.1	12.9		11.8	10.8	
PV1/2030	26.5		14.1	8.9	8.6	14.6		13.1	13.1		25.9		15.7	7.3	10.3	10.2		11.8	10.6	
PV1/1284			13.7	8.1	6.4															
PV1/534																				
PV1/2533																				
PV3/2005																				
PV3/2007	24.7		14.3	8.6	11.7	16.7		13.6	13.6		22.7		13.7	8.4	9.3	13.7		[11,6]	10.7	
PV3/2008	25.4		14	8.7	11.7	16.5		13.6	13.4		24		13.5	7.4	9.1	13.9		11.7	11	
PV3/2035																				
PV3/2036																				
PV3/128																				
PV1/566																				
PV1/2335																				
PV3/2037																				



Specimen #	Lower Teeth Measurements (mm)																			
<i>C. mediterraneum</i>	m2 - 1	m2 - 2	m2 - 3	m2 - 4	m2 - 5	m2 - 6	m2 - 7	m2 - 8	m2 - 9	m2 - 10	m3 - 1	m3 - 2	m3 - 3	m3 - 4	m3 - 5	m3 - 6	m3 - 7	m3 - 8	m3 - 9	m3 - 10
<b>Adult</b>																				
PV1/430	21.7		13.3	7	7.7	11.4		11.8	10.4											
PV1/232	20.4		11.7	6	6.2	12.5		11.3	9.6		24.5		10.6	5.7	6.1	10.6		10.3	9.4	
PV1/458	20.1		11.9	5.1	2	12.5		12.6	10.9		26.1		11.6	6	4.5	11.3		11.2	9.9	
PV1/766	21.8		11.6	7.7	8.1	12.5		11.1	10.4											
PV1/785																				
PV1/1296	18.6		11.2	3.4	2.7	8.8		10.7	9.3		25.4		10.6	5.1		8.6		9.8	8.5	
PV1/1924α	23.1		11.5	7.4	10.1	9.8		10.1	8.1		22.4		8.3			8.3		5.7	5.5	
PV1/1960	21.2		11.7	6.6	8.1	10.7		10.2	8.9		20.4		9.9	7.1	8.3	9.6		7.6	6.4	
PV1/2138	19.9		11.2	5.3	4.9	11.9		12.4	10.8		26.1		11	5.6	5	10.9		11.2	10	
PV1/2151 (α+β)	19		11.1	5.9	6.7	10.5		11	9.6		23.6		10.1	6.3	6.6	9.7		9.7	8.8	
PV1/2308	25.2		12.1	8.2	8.9	9.8		9.9	9		20.8					7.2				
PV1/2417	21.1		12.1	6.9	2.9	12.1		11.7	9.3		24.3		10.2	6.6	5.6	11.6		10.2	8.7	
PV1/2575																				
PV1/200	20.4		11.9	5.2	4.9	11		11.8			25		11.1	5.5	5	10.5		10.5	8.6	
PV1/276	21.6		12.1	6.7	8.2	12.8		11.1	9.6		24.4		11.1	7	6.5			8.6	8.4	
PV1/699	20.4		11.7	6.2	7.6	[11.5]		10.4	8.9		24.4		10.5	5.5	7.6	[10.6]		10	8.9	
PV1/840	20.7		11.9	5.3	5.9	10.7			10.4		23.8		11	6	6.9	10.1		10.6	9.7	
PV1/993	21.6		12	5.9	8.3	9.7		10.3	9.6		23.4		10.6	6.2	7.3	8.8		9.6	8.3	
PV1/1068	19.4		11.2	5.6	6.3	12.2		11.8	9.3		24.7		10.2	5.8	5.9	10.5		10.6	9.1	
PV1/1125	24.9		12.5	7.7	8.2	10.4		10	9.2		20.8		8.9	7.4	8.5	10.2		7.5	7	
PV1/1282																				
PV1/1287	22.7		13.3	7.7	8.7	13.5		12.2	11.4		26.6		12.2	7.8	8.3	12.1		11.4	9.9	
PV1/1913	23.6		12.7	8.1	9.1	12.1		12	11		26.4		11.2	7.6	5.7	10.5		11.2	9.4	
PV1/2060	20		11	5.9	6.7	12.8		10.3	10.2											
PV1/2202	23.3		12.3	7.2	8.4	10.5		9.4	8.7		21.7		9.6	6.5	6.4	8.8		7.4	6.5	
PV1/2454	23.9		11.4	6.6	7.6	7.8		8.7	7.7											
PV1/2577																				
PV1/87																				
PV1/1883																				
PV1/2058α																				
PV1/2058β																				
PV1/2082																				
PV1/1283																				
PV1/430 B											23.2		11.3	5.9	6.5	10.1		9.9	8.7	34.6
PV3/47	21.4		12.7	7.3	8.4	10.7		11.4	10.1											
PV3/60	20		12.1	6.1	7	11.2		11.6	10.1		24.2		11	6.1	8.1	10.3		9.4	8.4	
PV3/2000	26.6		12.5	8	11.7	8.7			8		24.3		9.9			7			5.7	
PV3/2004	23.6		11.7	7.2	8.1	10.3		10.6	9		21.5		9.5	7	6.3	9.2		7.7	6.9	
PV3/2006	22.3		13.4	6.7	8.7	12.1		11.1	10		22.8		10.2	7	7.6	9.8		8.4	6.8	
PV3/2002											25.9		11.4	7.8	7.9	11.3		9.8	8.3	45.4
PV4/9																				
PV1/219	19.8		11.3	5.7	5.5	9.4		11.6	9											
PV1/758	19.9		11.7	5	4.1	11.6		11.7	9.9		26.3		11.5	5.2	3	10		10.2	9	
PV3/68	[20,9]		13.4		8.2	10.6		12.1	10		25.5		11.5	5.5	8.2	10.5		10	9.2	
PV3/2046	21.1		[13]	4.4	3.2	13.4		13.8	12.6		22.7		13.7	5.7	4.1	12		12.7	10.8	
PV4/7, PV4/8	19.9		12.2	5.2	5.3	12.4		12.2	9.8		25		11.4	6.4	6.5	9.7		10.6	9.1	
<b>H. brachypus</b>																				
<b>Adult</b>																				
PV1/221																				
PV1/1090	21.6		12.8	7.1	8.5	13.5		10.9	9.4		24.7		11.6	6.3	7.1	11.9		9.8	8.7	
PV1/2153	[26]		13.1	8.9	10.8	12		11	9.7		24.5		10.8	8	8.3	9.9		7.9	7.4	
PV1/2469	23.2		13.9	7.6	8.5	10.1		7.7	8.3		27.9		12.4	8.3	7.4	11.8		10.9	9.5	
PV1/2030																				
PV1/1284																				
PV1/534											24.5		10.5	6.6	7.3	10.1		10.7	8.9	
PV1/2533											27.8		12.9			7.4		8.5	8.2	[36,8]
PV3/2005																				
PV3/2007	24.8		13.7	8.2	9.3	13.5		11.8	10.5											
PV3/2008	25.1		13.6	7.7	9.2	13.6		11.4	10.9		26.1		11.5	7.1	8	11.9		10.4	8.2	
PV3/2035																				
PV3/2036																				
PV3/128											25	26.1	11.2	6.7	6.7	11.6	11.5	10.4	9.2	40.8
PV1/566																				
PV1/2335											27	29	12.1	6	6.5	8.4	11.1	10.3	9.5	23.6
PV3/2037																				

Specimen #	Lower Teeth Measurements (mm)																			
<b>C. mediterraneum</b>	dp2 - 1	dp2 - 2	dp2 - 3	dp2 - 4	dp2 - 5	dp2 - 6	dp2 - 7	dp2 - 8	dp2 - 9	dp2 - 10	dp3 - 1	dp3 - 2	dp3 - 3	dp3 - 4	dp3 - 5	dp3 - 6	dp3 - 7	dp3 - 8	dp3 - 9	dp3 - 10
Juvenile																				
PV1/804	30.7		11.8	10.8	11.7	12.1		9.2	10.8		26		14.1	9.5	12.1	11.6		10.6	10.5	
PV1/1790	29.9		16.3		11.5	11		9.9	11.7		23.8		15.2		10.1	11.7		12.7	10.6	
PV1/18											26.9		12.3	8.6	11.1	10.6		9.1	8.5	
PV1/204	29.5		12.7	8.2	10.7	11.3		10.5	11.9		26.1		15.6	8.9	8.3	11.9		12.5	11.4	
PV1/432	29.7		13.1	10.1	11.6	11.8		9.1	10.7		26.4		15.3	10	12	12.5		11	10.5	
PV1/433	30		13.3	10.1	11.7	10.6		8.9	11		26.3		15	9.9	12.3	12.6		10.8	11.1	
PV1/917											27		13.7	8.3	9.9	12		10.9	10.1	
PV1/1058α											25.8		15.8	8.5	9			13.3	12.8	
PV1/1820	[24,9]		14.4								26.5		13			7.8		8.2	8	
PV1/1993	31.4		14.1	10.6	12.3	12.1		9.5	11.3		25.2		14.4	9.4	9.3	12.5		11	10.3	
PV1/2194	27.6		11.9	9.9	12.3	[10,6]		8.5	9.3		25.8		12.1	8	12.2	11.2		9.3	8.4	
PV1/2264											27.3		13.7	9.1	8.5	11			10.4	
PV1/2316	29.8		11.8			9.8		7.1	8.7		26.5		12.2	7.3	11.4	11.1		8.3	8.8	
PV1/2383	31.3		12.2	7.5	12.4	10.1		8.5	10.4		25.6		11.9	7.1	9.5	9.7		9	8.5	
PV1/2596	29.2		12	9.2	11.8	11.9		8.3	10.2		26.4		14	8.6	10.6	12.5		9.7	9.8	
PV1/317	30.9	30.3	12.1			7.2	11.5	6.6	8.2	17.2										
PV1/584	27.8		10.9	7.3	11.6	13.5		10.1	12.7	16.4										
PV1/899-B	32.9	33.2	12			6.7	9.7	6.8		22.4										
PV1/865											27.4	26.9	13.1			6.7	11.2	8.1	8.9	26.8
PV1/1130											27.2		11.9			5.8	11.6	7.7	7.9	22.1
PV1/1860											26.2		12.1			8.7		7.6	8.5	
PV1/65																				
PV1/567																				
<b>H. brachypus</b>																				
Juvenile																				
PV1/196	30.9		12.3	11.2	12.7	7.7		8.2	10.4		27.6		14.6	10.1	11.4	6.3		9.8	10.6	
PV1/333	34.6		12.6			8.6		6.6	8.4	18.1	27.9		14			7.7		8.4	8.6	23.1
PV1/832	30.7		11.8	8	11.9	10.4		8	10.2		27.8		13.1	8.2	12.4	9.6		8.9	9.5	
PV1/1198A									8.3		28.4		12.8			9.2		7.9	8.8	
PV1/1215																				
PV1/899-A											29.9	29.4	13.9			7.9	10.9	8.1	6.5	25.9
PV1/1187											28.5		14.2			7.9		7.8	7.8	
PV1/718																				
PV3/2043	36.8		17.4	12.4	15.6	13.1		11.7	13.8		30.1		16.7	10.7	12.1	13.7		12.7	10.9	
PV3/2045			17.5	[12]	15.5	13		11.3	12.3		30.1		16.5	12.1	14.8	15.1		12.3	11.5	
PV3/2009																				
Specimen #	Lower Teeth Measurements (mm)																			
<b>C. mediterraneum</b>	dp4 - 1	dp4 - 2	dp4 - 3	dp4 - 4	dp4 - 5	dp4 - 6	dp4 - 7	dp4 - 8	dp4 - 9	dp4 - 10	m1 - 1	m1 - 2	m1 - 3	m1 - 4	m1 - 5	m1 - 6	m1 - 7	m1 - 8	m1 - 9	m1 - 10
Juvenile																				
PV1/804	29.3		14.2	9.5	11.3	11.7		9.9	9.2											
PV1/1790	29.5		14.7	8.8	9.8	11.4		11.1	9.6		25.8		11.8							
PV1/18	27.7		12.4	8.8	9.9	8.2		7.6	6.7											
PV1/204	26.7		[16,1]	7.9	8	11.8		11.2			25.8		13.2	6.8	8.3	11.1		9.8	9.5	
PV1/432	28.4		15.1	10.1	10.6	11.8		9.7	9.4		23.4		10.4			8.1		8.6	7.4	
PV1/433	28.6		15	10.1	10.4	12.2		10.1	9.4		24.6		11.5			8.7		7.8	7.5	
PV1/917	28.9		12.5	8.8	9.4	9.8		9.4	8.4											
PV1/1058α	27.9		17	8.7	8.7	12.9		11.7	11											
PV1/1820																				
PV1/1993	27.9		13.9	9.3	9.3	11.6		9.2	8.6		25.8		11.8							
PV1/2194	28.8		12.2	8.3	11.5	8.6		8.4	6.9											
PV1/2264	31.1		13.6	8.5	8.3	9.3		9.9	9.3											
PV1/2316	29.6		11.7			8.3		6.5	7.4											
PV1/2383	28.3		12	8.2	10.6	6.9		7.6	6.8											
PV1/2596	28.3		12.8	8	9.9	10.8		9.1	8.7											
PV1/317																				
PV1/584																				
PV1/899-B																				
PV1/865																				
PV1/1130																				
PV1/1860																				
PV1/65	28.1	27.5	15.2	8.9	10.1	12	14.4	11	9	20.4										
PV1/567	29.6	29.4	15.1	10.2	9.9	11	12.8	9.2	8.4	19.7										
<b>H. brachypus</b>																				
Juvenile																				
PV1/196	31.4		15.1	10.3	10.3	4.6		9.5	9.2											
PV1/333																				
PV1/832	29.5		13.7	8.6	10.8	8		7.3	7.5											
PV1/1198A	30.8		12.7			7.7		7.9	8.3											
PV1/1215	30.2		12.3					8.9	7.6											
PV1/899-A																				
PV1/1187																				
PV1/718	30.5	29.2	12.9			4.7	10.3	6.8	6.3	22.1										
PV3/2043	33.3		15.5	9.5	10.8	13.1		11.5	10.2											
PV3/2045				9.8				11.3												
PV3/2009	31.1	30.8	10.9	[9,8]	11.3	10.4	14	6.8	7.7	24.2										

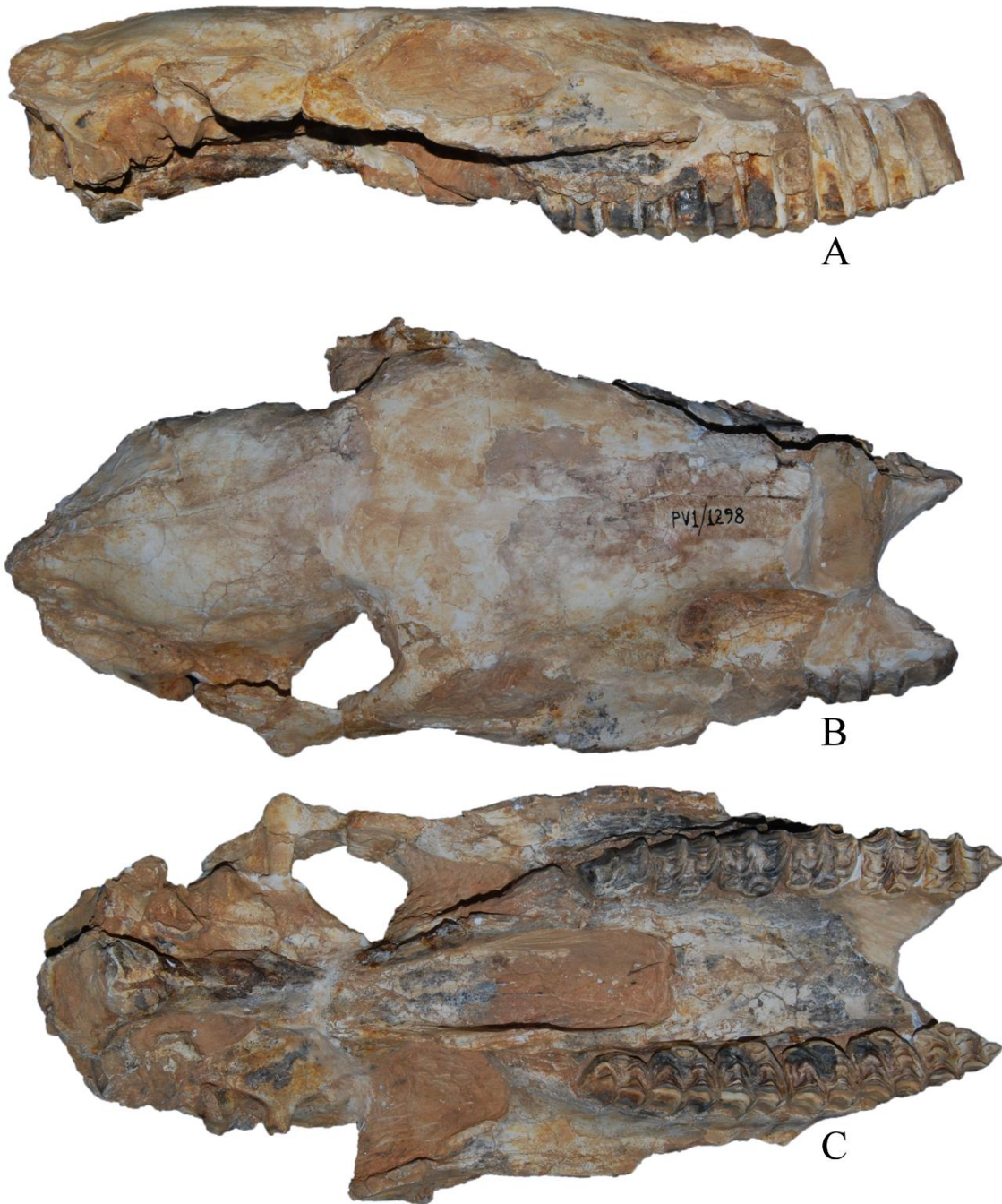


## PART I: CRANIA



100 mm

**Plate 1:** *Hippotherium brachypus* from the Late Miocene locality of Pikermi (PV1). Cranium EPTP PV1/689 in (A) right lateral aspect, (B) superior aspect, (C) inferior aspect.



**Plate 2:** *Hippotherium brachypus* from the Late Miocene locality of Pikermi (PV1). Cranium AMPG PV1/1298 in (A) right lateral aspect, (B) superior aspect, (C) inferior aspect.



100 mm

**Plate 3:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV1). Cranium EPTP PV1/1850 in (A) left lateral aspect, (B) superior aspect, (C) inferior aspect.



**Plate 4:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV1). Cranium EPTP PV1/1874 in (A) right lateral aspect, (B) superior aspect, (C) inferior aspect.



**Plate 5:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV1). Cranium EPTP PV1/1896 in (A) right lateral aspect, (B) superior aspect, (C) inferior aspect.





100 mm

**Plate 6:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV1). Cranium EPTP PV1/1988 in (A) right lateral aspect, (B) superior aspect, (C) inferior aspect.



A



B



C

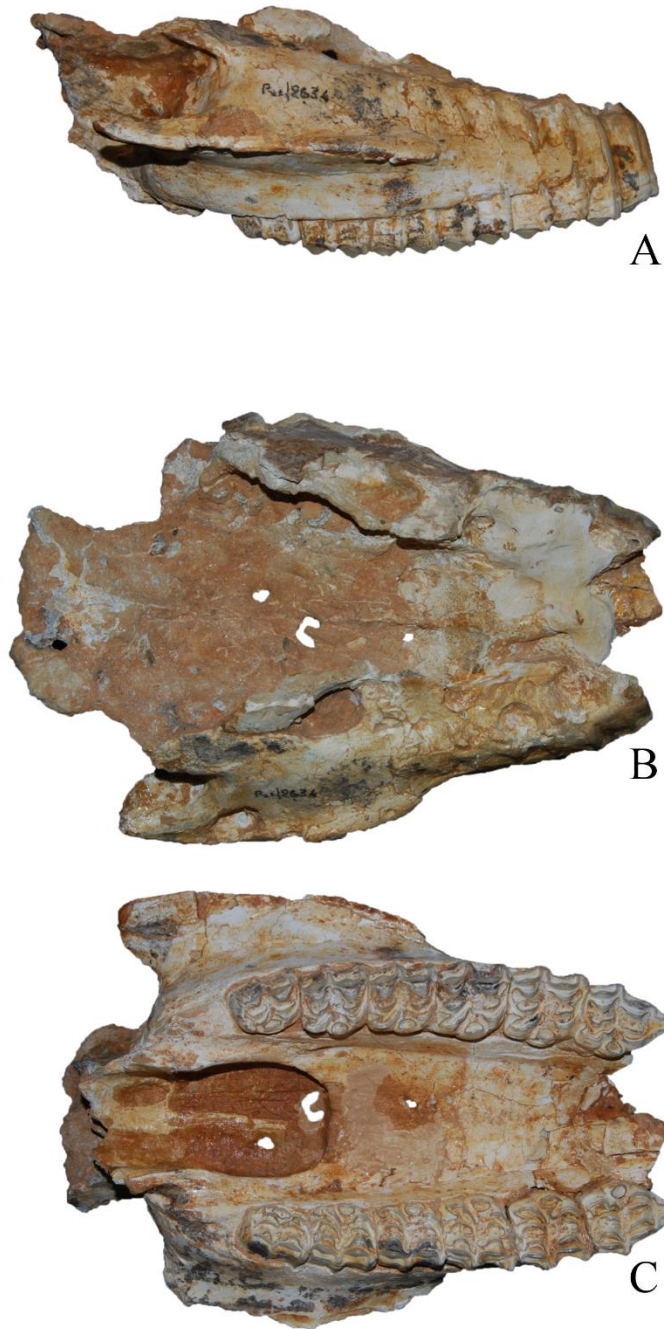
100 mm

**Plate 7:** *Hippotherium brachypus* from the Late Miocene locality of Pikermi (PV1). Cranium EPTP PV1/2008 in (A) right lateral aspect, (B) superior aspect, (C) inferior aspect.



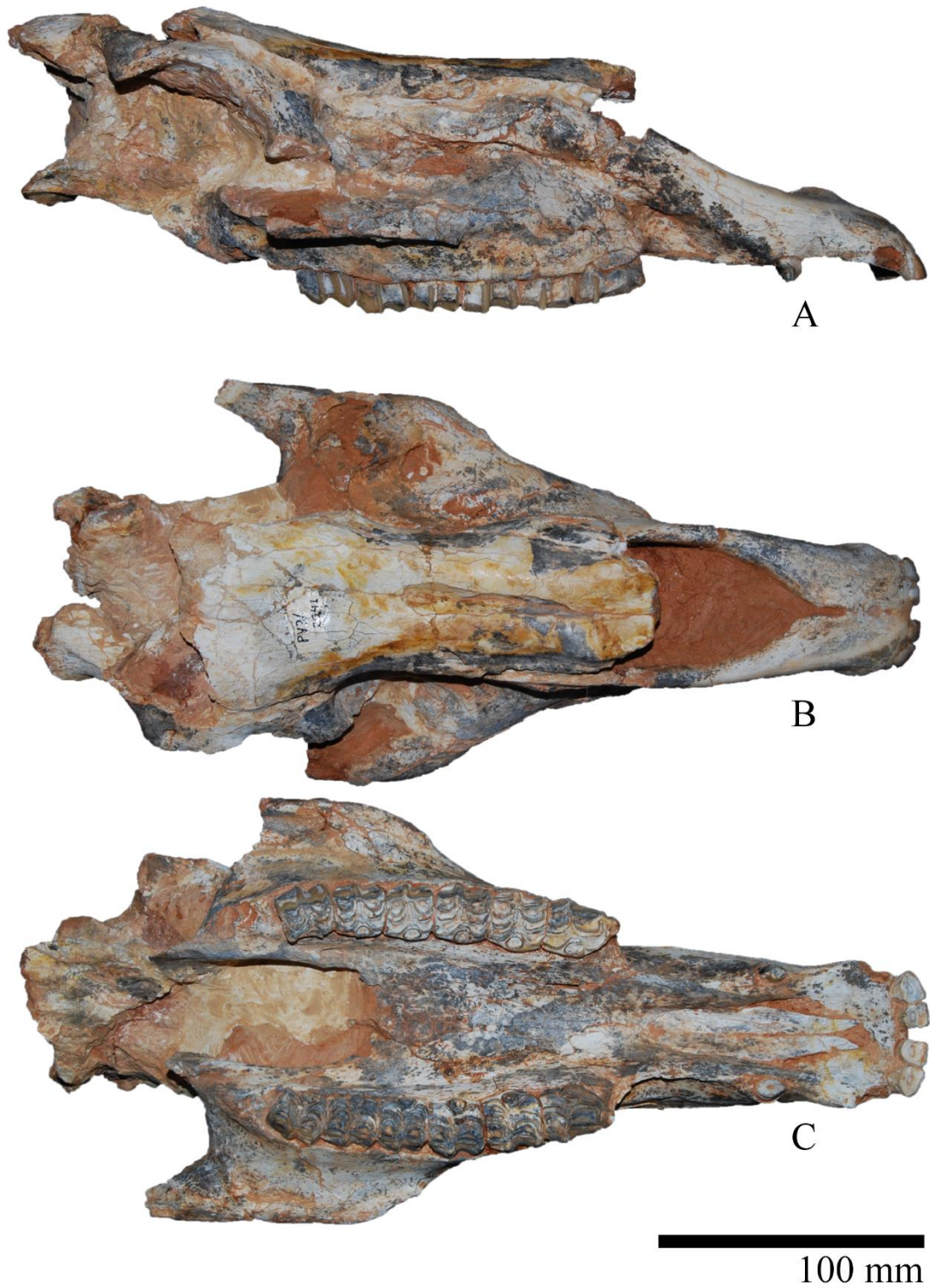
100 mm

**Plate 8:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV1). Cranium EPTP PV1/2205 in (A) left lateral aspect, (B) superior aspect, (C) inferior aspect.



100 mm

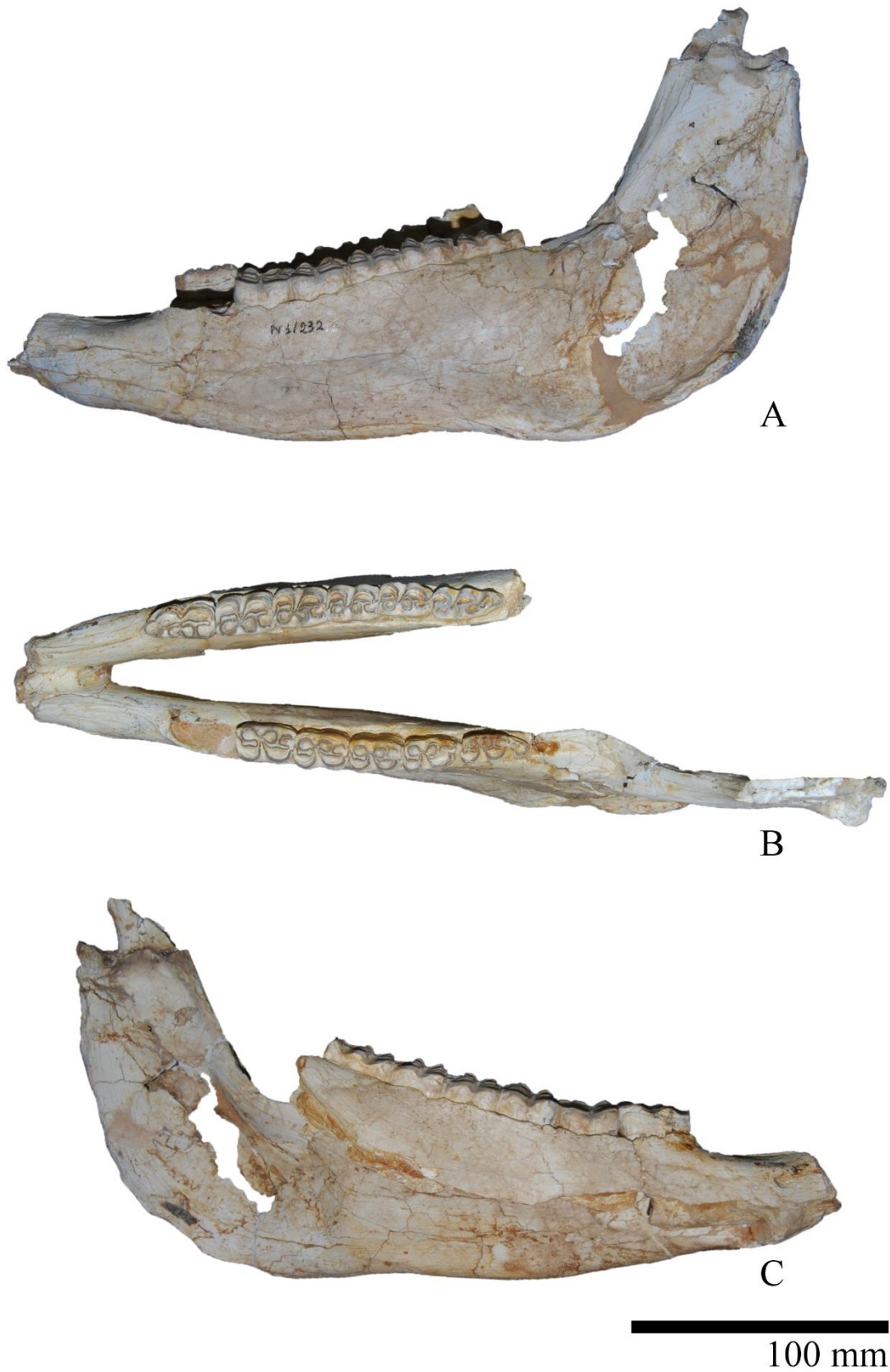
**Plate 9:** *Hippotherium brachypus* from the Late Miocene locality of Pikermi (PV1). Cranium EPTP PV1/2634 in (A) right lateral aspect, (B) superior aspect, (C) inferior aspect.



**Plate 10:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV3). Cranium AMPG PV3/2041 in (A) right lateral aspect, (B) superior aspect, (C) inferior aspect.



## **PART II: MANDIBLES**

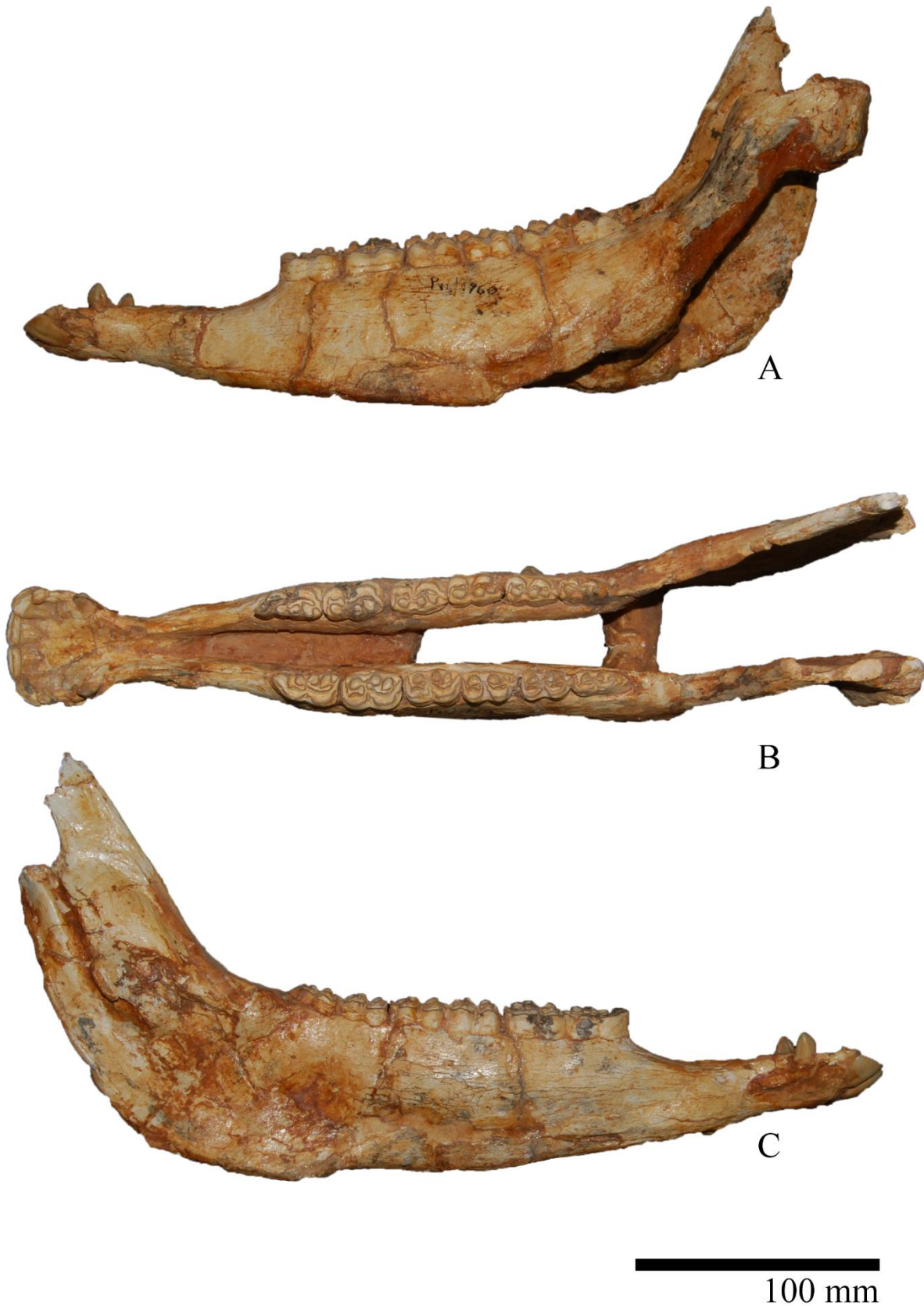


**Plate 11:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV1). Mandible EPTP PV1/232 in (A) left lateral aspect, (B) superior aspect, (C) right lateral aspect.

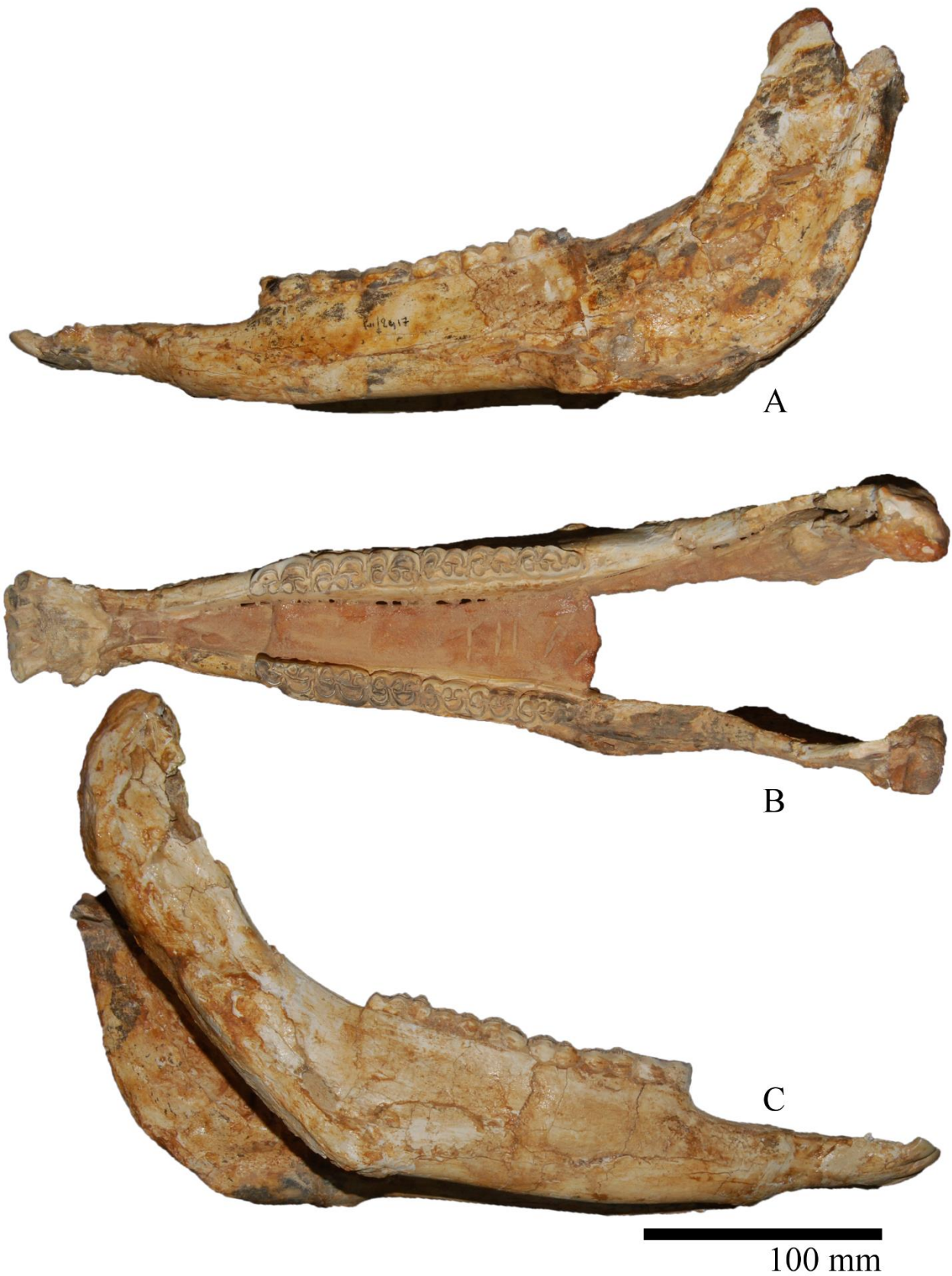


**Plate 12:** *Hippotherium brachypus* from the Late Miocene locality of Pikermi (PV1). Mandible EPTP PV1/1090 in (A) left lateral aspect, (B) superior aspect, (C) right lateral aspect.





**Plate 13:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV1). Mandible EPTP PV1/1960 in (A) left lateral aspect, (B) superior aspect, (C) right lateral aspect.



**Plate 14:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV1). Mandible EPTP PV1/2417 in (A) left lateral aspect, (B) superior aspect, (C) right lateral aspect.



100 mm

**Plate 15:** *Hippotherium brachypus* from the Late Miocene locality of Pikermi (PV1). Mandible EPTP PV1/2469 in (A) left lateral aspect, (B) superior aspect, (C) right lateral aspect.



100 mm

**Plate 16:** *Cremohipparion mediterraneum* from the Late Miocene locality of Pikermi (PV3). Mandible AMPG PV3/68 in (A) left lateral aspect, (B) superior aspect, (C) right lateral aspect.

APPENDIX C: List of prepared material for the NKUA/AMPG

Excavation site: PV1				
Specimen Nr.	Taphonomic code	Collection date	Taxonomic group	Description
PV1/1281	3030	5/10/2014	Hipparionini indet.	lower buccal tooth, dex
PV1/1282	3027	5/10/2014	<i>C. mediterraneum</i>	mandible, p2-m1, sin
PV1/1283		5/23/2014	<i>C. mediterraneum</i>	p2, sin
PV1/1284	1352, Block 237-243		<i>H. brachypus</i>	mandible, dp2-dp4 (?), sin
PV1/1285	3026	5/10/2014	Hipparionini indet.	P2, dex
PV1/1286	1360, Block 237-243		Hipparionini indet.	maxilla fragment, P2-P3, dex
PV1/1287	Block 237-243		<i>C. mediterraneum</i>	mandible, p2-m3, sin
PV1/1288	Block 210-218, No. 611		<i>Oioceros rothii</i>	frontlet with horn cores
PV1/1289	3031	5/10/2014	Bovidae indet.	mandible, m1-m3, dex
PV1/1290	3031	5/10/2104	Bovidae indet.	mandible, p2-m3, sin
PV1/1291			Bovidae indet.	mandible, p3-m3, sin
PV1/1292	Block 237-243		Bovidae indet.	mandible, dp3-m2, dex, juvenile
PV1/1293	3063	5/23/2014	<i>Sporadotragus</i> sp.	frontlet with horn cores
PV1/1294	984		<i>Sporadotragus</i> sp.	frontlet with horn cores
PV1/1295		10/10/2010	<i>C. mediterraneum</i>	maxilla fragment, P3-M1, sin
PV1/1296	3071	5/23/2014	<i>C. mediterraneum</i>	mandible with full dentition
PV1/1297		?/3/2010	Bovidae indet.	mandible, m2-m3, dex
PV1/1298		5/23/2014	<i>H. brachypus</i>	skull
PV1/1299		5/23/2014	Hipparionini indet.	incisor
PV1/1300	3059	5/23/2014	Bovidae indet.	maxilla fragment, dP3-M2, sin

Excavation site: PV3				
Specimen Nr.	Taphonomic code	Collection date	Taxonomic group	Description
PV3/2000		12/31/2013	<i>C. mediterraneum</i>	mandible, m1-m3, sin
PV3/2001		9/12/2013	Hipparionini indet.	upper buccal tooth, dex
PV3/2002		4/30/2013	<i>C. mediterraneum</i>	mandible, p2, sin
PV3/2003		7/23/2010	Hipparionini indet.	partial symphysis with incisors
PV3/2004		12/31/2013	<i>C. mediterraneum</i>	mandible, m1-m3, dex

PV3/2005	7/23/2010	<i>H. brachypus</i>	mandible, p1-p2, dex
PV3/2006	7/23/2010	<i>C. mediterraneum</i>	mandible, m1-m3, dex
PV3/2007	3/31/2013	<i>H. brachypus</i>	mandible, p3-m2, dex, possibly related to PV3/2008
PV3/2008	3/31/2013	<i>H. brachypus</i>	mandible, p3(partial)- m3, sin, possibly related to PV3/2007
PV3/2009	3/20/2011	<i>H. brachypus</i>	dp4, sin
PV3/2010	3/31/2013	Hipparionini indet.	partial symphysis with incisors
PV3/2011	3/31/2013	<i>H. brachypus</i>	maxilla fragment, dP1- dP4, dex
PV3/2012	4/30/2013	<i>H. brachypus</i>	maxilla fragment, P4-M3, sin
PV3/2013	9/12/2013	<i>C. mediterraneum</i>	maxilla fragment, dP2- M1, sin, dP2-M1, dex
PV3/2014	8/12/2013	<i>Palaeoreas lindermayeri</i>	frontlet with horn cores
PV3/2015	8/19/2014	<i>Palaeoryx pallasi</i>	frontlet with horn cores
PV3/2016	9/12/2013	<i>Gazellacapricornis</i>	horn core, dex
PV3/2017	9/12/2013	<i>Palaeoreas lindermayeri</i>	partial skull
PV3/2018	8/12/2013	<i>Tragoportax amalthea</i>	frontlet with horn cores
PV3/2019	9/13/2013	Bovidae indet.	maxilla fragment, P2-M3, dex
PV3/2020	3/31/2013	Bovidae indet.	mandible, p2-m2, dex
PV3/2021	4/30/2013	Bovidae indet.	mandible, m1-m2, sin
PV3/2022	4/29/2013	Bovidae indet.	mandible, m3, dex
PV3/2023	4/30/2013	Bovidae indet.	mandible, dp3-m1, sin, juvenile
PV3/2024	4/29/2013	Bovidae indet.	mandible, p2-m3, sin
PV3/2025	9/12/2013	Bovidae indet.	maxilla fragment, P2-P4, sin
PV3/2026	4/29/2013	<i>Tragoportax amalthea</i>	maxillae, P2-M3 (sin & dex)
PV3/2027	8/12/2013	Bovidae indet.	maxilla, P3-M3, sin
PV3/2028	4/29/2013	Bovidae indet.	maxilla, P3-M3, sin
PV3/2029	9/12/2013	Bovidae indet.	mandible, p4-m3, sin
PV3/2030	4/20/2013	Bovidae indet.	mandible, p2-m3, sin
PV3/2031	8/19/2014	Bovidae indet.	mandible, p3-m1, dex
PV3/2032 (A+B)	1/23/2013	<i>Palaeoreas lindermayeri</i>	frontlet with horn cores
PV3/2033 (A+B)	7/23/2010	<i>Gazellacapricornis</i>	horn cores

PV3/2034 (A+B)		8/12/2013	<i>Gazellacapricornis</i>	horn cores
PV3/2035		4/30/2013	<i>H. brachypus</i>	mandible, p2-p3(partial), sin, possibly related to PV3/2036
PV3/2036		4/30/2013	<i>H. brachypus</i>	mandible, p2, dex, possibly related to PV3/2035
PV3/2037		12/31/2013	<i>H. brachypus</i>	symphysis with incisors and canine, along with partial p1, sin & partial p1, dex
PV3/2038	"7"	4/29/2013	<i>C. mediterraneum</i>	P2, dex
PV3/2039	"36"	8/20/2014	Hipparionini indet.	upper buccal tooth, dex
PV3/2040		9/13/2013	Hipparionini indet.	partial premaxilla with incisors
PV3/2041	"33"	4/14/2014	<i>C. mediterraneum</i>	skull
PV3/2042		8/12/2013	<i>C. mediterraneum</i>	maxilla, P2-M2, dex
PV3/2043	"22"	9/12/2013	<i>H. brachypus</i>	mandible, dp1-dp4, dex, juvenile
PV3/2044	"22"	9/12/2013	Hipparionini indet.	mandible with two buccal teeth, dex
PV3/2045	"22"	9/12/2013	<i>H. brachypus</i>	mandible, p2-p4, sin
PV3/2046	"17"	4/14/2014	<i>C. mediterraneum</i>	mandible, p2-m3, dex
PV3/2047	"39"	8/19/2014	Hipparionini indet.	symphysis with incisors
PV3/2048 (A+B)		1/23/2013	<i>C. mediterraneum</i>	maxillae, P2-M3 (sin) & P2-M2 (dex)
PV3/2049		7/15/2010	<i>Protragelaphus skouzesi</i>	frontlet with horn cores
PV3/2050		9/12/2013	<i>Gazellacapricornis</i>	horn core, dex
PV3/2051		9/12/2013	<i>Gazellacapricornis</i>	horn core, sin
PV3/2052		23 ή 27/7/2010	Bovidae indet.	mandible, m2-m3, dex
PV3/2053		9/13/2013	Bovidae indet.	maxilla, m2-m3, sin
PV3/2054	2292	7/26/2011	<i>Protragelaphus skouzesi</i>	frontlet with horn cores
PV3/2055		10/26/2014	<i>Palaeoryx pallasii</i>	horn core, sin
PV3/2056	2365	7/27/2011	Bovidae indet.	mandible, p4-m3, sin
PV3/2057		8/12/2013	Bovidae indet.	maxilla, P2-M1, dex
PV3/2058 (A+B)		8/20/2014	Bovidae indet.	mandible, m3 (sin) & m2- m3 (dex)
PV3/2059 (A+B+Γ)	325	7/22/2010	<i>Protragelaphus skouzesi</i>	frontlet with horn cores