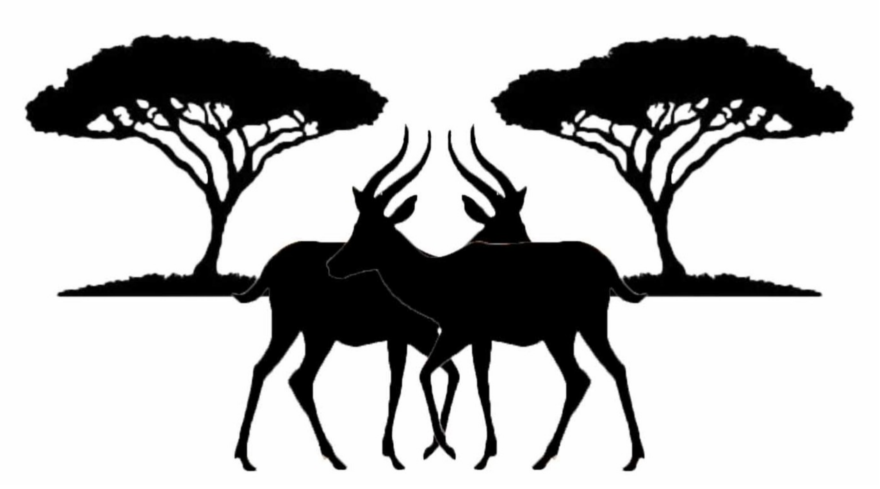
University of Patras
Department of Geology
Laboratory of Palaeontology and Stratigraphy

Study of the Villafranchian large mammal fauna from Karnezeika (Argolis, Peloponnese, Greece): Systematics, Taphonomy, Palaeoecology



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“The world is indeed full of peril, and in it there are many dark places; but still there is much that is fair, and though in all lands love is now mingled with grief, it grows perhaps the greater.”

-J.R.R.Tolkien

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Abstract

The Karnezeika locality lies in the southern part of Argolis prefecture and chronostratigraphically corresponds to the Lower Pleistocene. It consists a small doline formed in the local limestone, as the substrate is characterised mainly by Upper Triassic / Lower Jurassic carbonate rocks of the Pantokrator Formation of the Pelagonian Unit. Most likely the site served as a natural trap which gradually was filled with sediments, rocks and mainly mammal skeletal material from the wider area transferred there by the actions of water and gravity, thus creating favourable conditions for its fossilization. The large mammal fossil collection from Karnezeika is the subject of the current PhD study.

In total, 3358 identifiable specimens have been recorded. Apart from these, there are also more than 7000 catalogued and recorded specimens of quite small fragments of all kinds of bone. The large number of fragmented specimens shows that most of them were transported rather violently to the final place of burial and the transportation seems to have been quite fast since the bones show no particular signs of weathering nor abrasion; no traces of carnivore activity were recorded either. All these, in combination with the presence of bones with various Fluvial Transport Index values, as well as the lack of articulated elements and any sign of bioclastic sorting shows that the place of death was *peripheral* to the doline which means that the bones were transported from an area in close proximity and around the doline.

The large mammal fauna that was determined in the assemblage is vastly dominated by bovids including *Gazella bouvrainae*, *Gazellospira torticornis*, *Gallogoral meneghinii* and Caprini gen. et sp. indet., an assemblage which is quite unusual for post-Pliocene Greek localities where generally a large number of equid specimens occurs instead. Apart from four bovid taxa and an equid, three different cervid species, the giraffe *Palaeotragus inexpectatus*, the rhino species *Stephanorhinus etruscus*, seven carnivoran taxa, as well as scarce remains of a large cercopithecid were also determined, rendering Karnezeika as a primate-bearing Lower Pleistocene locality.

The bovid association *G. bouvrainae* – *G. meneghinii* – *G. torticornis*, combined with the three cervid species, is rather typical for the Middle Villafranchian faunas of Greece (2.6 – 1.8 Ma). In addition, the presence of numerous *G. meneghinii* individuals is of interest as well, since this taxon normally constitutes a quite rare element in the Greek fossil record. Moreover, the Karnezeika assemblage contains several carnivoran and artiodactyls representatives of mixed-habitats. These facts, in combination with the minimal presence of equids, which are represented only by a handful of specimens and the absence of typical open-landscape predators, most likely

show that the palaeoenvironment of Karnezeika was represented by rocky limestone terrains with hills and slopes.

Περίληψη

Η θέση Καρνεζέικα βρίσκεται στο νότιο τμήμα του νομού Αργολίδας και αντιστοιχεί στο Κατώτερο Πλειστόκαινο. Αποτελεί μια μικρή δολίνη σχηματισμένη στα ανθρακικά πετρώματα του υποστρώματος ηλικίας Ανώτερου Τριασικού / Κατώτερου Ιουρασικού του Σχηματισμού του Παντοκράτορα της Πελαγονικής ζώνης. Πιθανότατα η θέση λειτούργησε ως φυσική παγίδα η οποία σταδιακά γέμισε με ιζήματα, πετρώματα και κυρίως σκελετικό υλικό θηλαστικών από την ευρύτερη περιοχή, που μεταφέρθηκε εκεί από τις ενέργειες του νερού και της βαρύτητας, δημιουργώντας έτσι ευνοϊκές συνθήκες για την απολίθωσή τους. Η μεγάλη συλλογή απολιθωμάτων θηλαστικών από τα Καρνεζέικα είναι το αντικείμενο της τρέχουσας διδακτορικής μελέτης.

Συνολικά, έχουν καταγραφεί 3358 αναγνωρίσιμα δείγματα. Εκτός από αυτά, υπάρχουν επίσης περισσότερα από 7000 καταγεγραμμένα δείγματα πολύ μικρών θραυσμάτων κάθε είδους οστών. Ο μεγάλος αριθμός κατακερματισμένου υλικού δείχνει ότι τα περισσότερα από αυτά μεταφέρθηκαν μάλλον βίαια στον τελικό τόπο ταφής και η μεταφορά φαίνεται να ήταν αρκετά γρήγορη αφού τα οστά δεν παρουσιάζουν ιδιαίτερα σημάδια φθοράς ή τριβής. Δεν καταγράφηκαν ίχνη δραστηριότητας σαρκοφάγων. Όλα αυτά, σε συνδυασμό με την παρουσία οστών με διάφορες τιμές του Fluvial Transport Index, καθώς και την έλλειψη αρθρωτών στοιχείων και οποιοδήποτε σημάδι βιοκλαστικής ταξινόμησης, δείχνει ότι ο τόπος θανάτου ήταν περιφερειακός της δολίνης και τα οστά μεταφέρθηκαν από περιοχή σε κοντινή απόσταση και γύρω από αυτή.

Η μεγάλη πανίδα των θηλαστικών που προσδιορίστηκε, κυριαρχείται σε μεγάλο βαθμό από βοοειδή συμπεριλαμβανομένων των *Gazella bouvrainae*, *Gazellospira torticornis*, *Gallogoral meneghinii* και *Caprini* gen. et sp. indet.. Αυτό είναι ένα αρκετά ασυνήθιστο χαρακτηριστικό για τις μετα-Πλειοκαινικές ελληνικές θέσεις, όπου γενικά εμφανίζεται μεγάλος αριθμός δειγμάτων ιπποειδών. Εκτός από τέσσερα είδη βοοειδών και ένα ιπποειδές, προσδιορίστηκαν επίσης τρία διαφορετικά είδη ελαφιών, η καμηλοπάρδαλη *Palaeotragus inexpectatus*, ο ρινόκερος *Stephanorhinus etruscus*, επτά διαφορετικά σαρκοφάγα, καθώς και υπολείμματα ενός σπάνιου μεγάλου cercopithecid, καθιστώντας τα Καρνεζέικα ως μία από τις θέσεις με παρουσία πρωτεύοντος στο Πλειστόκαινο της Ευρώπης.

Η παρουσία των βοοειδών *G. bouvrainae – G. meneghinii – G. torticornis*, σε συνδυασμό με τα τρία ελάφια, είναι χαρακτηριστικά της πανίδας του Μέσου Βιλλαφράγκιου της Ελλάδας (2,6 – 1,8 Ma). Επιπροσθέτως, ενδιαφέρον παρουσιάζει και η παρουσία πολυάριθμων ατόμων *G. meneghinii*, ένα είδος που συνήθως αποτελεί ένα αρκετά σπάνιο στοιχείο στο ελληνικό αρχείο απολιθωμάτων. Επιπλέον, το σύνολο περιέχει πολλά σαρκοφάγα και αρτιοδάκτυλα που

εκπροσωπούν μικτά ενδιαιτήματα. Αυτές οι παρατηρήσεις, σε συνδυασμό με την εξαιρετικά φτωχή παρουσία ιπποειδών, τα οποία αντιπροσωπεύονται από ελάχιστα δείγματα και την απουσία τυπικών αρπακτικών ανοιχτού περιβάλλοντος, πιθανότατα δείχνουν ότι το παλαιοπεριβάλλον της θέσης Καρνεζέικα αντιπροσωπευόταν από βραχώδη ασβεστολιθικά υπόβαθρα με λόφους και πλαγιές.

Introduction

The current work constitutes a PhD project conducted in the Laboratory of Palaeontology and Stratigraphy of the Department of Geology, University of Patras. The study begun in January 2019 and was completed in September 2023. The aim of this project concerns, the study of the large-mammal fauna from the locality of Karnezeika as well as the respective taphonomy of the site, and acquisition of information concerning the site's formation, mammal structure and palaeoenvironment.

Although the systematic study of the locality started in 2019, the site was first discovered almost twenty years prior, during the early 2000's by quarry workers, employed by one of the limestone quarries operating in the area of Karnezeika and managed by the MARMYK Iliopoulos Company, as the quarry workers stumbled upon a karstic cavity with red earth infill and fossil bones. A former student of the Geology Department at the National and Kapodistrian University of Athens named Christos Rigos, who at the time, was conducting his practical training at the quarry, recognized the fossil material, and informed the quarry owner, Athanassios Iliopoulos. Mr Iliopoulos then decided to cut and extract the fossil bearing red earth infill of the cavity with the help of heavy quarry machinery as a 2×2×2m block and this block was placed afterwards at the side of the quarry. Christos Rigos later informed the Athens Museum of Palaeontology and Geology (AMPG) of the National and Kapodistrian University of Athens, and brought a number of fossil specimens to Professor Theodorou, and since then, this material remained under the AMPG's care but without an extensive study ever being carried out. Actually, Christos Rigos was the first one to work on this material preparing some of it. The 2×2×2m block was left at the side of the quarry for years and consequently the block started to break apart.

The laboratory of Palaeontology and Stratigraphy of the University of Patras was informed by Dr Athanasios Athanasiou about the existence of this fossiliferous material. Subsequently, the summer of 2017, the Research Committee of the University of Patras provided a short grant to cover the expenses for the transportation of the large fossiliferous blocks weighing more than 13 tons with a heavy duty lorry and crane from the quarry in Karnezeika to a suitable place outside the building of the Geology Department of the University of Patras for storage and later on for the preparation of the fossil material. Before the official start of this PhD study, a small part of this material was studied in the context of an Undergraduate Dissertation (Kokotini, 2018). Combined with the material from AMPG, some preliminary results on the fauna of Karnazeika were provided in the form of an oral presentation during the 15th International Congress of the

Geological Society of Greece (Kokotini et al., 2019).

Geological Setting

The Karnezeika locality lies in the southern part of Argolis County, between the Argolic gulf and a mountain range referred to as Adera (Figure 1). The geological background of the wider area is characterised mainly by carbonate rocks of Late Triassic / Lower Jurassic age of the Pantokrator formation (Gaitanakis et al., 2007), which now appear strongly karstified. The carbonate rocks that appear also in the Karnazeika locality present a rhythmic character that appears with the vertical alternation of shallow marine cycles, between lagoon (with beige or white/grey limestone) and epitidal (with white/beige limestone – dolomitic limestone) phases (Kostopoulou, 2018).

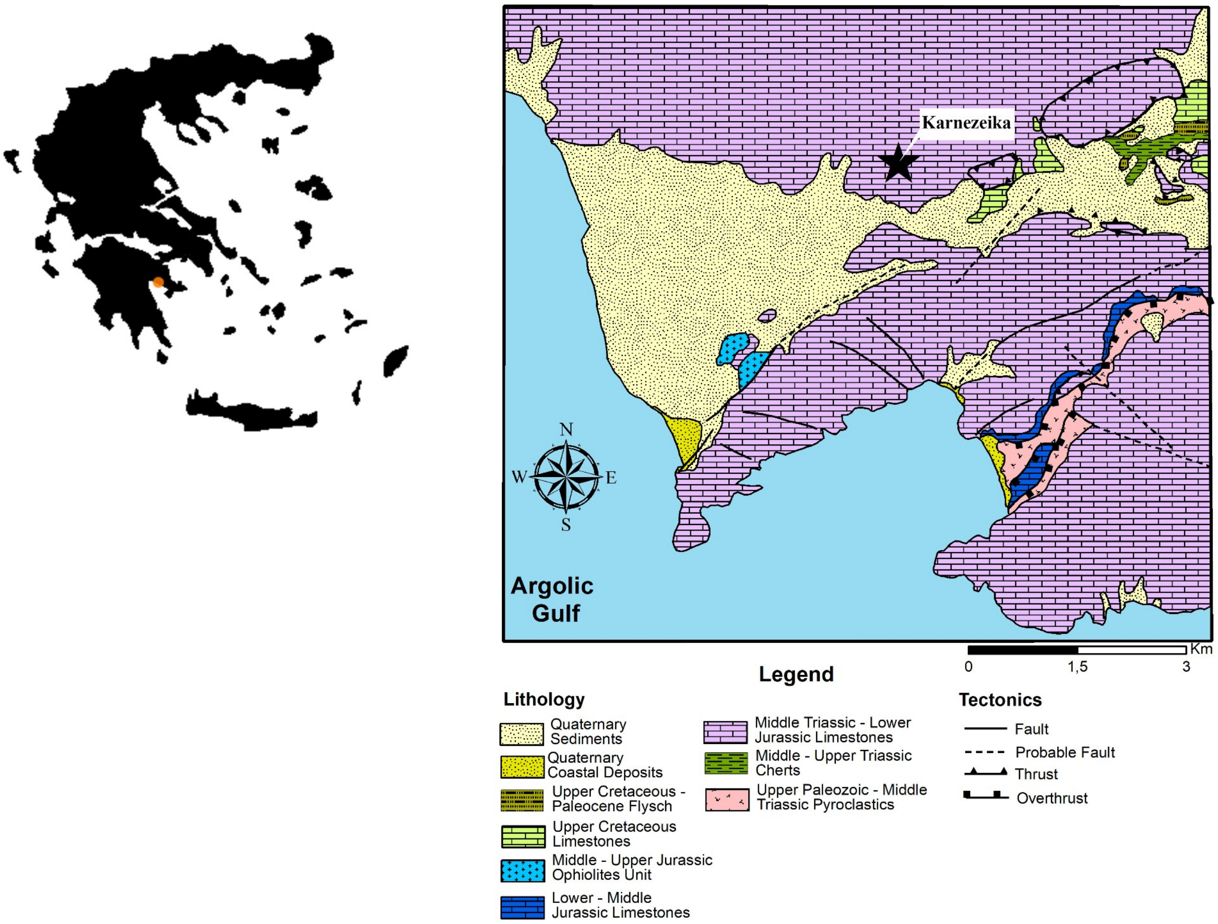

Figure 1: Map of Greece with indication of the Karnezeika locality (left) and geological map of the Karnezeika locality and the surrounding area (right).

Another important character of the area’s geology is the evidence of synsedimentary tectonic activity. This activity is based upon faults that affect only specific layers and not the whole formation. Other evidences include the grouping of peri-tidal deposits, as well as the appearance of sedimentary dikes of great diversity concerning their size and geometry (Kostopoulou, 2018). These phenomena are related to the shredding and the subsequent fast submersion of the carbonate platform of Pantokrator formation that took place during the Early Jurassic (Baumgartner, 1985).

With the later elevation of the area, the carbonate rocks, consisting mainly of limestone, favored the development of intense relief with substantial slopes resulting in the current presence of ravines and high altitudes (Matiatos, 2010; Kostopoulou, 2018). The main karstic structures that are mentioned by Kostopoulou (2018) for the wider area, include shallow surface grooves and dissolved cavities of small or very large dimensions, filled by red micritic matrix and fragments from the surrounding limestone. The Karnezeika locality also presents such geomorphological features, and most likely it was formed due to the collapse of a small karstic cavity inside the carbonate formations that created a small doline. Similar karstic geomorphs are also mentioned by the same author for the neighboring areas as well.

The Villafranchian

As mentioned earlier, some preliminary results concerning the Karnezeika fauna were provided in the form of an oral presentation during the 15th International Congress of the Geological Society of Greece by Kokotini et al. (2019). The identification of micro-mammals provided therein shows that the relative age of the locality corresponds to the Lower Pleistocene, and more specifically, to a chronological period usually mentioned in the literature as the Villafranchian.

The term “Villafranchian” was introduced by Pareto, (1865) in order to describe some Pleistocene terrestrial deposits that accommodated mammal fossils, around the village Villafrance d’ Asti, in the area of Piedmont in Northern Italy. The incorrect, however, original definition of the Italian geologist from both the stratigraphic and faunal points of view, as it was later turned out to be, including other reasons as well (Guérin & Faure, 1982), set the use of the term under serious question. Nonetheless, the general concept of the term was widely used in the bibliography for many years, as it is still used today, as a change would bring confusion among European researchers. Nowadays, however, the term Villafranchian is mainly being used as a biochronological term, in order to describe the mammal faunal units of a specific geochronological time frame (Late Pliocene – Early Pleistocene) of European sedimentary sequences, without paying any particular attention to the kind of the fossiliferous deposits (Kostopoulos, 1996). Thus, almost always the help of MN zonations (Mammal Neogene) (Agustí et al., 2001; Mein, 1975) is acquired, as well as the reference of typical localities.

The reason why this biochronological time range is important, is because it contains time periods during which significant environmental changes took place in the Northern Hemisphere, which in turn resulted in characteristic changes in the flora and fauna. These changes of course did not happen instantaneously, therefore, already since the beginning of the 60's (see Azzaroli, 1962; Bourdier, 1961; Howell, 1959), but also for many years later, there have been efforts to divide the Villafranchian in subsections, which often were based in specific faunas or large mammal families, such as the cervids (Heintz, 1968, 1970). Other important attempts to subdivide the Villafranchian include those of Azzaroli (1970), Mein (1975), Agustí et al. (1987), Mein (1990), and others as well, until finally the subdivision that also applies today prevailed, according to which the Villafranchian is divided into Early (3.5 – 2.6 Ma), Middle (2.6 – 2.0 Ma) and Late (2.0 – 1.0 Ma). Each of these subdivisions includes faunal units of specific typical localities, while as a whole, the Villafranchian spans from 3.5 – 1.0 Ma. The end of the Villafranchian is marked by a period (1.0 – 0.6 Ma) that usually is referred to as Epi – Villafranchian (Kahlke 2007) and constitutes the transition period from the Villafranchian faunas to those of the Galerian (Azzaroli, 1983). This subdivision is also used by the most recent, updated, general and descriptive history of the Villafranchian of Europe by Rook & Martínez-Navarro, (2010), however, these time limits may deviate at a 0.1 – 0.2 Ma level in the bibliography. In Greece, the term "Villafranchian" was introduced for the first time in 1958 but its usage began to acquire a biochronological meaning from 1985 and onwards, due to the extensive palaeontological excavations that took place mainly in Northern Greece (Kostopoulos, 1996).

The Early Villafranchian is the period for which there are much less data compared to the other time frames, mainly because of the relatively few known European localities. The Early Villafranchian belongs to the Early Pliocene and corresponds to MN16. As the typical locality of this period, usually is referred the basin of the Asto province of Northern Italy which also includes the historical fossiliferous site of Villafranca d'Asti (Pradella & Rook, 2007), and is known in the bibliography as the faunal unit of Triversa, named after the homonymous river that flows through the area. One more historical locality is also located in Northern Italy, and belongs to the lower strata of the Valdarno basin (Lower Valdarno) (Albianelli et al., 1997; Rook et al., 2013). Outside Italy, important localities bearing typical Early Villafranchian fauna are also present in the Haute – Loire area in Central/Southeastern France, like for example the Vialette locality (Lacombat et al., 2008) which contains, as the previous researchers mention, the earliest recordings of the *Equus* and

Canis genera in Europe. In addition to the above typical sites/faunas, significant finds have been found in Romania (Dacic basin), as for example the earliest European representative of *Mammuthus* (Lister & Van Essen, 2003), in Hungary (Virág & Gasparik, 2012), but also in Greece (Koufos, 2001, 2006), significantly contributing to the understanding of the fauna of that time. As Rook & Martínez-Navarro (2010) mention, the Early Villafranchian fauna consists mainly of the species *Tapirus arvernensis*, *Mammut borsoni*, *Anancus arvernensis*, *Sus minor*, *Mesopithechus monspessulanus*, *Leptobos stenometopon*, *Stephanorhinus elatus*, *Pseudodama lyra*, *Pliocrocuta perrieri*, *Chasmaporthetes lunensis*, *Homotherium crenatidens*, and *Acinonyx pardinensis.* These species indicate a wooded environment with tropical/subtropical elements that still remind of the Ruscinian (5.3 – 3.5 Ma). Specifically in Greece, the typical locality of reference for the Lower Villafranchian is undoubtedly the site Milia near Grevena (W. Macedonia). This locality has been quite extensively studied by a plethora of researchers (Crégut-Bonnoure & Tsoukala, 2017; Guérin & Tsoukala, 2013; Tsoukala et al., 2014; Tsoukala & Mol, 2016; van Logchem et al., 2010; Vlachos et al., 2018) and is characterised by important finds of the proboscidean *Mammut borsoni*, including the longest ever recorded tusks worldwide (Tsoukala, 2000). Other than that, in Milia many representative species of the Early Villafranchian were also found as the ones mentioned above, but in addition others such as the small sized deer *Croizetoceros ramosus*, the famous Antilopini *Gazella borbonica* and a new Bovini species, *Grevenobos antiquus*. Apart from Milia, the other few Greek localities that are mentioned in the literature are poor in material and of secondary importance (Koufos & Kostopoulos, 2016).

The Middle Villafranchian signals the passage from the Pliocene to the Pleistocene. With no doubt, Montopoli in the province of Tuscany in central Italy is the typical locality for the base of the Middle Villafranchian (Bernor et al., 2018; Cherin et al., 2013; Rook et al., 2017). In the stratigraphy of this site, the Gaus/Matuyama event can be clearly traced (Lindsay et al., 1980) during which the polarity of the planet shifted, which places Montopoli on the upper part of MN16 (MN16b). The fauna changes drastically for the first time and new species prevail, indicators of a more open environment, while other taxa that were indicators of wooded environments, such as *Mesopithecus* and *Tapirus*, disappear (Pradella & Rook, 2007). This reflects the environmental changes that occurred due to obliquity, the 41 kyr orbital cycle in the angle of the Earth's axis of rotation (DeMenocal, 2004; Raymo & Nisancioglu, 2003). During this period climate changed and more specifically in Europe it became colder and drier (Mosbrugger et al., 2005), favoring certain taxa and disfavoring other, while at the same time triggered waves of migration (Croitor & Brugal, 2007). One of these migrations is known in the bibliography as the "*Elephant – Equus* event" (Azzaroli, 1983) and characterizes the beginning of the Middle Villafranchian. This term however nowadays is avoided since both "true elephants" of the *Mammuthus* genus and *Equus* horses have already been found in Early Villafranchian faunas as mentioned earlier. One more typical and very important locality bearing Middle Villafranchian mammal assemblage is that of Saint – Vallier, in Drôme, Central/East France. Stratigraphically, it is located above Montopoli and belongs to MNQ17 (Guérin et al., 2004). The first extended study of the site's fauna already took place in the 50's by Viret (1954), while later, a plethora of researchers contributed so that Saint – Vallier became one of the most well studied localities of the Villafranchian in general (Argant, 2004; Cregut-Bonnoure & Valli, 2004; Delson, 2004; Eisenmann, 2004; Guérin, 2004; Suárez & Mein, 2004; Valli, 2004). In addition it also acts as a reference site for many other localities to date. Apart from Italy and France, important localities are also located in Spain which correspond to the upper part of the Middle Villafranchian. The most known localities are those of La Puebla de Valverde in the region of Aragón in the North-East (Andrés Rodrigo, 2011), Fonelas P-1 in Granada, at the South of the country (Arribas, 2008) and Villaroya in the province of La Rioja in the North, which until recently was considered to belong to the Early Villafranchian, but Pueyo et al., (2016) showed that it actually belongs to the Middle Villafranchian since it can safely be attributed above the Gaus/Matuyama boundary. Madurell-Malapeira et al., (2014) mention that the Middle Villafranchian faunas of Spain, in addition to the important taxa representative of this biochronological sub-unit, also contain some first recordings such as *Pachycrocuta brevirostris*, which, as the same authors mention, puts the "*Pachycrocuta* migration event" before the beginning of the Late Villafranchian. It is worth noting that the "*Pachycrocuta* event" is coinciding with another migration event known in the bibliography as the "Wolf event" (Azzaroli, 1983), but the *Canis* finds in the locality of Vialette (France), disprove the above designation. Nowadays, the term "*Pachycrocuta* event" is solely being used instead, as proposed by Martínez-Navarro, (2010). Furthermore, more important Middle Villafranchian local faunas are also located in the Balkans. One of them is the Varshets locality, in the province of Montana in Northwest Bulgaria (Spassov, 2000). Apart from the plethora of finds indicating a rich fauna including, among others, first records of species such as *Baranogale balcanica* (Spassov, 2001), Varshets is also important because of its geographic position, as an early station for the migration waves from Asia towards Europe. Characteristically, the OviBovini *Megalovis latifrons* appeared in Varshets far earlier before it expanded to Western Europe (Spassov & Crégut-Bonnoure, 1999). As far as the Greek peninsula is concerned, many important Middle Villafranchian local faunas are present (Koufos, 2001), which contributed and still do, to the understanding of the fauna and climate of that period and constitute bases of reference for localities bearing Villafranchian faunas all over Europe (Rook & Martínez-Navarro, 2010). The most significant of them are located in central and northern Greece and belong to the MN17 (Koufos & Kostopoulos, 1997a). Apart from those, more localities are detected all over Greece but are of secondary importance due to the fact that they either are not so well studied or have not provided rich or significant material in comparison with those mentioned below. The first locality to be mentioned is Vatera in the southern part of Lesvos (de Vos et al., 2002; Lyras & van der Geer, 2007). The locality has provided a quite rich fauna, including among others the rare Papionini *Paradolichopithecus arvernensis* as well as one of the larger land turtles in the world, that of the genus *Cheirogaster.* Opposite of the island of Lesvos in mainland Greece, there is another very important Greek locality in Southeastern Thessaly named Sesklo. An extended study of the fauna accompanied with palaeoecological and taphonomical elements is provided by Athanassiou, (1996) completing the previous study of (Symeonidis, 1992). Sesklo is characterised by the strong presence of the horse *Equus stenonis* (Athanassiou, 2018), but also by the first records of species such as the large sized gazelle, *Gazella aegaea* (Athanassiou, 2002a), as well as the carpine *Euthyceros thessalicus* (Athanassiou, 2002b). Another notable locality, Dafnero, is located southwest of Kozani, in Macedonia. The equids and carnivores are described by Koufos & Kostopoulos, (1993) and Koufos, (1993) respectively, while Kostopoulos, (1996) describes in detail the artiodactyls, including also the first finds of a new *Gazella* species named *Gazella bouvrainae* later by the same author. The last Greek Middle Vilalfranchian locality that will be mentioned is that of Volakas, northwest of Drama, Macedonia. Part of the material of this site was studied in the 60's by Sickenberg, (1967, 1968), who also identified a new giraffe and named *Macedonitherium martinii* (nowadays constitutes a synonym of *Palaeotragus inexspectatus* (Athanassiou, 2014)). Kostopoulos, (1996) described the artiodactyls of Volakas for the first time including a new subspecies of *Gallogoral meneghinii*, named *Gallogoral meneghinii sickenbergii*. Based on the above localities, Koufos & Kostopoulos, (2016) mention the following species as typical for the Greek Middle Villafranchian: *Paradolichopithecus arvernensis*, *Anancus arvernensis*, *Mammuthus meridionalis*, *Chasmaporthetes lunensis*, *Pliohyaena perrieri*, *Baranogale* cf. *helbingi*, *Meles thorali*, *Nyctereutes megamastoides*, *Vulpes alopecoides*, *Homotherium crenatidens*, *Lynx issiodorensis*, *Megantereon cultridens*, *Ursus* cf. *etruscus*, *E. stenonis* cf. *vireti*, *Stephanorhinus* cf. *etruscus*, *Palaeotragus inexpectatus*, *Metacervoceros* ex. gr. *rhenanus*, *Croizetoceros ramosus*, *Eucladoceros tegulensis*, *Euthyceros thessalicus*, *G. meneghinii*, *Gazella bouvrainae*, *Gazella aegea*, *Gazella borbonica*, *Gazellospira torticornis*, *?Procamptoceras* sp., και *?Caprini* indet. The species *S. etruscus*, *E. stenonis*, *G. meneghinii* and *G. torticornis* are also mentioned by Rook & Martínez-Navarro, (2010) as typical for the Middle Villafranchian in general. It is worth mentioning that an interesting phenomenon occurs in the Greek Middle Villafranchian which is the co-existence of three different Gazella species, while in the rest of Europe only one appears, *G. borbonica*.

The Late Villafranchian begins during the Olduvai period, near the Gelasian/Calabrian border and is signalled by migration events and many replacements of previous species by new ones (Azzaroli, 1983; Torre et al., 1992). Even though some of these migration events has been already proven that took place earlier, the faunal change of this period is a fact (Rook & Martínez-Navarro, 2010). The Late Villafranchian has a special significance in the world literature because during this period, among others, *Homo erectus* appears for the first time in Eurasia (Ferring et al., 2011). The base of the Late Villafranchian, according to Azzaroli (1977), is the faunal unit of Olivola (followed by the faunal unit of Tasso), with characteristic the expansion of the Bovini *Leptobos etruscus* that came to replace *Leptobos stenometopon.* One important typical locality with finds of these two faunal units are the upper strata of the Valdarno basin (Upper Valdarno) in Tuscany, Northern Italy (De Giuli & Masini, 1986; Mazza et al., 2004; Rook et al., 2013). Outside Italy, another typical locality is that of Senèze, in the area of Auvergne-Rhône-Alpe, in central/southeastern France. This locality belongs to MNQ18 (Delson et al., 2006; Paquette et al., 2021; Roger et al., 2000) and has been studied by a plethora of researchers (see references in Delson et al., 2006), thus providing a quite rich material, including new species. With the end of the faunal units mentioned, also cease the last appearances of residual species of the middle Villafranchian, such as the Antilopini *G. torticornis* or the Machairodontinae *M. cultridens* (Rook & Martínez-Navarro, 2010). Afterwards, the fauna changes dramatically, as seen by the example of one of the most important late Villafranchian localities, that of Dmanisi in the area of Kvemo Kartlii in southeast Georgia. This locality is celebrated by the scientific community worldwide due to the richest and oldest *Homo* finds in Eurasia (Lordkipanidze et al., 2007, 2013; Vekua et al., 2002), which prove that the appearance of *Homo erectus* in the Caucasus area was at least isochronous with its appearance in Eastern Africa, while also reinforcing the hypothesis that as a species it emerged in Eurasia and then spread from there (Ferring et al., 2011). Apart from the *Homo* finds, the locality has yielded rich material of other members of the fauna such as the giant bird *Pachystruthio dmanisensis*, the hyena *Pachycrocuta brevirostris* and the large sized deer *Arvernoceros* (Gabunia et al., 2000; Vekua, 2013; Zelenkov et al., 2019, Bartolini-Lucenti et al., 2022), as well as some records of species first appearances (Bukhsianidze & Vekua, 2006; Vekua, 2012). Another typical locality, Venta Micena, is located in the Iberian Peninsula near the town of Orce of South Spain. It consists probably the best studied locality of the late Villafranchian in the Iberian Peninsula and has provided numerous well – preserved specimens (Madurell-Malapeira et al., 2014; Palmqvist et al., 2005). It has provided among others, rich material of proboscideans (Ros-Montoya et al., 2012), first records of Asiatic species in Europe such as *Hemibos* sp. (Martínez-Navarro et al., 2011), new species records such as the canid *Canis orcensis* (Martínez-Navarro et al., 2021), as well as an impressive record of large carnivores (Arribas & Palmqvist, 1998; Martínez-Navarro & Palmqvist, 1995; Rodríguez-Gómez et al., 2017). Remaining in the Iberian Peninsula and stratigraphically almost at the same level, another important locality, Incarcal, is located in the northeastern edge of Spain (Girona), near the village of Crespià (Galobart & Maroto, 2003; Maroto et al., 2003). This locality consists in reality a complex of Karstic cavities, with the fossils appearing in the sedimentary infills of them. The material that has been provided, is less than that of Venta Micena, however, it is of great interest since it includes remnants of proboscideans (Ros-Montoya et al. 2012), macaques (Alba et al., 2016), as well as outstanding material of the large sized Machairodontinae *H. latidens* (Galobart et al., 2003). The last typical locality of Europe, outside Greece, that will be mentioned is Pirro Nord, also known as Cava Pirro. It is located in Eastern Italy, at the beginning of cape Gargano near the village of Apricena. This locality has provided rich material of carnivores (Petrucci et al., 2013), birds (Bedetti & Pavia, 2013), as well as first records of species such as *Bison degiulii* or *Capreolus sp. (*Arzarello et al., 2015). It also includes the useful for biostratigraphy rodent, *Allophaiomys ruffoi* (Arzarello et al., 2009). Nevertheless, the most important findings of the site are stone tools that certify the presence of the genus *Homo* in the area approximately 1.6 to 1.3 Ma (Arzarello et al., 2007, 2012, 2015). As far as the Greek peninsula is concerned, important localities are located mainly in North and central Greece. The most significant of these are limited in the Mygdonia basin east of Thessaloniki, in Macedonia. The Gerakarou locality of the Mygdonia basin, south of lake Koroneia and near the homonymous settlement, is one of these localities. It has provided abundant material with important finds such as *G. bouvrainae* that appears only in the Greek peninsula, and a new even smaller sized sub-species of the already small cervid *C. ramosus* that was named *C. ramosus gerakarensis* (Kostopoulos, 1996), as well as many finds of *Canis* (Koufos, 2014). Remaining in the Mygdonia basin, southeast of Gerakarou is the locality of Tsiotra Vryssi. This locality has provided a large number of perissodactyl, artiodactyl, proboscidean and carnivore findings (Konidaris et al., 2021), including an almost complete skull of the bear *Ursus etruscus* (Koufos et al., 2018). Another locality is that of Halykes in the county of Magnesia. Even though it has not provided a large quantity of material compared to the previous locality (Athanassiou, 1996, 2002c), it is important due to the fact that it is the southernmost studied locality of the late Villafranchian of Greece, giving data for the fauna of that period south of Macedonia.

The end of the late Villafranchian and consequently of the Villafranchian as a biochronological unit, coincides with the end of the Lower Pleistocene and occurs as the transition begins from the Galerian to the dawn of the Middle Pleistocene. During this transition, another biochronological unit is detected, which is usually referred to as the Epi – Villafranchian and is characterised by climatic changes corresponding to the 41 kyr periodicity (Bellucci et al., 2015). As the same authors mention, the passage from the late Villafranchian to the Epi – Villafranchian is signalled by the appearance in Europe of the cervid *Praemegaceros verticornis* and the bovid *Bison menneri*, but also of the suid *Sus* gr. *scrofa* as Martínez-Navarro et al., (2015) added. One of the main European Epi – Villafranchian localities is Untermassfeld (Kahlke, 2000, 2006, 2009), located in Thuringia, central Germany. It has provided plethora of different taxa as well as very rich material of the hippo *Hippopotamus amphibius antiquus* but also of the rhino S*tephanorhinus hunsheimensis*. The presence of *Homo* is also mentioned by some researchers (Landeck & Garcia Garriga, 2017, 2018), but is being questioned by others (Roebroeks et al., 2018). In Greece, the most important Epi – Villafranchian locality is located once again in the Mygdonia basin in Macedonia and is named Apollonia 1 after the nearby homonymous settlement, south of lake Volvi (Kostopoulos, 1996). The locality has provided rich material including new species such as the oviBovini *Soergelia briggitae* (Kostopoulos, 1996), the medium – large sized true horse *Equus apolloniensis* (Gkeme et al., 2021; Koufos et al., 1997) and the canid *Canis apolloniensis* (Koufos, 2018; Koufos & Kostopoulos, 1997b).

Material and Methods

Extraction and preparation of the specimens

The extracted 2×2×2 m block consisting of fossiliferous cemented terra rossa sediment and limestone clasts was placed under a sheltered area and then the extraction of the fossils began using hand tools. More specifically the tools used during this process were geological hammer, chisels, hard brushes in order to remove sediment and pebbles and soft ones for cleaning around of the fossils. The sediment was generally not well cemented and thus easy to work on. However, what made the extraction difficult was the extremely high content of limestone clasts ranging in size from a few centimetres to a few decimetres. The protocol that was followed for the extraction of the fossils was the following: the process started from the top of the block, as it was placed on the ground, and this was named as level zero (E0). During the extraction process, fossils were not removed but remained there until all of the level was cleared to a depth of ten to fifteen centimetres. Then, the layer was photographed as well as a rough sketch was drawn in order to depict the location and orientation of the fossils on the level, which were also given a special level code. Afterwards, the specimens were removed and transferred to the laboratory for final preparation as it will be described later. This process was repeated until the very last level, and the removal of the last fossil bones from the block.

All the removed sediment during the extraction process was not discarded but instead it was collected in hard plastic bags and stored in a warehouse of the Department. On these bags information concerning the date of collection, the block number, and the level of which it came from was written. We are aware of the presence of micro-vertebrates in the sediments, thus this could consist the material for another project concerning the extensive study of the micro-vertebrate fauna, which in the context of the present dissertation, their presence is simply certified.

Preparation

Due to the soft nature of the sediment, any chemical treatment of the material was not considered necessary as the mechanical cleaning of the fossils was sufficient. For this purpose, conventional hand tools such as needles, small chisels, brushes, scrapers etc. were used. After preparation, the next stage was the conservation of the fossils. All the fossil specimens were impregnated using a 10% solution of the acrylic resin Paraloid B-72 in acetone. Since some of the material did not come out intact, but broke or had already been broken due to taphonomic processes in the past, broken parts were restored and glued together using the acrylic resin UHU.

Coding

For the coding of the fossil specimens, the initials KZ were chosen, followed by a serial Arabic numeral. As it has already been mentioned, a small part of Karnezeika fossils had already been studied in the context of an undergraduate dissertation by Kokotini, (2018). For this reason, the coding of the fossil bones concerning the current project continued from where the previous ones had ended. Thus, the first specimen took the code number KZ312 and the last one KZ3358. Small fragments that were deemed unable to provide any information either taxonomically or taphonomically, were not coded.

Bone identification and determination

For the initial identification of the fossils, the special osteological atlases of Pales and Garcia, (1971, 1981) were used. Fossil bones were then initially divided into artiodactyls, perissodactyls and carnivores. Thereafter, each different morphotype of each, respectively, osteological element (e.g., metapodials, phalanxes, long bones, teeth etc.), was attributed to families such as Bovidae, Cervidae, Felidae etc. The determination of different taxa was based on a number of relevant publications (Heintz, 1963, 1970; Hillson, 1999, 2005; Brown and Gustafson, 2000; France, 2011; Wang, Peters and Barker, 2020 etc.). In addition the collections of the Palaeontological Museum of the Geology Department of the Aristotle University of Thessaloniki and the Museum of Palaeontology and Geology of the Geology Department of the National and Kapodistrian University of Athens, were used as comparative material.

Nomenclature

Description of the postcranial elements follows mainly the terminology given by König and Liebich, (2007). Regarding the description of the dental material, terminology was chosen depending on the taxon under study. Therefore, for the artiodactyls the terminology follows Bärmann and Rössner, (2011), for the equids the terminology follows Eisenmann et al., (1988), for the Rhinocerotidae the terminology follows van der Made, (2010), for the carnivores the terminology follows Wang et al., (2004), Hanko, (2007) Prat-Vericat et al., (2020), and finally for the primates the terminology follows Swindler, (2002).

Measurements

Apart from the description of the material, every studied osteological element is accompanied by basic measurements. For these measurements, no specific methodology was followed as it varied depending on the osteological element and the taxonomic family respectively. However, as a general rule, the anteroposterior diameter (Length or DAP) of each bone was measured, as well as the transverse diameter (Width or DT). Measurements were taken with the help of digital callipers to the nearest two decimals and are provided in millimetres.

Abbreviations

L: greatest length, DAP: antero-posterior / cranio-caudal diameter, DT: transverse diameter, prox: proximal end, dia: diaphysis, dis: distal end, med: medial, lat: lateral. Regarding the dentition, small characters (p, m) indicate the lower premolars and molars whereas capital ones (P, M) indicate the upper teeth, D or d: deciduous, L: length (mesiodistal diameter), occlusal, W: width (labiolingual or vestibular diameter), maximum. The present locality of Karnezeika is sometimes abbreviated as KZ. PCUP: Palaeontological Collection of the University of Patras; AMPG: Athens Museum of Palaeontology and Geology, National and Kapodistrian University of Athens.

Systematic Palaeontology

Primates

The Cercopithecidae is a diverse family of Old-World monkeys (Catarrhini) with a former wide distribution across Africa, Asia and Europe. Taxonomically, it is divided in two subfamilies, Cercopithecinae and Colobinae, both of which are present in the fossil record of Europe (Eronen and Rook, 2004), even though rather rare with respect to other families. In Europe, the cercopithecids appear in the Late Miocene (MN11) with the colobine *Mesopithecus* Wagner, 1839, and disappear in the late Pleistocene. During the Pliocene and the Pleistocene, the family showed an increased taxonomic diversification in Europe, represented by the genera *Macaca* Lacépède 1799, *Dolichopithecus* Depéret, 1889, *Theropithecus* Geoffroy Saint-Hilaire, 1843, and *Paradolichopithecus* Necrasov et al., 1961 (Szalay and Delson, 1979; Frost, 2017).

In the Greek cercopithecid fossil record, the colobine monkey *Mesopithecus* is the most frequent, known from several Upper Miocene localities of the central and northern parts of continental Grece (Koufos, 2009), such as Pikermi near Athens (with *M. pentelicus* Wagner, 1839) and Axios Valley near Thessaloniki (with *M. delsoni* de Bonis et al., 1990 and *M. monspessulanus* Gervais, 1849). In addition, another colobine monkey, *Dolichopithecus*, is known from the Lower Pliocene locality Megalo Emvolo near Thessaloniki (Koufos et al., 1991) and from a few isolated dental specimens found in Ptolemais basin (Doukas and De Bruijn, 2002). Spassov and Geraads, (2007) included the Megalo Emvolo remains to a new species, *D. balcanicus* Spassov & Geraads, 2007. However, this opinion was not followed by Koufos, (2009, 2022), who continued to refer the Megalo Emvolo sample to *D. ruscinensis* Depéret, 1889. As far as the Cercopithecinae are concerned, the first finds include some isolated dental remains from the locality of Tourkovounia near Athens, which were ascribed by Symeonidis and Zapfe, (1976) to *Macaca florentina* Cocchi, 1872. Very recently, new *Macaca* remains were unearthed from the locality of Marathousa-1 in Megalopolis basin, ascribed by Konidaris et al., (2022) to *M. sylvanus* cf. *pliocena* Owen, 1846, and from the nearby locality of Kyparissia (*M. sylvanus* Linnaeus, 1758, Konidaris et al. in press). Finally, the Villafranchian large cercopithecid *Paradolichopithecus* is currently known in Greece from two Lower Pleistocene localities: Vatera on Lesbos Island and Dafnero in NW Greece (de Vos et al., 2002, van der Geer & Sondaar, 2002, Lyras & van der Geer, 2007, Kostopoulos et al., 2018); both ascribed to the Eurasian species *Par. arvernensis* (Depéret, 1928). For a comprehensive and up-to-date review of the Greek fossil record of Cercopithecidae, see Koufos, (2022).

Order Primates Linnaeus, 1758
Infraorder Catarrhini Geoffroy Saint-Hilaire, 1812
Superfamily Cercopithecoidea Gray, 1821
Family Cercopithecidae Gray, 1821
Subfamily Cercopithecinae Gray, 1821
Tribe Papionini Burnett, 1828
Paradolichopithecus Necrasov, Samson & Radulesco, 1961
Type species *Dolichopithecus arvernensis* Depéret, 1928

Remark. Traditionally, the authorship of *Dolichopithecus arvernensis* was attributed to Depéret, (1929) where the species was fully described. However, recently, it has been known (Delson E. pers. comm.) that the first (i.e., original) announcement of this taxon was actually provided a year earlier by Depéret, (1928) himself. In this latter article, Depéret names his new species and provides a short but meaningful description of very basic features, that could satisfy the terms of name availability under the Article 12 of ICZN.

cf. ***Paradolichopithecus*** sp.

Figure 2

Material

One upper incisor (PCUP KZ1400); one left upper second molar M2 (PCUP KZ1852); one proximal part of a right radius (AMPG KRZ93).

Description

The specimen KZ1400 is a right incisor, most likely an upper one (Figure 2e–g). The tooth is ascribed to the same taxon due to similarities with primate incisors, though with some reservation, because of its unusual wear pattern. The occlusal surface is oval shaped (elongated mesiodistaly) and devoid of any morphological characteristics, as it is in advanced stage of wear. Almost all of the surface consists of exposed dentine. The centre of the surface is low while the

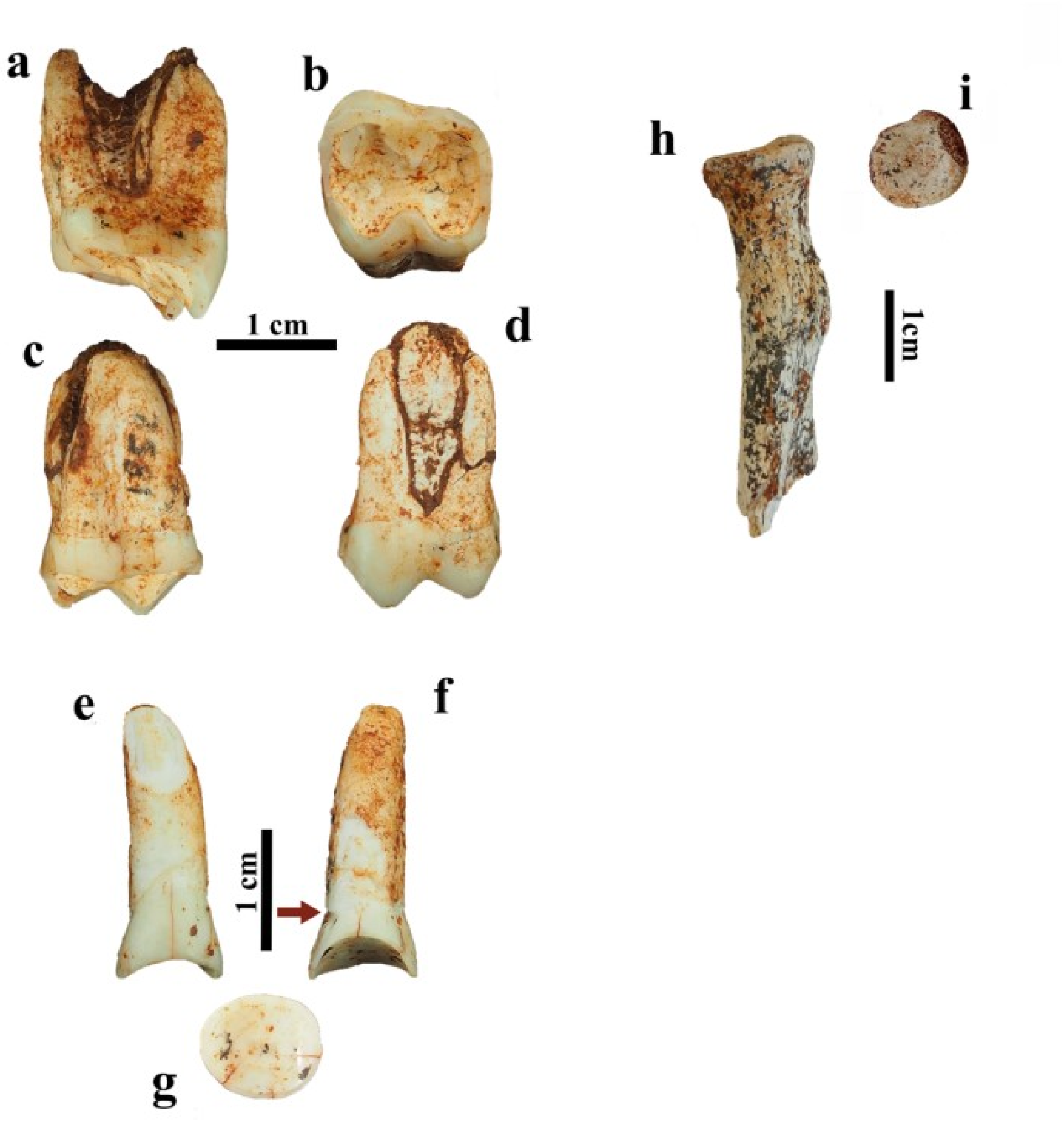

Figure 2: cf. Paradolichopithecus *sp., Karnezeika: (a)–(d) left M2(PCUP KZ1852), in mesial (a), occlusal (b), lingual (c) and buccal (d) view; (e)–(g) right I1 (PCUP KZ1400), in labial (e), lingual (f) and occlusal (g) view (the mesiodistal groove is indicated with an arrow); and proximal part of right radius (AMPG KZR93) in anterior (h) and proximal (i) view.*

mesial and distal enamel ridges are high, creating a valley-like structure. A longitudinal, mesiodistally oriented groove is present in the mesial side of the tooth, at the border of the crown and the cervix (see arrow in figure 2). This groove, as well as the tooth as a whole, is characterised by the presence of micro-cracks due to taphonomical modification, as well as black stains, most likely due to the presence of manganese oxides (Fernández-Jalvo and Andrews, 2016). Labially, the crown appears wide and relatively short. The root is robust and curves laterally towards its apex. Its cross-section is elliptical, slightly compressed mesiodistally. No basal bulge nor any lingual cingulum is observed.

The specimen KZ1852 is a well preserved isolated left upper molar, which retains all three of its roots (Figure 2a–d). The crown is almost square shaped (M2L×100/M2Wmax=96.5) and includes four low bilophodont cusps (two buccal and two lingual) following the typical bilophodont morphology for the molars of the Old World monkeys (Swindler, 2002). The tooth is in a very advanced stage of wear (stage F of Delson (1973), exposing largely the dentine in the entire occlusal surface and resulting in complete merging of the wear facets. The inner profile is also lost to wear, placing the individual to IDAS 4 (late adult) or IDAS 5 (senile) (*sensu* Anders et al. (2011). Enamel is only visible at the margins of the tooth. Due to the advanced wear, the occlusal surface appears much lower than the enamel margins and almost completely smooth, lacking any morphological characteristics. Nevertheless, despite this advanced stage of wear, the tips of the buccal cones remain relatively pointed. The lingual cones are much lower than the buccal cones. On the distal and mesial walls two contact facets can be clearly seen indicating that the tooth is a first or second molar and most likely the latter due to its dimensions (Table 1). Strong bulging appears in the buccal side of the paracone, as can be also observed in modern baboons and macaques. A well-developed cleft (*sensu* Delson, 1975) is visible on the lingual side of the tooth. A weak flaring is detectable, more evident in the lingual side, which was calculated based on Benefit (1993) and Singleton (2003) and found to be equal to 0.3. Such a low value may be due to the advanced stage of wear.

Table 1. Measurements of the teeth and radius of cf. *Paradolichopithecus* sp. from Karnezeika. M2L: maximum mesiodistal diameter of M2; M2Wmax: maximum buccolingual diameter of M2; M2Wmes: mesial (first lobe) buccolingual diameter of M2; M2Wdis: distal (second lobe) buccolingual diameter of M2; IL: maximum mesiodistal diameter of I; IWmax: maximum labiolingual diameter of I; RaLmax: maximum head diameter of the radius; RaWmax: minimum head diameter of the radius.

cf. *Paradolichopithecus* sp.		
Measurement	**n**	**value (mm)**
M2L	1	12.77
M2Wmax	1	13.24
M2Wmes	1	13.07
M2Wdis	1	11.53
IL	1	8.68
IWmax	1	7.77
RaLmax	1	21.15
RaWmax	1	19.20

The radius (AMPG KRZ93) preserves only the proximal part of the bone, broken a few centimetres distally of the well-developed radial tuberosity (Fig. 2h–i). The neck of the radius is short and slightly inclined in relation to the radial tuberosity. The head of the radius is sub-circular with a shallow articular surface.

Remarks

Characters shown by the upper M2 specimen KZ1852, such as the low cusps, the lingual cleft, the flaring and the wear pattern are typical of Papionini (Delson, 1973; Swindler, 2002; Frost and Kullmer, 2008). On the contrary, Colobinae are characterised by an increased crown relief and an asymmetrical curve of the distal margin of the upper teeth (Szalay and Delson, 1979). *Dolichopithecus* can be excluded based on its smaller dimensions and the presence of strong crown relief, commonly found in Colobinae (Szalay and Delson, 1979). Among known Plio-Pleistocene Eurasian Cercopithecidae, *Theropithecus* can easily be ruled out on the basis of its particular dental morphology with high crowns, columnar cusps and significantly developed enamel folding, as well as the characteristic double cross wear pattern (Jablonski, 1993; Frost, 2014). As far as the other three commonly known genera are concerned, placing *Macaca* on the one side and the group *Paradolichopithecus – Procynocephalus* on the other, their molar morphology is quite similar but they differ significantly in terms of size, as shown in Figure 3. The Karnezeika molar specimen seems to correspond metrically to the *Paradolichopithecus – Procynocephalus* group, while it appears consistently larger than all compared macaques. The occlusal surface dimensions can provide a safe criterion in distinguishing between *Macaca* and *Paradolichopithecus* dental remains (Alba et al., 2018), therefore attribution to the former can also be discounted.

Hence, based on the aforementioned morphological characters which are typical of the Papionini (excluding *Theropithecus)*, and the tooth dimensions (much larger than *Macaca*), the specimen KZ1852 most likely belongs to the genus *Paradolichopithecus*. Dental remains of *Paradolichopithecus* are practically indistinguishable from *Procynocephalus* and their phylogenetic relationships along with the possibility of synonymy is still a matter of debate (see Simons 1970, p.197; Szalay and Delson, 1979; Nishimura et al., 2010; Nishimura et al., 2014; Kostopoulos et al., 2018). Nevertheless, it is a common consensus that the latter is a Far-Asian form. Moreover, in Greece the presence of *Par. arvernensis* has been documented already in two localities: Vatera (Van der Geer and Sondaar, 2002; de Vos et al., 2002; Lyras and van der Geer, 2007) and Dafnero (Kostopoulos et al., 2018).

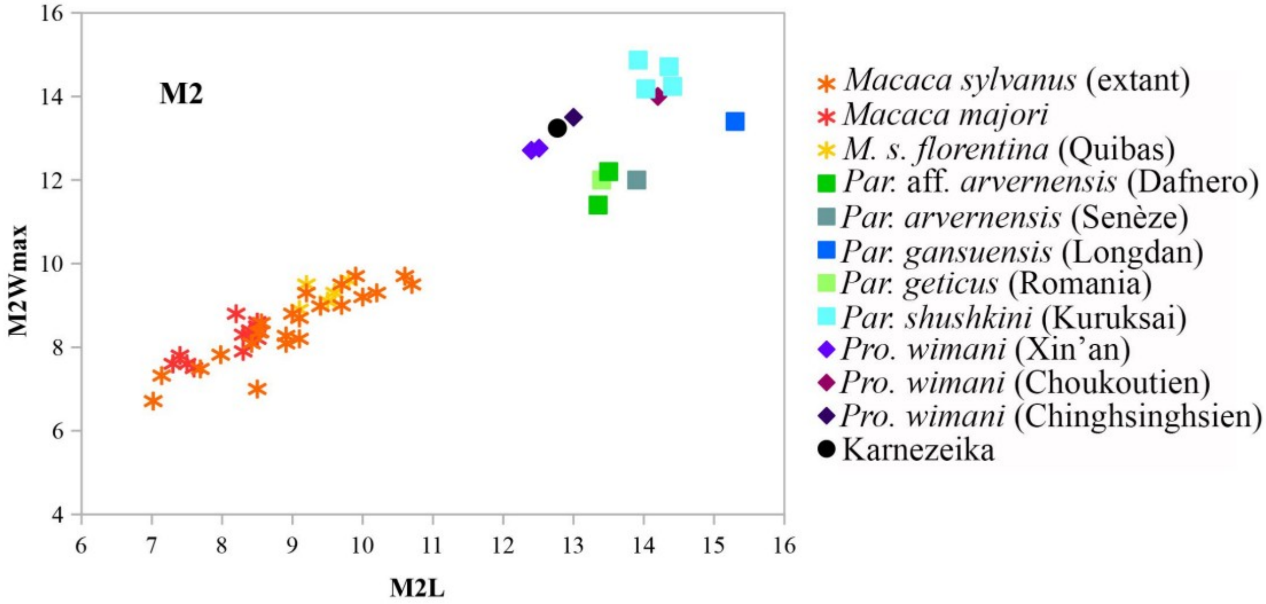

Figure 3: Bivariate plot of maximum length and width of the M2 of cf. Paradolichopithecus *sp. from Karnezeika compared with other Papionini. Data from Takai et al. (2008) and references therein, Alba et al. (2011), Kostopoulos et al. (2018) and the PRIMO database (http://primo.nycep.org).*

The incisor KZ1400 is quite problematic since it shows an unusual wear pattern. If its identification as a cercopithecid upper incisor is valid, then it is very likely that it belongs to the same individual as the molar KZ1852, based on the similar degree of wear and the overall preservation. However, the wear pattern seems not to correspond to the usual type found in cercopithecine incisors, in which the labial surface appears significantly inclined, uniformly worn and the lingual side being more triangularly shaped (Shellis and Hiiemae, 1986; Koufos and de Bonis, 2017). On the contrary, the Karnezeika specimen exhibits characters such as the valley-like structure and the interproximal grooving (*sensu* Formicola 1988), which resemble to some extend artificial modifications occurring in human populations (Ubelaker et al., 1969; Brown and Molnar, 1990; Molnar, 2008). Of course, no such scenario is proposed for the Karnezeika large cercopithecid, but the mechanism behind the formation of this feature might possibly be similar. The repetitive motion, when chewing some hard material, by moving it from the inside out of the animal's mouth, may have resulted in these particular characters (see Ryan (1979). This, however, would imply that such a motion must have been consecutive and a common habit in the animal's diet which can only be hypothesized with the current data.

The articular surface of the proximal end of the radius exhibits a quite rounded shape (RaLmax × 100/RaWmax = 110.15), which is similar to that of *Par. arvernensis* from Vatera

(RaLmax × 100/RaWmax = 111.28). *M. sylvanus florentina* is characterised by smaller dimensions and exhibits an even more rounded articular surface of the proximal end of the radius (RaLmax × 100/RaWmax = 105.88 – see Fig. 4(c-d) in Alba et al., (2011)). The studied radius from Karnezeika also differs from that of the modern baboon *Papio hamadryas* and the mandrill *Papio sphinx* as well. The two latter taxa have radii with an elliptical articular surface (see van der Geer and Sondaar, 2002).

Whatever the case, the similarities with *Paradolichopithecus* cannot be dismissed based on the studied molar and radius; on the other hand, the two isolated dental elements and the partially preserved radius cannot be considered as conclusive and a comparison at the species level is not reliable at the moment. Therefore, due to the scarcity of material and for propriety reasons, it is considered best to ascribe the Karnezeika large-sized primate to cf. *Paradolichopithecus* sp.

Biochronologically, the oldest *Paradolichopithecus* occurrence dates to around 3.2 Ma (Eronen and Rook, 2004), while the most recent known record dates to around 1.6 Ma.

Paradolichopithecus consists a rare find in Greece (Koufos, 2022) and in Europe as well, with only a few specimens referred to this genus. More specifically, in the Balkan area, apart from the Greek sites mentioned above (Vatera and Dafnero), the genus is also known from two Romanian localities: in Valea Graunceanului (Necrasov et al., 1961) and Malushteni (Delson, 1973). Similar dental finds with the ones described herein, were recently described in the same manner from the locality of Ridjake in Serbia (Radović et al., 2019). Nevertheless, the few new finds described herein from Karnezeika indicate the possible presence of this important cercopithecid taxon in Peloponnesus, widening further the distribution of *Paradolichopithecus* in Greece (see also Sianis et al., 2022b).

Carnivora

Carnivores play an important role in regulating the numbers of plant-consuming members of the macro- and micro-fauna in modern ecosystems, and this has been the case during the Pleistocene as well (Van Valkenburgh et al., 2016). Thus, carnivores constitute an important element of fossil accumulations and their study provides essential information on the palaeoecology of fossil assemblages. The Villafranchian carnivore guild of Greece is quite rich, comprising numerous species, the majority of which belong to canids and felids (Koufos, 2014). The Greek fossil record also includes some endemic species, such as *Canis apolloniensis* Koufos and Kostopoulos, 1997 and *Meles dimitrius* Koufos, 1992 (Koufos and Kostopoulos, 1997; Koufos, 2018; Savvidou, 2022). For a comprehensive review of the Greek fossil record of carnivores, see the corresponding chapters in Vlachos (2022).

Class: Mammalia Linnaeus, 1758
Order: Carnivora Bowdich, 1821
Family: Ursidae Fischer de Waldheim, 1817
Genus: *Ursus* Linnaeus, 1758

Ursus etruscus Cuvier, 1823

Figure 4

Material

The associated material consists of a few isolated teeth including one right and one left M1 (KZ2099, KZ3280), one right m2 (KZ3279), a partially preserved premolar (KZ2182) and a partially preserved canine (KZ3221). See also Figure 4.

Description

The molars are bunodont with broad and complex occlusal surfaces. Specimens KZ3280 and KZ3279 most likely belong to the same individual, based on the state of wear and overall preservation (Fig 4(a-c, e-g)). They were also found close to each other. The partially preserved specimens KZ2182 and KZ3221 (not figured) do not offer diagnostic characters, due to their fragmentary state, and are included herein based on size and general morphology.

The general shape of the M1 is rectangular (L×100/W= ~132). Buccally, the paracone and the metacone are large, prominent, and similar in size. A cingulum develops along their buccal wall. Mesially, the parastyle is well expressed and robust, but low. Distally, the metastyle is similar to the parastyle, yet slightly lower in KZ2099, and almost absent in the worn specimen KZ3280. Both styles are vertically oriented. The talonfield is relatively reduced and tuberculated, and is inclined backwards. On the lingual side, the protocone, the hypocone and a mesocone between them appear similar in morphology and size. They are well expressed, low and elongated. The protocone is slightly larger than the three aforementioned cones and retains its original shape with advancing wear, compared to the other two cones. On the contrary, the mesocone appears extremely weak in the worn specimen KZ3280. The lingual cingulum is weak, and does not extend distally beyond the hypocone. KZ3280: L: 19.10 mm / W: 14.92 mm; KZ2099: L: 22.16 mm / W: 16.33 mm.

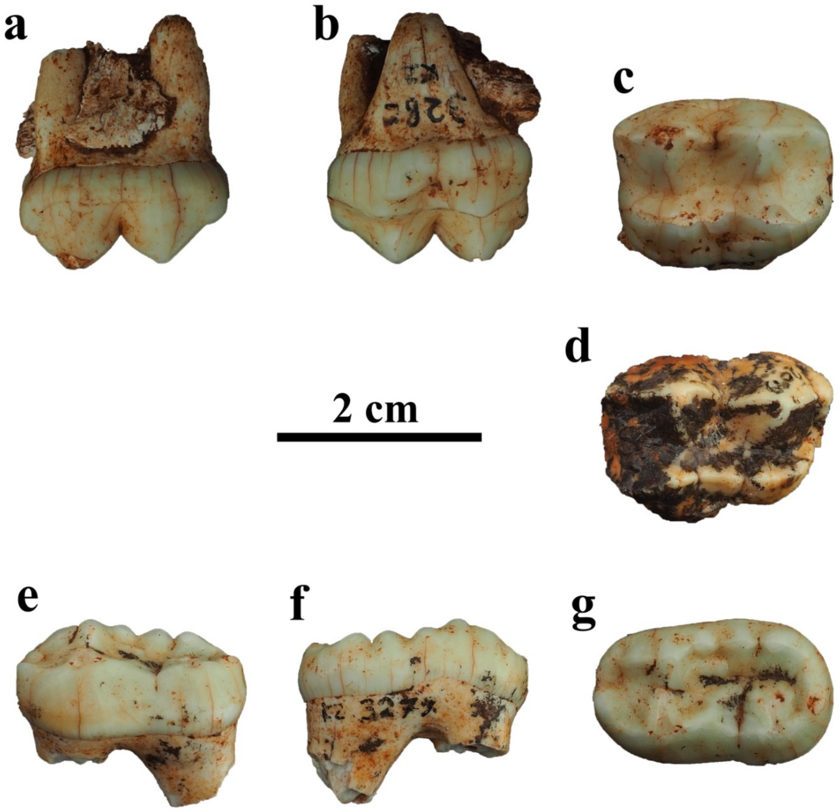

Figure 4: Ursus etruscus. Karnezeika. a-c, Left M1 (KZ3280) in vestibular (a), lingual (b) and occlusal (c) view; d, right M1 (KZ2099) in occlusal view; e-g, right m2 (KZ3279) in lingual (e), vestibular (b) and occlusal (g) view. Scale bar: 2 cm.

The m2 is elongated and shows a moderate central constriction. Buccally, the most prominent element is the metaconid, which is large and robust. Two moderately expressed metastylids can be observed on both sides of the metaconid, of which the mesial one is hardly distinguishable from the latter, due to the advanced stage of wear. The entoconid is bicuspid and strong, but low. Lingually, the protoconid and hypoconid are robust, though somewhat worn. There is a very weak cingulum at the base of the buccal wall. Occlusally, the enthypoconid appears connected with the hypoconid due to wear. KZ3279: L: 21.85 mm / W: 12.72 mm.

Remarks

The complex bunodont occlusal surface is typical of Ursidae and reflects their omnivorous dietary habits. After an absence of Ursidae during the Early Pliocene in the Greek fossil record (Kostopoulos and Vasileiadou, 2006), the family appears again in Villafranchian assemblages mainly with the genus *Ursus* and in one case with the short-faced bear *Agriotherium* from Milia, Grevena (Tsoukala et al., 2014). Compared with Plio-Pleistocene *Ursus* species (Fig. 5), the Karnezeika dental specimens differ strongly in terms of size from the large spelaeoid bears, such as *U. deningeri* von Reichenau, 1904, *U. spelaeus* Rosenmüller, 1794, and *U. ingressus* Rabeder et al., 2004, being clearly smaller. Compared to other smaller *Ursus* species, the Karnezeika bear exhibits characters such as: a rectangular M1 with similar sized metacone and paracone, moderately expressed buccal styles with the parastyle being slightly greater than the metastyle, presence of a well expressed mesocone in the lingual side, a weak lingual cingulum, and a bicuspid entoconid on m2, which are features most commonly found in *U. etruscus* (Viret, 1954; Mazza and Rustioni, 1992; Medin et al., 2017, 2019). Furthermore, the metaconid of m2 is not single-cusped as in *U. minimus* Devèze and Bouillet, 1827 (Baryshnikov and Lavrov, 2013). Also, the paracone of M1 is not significantly higher than the metacone, nor the metastyle almost absent as in *U. thibetanus* Cuvier, 1823 (Baryshnikov, 2010). Compared to *U. dolinensis* García and Arsuaga, 2001 from Trinchera Dolina, Spain (or *U. deningeri* as argued in Madurell-Malapeira et al., 2014; Medin et al., 2017) the buccal styles of M1 are not so reduced, while the m2 shows a central constriction in contrast to the Spanish specimens (García and Arsuaga, 2001).

Based on its metrical and morphological characters, the Karnezeika ursid is ascribed to *U. etruscus*, which is undoubtedly the typical ursid of the Villafranchian faunas of Europe. The oldest European *Ursus* representatives belong to *Ursus* ex. gr. *minimus-thibetanus (sensu* Mazza and Rustioni, 1994) and appeared in the Early Pliocene (Krause et al., 2008; Wagner, 2010). By the beginning of MN17, however, they either evolved to or were replaced by the etruscan bears of Asiatic origin (Rustioni and Mazza, 1993), which likely in turn gave rise to the brown and spelaeoid lineages (see Kurtén, 1968; Medin et al., 2017, 2019). Characters shown by the Karnezeika specimens such as the vertically oriented buccal styles of M1 and the three-cuspid metaconid of m2 seem to further confirm the ancestral position of *U. etruscus* in the spelaeoid lineage, since these are derived features typical of cave bears (see Medin et al., 2017 and references therein). In Greece, the species is known from many Early to Late Villafranchian assemblages (see Pappa and Tsoukala, 2022 for a detailed review). The best – preserved material comes from Tsiotra Vryssi, Mygdonia basin (Koufos et al., 2018).

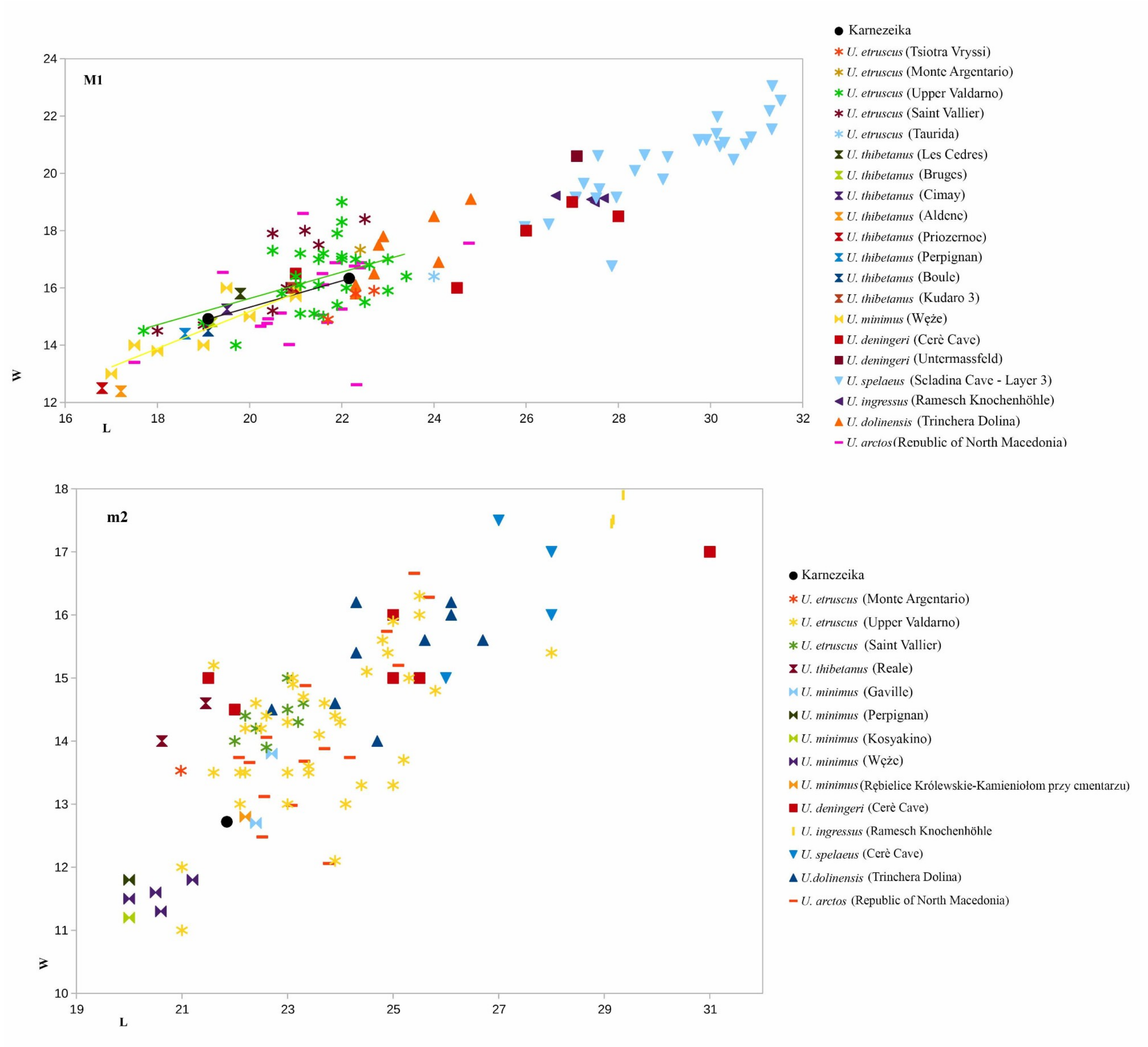

Figure 5: Scatter chart of the dental dimensions of Ursus etruscus *from Karnezeika and other comparable taxa. Diagram A corresponds to M1 and diagram B to m2. Data from (Viret, 1954; Ryziewicz, 1969; Mazza & Rustioni, 1992; Crégut-Bonnoure, 1996; García & Arsuaga, 2001; Rabeder et al., 2004; Wagner et al., 2008; Petrucci & Sardella, 2009; Rabeder et al., 2010; Rossi & Santi, 2011; Baryshnikov & Lavrov, 2013; Baryshnikov & Zakharov, 2013; Koufos et al., 2018; Charters et al., 2019; Biljana, 2020; Gimranov et al., 2020).*

Family: Mustelidae Fischer de Waldheim, 1817

Genus: *Baranogale* Kormos, 1934

Baranogale helbingi Kormos, 1934

Figure 6

Material

A partially preserved left hemimandible bearing p2, p3 and m1 (KZ2771), a partially preserved right hemimandible bearing m1 (KZ2896), a partially preserved left hemimandible bearing p2, p3 and m1 (KZ1300), a fragment of a left hemimandible bearing m1 (KZ3163) and possibly one isolated m2 (KZ1460) and two isolated canines (KZ515; KZ3335). Two calcanei and a talus bone are also attributed to this form, based on their overall small size.

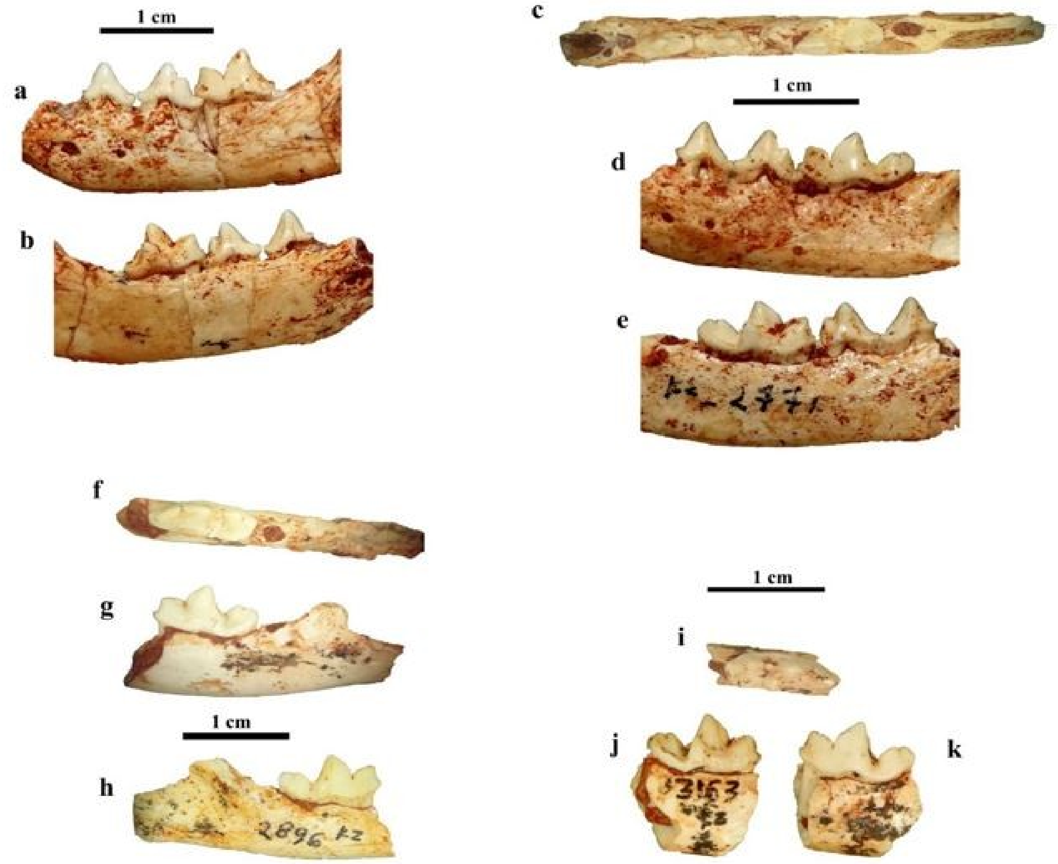

Figure 6: Baranogale helbingi. *Karnezeika. a-b, left hemimandible bearing p3, p4, m1(KZ1300) in vestibular (a) and lingual (b) view; c-e, left hemimandible bearing p3, p4, m1 (KZ2771) in occlusal (c), vestibular (d) and lingual (e) view; f-h, right hemimandible bearing m1 (KZ2896) in occlusal (f), lingual (g) and vestibular (h) views; i-k, left m1 (KZ3163) in occlusal (i), lingual (j) and vestibular (k) view. Scale bars: 1 cm.*

Description

All teeth are small and proportionally narrow, with pointed conids. Two equal-sized mental foramens are observed below the third lower premolar. See Figure 6.

The canine (not figured) is slender and shows a weak lingual crest.

The p3 is triangular and slender with a quite simple morphology. It has one main conid, which is very strong, high, and particularly pointed. A cingulid is present, forming cuspid-like protrusions both in the mesial and distal ends of the crown (Figures 6(a-b, d-e)).

The p4 is similar to p3, but it additionally has a secondary, well – developed conid on the distal side of the protoconid, developed parallel to the latter (Figure 6(a-b, d-e)). Moreover, the distal cingulid is stronger than in p3.

The m1 is narrow and elongated. The protoconid is strong, high and pointed. Its distal side is straight and almost vertical, while the mesial side curves smoothly backwards. Mesially, the paraconid forms a wide angle with the protoconid and these two are separated by a slit-like depression. The metaconid is not individualized. Distally, the talonid is high, particularly distally, and accounts for slightly less than the half of the total tooth length. On the buccal side of the talonid there is a moderately expressed hypoconid which is almost fused with the buccally displaced hypoconulid (Figure 6(d, h, k)). With advancing wear, the hypoconid and the hypoconulid merge with each other. No entoconid is observed. The lingual side of the talonid is devoid of conids, resulting in a completely smooth margin. A cingulid is present, but it is weaker than those in the premolars.

The m2 (not figured) is very reduced and has a trapezoidal occlusal surface with five cuspids.

The talus (not figured) is small and slender. The upper trochlea occupies almost half the total bone’s length. The lateral part of the upper trochlea appears wider and more robust than the medial part. A strong ridge is also present at the articular surface that accommodates the fibula. The neck of the talus is short and is placed in the medial part of the bone. The head of the talus is not particularly prominent.

The calcaneus (not figured) is small and slender and fits with the talus, indicating that they both belong to the same individual. The sliding groove of the superficial flexor tendon is wide, shallow, and does not show a steep slope. The sliding groove of the external flexor tendon is wide, without particular elevation and shows a weak curving. The posterior side of the main body of the calcaneus is quite thin.

Remarks

Most of the Karnezeika carnivore material belongs to this small-sized mustelid representative. *Meles thorali* Viret, 1954 is larger (Table 1), possesses a wide talonid and a strong individualized metaconid in m1, and there is no additional cuspid in p4 (Viret, 1954). In *Lutra* Brisson, 1762 the talonid of m1 is wider than the trigonid, while the teeth are also larger in size (Willemsen, 1992; Cherin and Rook, 2014). *Pannonictis ardea* Gervais, 1859 is larger as well and also shows stronger cinguli and a proportionally smaller talonid (Peters and de Vos, 2012). *Vormela* Blasius, 1884, is smaller in size, shows a strong reduction of the alveolus of the mesial p3 root and typically has a high and thick mandible with an almost vertical symphysis (Spassov, 2001). These are characters not observed in the Karnezeika specimens. Furthermore, *V. peregusna* Guldenstaedt, 1884 and *V. prisca* (Teilhard de Chardin and Leroy, 1945) do not exhibit a secondary cuspid in p4. The Villafranchian *V. petenyii* Kretzoi, 1942, does show a bicuspid p4, but the secondary cuspid is more reduced. On the contrary, the characters of the Karnezeika specimens, such as p3 and p4 with the elevated cingulid, p4 with a secondary cuspid, a small metaconid located distally to the protoconid of m1, and the described morphology of the talonid, fit very well with the description for *Baranogale helbingi* (Kormos, 1934; Viret, 1954). Spassov (2001) included a new species in *Baranogale*, namely *B. balcanica* Spassov, 2001, from Varshets, Bulgaria. This species differs from *B. helbingi* by its smaller size, reduced p2, and plesiomorphic condition of p4 and m2 (Spassov, 2001). Hence, based on the aforementioned observed morphological characters and size, the Karnezeika mustelid is referred to *B. helbingi*. This is a rare species, mentioned from only a handful of European Villafranchian assemblages (see Spassov, 2001 for a review) that belong to three geographic regions: Western Europe, in the localities of Saint Vallier and Etouaires, France (Schaub, 1949; Viret, 1954); Central Europe, in the localities of Villány and Csarnóta 2, Hungary (Kormos, 1934; Jánossy, 1986), as well as in Podlesice and Węże, Poland (Kowalski, 1959; Stach, 1961); South-East Europe, in the locality of Dafnero (referred to as *B.* aff. *helbingi*) and now in Karnezeika, Greece (Koufos and Kostopoulos, 1997; Sianis et al., 2021, 2023). Nevertheless, the specimens from the above-mentioned sites show inhomogeneous characters in size and morphology of the corresponding dental material beyond the normal population's variability, thus pointing towards the possible co-occurrence of different subspecies. Spassov (2001) was the first to hypothesize this, however, the scarce material in the fossil record was not considered enough for a safe establishment. Furthermore, Kowalski (1959) had already noticed size differences between the Polish/Hungarian and Saint Vallier specimens, without being able, though, to provide a plausible explanation for this variability.

As seen in Figure 7, the Karnezeika and Saint Vallier specimens appear larger than the rest, but still not as large as *B.* aff. *helbingi* from Dafnero. Apart from similarity in size, they are also very similar morphologically, with no clear differences observed. The same is true for the *B. helbingi* holotype from Villány, even though it is smaller. Comparing the specimens from Karnezeika with the Dafnero specimen, the latter has more conical premolars separated by a diastema, a reduced mesial cingulid on the premolars, a reduced secondary cuspid in p4, a higher paraconid in m1, and a non-elevated talonid. The specimens from Węże appear generally similar to those from Karnezeika and Saint Vallier but show weaker cingulid protrusions in p3 and a weaker accessory cuspid in p4, while the hypoconulid is more independent from the hypoconid. The orientation of the canine in relation to the main axis of the mandible is also very different from that observed in the Saint Vallier specimen. The Podlesice specimen shows more conically-shaped premolars and the distal cingulid of p4 is less developed. Additionally, despite the poor preservation of m1, its talonid appears flattened and not elevated. The specimens from Etouaires show premolars similar to those of Karnezeika, but the m1 has a hypoconulid more independent from the hypoconid and the carnassial notch is less deep. The canine's orientation with the axis of the mandibular corpus is similar to that observed in the Saint Vallier specimen, but the anterior and posterior margins have a significantly stronger morphology. These observations are better visualized in Table 2. Leaving size aside, it is evident that the specimens from Karnezeika, Saint Vallier, and Villany, which are part of faunas corresponding to the Middle Villafranchian (MN17-MN18) are identical, while they also seem to show a connection with those from Etouaires (Early Villafranchian). Interestingly enough, the specimen from Podlesice, which according to Spassov (2001) is the oldest occurrence of the species (early Ruscinian), shares some morphological characters with *B.* aff. *helbingi* from Dafnero (MN17), despite the latter being much larger and far more recent. The Węże specimens are clearly different from those of Dafnero and Podlesice and more similar to the rest. It is established that mustelids show broad individual variation (Kowalski, 1959) and also strong sexual dimorphism (Moors, 1980). Therefore, we believe that the size differences observed among the various specimens can be explained by individual or sexual variation. Also, it is reasonable to take into account the possible error of manual measuring of small-sized specimens from various different researchers. On the contrary, more attention should be paid to morphological differences.

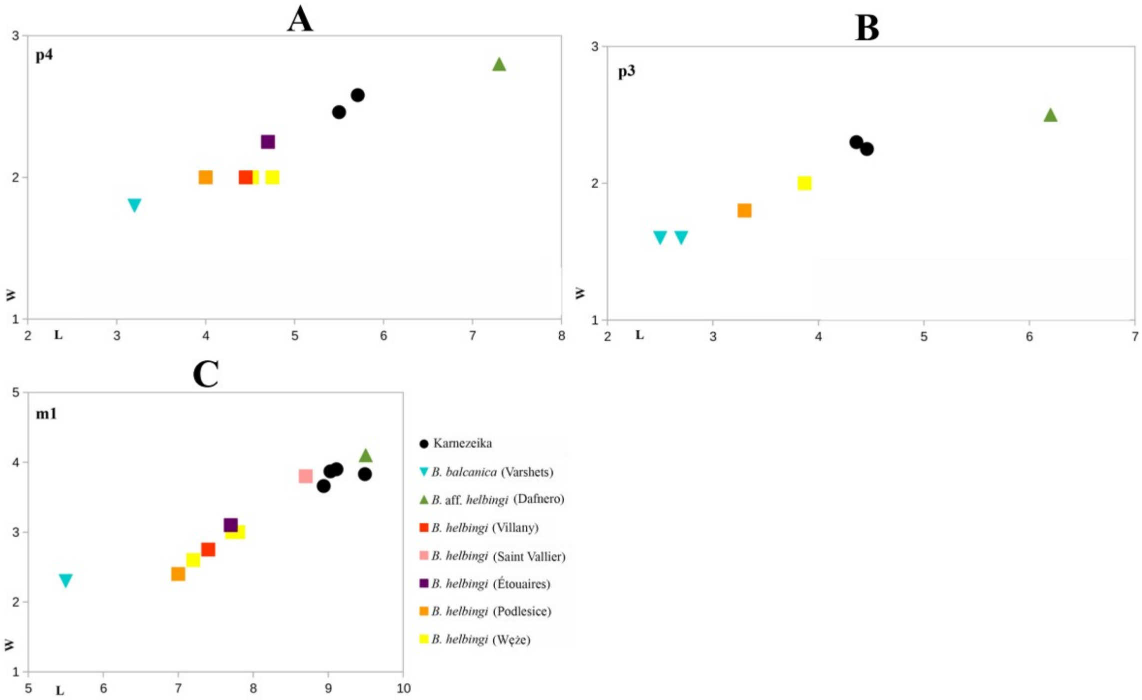

Figure 7: Scatter chart of the dental dimensions of Baranogale helbingi *from Karnezeika and other comparable species. Diagram A corresponds to p4, diagram B to p3 and diagram C to m1. Data from (Viret, 1954; Kowalski, 1959; Stach, 1961; Koufos & Kostopoulos, 1997; Spassov, 2001 and references therein).*

In conclusion, based on the above comparisons (see also Table 2), we discuss the following:

1)The specimens from Villány (holotype), Saint Vallier, and Karnezeika belong to the same form which most likely dominated the European *Baranogale* record during the Middle Villafranchian. Their diagnosis follows that of *B. helbingi* Kormos 1934. Furthermore, they differ from other forms in having a combination of elements such as an almost right angle between the main axis of the canine and the mandibular corpus axis; an almost parallel angle between the base of the canine crown and the mandibular corpus axis; a smooth anterior margin of the canine with a tendency to create a step-like structure in the posterior margin; a high p3; strong cingulum protrusions in the premolars; an elongated p4 with a strong accessory cuspid; a deep carnassial notch in the m1; a hypoconulid that is almost fused with the hypoconid; an elevated talonid.

2) The specimens from Etouaires show similar characters to those mentioned above, however, more primitive. Since they belong to an earlier fauna unit, we believe that it maybe represents an ancestral form of *B. helbingi*.

Table 2. Morphological differences and similarities in various characters of lower teeth among the known *B. helbingi* specimens.

		Villány	**Podlesice**	**Wężе**	**Saint Vallier**	**Etouaires**	**Dafnero**	**Karnezeika**
c	Angle between the main axis of the canine and the mandibular corpus axis	-	-	acute	almost right	almost right	-	-
	Angle between the base of the canine's crown and the mandibular corpus axis	-	-	acute	almost parallel	parallel	-	-
	Anterior margin	-	-	smooth	smooth	angular	-	smooth(?)
	Posterior margin	-	-	smooth	tends to create step-like structure	step-like	-	tends to create step-like structure(?)
	Lingual ridge	-	-	-	strong	strong	-	weak(?)
p3	High/Short	high	high	short	high	high	short	high
	Cingulid protrusions	strong	only posterior (strong)	weak	strong	strong	only posterior (strong)	strong
	Diastema	absent	absent	absent	absent	absent	present	absent
p4	Shape	elongated	less elongated	elongated	elongated	elongated	elongated	elongated
	Cingulid protrusions	strong	only posterior (strong)	strong	strong	strong	only posterior (strong)	strong
	Accessory cuspid	strong	weak	weak	strong	strong	weak	strong
m1	Carnassial notch depth	deep	-	deep	deep	less deep	shallow	deep
	Hypoconid-Hypoconulid	almost fused	-	more independent	almost fused	more independent	-	almost fused
	Talonid	elevated	flattened	elevated	elevated	elevated	flattened	elevated

3) The specimen from Podlesice does include traits typical of *B. helbingi*, but also includes elements that are not present in the holotype (see Table 2). This could potentially be explained by considering this form as belonging to a different stock of possibly Asian or African origin. Since the Podlesice specimen is the older fossil of the species, this stock may have given rise to the European *B. helbingi* lineages in Europe, but could also have been replaced by other forms. The specimen from Dafnero could reflect its Asian or African descendant, which re-invaded Europe during the Early Pleistocene.

4) Based on our current knowledge of the Węże specimen, we refrain from drawing further conclusions concerning this form. It could correspond to an intermediate form of the above.

It should be noted, however, that the degree of intra-specific variance among similar and/or related species is not fully known and there is not yet enough evidence to fully support the above hypotheses, As such, the previous made remarks aim to act as possible guidelines to future studies, since drawing final conclusions concerning the taxonomic status of this taxon goes beyond the scope of the current manuscript.

Mustelidae indet.

Material

One partially preserved left m1 (KZ2173); one left lower canine (KZ1598).

Description

The canine is short and its tip is relatively rounded. It shows a strong lingual crest. L: 6.65 mm; W: 4.00 mm.

The m1 is relatively robust, however, fragmented and the talonid is missing. The protoconid is strong and wide. The metaconid is well expressed, short, and individualized with a rounded tip. Mesially, the paraconid is similar to the metaconid and of equal size. The carnassial notch is weak. No cingulid is observed. L: >6.86 mm; W: 4.11 mm.

Remarks

The general size and morphology of the preserved dental material point towards the presence of another mustelid larger than *Baranogale*. The material, however, is very scanty and incomplete and lacks any diagnostic features. Therefore, we refrain from ascribing these teeth to a taxon of the genus or species level.

Family: Canidae Fischer de Waldheim, 1817

Genus: *Vulpes* Frisch, 1775

Vulpes alopecoides Del Campana, 1913

Figure 8

Synonyms:

2019 — *Vulpes* sp. — Kokotini et al., table 1.

Material

One right M1 (KZ2492), one left p2 (KZ1597), one right m1 (KZ2493), one left m1 (KZ906), one right m2 (KZ1103), two left m2 (KZ728, KZ1062). See also Figure 8.

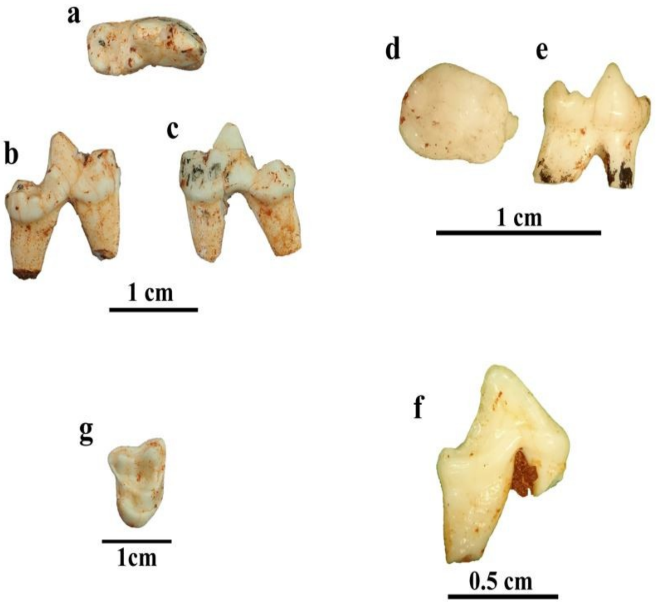

Figure 8: Vulpes alopecoides. *Karnezeika. a-c, Left m1 (KZ906) in occlusal (a), lingual (b) and vestibular (c) view; d-e, left m2 (KZ1062) in occlusal (d) and vestibular (e) view; f, left p2 (KZ1597) in lingual view; g, right M1 (KZ2492) in occlusal view. Scale bars: 1 cm (a-c, g), 5 mm (d-f).*

Description

The M1 (Figure 8(g)), is relatively slender and buccolingually elongated with respect to its mesiodistal diameter (L×100/W=79). In occlusal view, the protocone is robust and is connected through prominent ridges to the protoconule (mesially) and the entocone (distally). The hypocone is almost as developed as the protocone and is accompanied by a prominent lingual cingulum. Buccally, the paracone is markedly larger and higher than the metacone, while both are very pointed and well developed. The buccal cingulum is strongly expressed and prominent. Distally, a ridge connects the buccal cingulum with a small but well expressed entocone, and continues until it reaches the protocone. Mesially, the mesial cingulum is evident but not as prominent as the buccal one. A large sub-triangular depression is present in the middle of the occlusal surface, between the protocone, the entocone, the paracone, and the metacone.

The p2 (Figure 8f) is slender and elongated. The protoconid is strong and high, placed towards the mesial part of the tooth. No accessory cuspid is present on its distal side. Lingually, there is a well-expressed cingulid that protrudes upwards at the distal side of the tooth. The cingulid is quite reduced buccally and mesially.

The protoconid of m1 (Figure 8(a-c)) is very strong and high and tilts distally. The paraconid is much lower but appears to be strong as well and is located exactly above the mesial border of the mesial root. These two conids are separated through a small furrow. Lingually, the metaconid appears individualized, prominent but low (Fig. 8(a-b)). The hypoconid is well expressed but relatively small. The entoconid is well expressed and similar in size and height with the hypoconid. A small cuspulid can be detected between the entoconid and the metaconid. In occlusal view, the talonid is square shaped and occupies approximately 1/3 of the tooth’s total length.

The m2 (Figure 8(d-e)) is relatively elongated mesiodistally (somewhat oval-shaped) in relation to its buccolingual diameter. Mesially, a vestigial paraconid is observed which is hardly visible in worn specimens (e.g., KZ 1103). The metaconid is strong and high, similar to the protoconid. Distally, the hypoconid is well expressed and higher than the weaker and lower entoconid. At the lingual side, between the entoconid and the metaconid, a small additional cuspid is also present. The talonid is relatively deep and well expressed. The buccal side is characterised by a prominent cingulid.

Remarks

The aforementioned dental material shows the general canid morphology and belongs to a small representative of the family based on dental dimensions (Table 3). Based on the literature, three Canidae genera occur in the Villafranchian assemblages of Europe: *Nyctereutes* Temminck, 1838, *Vulpes* Frisch, 1775 and *Canis* Linnaeus, 1758 (including the subgenus *Xenocyon* Kretzoi, 1938) (Cherin et al., 2014; Bartolini Lucenti and Rook, 2016; Bartolini Lucenti, 2018; Bartolini Lucenti and Madurell-Malapeira, 2020; Bartolini Lucenti and Spassov, 2022; Koufos, 2022b). The morphological characters described above, such as the buccolingually elongated upper molar, the presence of a strong and prominent buccal cingulum on M1, the robust M1 hypocone, the mesiodistally elongated m1, the presence of a reduced but individualized metaconid on m1, the equally sized entoconid and hypoconid, the presence of an accessory cuspid in the m1 talonid, the similar sized protoconid and metaconid on m2, the prominent m2 buccal cingulid and the presence of an accessory cuspid in the distolingual side of m2 are typical features of *Vulpes* (Bartolini Lucenti and Madurell-Malapeira, 2020). A metric comparison with some of the known Early Pleistocene species also points toward this genus (Fig. 9), showing a clear grouping with *Vulpes*. The Ltalonid×100 / Lm1 index was also calculated and found to be equal to 28 – almost identical to the index (28.2) mentioned by Koufos and Kostopoulos (1997) for *V. alopecoides* from the locality of Dafnero, N. Greece, in contrast with the value of 33.7 mentioned by the same authors for *N. megamastoides* Pomel, 1842. The latter also has less elongated M1 with a more square-shaped occlusal surface, a prominent parastyle, a large protoconule, and an enamel bulging of the cingulum on the mesial side. Furthermore, the metaconid in the m1 of *N. megamastoides* is more robust and larger and the talonid basin is also larger (Rook et al., 2017). The small dimensions of the Karnezeika dental specimens as seen in Figure 9, could rule out the possibility of their inclusion to a *Canis* representative. Compared to small-sized dogs, such as *Canis accitanus* Garrido and Arribas, 2008 from Fonelas P-1, the Karnezeika canid is still smaller, while it also does not exhibit a bilobed hypocone in the M1, as mentioned in the species diagnosis (Garrido and Arribas, 2008). Compared with the Greek canid *Canis apolloniensis* Koufos and Kostopoulos, 1997, from Apollonia 1 in N. Greece, the latter shows a weak buccal cingulum in the M1, a shallower main basin and more robust cones. The m1 is not as slender and has a bicuspid talonid, while no entoconid is present in m2 (Koufos and Kostopoulos, 1997; Koufos, 2018). The Karnezeika canid clearly belongs to a small-sized representative, which, based on both metric and morphological characters, can only belong to a species of the genus *Vulpes*. Until recently, Villafranchian foxes were attributed to three species, *V. alopecoides*, *V. praeglacialis* Kormos, 1932 and *V. praecorsac* Kormos, 1932. Recently, Bartolini Lucenti and Madurell-Malapeira (2020) referred all European foxes of the Plio-Pleistocene to *V. alopecoides*, based on the observed variation in tooth morphology which is non-important, since it is less than the variation observed in extant fox species. As such, they suggest that it is better to include the aforementioned Early Pleistocene European forms to one species, of which *V. alopecoides* has priority. We follow their suggestion.

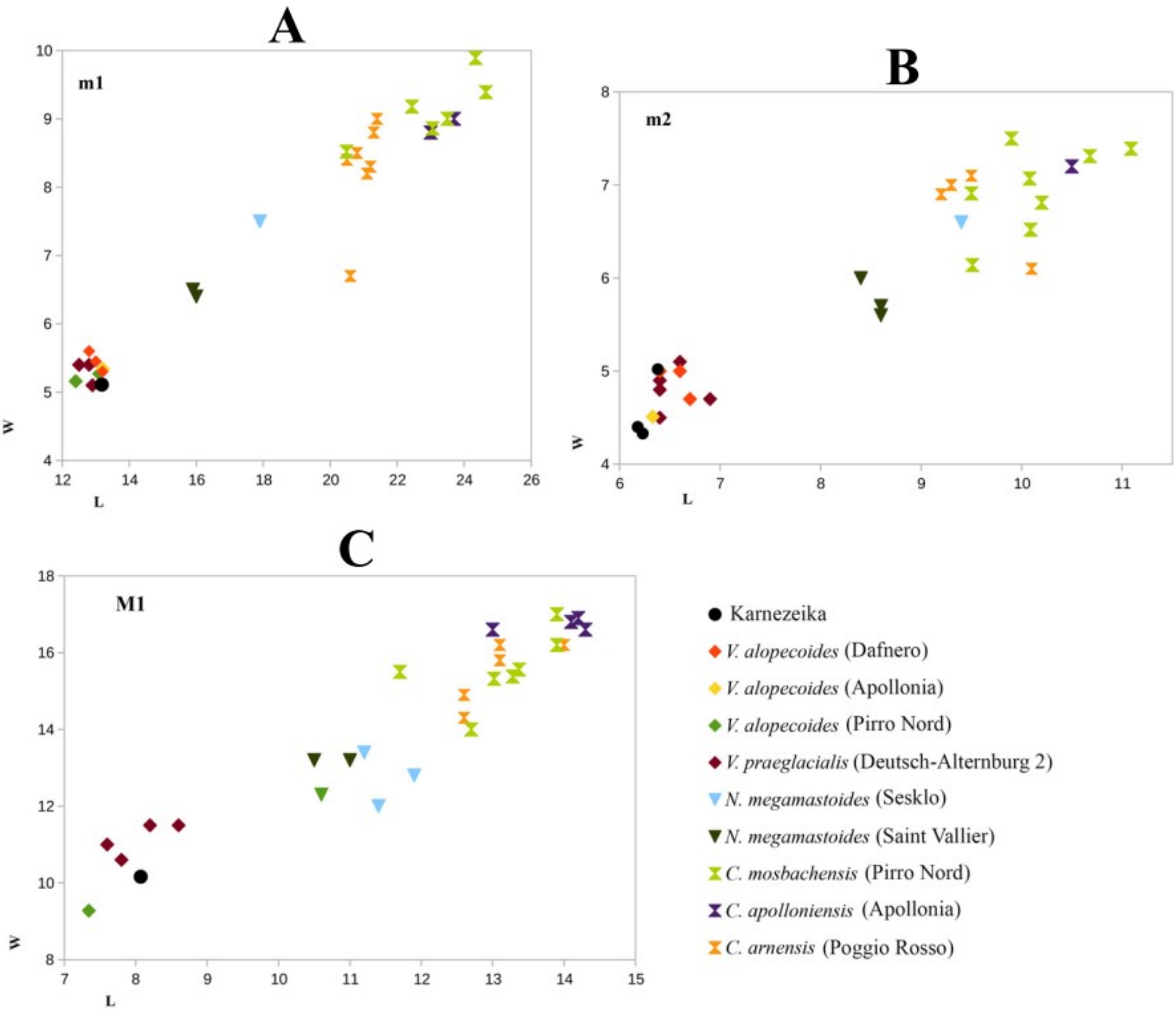

Figure 9: Scatter chart of the dental dimensions of Vulpes alopecoides *from Karnezeika and other comparable taxa. Diagram A corresponds to m1, diagram B to m2 and diagram C to M1. Data from (Viret, 1954; Athanassiou, 1996; Koufos & Kostopoulos, 1997; Petrucci et al., 2013; Bartolini-Lucenti & Rook, 2016; Bartolini-Lucenti, 2017).*

The first record of *Vulpes* in Europe comes from Bulgaria during the MN15, ascribed to *Vulpes* sp. based on an isolated P4 (Spassov, 2000) and Ukraine (Odessa Catacombs – MN15), referred to *V. praecorsac* (Odintzov, 1965). Since then, even though the remains are usually scarce and/or fragmentary, foxes seem to have an uninterrupted presence in the European mammal record, which continues until today with the extant red fox species *V. vulpes* Linnaeus 1758. For an extensive and well-structured review of the fossil record of Plio-Pleistocene foxes, see Bartolini Lucenti and Madurell-Malapeira (2020). In the Greek fossil record, the genus is well documented in many Pleistocene localities of mainland Greece (Koufos, 2022b). *Vulpes alopecoides* (including synonym species) is mentioned from Dafnero 1 (Koufos and Kostopoulos, 1997), Apollonia 1 (Koufos, 2018), Petralona (Baryshnikov and Tsoukala, 2010), Volax (Sickenberg, 1968), and Sesklo (Athanassiou, 1996).

Table 3. *Vulpes alopecoides* from Karnezeika. Dental measurements (in mm).

Specimen		**L**	**W**
KZ2492	M1	8.07	10.16
KZ1597	p2	6.13	2.34
KZ2493	m1	-	4.81
KZ906	m1	13.18	5.11
KZ1103	m2	6.23	4.33
KZ728	m2	6.18	4.4
KZ1062	m2	6.38	5.02

Family: Hyaenidae Gray, 1821

Genus: *Pachycrocuta* Kretzoi, 1938.

Pachycrocuta brevirostris Gervais, 1850

Figure 10

Synonyms:

2019 — *Pachycrocuta brevirostris* — Kokotini et al., table 1.

Material

A partially preserved left hemimandible bearing m1 (KRZ158), curated in AMPG (Figure 10).

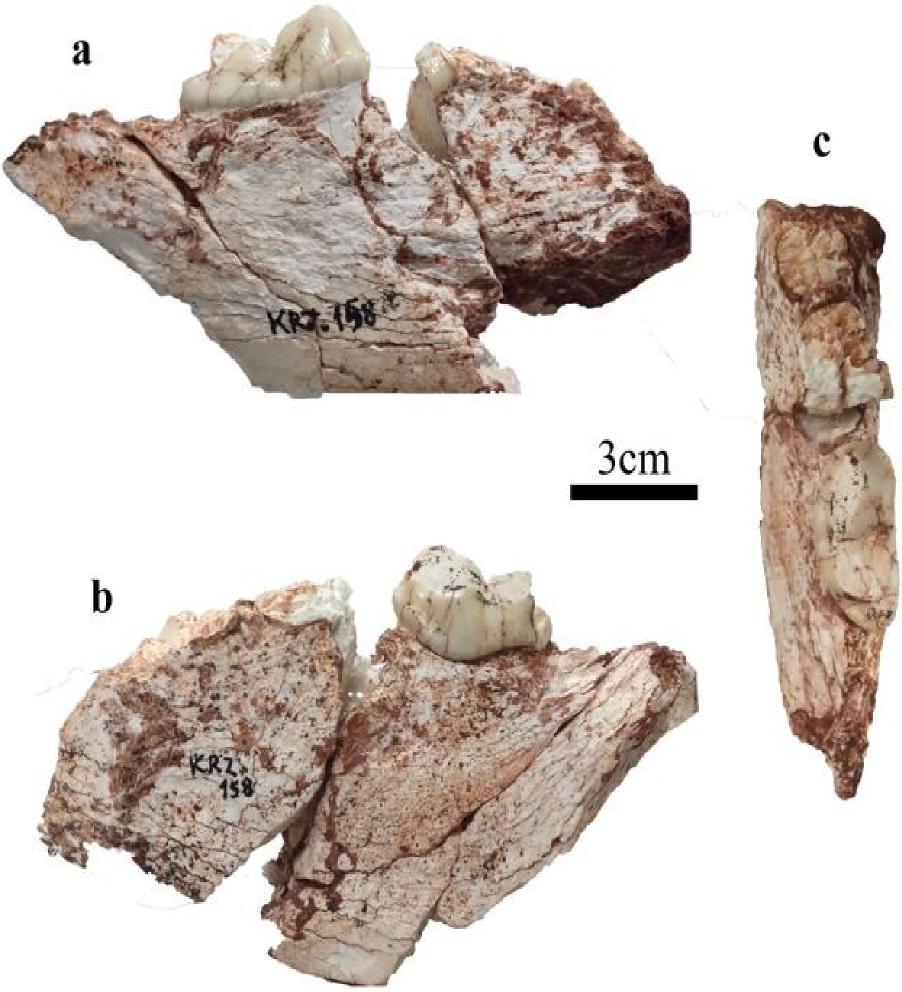

Figure 10: Pachycrocuta brevirostris. *Karnezeika. Left hemimandible bearing m1 (KRZ158) in lingual (a), vestibular (b) and occlusal (c) view. Scale bar: 3 cm.*

Description

The m1 is robust and bears a small talonid. Both the paraconid and the protoconid are strong, but the former is larger and the two are separated by a slit-like depression. No metaconid is observed (Figure 10(a-c)). Due to wear, both conids exhibit smooth occlusal surfaces and are relatively flat. The carnassial notch is rather shallow. There is a jugged and relatively short cingulum in the mesiobuccal side of the tooth, which becomes smoother as it extends mesially and mesiolingually. Distally, the talonid is short, wide, and oriented upwards (Figure 10(b-c)). It includes one well expressed cuspid in its center (hypoconid), which fits morphotype E described/figured in Liu et al. (2021, Fig. 5). L: 28.89 mm; Ltal: 3.92 mm; W: 13.94 mm.

Remarks

The robustness of the tooth, in combination with the large paraconid–protoconid blade and the small talonid, are features typical of the Hyaenidae. The Karnezeika specimen lacks the blade-like hypoconid shown in *Chasmaporthetes* Hay, 1921 (Kurtén and Werdelin, 1988), while it is also more massively built, since *Chasmaporthetes* was not committed to bone crushing dietary habits and still retained sectorial dentition (Ferretti, 1999). Compared to *Pliocrocuta perrieri* Croizet and Jobert, 1828, the Karnezeika hyaenid is larger (Figure 11) and does not exhibit the characteristic of the former bicuspid talonid (Werdelin and Sanders, 2010) nor a metaconid. The talonid is short but not greatly reduced as in *Crocuta* Kaup, 1828. *Parahyaena howelli* Werdelin, 2003 exhibits a m1 with a distinctly developed metaconid, as well as a bicuspid talonid (Werdelin, 2003). The large dimensions of the studied tooth, the absence of a metaconid and the short, unicuspid talonid are actually typical of the giant hyena *Pachycrocuta brevirostris* (Gervais, 1850) (Howell and Petter, 1980; Werdelin, 1999; Werdelin and Sanders, 2010; Liu et al., 2021) and therefore the Karnezeika specimen is ascribed to this species.

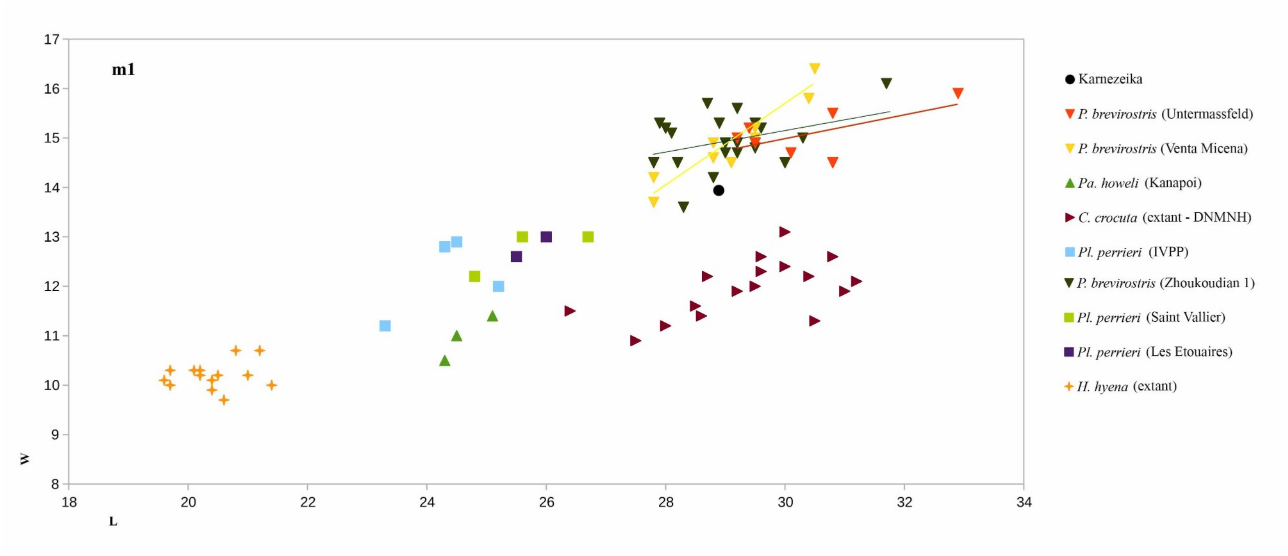

Figure 11: Scatter chart of the dental dimensions of Pachycrocuta brevirostris *from Karnezeika and other comparable taxa. Data from (Turner, 1984; Turner & Antón, 1996; Werdelin, 2003; Tseng et al., 2016; Iannucci et al., 2021 and references therein; Liu et al., 2021). DNMNH: Ditsong National Museum of Natural History; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences.*

The giant short-faced hyena *P. brevirostris* had a wide distribution in Eurasia, from West (e.g., Spain, Palmqvist et al., 2011) to the Far East (e.g., China, Liu et al., 2021) and its appearance in large mammal faunas of Europe, usually signals/marks the beginning of the late

Villafranchian (Rook and Martínez-Navarro, 2010; Iannucci et al., 2021). The species, even though represented by scarce material, is known in Greece from several late Early Pleistocene and more recent localities (Koufos, 2022d).

Family: Felidae Fischer de Waldheim, 1817

Genus: *Felis* Linnaeus, 1758

***Felis* sp.**

Figure 12

Material

One left upper carnassial – P4 (KZ2295). See Figure 12.

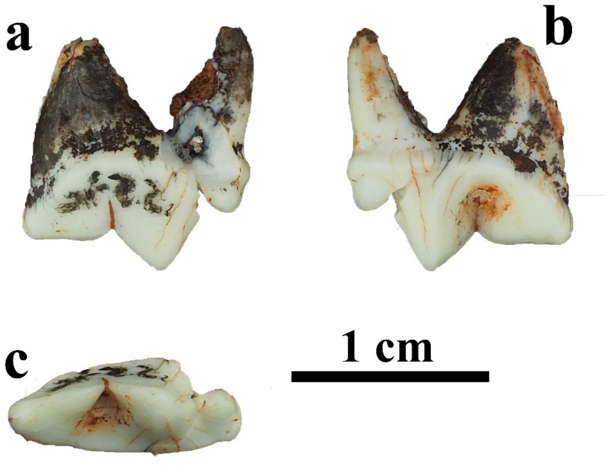

Figure 12: Felis *sp. Karnezeika. a-c, Left P4 (KZ2295) in lingual (a), vestibular (b) and occlusal (c) view. Scale bar: 1 cm.*

Description

The upper carnassial does not preserve the protocone area. The paracone is strong, prominent and pointed. Distally, the metacone is moderately expressed and is hardly separated from the metastyle. Both, together with the paracone, form the main cutting blade of the tooth. Mesially, the parastyle is well expressed but low. Mesiobuccally of the parastyle, the cingulum is locally thickened, but it is generally weak along the buccal side of the tooth. A deep circular depression forms buccally between the metacone and the paracone. On the lingual side, these two cones are separated by a small slit-like furrow. Measurements: Length: 11.41 mm; Width: ~5.5 mm; Paracone length: 4.44 mm; Metacone length: 4.51 mm.

Remarks

Only one specimen is included in this small-sized felid, but it is considered enough for a safe taxonomy at the genus level. The above described upper carnassial is characterised by its small dimensions and typical felid morphology. Figure 13 shows very well the size correlation with the smallest of them, those of the genus *Felis*, while being significantly smaller than the dimensions reported for *Lynx* Kerr, 1792 and consequently larger felids. Hence, the Karnezeika cat may be referred to the genus *Felis*.

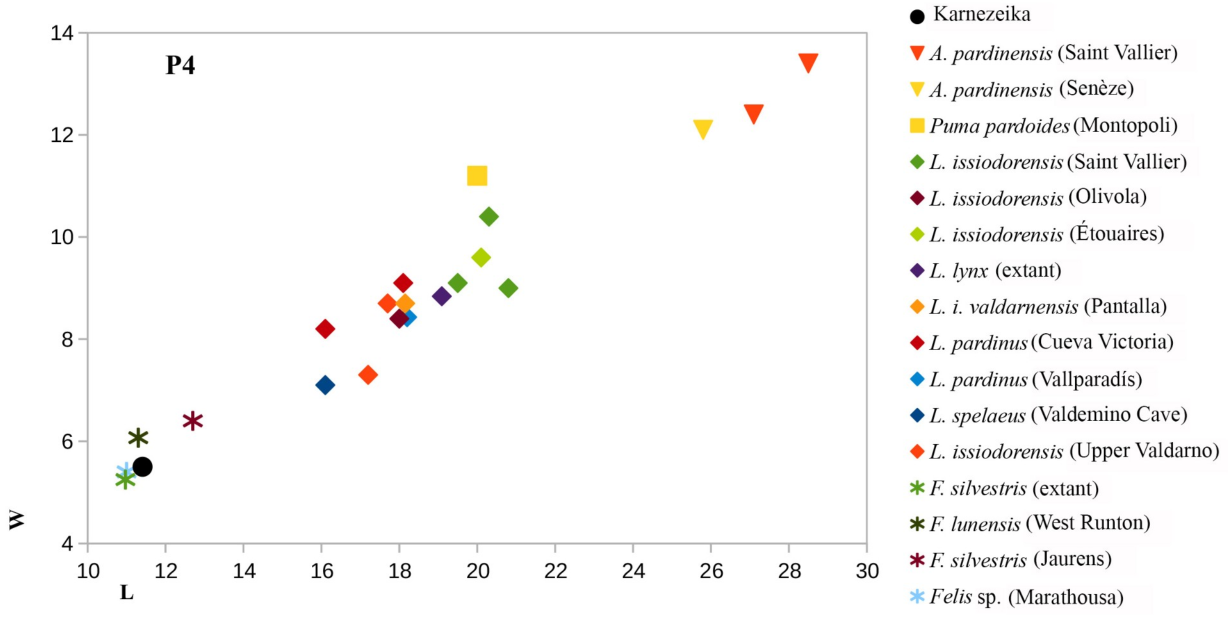

Figure 13: Scatter chart of the dental dimensions of Felis *sp. from Karnezeika and other comparable taxa. Data from (Viret, 1954; Kurtén, 1978; Ballesio, 1980; Argant, 2004; Lewis et al., 2010; Cherinet al., 2013a, 2013b; Ghezzo et al., 2015; Boscaini et al., 2016; Konidaris et al., 2018).*

Only one species of small cat is known in Villafranchian assemblages, *F. lunensis* Martelli, 1906, the probable ancestor of the extant European wildcat *F. silvestris* Schreber, 1777

(Kurtén, 1965; Lewis et al., 2010). However, due to the existence of only a single, damaged specimen in the studied material, as well as the inability to compare it to the species' type material (the holotype is a hemimandible; Martelli, 1906; Kurtén, 1965, Pl.1 Figs. A-B), or any other well-documented sample (pre-Olduvai small cats are very rare), we refrain from assigning the Karnezeika small cat to a species.

Subfamily: Machairodontinae Gill, 1871

Genus: *Megantereon* Croizet and Jobert, 1828

Megantereon cultridens Cuvier, 1824

Figure 14

***Synonyms**:*

2019 — *Panthera gombaszoegensis* — Kokotini et al., table 1.

Material

One isolated right I3 (KZ1454); one fragmentary m1 (KZ977); one isolated right i3(?) (KZ2905); The distal part of a right humerus (KRZ41) curated in the AMPG; one right proximal phalanx of digit I (thumb) (KZ634); one incomplete distal phalanx (KZ1676). The two incisors are included here based only on overall morphology and size, which better fit that of a large felid. See also Figure 14.

Description

The I3 (not figured) is short and robust. The lingual side of the crown is completely obliterated, most likely due to attrition by contact with the lower teeth, and appears flat and smooth. Under the stereo-microscope the surface is filled with shallow grooves of varied orientations. L: 13.12 mm; W: 8.16 mm.

The lower incisor (not figured), possibly i3, is more slender than I3. The wear surface of the tooth appears toward be laterally inclined to its main axis. Occlusally, there is a relatively deep groove that follows the aforementioned inclination. Both the lingual and labial sides of the tooth are obliterated as in I3, forming flat and smooth surfaces. Under the stereo-microscope, these surfaces are filled with linear markings that again follow the lateral inclination. L: 10.82 mm; W: 8.34 mm.

Figure 14: Megantereon cultridens. *Karnezeika. a-c, Right humerus (KRZ41) in cranial (a), caudal (b) and distal (c) view. Scale bar: 5 cm (a-b), 3 cm (c).*

The humerus (Figure 14(a-b)) includes the characteristic supracondylar foramen of the Felidae family and appears to belong to a large-sized form. A strong ridge is observed in the cranial side of the diaphysis and a widening of the bone in the medial side. The lateral epicondyle is relatively weak while the medial epicondyle is strong and oriented backward. The entepicondylar foramen is elongated and inclined approximately 45° with respect to the main bone axis. Strongly expressed radial and coronoid fossae are also observed. The angle of the capitulum with the trochlea is well rounded. The olecranon fossa extends towards the medial side but also protrudes slightly towards the trochlea as well (see Figure 14b).

The proximal phalanx (not figured) of the first digit is short and robust. The proximal articular facet is asymmetrical, with a sub-rectangular articular facet on the lateral side.

Remarks

Compared with other Villafranchian Felidae (Table 4), the humerus from Karnezeika is definitely larger than *Puma* and smaller felids, such as *Lynx*. On the contrary, the Karnezeika specimen is metrically closer to larger felid forms such as the Villafranchian Machairodontinae *Homotherium* Fabrini, 1890 and *Megantereon*, but also the Pantherinae *Panthera* Oken, 1816. Comparison of the proximal phalanx with those of extant felids (Figure 15), showed a metrical affinity with large Pantherinae such as *Pa. leo* Linnaeus, 1758 and *Pa. tigris* Linnaeus, 1758. Direct comparison of the Karnezeika humerus with that of *Homotherium* from Sesklo (Athanassiou, 1996) showed significant differences in both size and morphology, ruling out any close taxonomic relationship. More specifically, *Homotherium* lacks the strong cranial ridge and widening present in the diaphysis of the Karnezeika specimen, and has a more rounded supracondylar foramen. Furthermore, the lateral condyle is stronger and the angle between the capitulum and the trochlea is more angular.

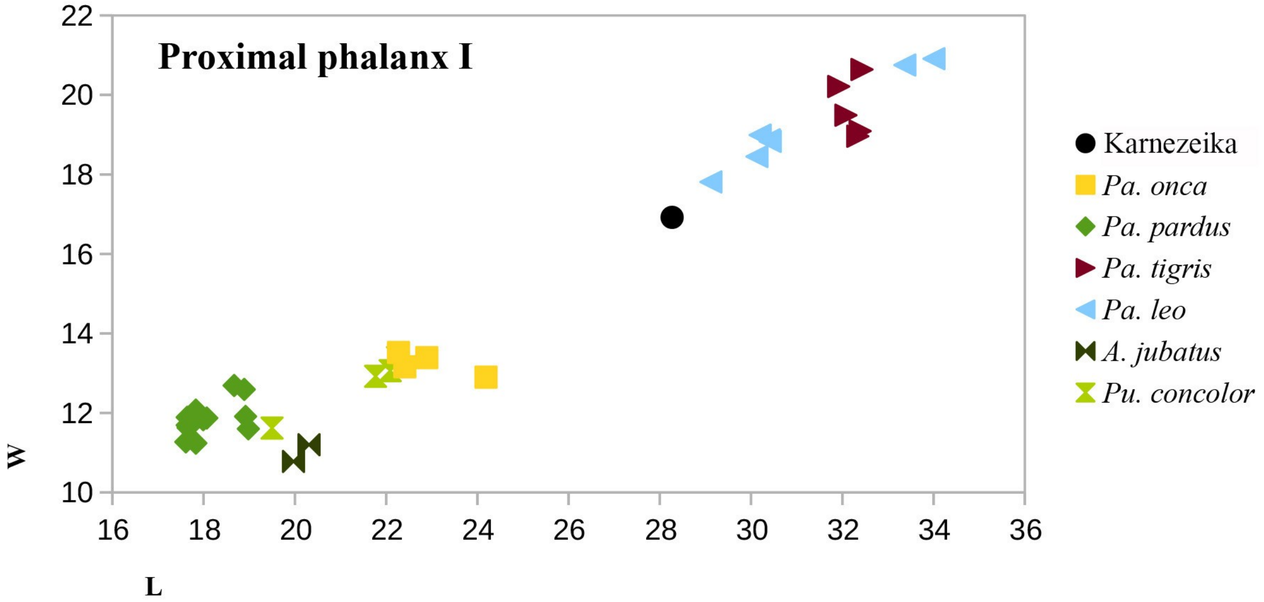

Figure 15: Scatter chart of the proximal phalanx I specimen of M. cultridens *from Karnezeika compared with extant felids. Data from Salesa et al., 2010.*

Panthera occurs during the Villafranchian with one species, which Hemmer et al. (2010) refer to as *P. onca* Linnaeus, 1758, including the subspecies *P. o. toscana*, *P. o. gombaszogensis* and *P. o. georgica*. More recently, Argant and Argant (2011) reverted to the more common species name of *P. gombaszogensis* Kretzoi, 1938, retaining however the three subspecies

(*P. g. toscana*, *P. g. gombaszogensis*, and *P. g. georgica)*. The latter authors argued that since these Plio-Pleistocene forms differ significantly from the extant jaguar (*P. onca*), especially in the post-cranial skeleton, they cannot be ascribed to the same species. We follow their suggestion. Unfortunately, no comparable material is available for *P. g. georgica* from Dmanisi, nor from the most common smaller-sized *P. g. toscana*. Even though the state of preservation does not allow the observation of some characters, direct comparison with *P. gombaszogensis* from Halykés (Athanassiou, 1996, 2002), showed significant differences. Apart from the larger size, the *P. gombaszogensis* humerus includes a wider angle between the capitulum and the trochlea as well. The medial epicondyle appears also much larger and robust.

Table 4. The dimensions (in mm) of the humerus of *M. cultridens* from Karnezeika and comparison with other Felidae of the Plio – Pleistocene. Data from (Ballesio, 1963; Athanassiou, 1996; Argant, 2004; Christiansen & Adolfssen, 2007; Madurell-Malapeira et al., 2010; Argant & Argant, 2011; Hemmer *et al*., 2011).

	DML dis	**DAP dis**	**DML trochlea**	**DML ol. fossa**	**DML dia**
Karnezeika	66.32	38.12	51.54	23.85	23.26
H. crenatidens (Sesklo)	81.4	57.2	58	35	277
H. crenatidens (Senèze)	85.5	57	56.5		28.5
M. cultridens (Senéze)	77.4 – 79.3 (n=2)		51.1 – 53.6 (n=2)		24.8 – 27.2 (n=2)
P. g. gombaszogensis (Chateau Breccia)	79.5 – 80.6 (n=2)	48.4 – 49.3 (n=2)	52.1 – 55.5 (n=2)		
P. gombaszogensis (Halykes)	76.3		52.46		
A. pardinensis (Dmanisi)	60.2	43.4	45.5	27.5	24.5
A. pardinensis (Saint Vallier)	56.2 – 58.5 (n=2)	31.1 – 34.3 (n=2)			19.2 – 21.1 (n=2)
P. pardoides (La Puebla de Valverde)	41.4	24.8			15.9

Concerning the comparison with *Megantereon*, the only available data come from Christiansen and Adolfssen (2007) for *M. cultridens* from Senèze, which also is the only well-documented *Megantereon* species from the Greek Middle Villafranchian localities (Koufos, 2014, 2022d). Table 5 shows the metric comparison of *M. cultridens* from Senèze and the Karnezeika form following the methodology of Christiansen and Adolfssen (2007). They appear quite similar in size and taking into account the low number of specimens for both the Senéze and Karnezeika forms, the small metric differences most likely correspond to individual variation.

Morphologically, Christiansen and Adolfssen (2007) mention a characteristic flaring of the olecranon fossa toward the lateral, which is also observed in the Karnezeika specimen. Similarities also occur in the morphology of the coronoid fossa (with a characteristic higher than wide shape) and in the morphology of the entepicondylar foramen (slit-like shaped). In addition, Christiansen and Adolfssen (2007) report a wide angle between the capitulum and the trochlea, and the distal projection of the trochlea beyond the capitulum, both characters present in the Karnezeika specimen as well.

Felid postcranial elements seldomly offer taxonomically diagnostic characters. Nevertheless, taking size into account, limits the possible candidate taxa. Many morphological and metric characters, point towards *Megantereon* which also fits well the chronostratigraphic context. The species-level taxonomy of this large predator has been a matter of debate for years (see Lewis and Werdelin, 2010 and references therein). However, there is a general consensus that all pre-Olduvai European specimens belong to *M. cultridens* (Sardella et al., 2008), whereas controversy concerns the later forms (e.g., *M. whitei*, *M. adroveri*), which some authors consider of African origin that replaced *M. cultridens* (Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 2007), while others propose a continuous lineage instead (Werdelin and Lewis, 2000; Lavrov et al., 2022). Although no diagnostic species-level characters are present in the Karnezeika material, we consider the similarity with the Senèze specimens, in combination with the age of the locality, sufficient to ascribe this felid to *M. cultridens*. This species is rare in Greece, to date reported from Makinia, Volax, and Apollonia 1 (Sickenberg, 1968; Symeonidis et al., 1985; Koufos, 1992, 2022d).

No other large felids are recorded in the locality; therefore, the two incisors described above are included to *M. cultridens* as well.

Discussion

The locality has yielded material of fossil carnivora belonging to seven different taxa. These are the ancestor of the modern African zorilla, *B. helbingi*; the ancestor of the modern European fox, *V. alopecoides*; the Etruscan bear *U. etruscus*; the dirk-toothed cat *M. cultridens*; a small-sized wildcat mentioned currently as *Felis* sp.; the giant short-faced hyena *P. brevirostris*; and an indeterminate mustelid mentioned herein as Mustelidae indet. The carnivore guild includes members such as *M. cultridens* and *B. helbingi*, which are rather typical of the middle Villafranchian of Greece (Koufos, 2014).

Table 5. Supplementary measurements (in mm) of the *M. cultridens* humerus from Karnezeika compared to the *M. cultridens* specimen SE311 from Senéze. Data from (Christiansen & Adolfssen, 2007).

	Karnezeika	**SE311 (Left)**	**SE311 (Right)**
Articular Length	-	262.4	262.5
Least circumference		93.5	87.3
DAP dia	27.25	32.3	30.8
DML dia	22.85	27.2	24.8
Capitulum DAP	25.98	27.3	26.8
Capitulum DML	25.86	27.2	26.6
Trochlea DAP	32.31	31	31.1
Trochlea DML	22	15.3	15.1
Articular Width	49.33	53.6	51.1
Distal Width	67.89	77.4	79.3

Baranogale is a rare taxon and its presence in Karnezeika with well-preserved material is quite fortunate. Due to this rarity, its taxonomic status was and still remains unclear, but we consider that the current work contributes to the study of this enigmatic taxon. As such, the *B. helbingi* form from Villany, Saint Vallier and Karnezeika may have been the dominant European *Baranogale* during the middle Villafranchian, while the rest may either consist ancestral forms or represent different lineages of Asian or African origin. Nevertheless, new information must arise in order to acquire a clear image concerning the taxonomic status of this taxon. I hope that new finds in the future will provide further evidence to strengthen my proposal concerning species variability in the European fossil record.

Cervidae

Order: Artiodactyla Owen, 1848
Family: Cervidae Gray, 1821
Genus*:* *Croizetoceros* Heintz, 1970

Croizetoceros ramosus (Croizet & Jobert, 1828)

Figure 16

Material

Part of the left (KZ375) and right (KZ3135) hemimandible with p3, m1, m2, one isolated upper molar M1 (KZ795), one isolated lower molar m1 (KZ3164), the proximal part of a metacarpal, part of a horn core (KZ2969) and a deciduous d4 (KZ640).

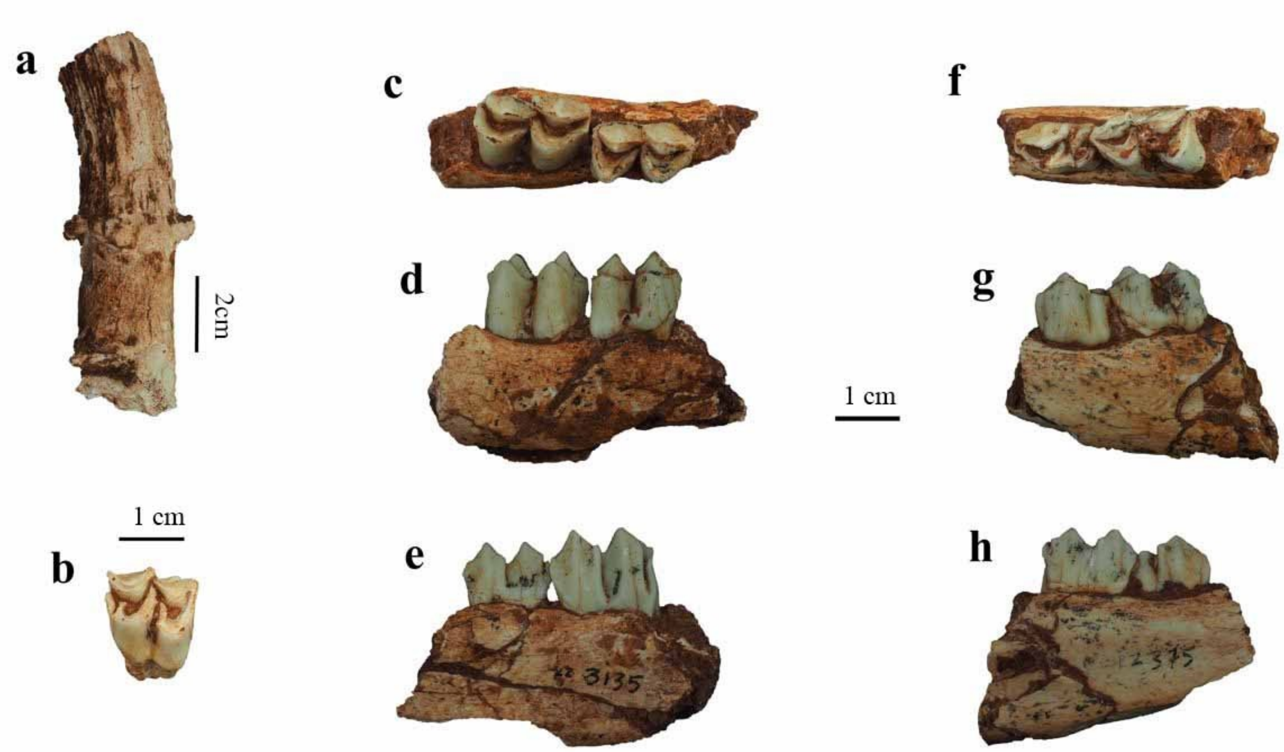

Figure 16: Croizetoceros ramosus. *Karnezeika. a, antler fragment (KZ2969); b, right M1 (KZ795) in occlusal view; c-e, part of left hemimandible with m1 and m2 (KZ3135) in occlusal (c), vestibular (d) and lingual (e) views; f-h, part of right hemimandible with p4 and m1 (KZ375) in occlusal (f), vestibular (g) and lingual (h) views.*

Description

The material is characterised by generally small size, comparative to that of the *Gazella* in bovids. All corresponding specimens bear characteristic Cervidae features.

Two antler fragments have been found but only one is relatively well preserved (Fig. 16a). It is broken a few centimeters above the burr and before the first tine. Its cross section is rounded and the antler shows backwards bending. The pedicle appears long.

The upper molar (Figure 16b) is brachyodont and consists of two lobes, the posterior of which being slightly larger and higher. The protocone is relatively rounded as it is the metaconule, without any of the two protruding more than the other, outwards. The paracone is strong while the metacone is quite weak but leans more inwards. A strong mesostyle and parastyle can be observed whereas the metastyle is weaker. A metaconule fold can also be detected.

p4 (Figure 16(f-h)) appears completely molarised resulting in the two posterior conids being fused thus creating a common occlusal surface on the buccolingual axis of the tooth. The mesolingual conid as well as the mesolabial, are weak but wide. Due to molarization, a weak metastylid can also be observed.

m1 (Figure 16(c-e, f-h)) consists of two lobes of quite similar morphology. Both the metaconid and the entoconid are narrow and relatively strong. The protoconid and the hypoconid are semi-triangular. In lingual side, a strong metastylid can be observed which appears weaker in worn specimens. The mesostylid is weak, small and located near the base of the tooth. No entostylid is detected. Between the two lobes, a strong ectostylid appears.

m2 (Figure 16(c-e)) is similar to m1. It can be distinguished from it by the larger size and also the weaker ectostylid.

d4 (not figured) consists of three almost identical lobes, the size of which increases smoothly from the anterior to the posterior. The labial conids appear narrow and are well expressed, as are the lingual. The entostylid and the anterior stylid are weak, in contrast with the metastylid which is strong.

Only the proximal part of the metacarpal is preserved (not figured). It appears small and quite slender. The posterior side of the diaphysis is extremely concave. The articular surface has a trapezoidal shape and in the center of it appears an oblong depression. The metacarpal tuberosity is well developed.

Remarks

The main characteristic of the studied material is the overall small size. Having this in mind and according to the literature, the only possible candidate is the well – known small sized cervid *C. ramosus* which is a common finding during the Villafranchian (Kostopoulos and Athanassiou, 2005; Koufos and Kostopoulos, 2016). The dental morphology with the molarised p4, the absence of a *Palaeomeryx* fold and the presence of a metaconule fold (Heintz, 1970; Croitor, 2018), also point towards this direction. The antler morphology would be taxonomically very useful, but unfortunately only the dimensions of the pedicle are useful in our case, which are given in Table 6. The dimensions fit well within the ranges of the Saint Vallier and Gerakarou forms, while they appear larger than the Spanish forms.

Table 6. Pedicle dimensions (in mm) of the Karnezeika *C. ramosus* compared to that of other forms. Data from (Heintz, 1970; Kostopoulos, 1996; Valli, 2004).

	n	**DT**	**DAP**
Karnezeika	1	28.96	>25
C. ramosus (Gerakarou)	8	20 – 35.5	19 – 29.5
C. ramosus (Saint Vallier)	6	17 – 28	19 – 26.5
C. ramosus (La Puebla de Valverde)	4	20 – 25.5	19 – 26.5
C. ramosus (Villaroya)	4	29.2 – 35.5	26 – 30.3

Concerning the teeth, apart from the morphology mentioned above, similarities with *C. ramosus* also appear in the size as all dental elements fit well within the ranges of all the other known representatives of the species (Table 7).

Table 7. Teeth dimensions (in mm) of the Karnezeika *C. ramosus* and comparison with other forms. Data as in table 6 with the addition of Athanassiou (1996).

		Length	**Width**
Karnezeika	p4	10.77	6.79
C. ramosus (Gerakarou)	p4	9.8 – 12.3 (n=13)	7 – 7.9 (n=13)
C. ramosus (Sesklo)	p4	11.4 – 12.5 (n=3)	8.2 – 8.4 (n=3)
C. ramosus (Saint Vallier)	p4	11 – 12.5 (n=12)	6.5 – 9 (n=20)
C. ramosus (La Puebla de Valverde)	p4	10 – 12.5 (n=25)	7 – 8.5 (n=24)
C. ramosus (Villaroya)	p4	10.5 – 13.5 (n=47)	7.5 – 9.5 (n=46)
Karnezeika	m1	13.15 – 13.81 (n=3)	7.07 – 7.47 (n=3)
C. ramosus (Gerakarou)	m1	11.65 – 14.6 (n=15)	8.3 – 13.2 (n=17)
C. ramosus (Sesklo)	m1	12.7 – 13.6 (n=2)	9.4 – 9.8 (n=2)
C. ramosus (Saint Vallier)	m1	13 – 15 (n=17)	8 – 11.5 (n=15)
C. ramosus (La Puebla de Valverde)	m1	11.5 – 15.5 (n=33)	8.5 – 10 (n=25)
C. ramosus (Villaroya)	m1	11.5 – 16 (n=34)	9.5 – 10.5 (n=32)
Karnezeika	m2	14.92	8.33
C. ramosus (Gerakarou)	m2	14.4 – 16.1 (n=14)	9.3 – 10.5 (n=12)
C. ramosus (Sesklo)	m2	14.9 – 15.2 (n=2)	10.4 – 10.6 (n=2)
C. ramosus (Saint Vallier)	m2	14.5 – 16.5 (n=16)	9 – 12 (n=22)
C. ramosus (La Puebla de Valverde)	m2	13 – 17.5 (n=33)	9.5 – 11.5 (n=29)
C. ramosus (Villaroya)	m2	14.5 – 16.5 (n=33)	10 – 11.5 (n=33)

Measurements and comparison of the proximal part of a metacarpal, are given in Table 8. Again, the Karnezeika specimen fits well the ranges of the other European forms, even though it is on the lower side of them and fits better with the characteristically smaller form of Gerakarou.

Table 8. Dimensions of the metacarpal proximal epiphysis of the Karnezeika *C. ramosus* and comparison with other known representatives of the species. Data as in table 6.

	DTprox	**DAPprox**
Karnezeika	21.35	15.52
C. ramosus (Gerakarou)	21 – 24.2 (n=3)	15.6 – 18 (n=3)
C. ramosus (Saint Vallier)	24 – 28 (n=14)	18 – 21 (n=13)
C. ramosus (La Puebla de Valverde)	23 – 26.5 (n=16)	17 – 19.5 (n=16)
C. ramosus (Villaroya)	21.5 – 28 (n=27)	17 – 20.5 (n=17)

The small sized cervid that appears in Karnezeika can be safely ascribed to *C. ramosus*, not only because of the morphological and metrical similarities mentioned above, but also because of the lack of possible candidates during the Villafranchian. In the Greek peninsula, two different forms of *Croizetoceros* occur, *C. ramosus* similar to the “classic” western European forms (e.g., Saint Vallier, La Puebla de Valverde etc.) and a smaller form which Kostopoulos (1996) named *C. r. gerakarensis* after the holotype locality of Gerakarou. The latter, is characterised by differences in the antler morphology as well as in the lower second premolar (Kostopoulos and Athanassiou, 2005), which is considered a result of the isolation of the Greek *C. ramosus* population during the late Villafranchian (Kostopoulos and Athanassiou, 2005). In the *C. ramosus* material from Karnezeika, there are not enough morphological features preserved on the antlers, nor is the p2 to compare it with the Gerakarou form or any other subspecies (e.g., *C. r. minor* from Senèze), therefore there can be no inclusion to such.

cf. *Metacervoceros rhenanus*

Figure 17

Material

The corresponding material is scanty including a fractured isolated M2(?) (KZ3314) and a maxilla fragment bearing P2, P3 (KZ3116).

Description

All teeth are brachyodont. The lingual cones of P2 appear rounded and similar in shape. They are separated through a wide but weak groove which does not reach the base of the tooth. In labial side, a quite strong anterolabial cone can be observed, while the posterolabial cone is of clear expression but weaker. Of clear but weak expression appears also the anterior style which curves from the middle of the tooth and towards the base, while the posterior style is practically non existent. A central fold can be detected in the occlusal surface, as well as a weak cingulum at the base.

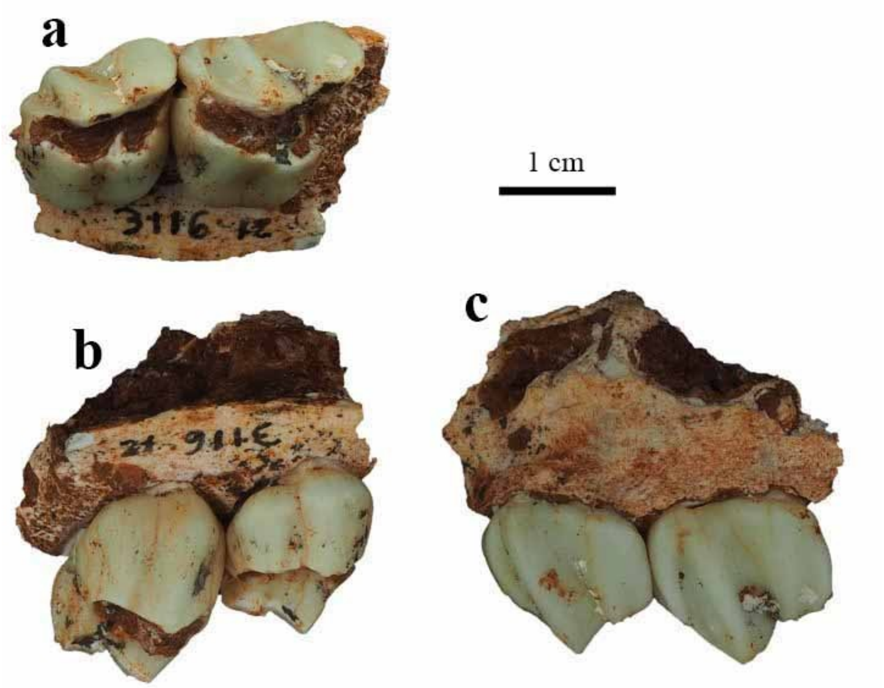

Figure 17: cf. Metacervoceros rhenanus. *Karnezeika. a-c, part of the left side of the maxilla with P1 and P2 (KZ3136) in occlusal (a), lingual (b) and vestibular (c) views.*

P3 is quite similar to P2. However, the anterolabial cone appears weaker, while the anterior style stronger and fuses with the anterolabial cone at the base. The posterior style is somewhat more clearly expressed but weak nonetheless.

The upper molar (not figured), probably a M2, consists of two lobes, the posterior which is larger than the anterior and protrudes more lingually. The protocone and the metaconule are semi-triangular and relatively weak. The metacone appears extremely weak, while the paracone, even though there is a fracture, appears strong. Strongly expressed are also the metastyle and the mesostyle and less the parastyle. Both the paracone and the metacone are significantly inclined inwards. As in the premolars, a weak cingulum can be observed at the base of the tooth, while between the two lobes appears a small entostylid.

Remarks

Despite the poor material, it is clear that those teeth belong to a cervid, as shown by the general morphology of the teeth, which however is definitely larger than *Croizetoceros*, but smaller than the large-sized *Eucladoceros* (Table 9).

Table 9. The dimensions of cf. *M. rhenanus* from Karnezeika and comparison with other known Villafranchian Cervidae. Data from (Heintz, 1970; Kostopoulos, 1996; Valli, 2004).

		Length	**Width**
C. ramosus (Gerakarou)	P2	9 – 10.7 (n=9)	8 – 9.1 (n=9)
C. ramosus (Saint Vallier)	P2	10- 12 (n=14)	9 – 10.5 (n=18)
Karnezeika – cf. *M. rhenanus*	P2	12.37	12.23
M. rhenanus (Dafnero)	P2	13.90	12.80
M. rhenanus (Saint Vallier)	P2	11.5 – 13.5 (n=10)	11 – 13 (n=14)
M. rhenanus (Senéze)	P2	12 – 14.5 (n=29)	11 – 13 (n=29)
E. ctenoides (Gerakarou)	P2	15.7	15.5
Eucladoceros (Senéze)	P2	16 – 20 (n=32)	14 – 17.5 (n=32)
C. ramosus (Gerakarou)	P3	9 – 10.1 (n=11)	9.5 – 11 (n=11)
C. ramosus (Saint Vallier)	P3	9 – 11 (n=14)	10 – 13 (n=20)
Karnezeika – cf. *M. rhenanus*	P3	13.19	13.53
M. rhenanus (Dafnero)	P3	11.9- 12.5 (n=2)	12.2 – 13.4 (n=2)
M. rhenanus (Volakas)	P3	13.5 – 13.6 (n=2)	13
M. rhenanus (Saint Vallier)	P3	11.5 – 13.5 (n=3)	12 – 15.5 (n=16)
M. rhenanus (Senéze)	P3	12 – 14 (n=33)	12 – 14.5 (n=31)
E. ctenoides (Gerakarou)	P3	16.1 – 16.7 (n=2)	19
Eucladoceros (Senéze)	P3	16 – 19.5 (n=38)	16.5 – 20 (n=37)
C. ramosus (Gerakarou)	M2	14 – 17 (n=13)	15.3 – 16.7 (n=13)
C. ramosus (Saint Vallier)	M2	14.5 – 17 (n=15)	14.5 – 18 (n=26)
Karnezeika – cf. *M. rhenanus*	M2(?)	17.72	16.5
M. rhenanus (Dafnero)	M2	18.25	18.1
M. rhenanus (Volakas)	M2	19.7 – 20.4 (n=2)	20 – 20.3 (n=2)
M. rhenanus (Saint Vallier)	M2	16.5 – 19.5 (n=8)	17 – 20 (n=22)
M. rhenanus (Senéze)	M2	16 – 20.5 (n=35)	11 – 13.5 (n=33)
E. ctenoides (Gerakarou)	M2	29.75	26.6 – 26.9 (n=2)
Eucladoceros (Senéze)	M2	22.5 – 28.5 (n=31)	22 – 27.5 (n=30)

The three different Cervid genera shown in Table 9 are the only cervid taxa mentioned for the middle Villafranchian of Greece (Kostopoulos and Athanassiou, 2005). The middle-sized form of the three, however, has created the strongest controversy and confusion between researchers (Heintz, 1970; Spaan, 1992; de Vos, Mol and Reumer, 1995; Di Stefano and Petronio, 1998; Croitor and Bonifay, 2001; Croitor, 2006; Garrido, 2008), concerning its taxonomy and phylogeny. Still, no consensus has been achieved for this *Dama*-like cervid, but herein, I follow the proposal by Croitor and Bonifay, (2001), considering *Metacervoceros* a valid genus, which includes the species *M. pardinensis* and *M. rhenanus*. Dental characters shown by the Karnezeika specimens such as the vertical groove separating the lingual cones of P3, the enamel fold of P2 and the weak cingulum fit the descriptions of *M. rhenanus* (Croitor and Bonifay, 2001; Kostopoulos and Athanassiou, 2005; Croitor, 2018). However, all data coming from such scarce material are not enough for a safe determination, therefore, and since characters point towards the presence of *M. rhenanus*, it is best to currently mention the middle-sized deer from Karnezeika as cf. *Metacervocerus rhenanus*.

Genus*: Eucladoceros* Falconer, 1868

?***Eucladoceros* sp.**

Figure 18

Material

Part of a right antler (KZ1737), fragment of the antler’s tine split off (KZ1505), talus (KZ1442), two calcanei (KZ1905, KZ522), one incomplete metatarsal without DE (KZ1800), proximal parts of tibiae (KZ2011, KZ2175), distal part of the metacarpal (KZ2810), two proximal parts of radius (KZ1502, KZ1439), distal part of radius (KZ1654), two proximal parts of ulna (KZ2607, KZ498), parts of the scapula (KZ548, KZ1503, KZ2311), two cuboscaphoids (KZ2300, KZ1506), four distal phalanxes (KZ1293, KZ2977, KZ437, KZ2916).

Description

The corresponding material is characterised by its large size and its typical cervid – like features.

Specimen KZ1737 (Figure 18) is a right lower antler fragment with the pedicle including a very small part of the frontal bone attached to it. It is broken a few centimeters (~3cm) above the burr. It is quite massive and shows lateral compression.

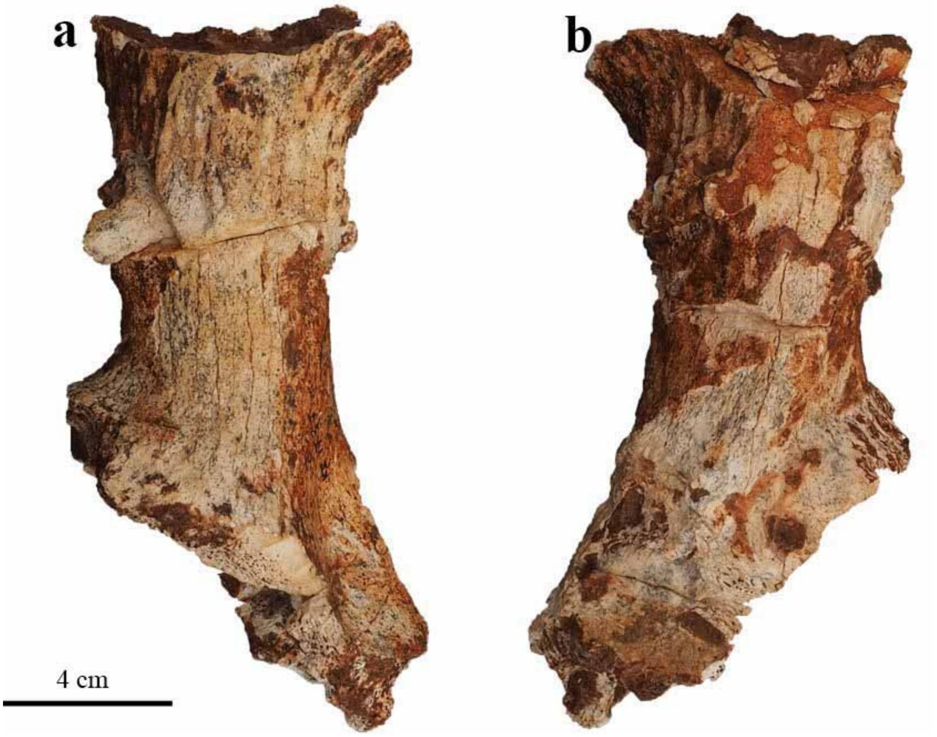

*Figure 18: ?*Eucladoceros *sp. Karnezeika. a-b, part of a right antler (KZ1737) in posterior (a) and anterior (b) views.*

Only the distal part of the metacarpal is preserved. The posterior side of the diaphysis appears concave but becomes flat near the distal epiphysis. On the contrary, the anterior side is very convex, almost angular. The trochleas develop parallel to the main bone axis, while the condyles deviate slightly. The gap between the trochleas is small.

Only part of the diaphysis of the metatarsal is preserved with the distal end missing, while the proximal epiphysis is destroyed. The bone is straight and robust. The posterior side is extremely concave and becomes flat near the distal end. On the anterior side, the MtIII + MtIV merging groove can be clearly seen. The merging groove is not located in the center but towards the lateral with the medial part of the diaphysis being lifted higher than the lateral.

The calcaneus is quite robust. The calcaneal tuberosity is massive and wide. The sliding groove of the superficial flexor tendon is deep and wide. The sliding groove of the external flexor tendon is quite lifted and forms a wide angle with the main body of the calcaneus. The posterior side of the body of the calcaneus is very wide, in contrast with the anterior side which is almost angular.

The articular surface of the talus, that accommodates the calcaneus is square shaped. Above that articular surface, on the posterior side, a groove is detected, which develops parallel to the transverse axis of the bone. The two parts of the upper trochlea do not show any particular inclination. The lateral part of the lower trochlea is larger than the medial and shows a flat base as well as a swollen continuous ridge. The anterior fossa is relatively deep and wide and has an elliptical shape. In medial side, a strong ridge can be observed at the upper part.

The anterior surface of the distal phalanx is straight and the anterior part of the solar border is quite sharp. The extensor process is strong and clearly separated from the articular surface which is divided in a lateral and a medial part through a weak ridge. The lateral part protrudes significantly backwards. The three left distal phalanxes that are preserved, are tilted medially when the base of the phalanx rests on a stable level.

Remarks

This taxon includes mainly postcranial elements and a few antler fragments that point towards the direction of a fairly large sized deer. The dominant large deer of the Villafranchian is *Eucladoceros* (Heintz, 1970; Kostopoulos and Athanassiou, 2005; Garrido, 2008). As in most ruminants, cervids are usually described based on antler morphology and dentition with proportions of postcranial bones serving as complementary data. Unfortunately, the large sized cervid from Karnezeika does not offer such data making its precise determination practically impossible. The genus *Eucladoceros* has a rich systematic history with many synonyms and controversies (Heintz, 1970 — table 75; Azzaroli and Mazza, 1992; Spaan, 1992; de Vos, Mol and Reumer, 1995; Croitor and Bonifay, 2001; van der Made and Dimitrijević, 2015). Croitor, (2018) recognizes two valid species for south and western Europe: The rare *Eucladoceros dicranios* and the most common *Eucladoceros ctenoides* which includes plethora of synonyms (*E. senezensis*, *E. tegulensis*, *E. falconeri*, *E. tetraceros* etc.), proposing, however, the introduction of some of them as temporal and local subspecies, with the main diagnostic feature being the morphology of the antlers. Apart from *Eucladoceros*, another large cervid mentioned from Greek localities is that of *Arvernoceros* from the Epi – Villafranchian (Croitor and Kostopoulos, 2004), even though its taxonomy is disputed by some researchers (van der Made and Dimitrijević, 2015; Pfeiffer-Deml, 2020).

As shown in table 10, the only available character that can be used, as far as the antler fragment is concerned, is the pedicle. However, the given ranges for both *Eucladoceros* and *Arvernoceros* are quite large and almost identical. Specimen KZ1737 is also broken before the first tine therefore it is clear that no important data can be extracted from it.

Concerning the postcranial elements of the large sized Karnezeika cervid, which were well preserved to be measured, their measurements are provided in Table 11. It is therefore clear that there is a wide range of overlap between the two species. Furthermore, Pfeiffer-Deml, (2020) mentions that most morphological characters of *A. ardei* and *Eucladoceros* postcranial elements are similar and cannot be used to separate them. Instead, the morphology of the teeth and especially of the antlers are the only safe diagnostic criteria which are unfortunately absent from the large Karnezeika cervid.

Although some metric features fit better with *Eucladoceros* which is the only one that has been found in the middle -late Villafranchian of Greece, the available data are not considered enough for a safe determination. Therefore, the large sized cervid from Karnezeika will be mentioned as ?*Eucladoceros* sp.

Table 10. Basic dimensions of the Karnezeika large cervid pedicle and the comparison with the two most common species given by (Heintz, 1970).

	DTpedicle	**DAPpedicle**
KZ1737	45.58	46.58
E. ctenoides (Senéze)	26 – 55 (n=26)	26 – 57 (n=26)
A. ardei (Etouaires)	24 – 52 (n=26)	26.5 – 50 (n=26)

Table 11. Measurements of the metacarpal and the radius of the Karnezeika large cervid and comparison with large cervids from other localities. Data from (Heintz, 1970; Athanassiou, 1996; Kostopoulos, 1996; Croitor and Kostopoulos, 2004). NOTE: Specimens from Etouaires given by Heintz, (1970), belong to *P. ardei* + *C. perrieri* mixed, which however are characterised by the same size since their separation was not, at the time, possible by morphological means.

	DTprox	**DAPprox**	**DTdia**	**DAPdia**	**DTdis**	**DAPdis**
	Metacarpal					
Karnezeika			28.36	28.08	46.72	29.71
E. ctenoides (Senéze)	38 – 50 (n=36)	28 – 36.5 (n=32)			40.5 – 51.5 (n=32)	26 – 33.5 (n=32)
E. ctenoides (Saint Vallier)	43 – 52.5 (n=8)	32.5 – 38.5 (n=8)			44.5 – 53.5 (n=4)	28.5 – 35.5 (n=4)
E. ctenoides (La Puebla de Valverde)	40.5 – 51.5 (n=9)	29.5 – 35 (n=9)			42.5 – 51.5 (n=5)	27.5 – 36 (n=7)
E. ctenoides (Gerakarou)	36.6 – 38.9 (n=4)	25.2 – 25.8 (n=4)	23.5	22.5 – 23 (n=2)		
E. ctenoides (Sesklo)	40.9	28	26		46	28.4
Arvernoceros cf. *verestchagini* (Apollonia)	65.3 – 67.9 (n=5)	46 – 49.7 (n=5)			64.4 – 70 (n=4)	40.6 – 44.4 (n=4)
A. ardei/C. perrieri (Etouaires)	35.5 – 48.5 (n=54)	25 – 35 (n=54)			36.5 – 45.5 (n=28)	24.5 – 31 (n=28)
	Radius					
Karnezeika	60.13	33.26	39.33	22.6	59.14	29.03
E. ctenoides (Senéze)	49 – 63 (n=32)	28 – 37 (n=33)			46.5 – 61.5 (n=33)	25 – 35 (n=33)
						(Continues)

E. ctenoides (Saint Vallier)	53 – 61.5 (n=8)	32.5 – 37.5 (n=8)			53.5 – 60 (n=6)	31.5 – 36.5 (n=5)
E. ctenoides (La Puebla de Valverde)	52.5 – 60 (10)	27.5 – 35.5 (n=6)			48 – 57 (n=5)	27.5 – 35.5 (n=6)
E. ctenoides (Volakas)	57.1	34.6	39	23.5	46 – 48.2 (n=2)	27.3 – 31.6
Arvernoceros cf. *verestchagini* (Apollonia)	89.8	47.6			75	60.7
A. ardei/C. perrieri (Etouaires)	46 – 58 (n=38)	26 – 34.5 (n=38)			43 – 55 (n=27)	26.5 – 33 (n=27)

Giraffidae

Family: Giraffidae Gray, 1821
Subfamily: Palaeotraginae Pilgrim, 1911
Genus: *Palaeotragus* Gaudry, 1861

Palaeotragus inexpectatum Samson & Radulesco, 1966

Figure 19

Material

A few isolated upper teeth, one part of a mandible bearing p3, p4 (KZ815), parts of the trochleas of the metapodials's distal epiphyses, two fragments of the olecrana and one fragment of the scapula. The skeletal elements are ascribed to this taxon based on their size which does not fit any of the other artiodactyla.

Description

The respective material is fragmentary, scarce and seems to belong to one young adult individual based on the absence of dental wear.

Part of the mandible is preserved, bearing p3 and p4, along with the interalveolar margin which contains no trace of any mental foramen.

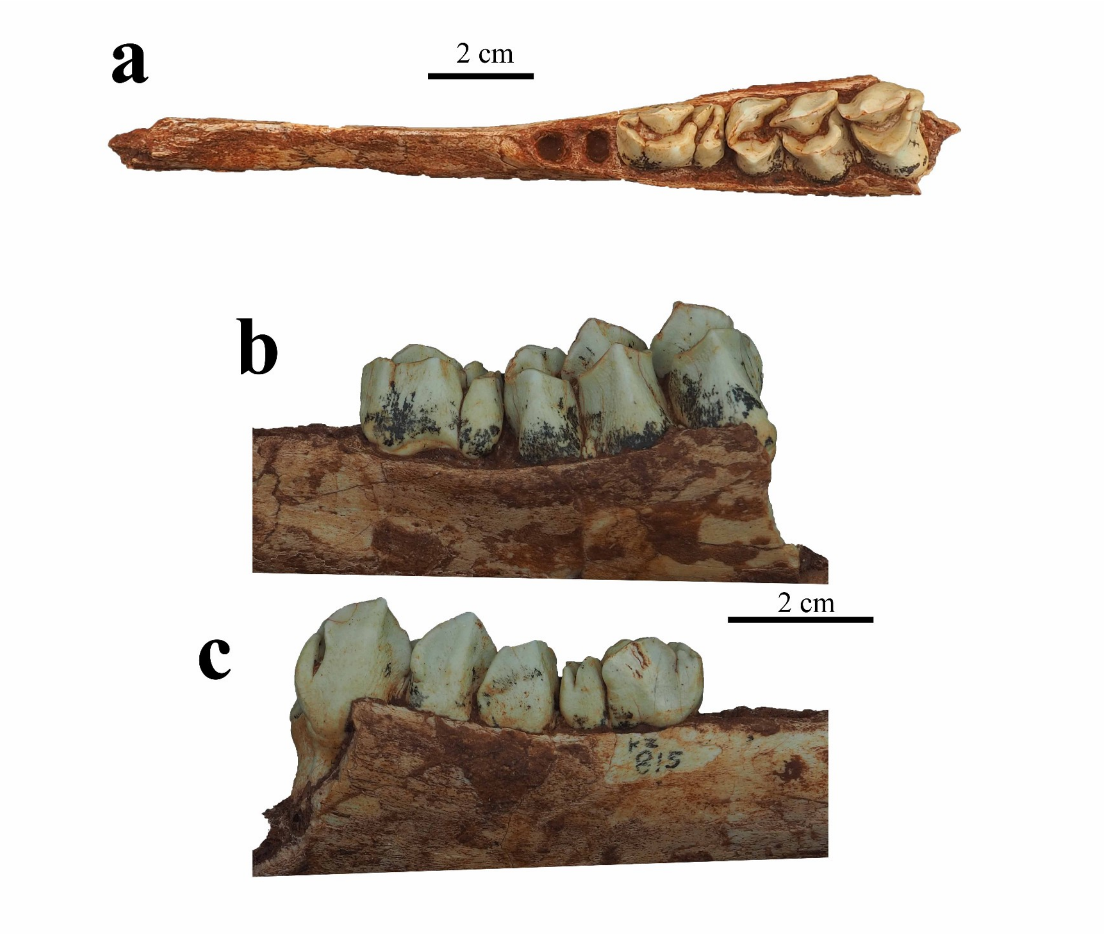

Figure 19: Palaeotragus inexpectatum. *Karnezeika. a-c, part of left hemimandible with p3 and p4 (KZ815) in occlusal (a), vestibular (b) and lingual (c) views.*

The teeth are brachydont, bulky, with significantly wrinkled enamel and completely unworn. The p3 is completely molarised with the posterolabial and posterolingual conids developing at an angle almost vertical to the anteroposterior axis of the tooth. Both the mesolingual and mesolabial conids are strong and wide but lack connection. The p4 consists of three lobes, the anterior lobe differs significantly from the other two. The anterolingual conid is strong and extremely wide. It develops at an angle with the buccolingual axis of the tooth, being intensively inclined anteriorly. As a result, the anterior part of the lobe (the part where, usually, the anterior stylid is located) is displaced outwards and fuses with the anterior cristid of the posterolabial conid. On the contrary, the posterior part of the lobe (where the posterior cristid of the anterolingual conid should be) develops in an opposite direction from the posterior cristid of the anterolabial conid resulting in the formation of an opening inside the lobe. Part of the middle lobe enters that opening. The middle and the posterior lobes have a similar morphology with the latter which is slightly larger than the rest. Both the metaconid and the entoconid are strong and wide, whereas also strong appear the metastylid and the entostylid. The labial conids are angular while the base of each lobe appears swollen. Between the lobes, small ectostylids can be detected.

The P2 (not figured) is brachydont with wrinkled enamel. The anterior part of the tooth appears lower than the posterior part. The anterolingual cone as well as the posterolingual one, is quite weakly expressed and the surface of the tooth is uniform between them. On the labial side, a very strong and high posterolabial cone can be detected which is separated by a gap from a similarly expressed anterior style. The posterolingual cone is extremely weak, almost nonexistent, while a strong posterior style can be observed. The base of the posterior style protrudes and creates an enamel mass that bends towards the front.

The P3 (not figured) consists of two lobes, one anterior which is lower and wider and one posterior which is narrower and taller. The protocone is of clear but weak expression and the anterolingual crista develops straight. Opposite of the protocone in the buccal size, a strong and wide paracone appears which is separated by a gap from a strong parastyle, as in P2. The posterior lobe includes a weak metacone that tilts outwards, between two strong and similar in structure styles (mesostyle and metastyle). The styles are wider at base than at the top.

Measurements of the teeth are given in table 12.

Table 12. Measurements of the teeth of the Karnezeika Giraffid. The p2-p4 length is approximate since p2 is absent from the mandible. *(The three different widths correspond to each different lobe of p4 beginning from the anterior towards the posterior).

Specimen		**Length**	**Width**
KZ815	p3	18.93	11.43
KZ815	p4	34.12	13.77/15.4/16.64 *
KZ815	p2-p4	~70.66	-
KZ2906	P2	18.44	12.09
KZ2463	P3	~27.68	16.59
KZ3273	P3	26.37	16.46

Remarks

As mentioned above, the studied material seems to belong to one young adult individual. Unfortunately, no rich corresponding material was found in the literature nor in the visited palaeontological collections to compare the finds from Karnezeika. Therefore, the only available specimen that was used for taxonomical purposes is KZ815, as a similar specimen (even though sub-adult) is mentioned from Sesklo (Athanassiou, 1996; Kostopoulos and Athanassiou, 2005). The general morphology of the teeth in combination with the strong brachyodontism, wrinkled enamel, molarised p3 with characteristic developed posterior conids as well as the lack of a transverse connection of the mesolingual and mesolabial conids (Van Der Made and Morales, 2011) and the absence of mental foramens, show that this mandible belongs to a representative of the Giraffidae. Comparing the size of the teeth of the Karnezeika giraffid with the giraffe from Sesklo, which was the only available material to compare with, a good analogy occurs and the two specimens seem to be similar in size (Table 13) as well as in morphology.

Table 13. Measurements of the lower teeth of the Karnezeika Giraffid and comparison with the specimen from Sesklo. *(The three different widths correspond to each different lobe of d4 and p4 beginning from the anterior towards the posterior).

		Length	**Width**
Karnezeika	p3	18.93	11.43
P. inexpectatum **(Sesklo)**	d3 (n=2)	21 – 22.2	11.5 - 12
Karnezeika	p4	34.12	13.77 / 15.4 / 16.64 *
P. inexpectatum **(Sesklo)**	d4	34.5	14.10 / 15.2 / 17.00 *

Traditionally in Greece, Villafranchian giraffids were usually ascribed to *Mitilanotherium martinii* following the finds from Volakas, described by Sickenberg (1967). Later, Kostopoulos and Athanassiou, (2005), proposed the possible synonymy of the aforementioned species as a junior synonym of *Mitilanotherium inexpectatum*, until almost a decade later, new finds from Sesklo drove Athanassiou (2014) into the conclusion that the taxonomy of this Plio – Pleistocene giraffid was mistreated due to the general scarcity of the material, while in reality all the Villafranchian paleotragines belong to the same species *Palaeotragus inexpectatum*, extending the range of this late Miocene genus into the Pleistocene. Therefore, due to the lack of species diversity of Villafranchian giraffids, along with the great similarity with the juvenile mandible mentioned by Athanassiou, (1996); Kostopoulos and Athanassiou, (2005) from Sesklo, it is safe to ascribe the Karnezeika giraffe to *Palaeotragus inexpectatum*.

Bovidae

Bovidae represent the most taxonomically diverse group in the fossil record of Greece, comprising a high number of taxa (see Kostopoulos 2022 for a comprehensive review). During the early Pleistocene the family, as represented in the so-called Villafranchian faunas, included many well-known and characteristic taxa that occurred throughout Europe, such as *Leptobos etruscus*, *G. torticornis* and *G. meneghinii* (Kostopoulos 2006, 2022), but also some enigmatic species, such as the possible caprine *Euthyceros thessalicus* (Athanassiou 2002a), or the antilopine *A. koufosi* (Kostopoulos 1998).

Family: Bovidae Gray, 1821

Subfamily: Antilopinae Baird, 1857

Genus: *Gazella* de Blainville, 1816

Gazella bouvrainae Kostopoulos and Athanassiou, 1997

Figure 20

Material

Because of the large number of specimens, the corresponding material of this taxon is not listed here.

Description

The majority of the bovid material from Karnezeika belongs to a small-sized representative with long and slender postcranial bones as well as mesodont teeth. All skeletal and dental elements show homogeneity in size and shape, with the exception of the horncores.

The *Gazella* horncores from Karnezeika can be separated in two size groups, namely size group A and size group B, respectively. None of the specimens is complete, as all are broken a few centimetres above the base. The horncores of both size groups do not differ particularly in morphology. Their cross-section, throughout their preserved length, is oval/circular. The horncores are also slightly inclined caudally, while in cranial or caudal view they show a slight lateral divergence. All specimens show shallow longitudinal grooves along their rostromedial side. Basal horncore measurements along with their cross-section compression index (DT/DAP×100) are provided in Table 14.

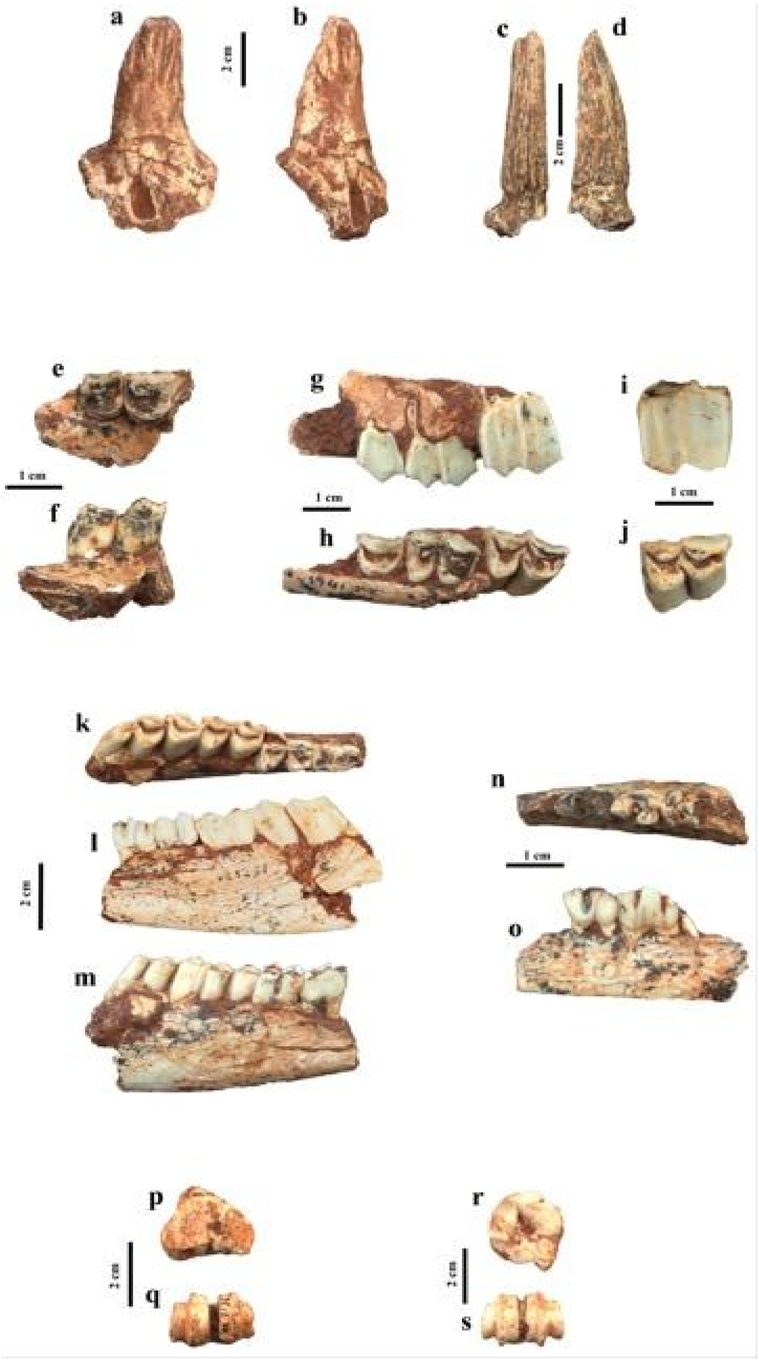

Figure 20: G. bouvrainae. *Karnezeika. a–b, Left horncore, size group B (KZ2512), in anterior (a) and medial (b) view; c–d, left horncore, size group A (KZ1158), in anterior (c) and medial (d) view; e–f, left part of maxilla with P2, P3 (KZ1301), in occlusal (e) and lingual (f) view; g–h, left part of maxilla with P4, M1, M2 (KZ1941) in labial (g) and occlusal (h) view; i–j, left M3 (KZ3046), in labial (i) and occlusal (j) view; k-m, right part of mandible with p4, m1, m2, m3 (KZ1231), in occlusal (k), lingual (l) and labial (m) view; n-o, right part of mandible with p3, p4 (KZ1762), in occlusal (n) and lingual (o) view; p–q, right metacarpal (KZ357), in proximal (p) and distal (q) view; r–s, left metatarsal (KZ2974), in proximal (r) and distal (s) view.*

Table 14: Metric characteristics (in mm) of the horn-core base (b) of *G. bouvrainae* from Karnezeika.

	Specimen	**DTb**	**DAPb**	**Index (DT/DAP)×100**
Size group A	KZ1158	16.06	18.86	85.2
	KZ2303	16.34	17.88	91.4
	KZ3227	13.38	16.55	80.8
Size group B	**Specimen**	**DTb**	**DAPb**	**Index (DT/DAP)×100**
	KZ2512	22.41	24.17	92.7

Most dental elements consist of isolated specimens; the tooth-bearing mandibular or maxillary specimens are few and incomplete. The dental measurements are provided in Table 15.

The P2 is slightly elongated (L×100/W=112–133, n=4) in occlusal view. The fossa is separated by a central fold into a small anterior and a larger posterior part. Lingually a slight bilobation is observed separating the lingual cone to a small anterolingual cone and a larger posterolingual one. At the labial side, an anterolabial well-developed cone stands out, separated from a weakly expressed anterior style through a narrow groove. The posterior style is very weak.

The P3 is almost square shaped (L×100/W=85-104, n=8) in occlusal view. In less worn specimens, a central fold is visible in occlusal view (e.g., specimens KZ2287, KZ2147), whereas in more worn specimens this fold connects the lingual cone to the labial wall, and occlusally, two fossae are formed, a larger anterior one and a smaller posterior (e.g., KZ1301). Lingually, one wide cone is observed, slightly displaced posteriorly. Labially, a well-expressed labial cone is present approaching an equally strong anterior style. The latter fuses at the base with the anterolabial cone. The posterior style is quite strong as well, but appears thinner than the anterior style, and usually protrudes more towards the labial side.

The P4 morphology is quite similar to that of P3 in occlusal view (L×100/W=84-123, n=9). A central fold can be observed occlusally. Moreover, the anterolabial cone is less prominent and located in the middle of the labial side, rather than being displaced anteriorly as in P3.

The M1 and M2 are mesodont. Occlusally, all specimens show a metaconule fold, while in the most worn teeth, usually one circular fossetta can be detected in the occlusal surface between the lobes. Lingually, the anterior lobe is triangular, while the posterior is sub-triangular. The protocone is strong, pointed and protrudes more lingually than the weaker and wider metaconule. In labial side, the paracone as well as the mesostyle are strong, while the metacone is extremely weak to absent. Both the parastyle and but less the metastyle are clearly expressed but are not as prominent as the mesostyle. The second upper molars are similar to the first ones but larger.

The M3 generally exhibits similar structure and morphology to M1 and M2. The anterior and the posterior lobes are more rounded while the metastyle shows a wing-like protrusion at the base.

The p2 appears triangular (L×100/W=159-262, n=6) in occlusal view. Lingually, an extremely strong and wide mesolingual conid is present. The posterolingual conid and the anterior stylid are clear but weak. The anterior valley is shallow but wide. In the labial side, a faint but wide mesolabial conid can be seen. The posterolabial conid is faint as well.

The p3 is fairly molarised and almost equal in length with the p4 (p3/p4=0.9, n=1). Occlusally, the separation of the anterior conid from the anterior stylid is clear in unworn specimens but they appear fused as wear takes place. Lingually, the mesolingual conid is somewhat weak. The posterolingual conid is similar to the mesolingual one, while the posterior stylid is almost absent. The anterior valley is deep and wide. Occlusally, the posterior valley appears narrow and shallow, while it is lingually closed. In labial side, the mesolabial conid is quite faint, while the posterolabial conid is very strong.

The p4 appears fairly moralised as well and somewhat triangular (L×100/W=139-188, n=11) in occlusal view. The two posterior conids are fused and create a common occlusal surface across the buccolingual axis of the tooth. Similar to p3, the anterior conid is easily separated from the anterior stylid in unworn teeth, but they appear fused occlusally in worn specimens. Lingually, the mesolingual conid appears strong and in most specimens creates protrusions towards both the anterior and the posterior. The posterolingual conid and the anterior conids are strong. The anterior valley is deep and vertical (e.g., specimen KZ2294) or sometimes slightly tilted towards the posterior (e.g., specimen KZ2793). The posterior valley is deep and narrow. Labially, the mesolabial conid is weak while the posterolabial conid quite strong. A shallow and wide groove is present in front of the latter.

The m1 is mesodont. Both lobes appear quite similar in shape and size. In lingual side, the metaconid and the entoconid are weak. The mesostylid and entostylid are clearly expressed but also weak, and fuse with the corresponding conids near the base of the crown. The metastylid is extremely weak, almost absent. Labially, the protoconid and the hypoconid are triangular, without one of them protruding more towards the labial side than the other does. In some specimens where the anterior part of the tooth is well preserved, a trace of a weak anterior cingulid can be observed. A small and short ectostylid is also present.

The m2 is similar to m1 but larger in size. Additionally, in lingual side, the metastylid appears stronger in some unworn specimens. The same is true for the entostylid with a noticeable protrusion towards the posterior. Labially, the anterior cingulid is stronger and completely visible in all specimens.

In m3 the anterior lobe is larger than the other two and slightly more sub-triangular. The third lobe is cylindrically shaped and leans anteriorly, while also showing a quite rounded occlusal surface. Lingually, the lingual conids resemble these of m1 and m2. The metastylid is weak, while no entostylid is observed. In labial side, the conids resemble these of m1 and m2 as well. The anterior cingulid is weak as in m1, while the ectostylid is vestigial.

D2 is generally similar to P2. Occlusally, in unworn specimens, a central fold connects the labial wall to the lingual, splitting the anterior fossa in two. In worn specimens the anterior fossa appears undivided. In lingual side the protocone is strong and prominent. In the labial side, an extremely strong anterior cone can be observed as well as a very faint paracone. The mesostyle is strong and prominent. The anterior style is moderately developed.

The D3 exhibits a central fold in the occlusal surface of the posterior lobe in all specimens. In lingual side, the lingual wall of the anterior lobe is almost flattened and the two lobes are separated by a narrow and shallow groove. The protocone is weak. Labially, the anterior cone is very strong and prominent, while the paracone is very weak. The observed mesostyle and the parastyle are also well expressed. A strong anterior style is also present which develops labially.

The D4 is generally similar to D3 but larger. The anterior lobe is triangular and the posterior one is sub-triangular. Lingually, the separation of the two lobes is much clearer. The protocone and the metaconule are weak. Labially, a strong paracone stands out while the metacone is moderately expressed. The labial styles are strong. The parastyle fuses at the base with the paracone.

In d4 the anteroposterior diameter of the three lobes increases significantly from the base to the top. Lingually, the anterolingual conid is quite stronger than the other lingual conids. The anterior stylid and the metastylid are strong while no mesostylid is observed. The entostylid is weak but prominent. The labial conids are similar and triangular in shape, being weak but well expressed. An ectostylid can be detected between the middle and the posterior lobe, the size of which varies per specimen.

Table 15: Teeth measurements (in mm) of *G. bouvrainae* from Karnezeika.

	n	**L**	**L (mean)**	**W**	**W (mean)**	**(L×100)/W**
P2	4	8.63–9.75	9.00	6.5–8.38	7.6	112–133
P3	8	8.41–9.86	9.01	8.1–10.37	9.72	85–104
P4	9	8.95–10.28	9.35	8.35–10.73	9.15	84–123
M1	18	13.06–15.05	14.19	9.48–11.88	10.70	116–157
M2	14	14.79–16.39	15.62	9.99–14.08	11.84	109–157
M3	11	14.35–16.12	15.28	9.26–11.06	10.15	137–160
	n	**L**	**L (mean)**	**W**	**W (mean)**	**(L×100)/W**
p2	6	5.07–8.66	6.61	2.15–4.49	3.45	159–262
p3	27	9.05–11.01	9.66	4.40–6.03	5.15	166–214
p4	11	9.98–11.25	10.50	5.46–7.98	6.39	139–188
m1	14	10.82–13.47	12.55	5.87–8.33	7.44	133–218
m2	18	13.32–16.54	14.49	6.58–8.25	7.26	161–232
m3	14	17.76–20.42	19.25	6.66–8.13	7.32	242–288

All long bones of hindlimbs and forelimbs are elongated and slender. In humerus, the olecranon fossa is quite deep and narrow while its shape is semi-circular. In radius, no radial tuberosity is observed, although a noticeable depression in the lateral part of the upper end below the articular surface is evident. The metacarpals and the metatarsals are both extremely slender, while the metacarpal tuberosity appears strong. In femur, the greater trochanter is strong, the supracondyloid fossa appears relatively shallow and wide, whereas the intercondyloid fossa is relatively deep. In tibia, the intercondyloid tubercles are tall and strong. The calcaneus is short and slender, while the calcaneal tuberosity is strong and wide. The sliding groove of the superficial flexor tendon is shallow and wide. The posterior part of the main body of the calcaneus is also wide.

The sulcus for the external flexor tendon is extremely lifted and, in some specimens, forms an acute angle with the main body of the calcaneus. The talus is small sized and has a rectangular shape. The articular surface that accommodates the calcaneus is also rectangularly shaped and narrower at the bottom than at the top. Above the articular surface that accommodates the calcaneus, a groove slightly displaced towards the medial, or horizontal in some specimens, can be observed. The anterior fossa is deep, wide and semi-circular. A strong ridge can be detected on the top part of the medial side of the bone. The proximal phalanxes are quite small, long and slender, with a quite prismatic shape. The distal phalanges are extremely small sized. The anterior surface is slightly convex in some specimens and straighter in others. The front part of the plantar border is relatively rounded.

Remarks

According to Kostopoulos and Athanassiou (1997) and Athanassiou (2002b), three *Gazella* species occur in the Plio-Pleistocene of the Greek peninsula. These are, the widely spread, but less common in Greek localities, *G. borbonica* Depéret, 1884, *G. bouvrainae*, which is absent from the rest of Europe, but most common in Greece, and the rare *G. aegaea* Athanassiou, 2002, which has only been found in Sesklo (Thessaly) and Vatera (Lesvos). By examining the horncores of the Karnezeika *Gazella*, *G. aegaea* can easily be ruled out as a possible candidate, since it represents a large-sized taxon with strongly laterally compressed horncores (Athanassiou 2002b). These characters are completely absent from the much smaller Karnezeika *Gazella*, whose horncores have an oval/sub-circular cross-section. Such a cross-section is typical for *G. bouvrainae*, but also for the female individuals of *G. borbonica* (Table 16). Male individuals of *G. borbonica* show horncores more laterally compressed, which do not fit any of the two Karnezeika *Gazella* size groups.

Data from Table 16 can safely place size group B in the range of *G. bouvrainae*. However, the small general size in correlation with the strong roundness of size group A make it hard to distinguish between *G. bouvrainae* and female individuals of *G. borbonica*. Because of the fact that *G. borbonica* is known to show sexual dimorphism (Heintz 1975; Crégut-Bonnoure and Valli 2004; Andrés Rodrigo 2011), as also do the extant gazelles (Wronski et al. 2010), there is a possibility that the two size groups, A and B, also correspond to the same trend (even though it had never been noted for *G. bouvrainae* before), with size group B being the male stock and size group A the female counterpart. All gazelle species that show sexual dimorphism (fossil as well as extant) seem to develop an analogy, where the female horncore cross-sections are more circular than those belonging to males, as it has also been observed by de Vos et al. (2002).

Table 16: Maximum and minimum ranges of DT and DAP (in mm) for the base of the horncore of various *Gazella* fossil forms and of the pedicle of some extant species. Data from Heintz (1969); Kostopoulos and Athanassiou (1997); Athanassiou (2002b) and D. S. Kostopoulos pers. data.

	DT	**DAP**	**(DT/DAP)×100**
Size group A	13.38–16.34 (n=3)	16.55–18.86 (n=3)	80.8–91.4
Size group B	21.08–22.41 (n=2)	24.12–24.17 (n=2)	87.4–92.7
G. bouvrainae (Gerakarou)	21.0–24.1 (n=4)	24.0–28.0 (n=4)	81.4–90.0
G. bouvrainae (Dafnero)	22.5–27.4 (n=3)	33.0–35.1 (n=3)	68.2–78
G. bouvrainae (Sesklo)	22.7–26.0 (n=9)	30.5–32.4 (n=8)	72.1–81.9
G. aegaea (Sesklo)	27.5–31.0 (n=7)	44.0–45.5 (n=7)	61.5–69.7
G. borbonica ♂ *(*La Puebla de Valverde)	18.0–26.0 (n=86)	27.0–35.7 (n=94)	60.9–76.2
G. borbonica ♀ *(*La Puebla de Valverde)	11.5–16.0 (n=47)	13.0–19.5 (n=47)	76.5–93.8
G. dorcas ♂	18.3–23.6 (n=17)	25.5–31.5 (n=17)	65.4–86.1
G. dorcas ♀	11.0–13.7 (n=17)	12.0–15.5 (n=17)	82.8–94.9
E. rufifrons ♂	20.0–21.5 (n=5)	26.5–35.3 (n=5)	60.9–75.5
E. rufifrons ♀	12.0–14.0 (n=5)	13.7–18.2 (n=5)	74.2–87.6
E. thomsoni ♂	17.5–21.5 (n=6)	28.8–35.0 (n=6)	57.1–63.3
E. thomsoni ♀	8.4–10.3 (n=6)	9.3–14.0 (n=6)	78.6–91.2

This can be seen in Figure 21. At first glance, size group B seems unlikely to be the male counterpart of size group A, since it shows higher index values. However, in gazelle species that have less laterally compressed horncores, such as *G. dorcas*, there is an overlapping area between males and females. This might be the case with the Karnezeika material, whose small sample size likely does not depict the original variation of the two size groups.

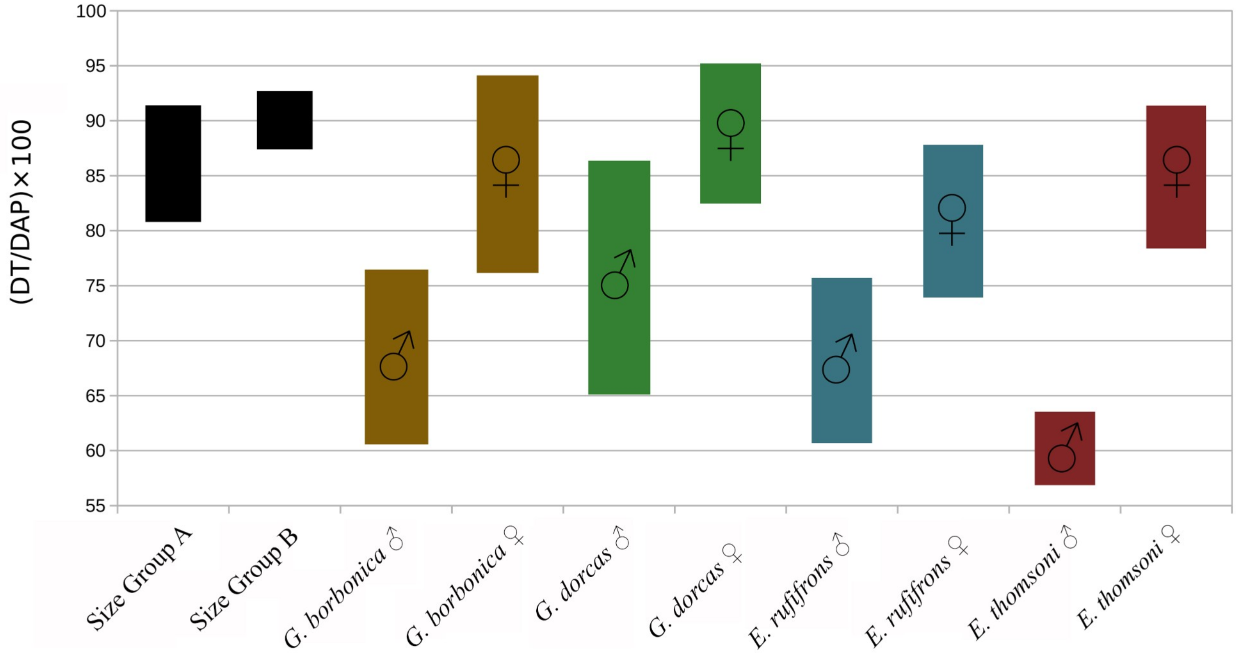

Figure 21: Bar chart comparing the horncore's cross-section compression index (DT/DAP)×100 of different gazelle species that present sexual dimorphism with those of size group A and size group B from Karnezeika. Notice the emerging pattern where index values for male horncores are always lower.

The examination of the dental material, on the contrary, does not show any heterogeneity in morphology or in size. Insignificant small differences can be observed between specimens but most likely they are the result of intraspecific variation or different stages of wear. Nevertheless, gazelle teeth, especially isolated specimens, which mostly is the case in the Karnezeika dental material, seldom offer diagnostic characters for species-level taxonomy. However, the metric study of this dental material shows a resemblance, as far as general size is concerned, towards *G. bouvrainae* (Figure 22).

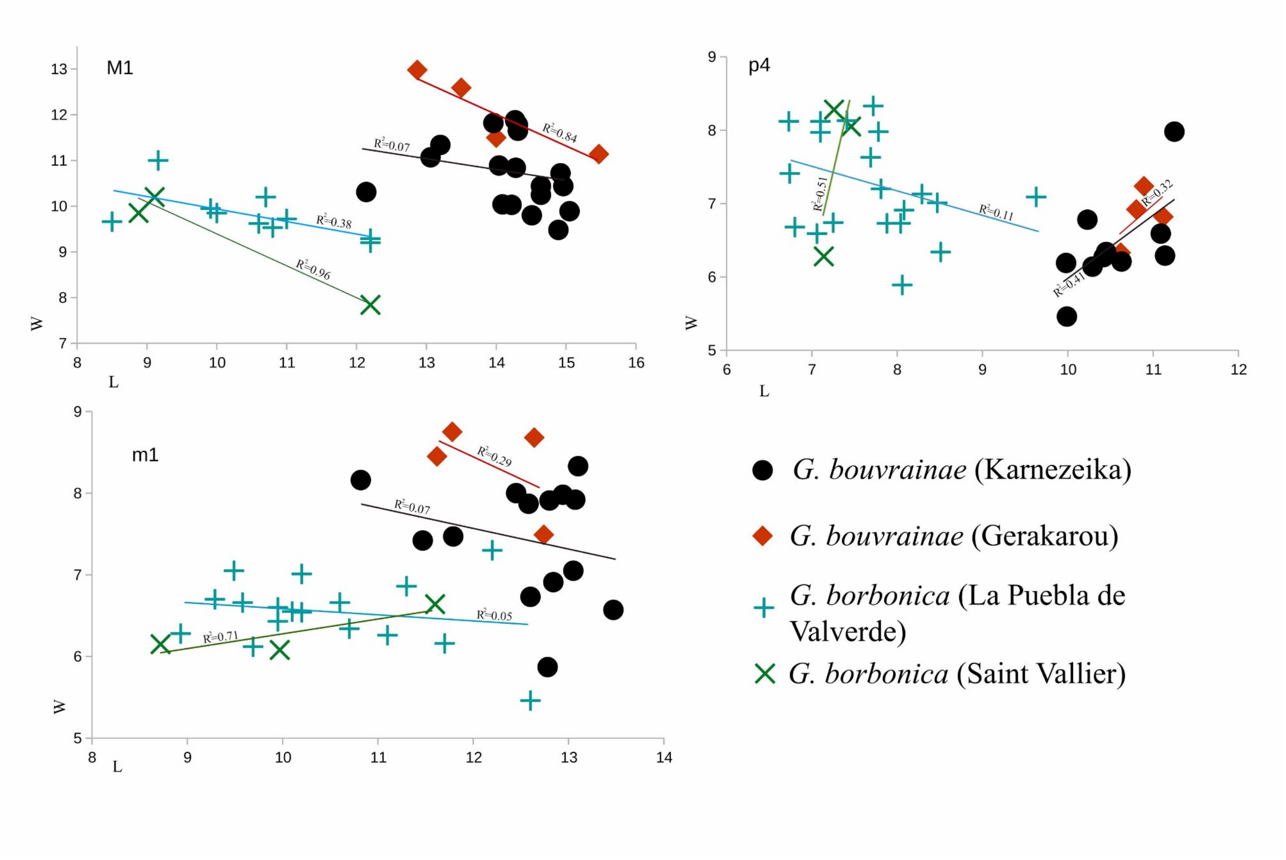

Figure 22: Scatter charts of dental dimensions of G. bouvrainae *from Karnezeika compared with* G. bouvrainae *from Gerakarou and* G. borbonica. *Data for* G. borbonica *from Andrés Rodrigo (2011).*

Same observations occur for the postcranial elements as well, as all data show sizes most compatible with that of *G. bouvrainae* with the metapodials and talus being the most diagnostic (Tables 17, 18 & 19).

Table 17. Linear measurements (in mm) of the metacarpal III-IV of the *G. bouvrainae* from Karnezeika. Data from Kostopoulos (1996) and Andrés Rodrigo (2011).

	DT prox	**DAP prox**	**DT dis**	**DAP dis**
G. bouvrainae (Karnezeika)	19.71–21.67 (n=9)	15.33–17.65 (n=9)	20.75–22.31 (n=11)	13.85–15.60 (n=11)
G. bouvrainae (Gerakarou)	20.5–23.5 (n=4)	15.50–17.80 (n=4)	21.7 (n=1)	14.30 (n=1)
G. borbonica (La Puebla de Valverde)	18.04–20.17 (n=33)	12.69–15.68 (n=34)	17.29–19.59 (n=39)	13.05–14.84 (n=35)
G. borbonica (Saint Vallier)	18.71 (n=1)	13.91 (n=1)	18.40 (n=1)	13.99 (n=1)

Table 18. Linear measurements (in mm) of the metatarsal III-IV of the *G. bouvrainae* from Karnezeika. Data from Kostopoulos (1996) and Andrés Rodrigo (2011).

	DT prox	**DAP prox**	**DT dis**	**DAP dis**
G. bouvrainae (Karnezeika)	18.33–21.65 (n=8)	19.75–22.35 (n=8)	20.69–22.91 (n=9)	14.25–16.06 (n=9)
G. bouvrainae (Gerakarou)	18.70–19.50 (n=4)	17.00–21.00 (n=5)	20.00–22.70 (n=5)	14.90–15.70 (n=4)
G. borbonica (La Puebla de Valverde)	16.80–20.15 (n=33)	19.13–22.44 (n=32)	19.00–20.47 (n=15)	13.46–15.97 (n=19)

Table 19. Linear measurements (in mm) of the talus of the *G. bouvrainae* from Karnezeika. Data from Kostopoulos (1996) and Andrés Rodrigo (2011).

	L med	**DAP max**	**L lat**	**DT dis**
G. bouvrainae (Karnezeika)	25.53–28.91 (n=18)	14.36–16.93 (n=19)	26.31–30.65 (n=17)	15.12–18.42 (n=19)
G. bouvrainae (Gerakarou)	27.70 (n=1)	15 (n=1)	29.70 (n=1)	17.05 (n=1)
G. borbonica (La Puebla de Valverde)	22.78–24.82 (n=17)	14.05–17.13 (n=17)	24.10–26.83 (n=14)	14.92–16.65 (n=15)
G. borbonica (Saint Vallier)	25.84–24.9 (n=2)	15.18 (n=1)	26.71–26.96 (n=2)	15.81–15.84 (n=2)

All elements studied above point to a closer affinity of the Karnezeika *Gazella* with *G. bouvrainae* in terms of size, while being consistently larger than *G. borbonica.* Based on the current data, horncores of size group A cannot straightforwardly be attributed to the same species. Taking into account the fact that ~26% of the total gazelle material from Karnezeika belongs to juvenile individuals, we consider three possible interpretations:

1) Size group A belongs to juvenile or female individuals of *G. bouvrainae*.

2) Size group A belongs to female individuals of some other species (e.g.,, *G. borbonica)*.

3) Size group A belongs to some other, smaller sized, until currently unknown species.

As there is no evidence in the existing dental and postcranial material to support the presence of *G. borbonica* or other gazelle species in the locality, we consider the interpretations 2 and 3 as less plausible. The first interpretation remains as the most probable one, although a comparison with juvenile *Gazella* individuals is currently not possible.

Genus *Gazellospira* Pilgrim and Schaub, 1939

Gazellospira torticornis Aymard, 1854

Figure 23

Material

Three horncore fragments (KZ848, KZ3191, KZ429), an isolated M1 (KZ1919), two isolated M3 (KZ3245, KZ1874), one complete metacarpal III-IV (KZ1900), two complete proximal phalanges (KZ1884, KZ1957) and one complete medial phalanx (KZ629).

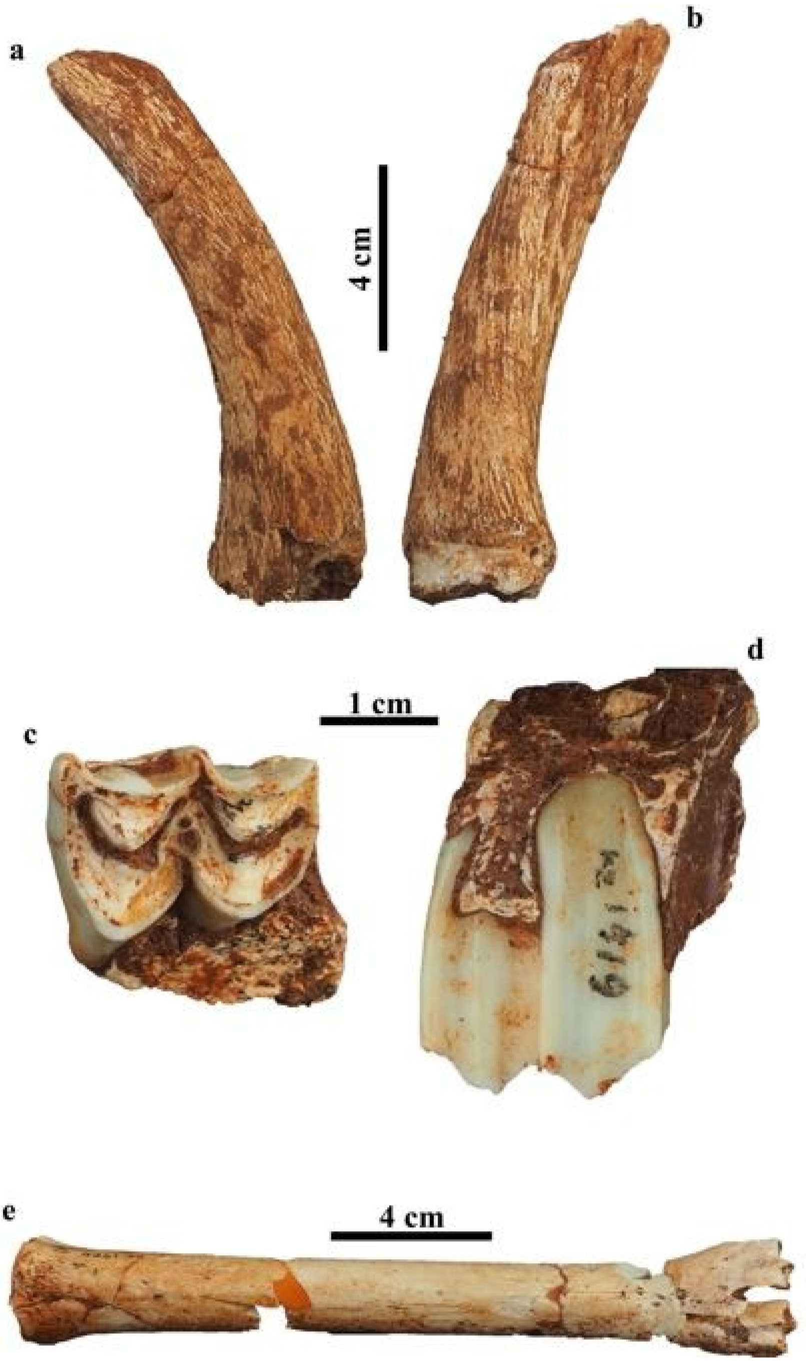

Figure 23: G. torticornis. *Karnezeika. a–b, right horncore (KZ848), in cranial (a) and caudal (b) view; c–e, left M1 (KZ1919), in occlusal (c) and labial (d) view; e, right metacarpal (KZ1900), in dorsal view.*

Description

The studied horn-core specimens (Figure 23(a-b)) consist of fragments broken near the base. They seem to be placed above the orbits and show a weak heteronymous torsion, completing one gyre. They are moderately compressed laterally and they are weakly inclined caudally and laterally. No keel is observed and specimen KZ848 shows a shallow groove that runs along the posterior side. The cross-section at the base is elliptical (measurements provided in Table 20).

Table 20: Measurements (in mm) of the horncore bases (b) of *G. torticornis* from Karnezeika.

	DAPb	**DTb**
KZ848	38.53	27.18
KZ3191	37.84	28.52
KZ429	39.02	29.90

The M1 is mesodont. In occlusal view, two round fossettes can be seen between the two lobes. Lingually, the anterior lobe is triangular, while the posterior one is sub-triangular. The protocone is strong, pointed and protrudes slightly more towards the lingual side than the wider metaconule. Labially, the paracone appears strong, while the metacone is weaker. The three labial styles are strong. The mesostyle develops in a straight line all along its length, while the parastyle and the metastyle are curved from the middle of the crown to the base, with the parastyle fusing at the base with the paracone.

The M3 is quite similar to M1, but labially the metacone appears even weaker, while the metastyle is wider at its base forming a wing-like protrusion.

The metacarpal III-IV (Figure 23e) is long and slender. The proximal articular surface is approximately trapezoidal. The distal epiphysis is narrow. The caudal face of the diaphysis is transversely mostly concave, particularly near the proximal end, while it appears flat near the distal end. The metacarpal tuberosity below the proximal articular surface at the anterior side, appears relatively strong. Only one complete proximal phalanx has been preserved along with the proximal part of one more. They are long and slender. The medial phalanx is relatively slender with the proximal part being wider than the distal.

Remarks

The body size of this bovid is intermediate between *Gazella* and *Gallogoral*. Although the available material is limited, it exhibits characters quite significant for its taxonomy. The horncore characters, such as the lateral compression and the open, heteronymous spiral, point towards the genus *Gazellospira* (Pilgrim and Schaub 1939). The same is true for the long and slender metacarpal III-IV, with its cervid-like, concave caudal face of the shaft (Pilgrim and Schaub 1939; Duvernois and Guérin 1989). The dental and other postcranial elements referred to this species are included here based on their size.

The heteronymous torsion of the horncores is a diagnostic character that appears only in two Antilopini of the Greek Villafranchian (Kostopoulos 2006, 2022), *G. torticornis* and the enigmatic and rare *A. koufosi* (Kostopoulos, 1998). The latter has horncores that differ significantly from the Karnezeika specimens being curved strongly caudally and laterally (Kostopoulos 1998). *Gazellospira* includes the Eurasian form *G. torticornis* and the Far Eastern form *G. zdanskyi* (Teilhard de Chardin and Trassaert, 1938) (previously referred to as *G. gromovae* Dmitrieva, 1975 — Hermier et al. 2020). As far as the general size of the horncore bases is concerned, Hermier et al. (2020) mention that the horncore base dimensions of *G. torticornis* show a wide geochronologic and geographic variation, with size generally decreasing from older (La Puebla de Valverde, MNQ17) to more recent sites (Fonelas, MNQ18). As shown in Figure 24, the DTb/DAPb ratio of the Karnezeika specimens matches that of *Gazellospira*, especially the smaller horncores from Fonelas (Garrido 2008).

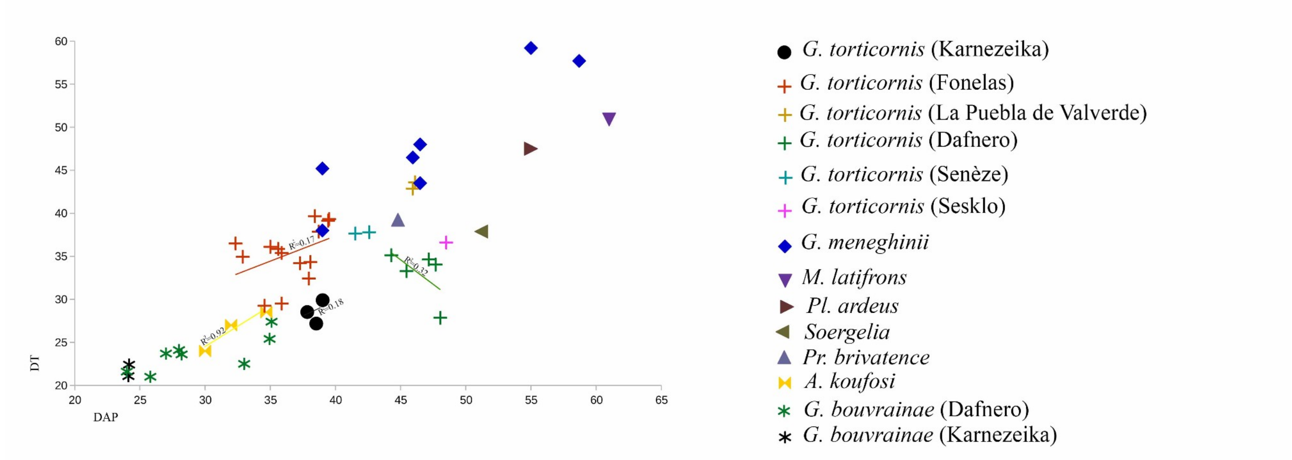

Figure 24: Scatter chart of the KZ G. torticornis *horncore basal measurements compared with other comparable taxa, as well as other forms of* G. torticornis *from different localities. Data from. Duvernois and Guérin (1989); Kostopoulos (1996, 1998); Athanassiou (2005); Hermier et al. (2020).*

Concerning the dental material, some characters, such as the well-developed buccal styles and the strong and protruding metastyle of M3 have also been reported for *G. torticornis* (Athanassiou 2005; Andrés Rodrigo 2011; Hermier et al. 2020). Furthermore, the dimensions of the Karnezeika specimens correspond to the ranges provided for the species with the possible exception of the length of M3, which seems to be slightly lower (Table 21).

Table 21. The dimensions (in mm) of the KZ *Gazellospira* molars and comparison with other *G. torticornis* populations. Data from Kostopoulos (1996); Athanassiou (2005); Andrés Rodrigo (2011).

		Length	**Width anterior lobe**	**Width posterior lobe**
KZ1919	M1	17.97	13.13	11.47
Dafnero	M1	20.8–21.9 (n=3)	13.0–14.5 (n=3)	11.3–14.4 (n=2)
Sesklo	M1	13–24.4 (n=9)	14.0–20.0 (n=8)	
Villarroya	M1	16.91–23.45 (n=11)	14.25 –17.94 (n=19)	12.85 – 18.61 (n=22)
La Puebla de Valverde	M1	20.07–20.55 (n=2)	14.93–16.38 (n=5)	14.31–15.35 (n=5)
KZ3245	M3	18.72	12.13	10.03
KZ1874	M3	19.08	11.72	10.64
Dafnero	M3	20.57–23.34 (n=14)	10.74–14.78 (n=14)	8.92–11.64 (n=14)
Sesklo	M3	24.6–26.0 (n=2)	19.0–21.0 (n=2)	
Villarroya	M3	21.8–27.11 (n=24)	11.66–19.37 (n=26)	10.09–17.51 (n=25)
La Puebla de Valverde	M3	23.45–24.91 (n=4)	12.53–14.96 (n=4)	10.91–12.90 (n=4)

Compared to *G. torticornis* from other sites the dimensions of the metacarpal III-IV (Table 9) are quite small, especially its total length. Such low values have been reported only for the Dafnero sample (Hermier et al. 2020 — Appendix C). However, as shown in Table 22, the dimensions of the Karnezeika specimen KZ1900 do not seem to correspond to any other comparable bovid.

Table 22. The dimensions (in mm) of the Karnezeika *Gazellospira* metacarpal III-IV KZ1900 and comparison of that of *G. torticornis* from various sites. Data from Kostopoulos (1996); Athanassiou (2005); Andrés Rodrigo (2011); Vislobokova et al. (2020).

	DT prox	DAP prox	DT dia	DAP dia	DT dis	DAP dis	L
KZ1900	27.11	20.98	17.83	15.38	28.16	18.86	188.5
Dafnero	30.57–37.4 (n=11)	22.25–27.31 (n=11)	19–24.41 (n=5)	17.8–22.4 (n=5)	31.69–38.34 (n=2)	22.9–23 (n=2)	186.9–229.47 (n=5)
Sesklo	31.5–36.9 (n=7)	21.5–24.9 (n=7)	19.5–24.5 (n=4)		35.2–40.9 (n=5)	24.3–27.3 (n=5)	
Villarroya ♂	36.78–41.9 (n=21)	26.72–30.23 (n=22)	21.73–25.22 (n=18)	20.48–25.64 (n=18)	36.7–40.35 (n=12)	25.51–29.05 (n=14)	234.61–254.84 (n=9)
Villarroya ♀	32.84–35.69 (n=10)	23.5–26.18 (n=11)	19.24–21.44 (n=9)	18.81–22.6 (n=9)	31.11–34.17 (n=6)	23.63–25.9 (n=7)	229.79–239.45 (n=8)
La Puebla de Valverde ♂	36.73–41.08 (n=2)	27.67 (n=1)	22.91 (n=1)	22.51 (n=1)			
La Puebla de Valverde ♀	33.16–36.04 (n=5)	22.17–25.34 (n=5)	18.57–22.09 (n=4)	18.62–21.74 (n=4)	32.12–33.96 (n=6)	22.52–23.69 (n=6)	220.7–228.75 (n=5)
Senèze ♀	33.3 (n=1)	25.69 (n=1)	20.26 (n=1)	20.23 (n=1)	34.19 (n=1)	23.1 (n=1)	230.0 (n=1)
Taurida Cave	32.5	23.7	18.7	17.1	34.7	22.9	219.0

The metacarpal, being long and slender, deviates significantly from the metacarpal proportions of the OviBovini (e.g., *Megalovis* or *Soergelia*) and does not fit the robustness of the common Villafranchian Rupicaprini, *Gallogoral* or *Pliotragus*. Furthermore, the Karnezeika metacarpal is longer and larger in overall size than *Gazella* but also than *Procamptoceras*. Based on all the above, it is concluded that the aforementioned material belongs to a small sized form or individual of *G. torticornis.* Metapodials of this species show a trend of decrease in length not only from older to more recent localities, but also from northern latitudes to southern ones (Hermier et al. 2020). This has been further confirmed by Vislobokova et al. (2020) for *G. torticornis* samples from Crimea.

Subfamily: Caprinae Gill, 1872

Tribe: Rupicaprini Brookes, 1828

Genus: *Gallogoral* Guérin, 1965

Gallogoral meneghinii Rütimeyer, 1878

Figure 25

Material

Numerous isolated teeth and disarticulated postcranial elements of forelimbs and hindlimbs as well as few horncore fragments (Figure 25). Because of the extremely large number of specimens, these are not listed here.

Description

Only a single relatively well preserved horncore specimen was found (KZ880), but it is enough to provide crucial diagnostic features. Specimen KZ880 is a horncore fragment broken relatively near the base. It is large, robust and straight, untwisted, and slightly tilted caudally. Its cross-section is circular, without a keel. Measurements are provided in Table 23. Based on an uncatalogued specimen from Karnezeika curated in the AMPG, which preserves a part of the frontal bone with the base of the fragmented left horncore, the KZ880 horncore is placed behind the orbit and is directed dorsally.

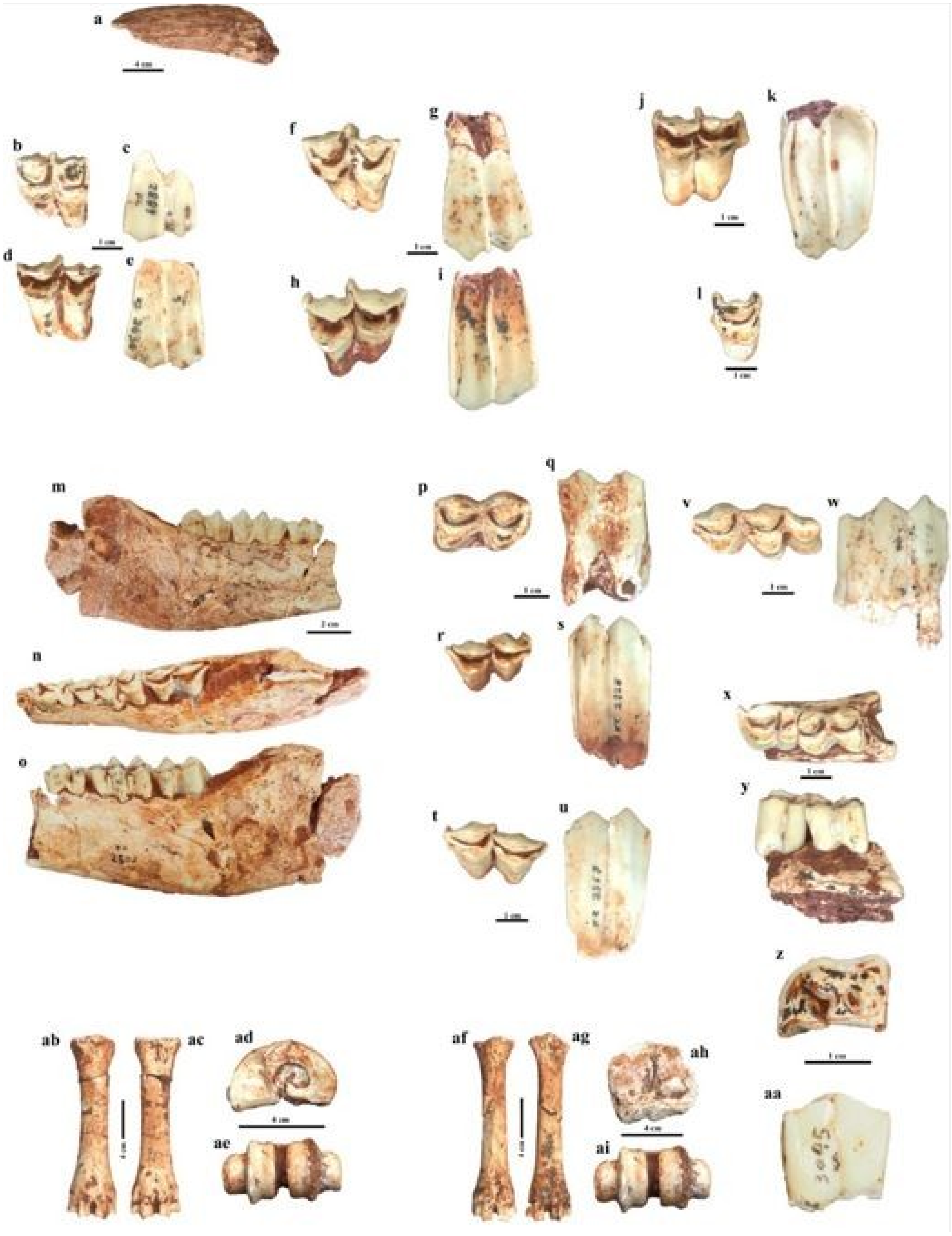

Figure 25: G. meneghinii. *Karnezeika. a, Right horncore fragment (KZ880), in lateral view; b–c, worn right M1 (KZ12889), in occlusal (b) and labial (c) view; d–e, unworn right M1 (KZ2630), in occlusal (d) and labial (e) view; f–g, worn right M2 (KZ2624), in occlusal (f) and labial (g) view; h–i, unworn left M2 (KZ1455), in occlusal (h) and labial (i) view; j–k, left M3 (KZ2432), in occlusal (j) and labial (k) view; l, right P3 (KZ3281), in occlusal view; m–o, left part of mandible with d3, d4, m1 (KZ2503), in lingual (m), occlusal (n) and labial (o) view; p–q, worn right m1 (KZ2758), in occlusal (p) and lingual (q) view; r–s, unworn right m1 (KZ2728), in occlusal (r) and lingual (s) view; t–u, left m2 (KZ2367), in occlusal (t) and lingual (u) view; v–w, left m3 (KZ2916), in occlusal (v) and lingual (w) view; x–y, left part of mandible with p4, m1 (KZ2439), in occlusal (x) and labial (y) view; z–aa, right p3 (KZ3045), in occlusal (z) and lingual (aa) view; ab–ae, left metacarpal (KZ2647), in cranial (ab), caudal (ac), proximal end (ad) and distal end (ae) view; af–ai, left metatarsal (KZ2811), in cranial (af), caudal (ag), proximal end (ah), and distal end (ai) view.*

The P2 is high. Occlusally, a central fold divides the fossa in two parts connecting the lingual and the labial walls. Lingually, the tooth appears bilobated with an anterolingual and a slightly larger posterolingual cone. Labially, the anterolabial cone is extremely strong, in contrast with the posterolabial cone which appears extremely weak and difficult to locate in specimens with advanced stages of wear. Both the posterior and anterior styles appear somewhat weak with the latter disappearing or fusing with the anterolabial cone at the base of the crown.

The P3 and P4 are similar in morphology. They are relatively hypsodont with an approximately square-shaped (L×100/W=76-116, n=9) occlusal outline. A central fold can be detected in some specimens (e.g.,, KZ2996, KZ3281, KZ2625). The lingual cone appears close to the middle of the lingual side, concerning P3, but it is slightly displaced towards the anterior in P4. Therefore, the lingual side of the P3 appears relatively rounded, whilst in P4 is more flattened. The labial side, is characterised by the presence of very strongly expressed anterior and posterior styles, which are almost vertically oriented. The paracone of both premolars appears quite weak (weaker in P4) and is located almost at the middle of the labial side of the tooth.

The M1 is hypsodont. The two lobes have a slightly wrinkled enamel surface. Occlusally, an elongated fossetta, developing almost parallel to the labiolingual axis of the tooth, appears in worn specimens. A metaconule fold is also traced. Lingually, the protocone is pointed, whereas the metaconule is more rounded and less prominent. Labially, the paracone is strong and appears to fuse with the parastyle at the crown base. The metacone is similar but relatively weak and does not appear to fuse with the metastyle respectively. The labial styles are very prominent, especially the mesostyle, which is directed labioanteriorly in many specimens.

The M2 is similar in morphology with M1 but larger. In addition, occlusally, the fossetta, even though it maintains the same orientation and shape with the fossetta of M1, it appears split in two. Labially, the metacone appears to fuse with the metastyle.

The M3 is similar to the other two molars. Labially, the metacone is quite weak and tapers towards the base. The metastyle is wide and very prominent, forming a wing-like protrusion at the base.

The p2 has an approximately triangular shape (L×100/W=139-186, n=16). Lingually, the mesolingual conid is moderately expressed. The anterior stylid appears strong. Both the anterior and posterior valleys are quite shallow. The posterolingual conid is weak. Labially, the mesolabial and posterolabial conids are similarly weak and of equal size.

The p3 is moderately molarised. Occlusally, worn specimens show a unified posterior occlusal surface and a fossetta in place of the posterior valley, while the back valley is absent. In unworn specimens, the back valley appears elongated and narrow and the posterior valley is significantly reduced. In lingual view, the anterior stylid stands out, whereas the conids are moderately expressed. The anterior valley is relatively deep and wide occlusally but closed lingually. The posterolingual conid appears weakly developed. Labially, the mesolabial conid is wide but weak. The posterolabial conid is similar. They are separated through a relatively deep and wide depression.

The p4 is highly molarised. In some worn specimens, a fossetta can be seen in the occlusal surface between the two 'lobes'. Lingually, the mesolingual conid is wide but weak, while the posterolingual conid is similarly weak but smaller. Characteristic is the strong expression of the anterior stylid. Labially, the mesolabial conid is wide and moderately expressed, whereas the posterolingual conid is similar but smaller.

The m1 and m2 are similar in morphology and have relatively wrinkled enamel. However, the m2 is quite larger in size. Lingually, in less worn specimens, both the metaconid and the entoconid appear quite strong and narrow. On the contrary, in worn specimens they become weaker and wider. A very strong mesostylid and a weaker entostylid are detected, whereas the metastylid is very weak to absent. In completely unworn specimens, the top part of the entostylid protrudes and extents posteriorly. In labial side, the protoconid appears strong and pointed while the hypoconid is similar, but relatively more acute and slightly more protruding labially. In completely unworn specimens a weak anterior cingulid can be seen, easily detectable from the middle of the crown upwards.

The m3 is generally similar in morphology with the other two molars, however a vestigial ectostylid is also present. The third lobe is simple and moderately compressed labiolingually. Lingually, the entoconulid is very weak, almost totally reduced. In some specimens (e.g., KZ2531, KZ2548), the lingual wall of the third lobe fuses with the corresponding wall of the middle lobe creating a uniform plane, while in some others the two walls are separated by a shallow but wide depression. Labially, the hypoconulid appears weak.

The D3 exhibits, occlusally, a vestigial central fold in the anterior lobe of some specimens (e.g., KZ2612). Lingually, the protocone is slightly displaced towards the anterior and the lingual wall of the anterior lobe behind it is completely flat. The metaconule is moderately expressed. In some specimens (e.g., KZ2368, KZ3285), a structure similar to an anterior cingulid is present. Labially, the paracone is very strong, while the metacone is weaker but clear. The labial styles are also strong with the mesostyle being the strongest.

The D4 is generally similar to D3 but larger. The anterior lobe is smaller and more triangular, while the posterior one is larger and more squared. In lingual side, the separation of the two lobes is much clearer. The protocone is moderately expressed and pointed while the metaconule is very weak and rounded. The structures present in the labial side are the same as in D3.

The d4 exhibits lobes of approximately the same size. The labial conids are slightly pointed but weak. Large sized ectostylids are also present. The lingual conids are weak. The stylids appear relatively strong with the anterior stylid and entostylid fusing at the base with the corresponding conids.

All long bones of hindlimbs and forelimbs are relatively short and robust. In humerus, the coronoid fossa is wide and deep and occupies almost the entire supra-articular area, while the olecranon fossa is quite deep and relatively narrow, with an oval/semi-triangular shape. In radius, no radial tuberosity is observed. The lateral eminence bears a wide articular surface and is inclined. The anconeal process of the olecranon appears strong and curved. In the metacarpal III-IV, the proximal articular surface is trapezoidal, and the trochleas of the distal epiphysis are strong. The palmar surface of the shaft is flat throughout its length, with the exception of the area 1-3 cm below the proximal end. The metacarpal tuberosity is weak. In femur, the supracondyloid fossa appears relatively shallow but very wide, while the intercondyloid fossa is relatively deep and rounded. In tibia, the intercondyloid tubercles are high and strong. The tibial tuberosity is very strong and forms a wide extensor groove with the lateral condyle. The tibial crest tilts slightly laterally and is quite strong. The metatarsals III-IV are similar to the metacarpals. In calcaneus, the calcaneal tuberosity is strong and wide. The sliding groove of the superficial flexor tendon is shallow and wide, whereas the sulcus for the external flexor tendon is quite lifted and forms a wide angle with the main body of the calcaneus. The caudal side of the main body of the calcaneus appears wide. The talus is very robust. Its anterior depression is deep and semi-circular in shape. A strong tubercle is observed at the proximal part of its medial side. The proximal and medial phalanxes are short and robust. The anterior surface of the distal phalanx is convex. The front part of the plantar border is rounded. The extensor process is relatively weak and very wide.

Remarks

Even though incomplete, the horncore fragment KZ880 and the uncatalogued specimen stored in AMPG mentioned above, provide useful information about morphology and proportions (Table 23).

Table 23. Metric characteristics (average values, in mm) of the KZ880 *G. meneghinii* horncore base (b) specimen and other comparable taxa. Data from Guérin (1965); Duvernois and Guérin (1989); Kostopoulos (1997); Crégut-Bonnoure and Dimitrijević (2006); Martínez-Navarro et al. (2012).

	DAPb	**DTb**	**(DT/DAP) ×100**
KZ880	45.7	45.2	98.90
G. meneghinii (Volakas)	55 (n=1)	59.2 (n=1)	107.6
G. meneghinii (Senèze)	45.94 (n=5)	46.48 (n=5)	101.18
M. latifrons (Senèze)	61 (n=1)	50.9 (n=1)	83.44
Soergelia (Venta Micena)	51.19 (n=10)	37.88 (n=10)	74.0
Pr. brivatense (Senèze)	44.8 (n=4)	39.25 (n=4)	87.61
Pl. ardeus (Senèze)	55 (n=2)	47.5 (n=2)	86.36

Comparing the characteristics of the KZ880 horncore with other taxa of comparable size, the genus *Gazellospira* can easily be ruled out, since no trace of twisting or keel is observed (Pilgrim and Schaub 1939). In *Megalovis* Schaub, 1923, the horncores are placed well behind the orbits, oriented dorsolaterally showing elliptical cross-section (Schaub 1923; Crégut-Bonnoure 2020). *Soergelia* Schaub, 1951 shows large horncores of elliptical cross-section (Crégut-Bonnoure 2020 and references therein) as well as completely different index (DT/DAP) ×100 than the Karnezeika specimen. In *Procamptoceras* Schaub, 1923 the horncores are placed above the orbits, rather than behind them and develop upwards (Duvernois and Guérin 1989). They are also smaller in size. *Pliotragus* Kretzoi, 1941, however, does have horncores placed behind the orbits, but they are curving laterodorsally (Duvernois and Guérin 1989), unlike the specimen accommodated in AMPG. *Eythyceros* Athanassiou, 2002 has horncores of special morphology, with an almost semicircular cross-section, as well as a keel (Athanassiou 2002a). Finally, compared to the genus *Gallogoral*, the KZ sample is completely identical. The very good similarity is also perceived by the DAP×100/DT index which is close to the *Gallogoral* values of both Volakas and Senèze forms (see Guérin 1965; Kostopoulos 1997).

The examination of the teeth did not provide enough data for a safe determination, other than their overall morphometric similarity with *Gallogoral* (Duvernois and Guérin 1989; Kostopoulos 1997). This, however, is not particularly useful; especially considering the fact that almost all studied dental material consists of isolated teeth. Nevertheless, the absence of a strong anterior cingulid (pli caprin) in lower molars rules out an attribution to *Gazellospira*, while the dimensions of the teeth show a taxon larger than *Procamptoceras* (Figure 26, measurements are provided in the Appendix).

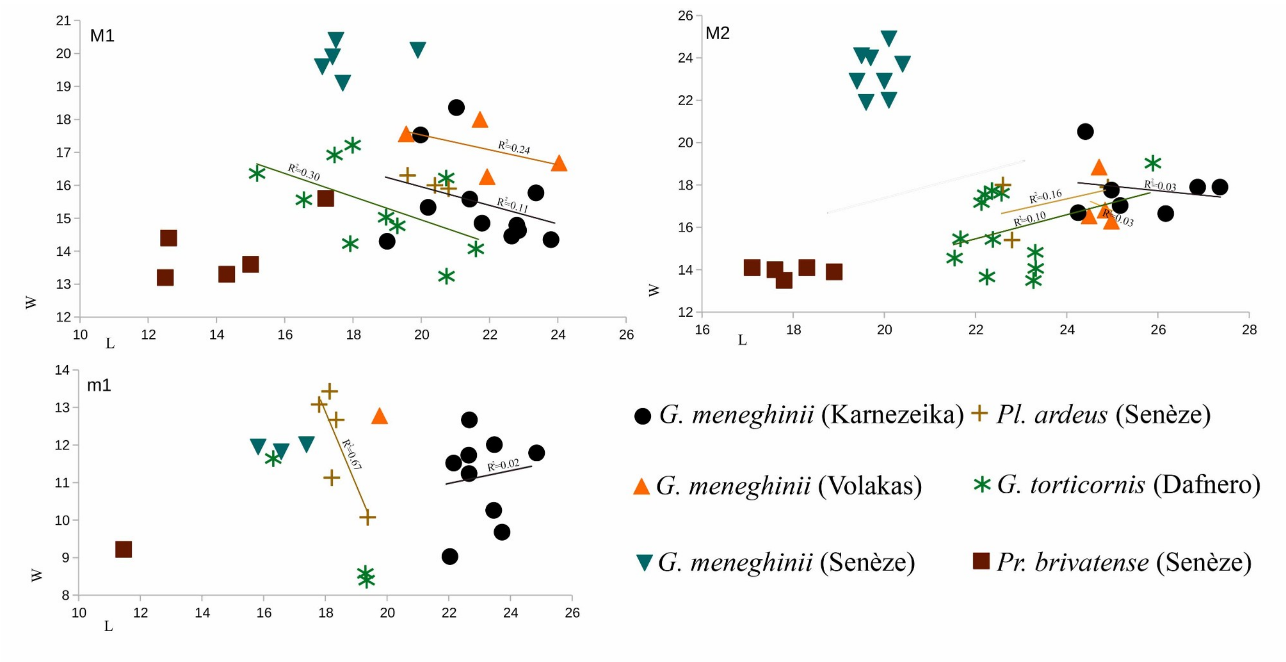

Figure 26: Scatter charts of dental dimensions of G. meneghinii *from Karnezeika and other comparable taxa. Data from Duvernois and Guérin (1989); Kostopoulos (1996); Hermier et al. (2020).*

The metapodials are short and robust, making them highly unlikely to belong to an 'antelope' in the strict sense, such as *Gazellospira*. Metric comparison of both metapodials is shown in the logarithmic (Simson) diagrams of Figure 27. The metapodials appear larger than those of *Procamptoceras*, while they are smaller than those of *Megalovis*. On the contrary, they show more similarity with *Gallogoral*, *Pliotragus* and *Soergelia*.

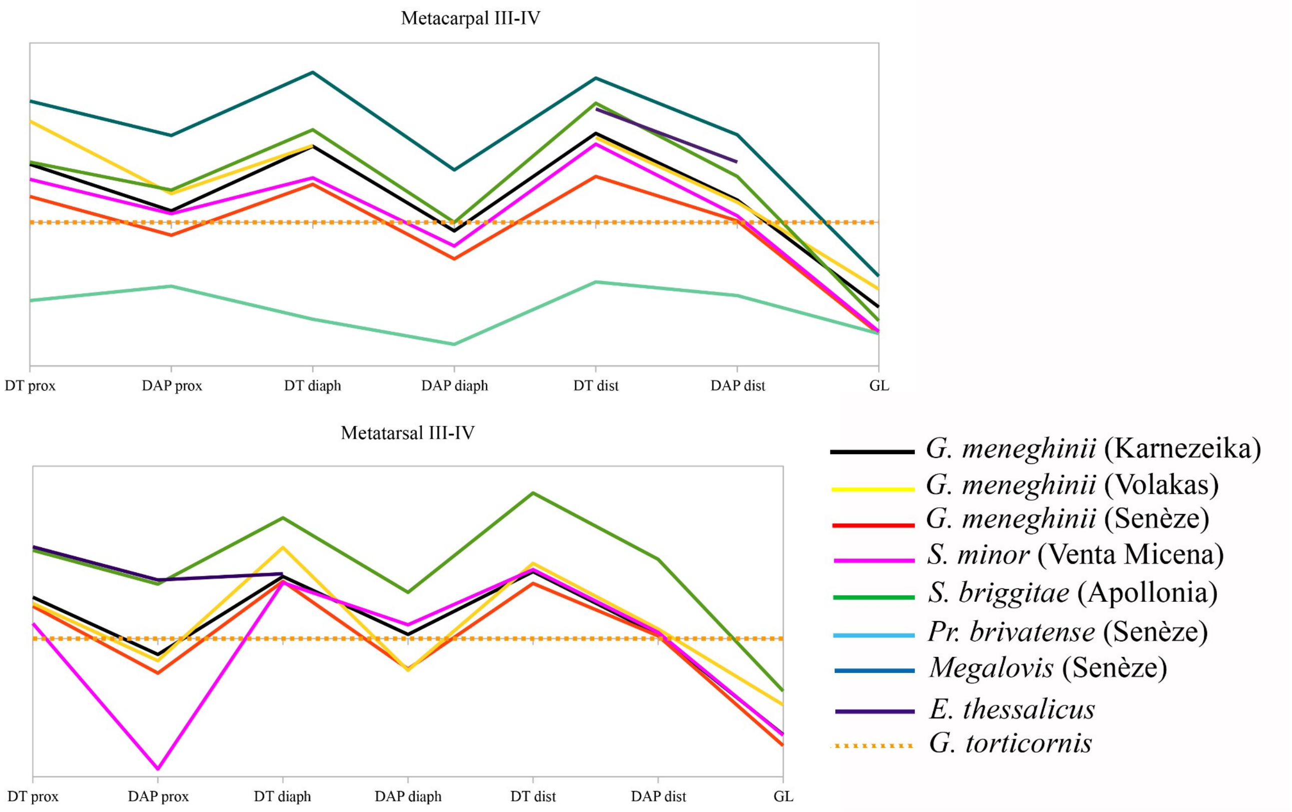

Figure 27: Logarithmic (Simpson) diagram of the metric characteristics of the metacarpal III+IV (top) and metatarsal III+IV (bottom) of G. meneghinii *from Karnazeika, as well as other related taxa, standardised with* G. torticornis. *Data from De Giuli and Masini (1983), Duvernois and Guérin (1989), Kostopoulos (1996), Athanassiou (2005), Andrés Rodrigo (2011).*

Based on all the above data the Karnezeika middle to large sized bovid can safely be ascribed to the genus *Gallogoral* known by a single species: *G. meneghinii* Rütimeyer, 1878. Further attribution to one of the three different known subspecies (*G. meneghinii meneghinii*, *G. meneghinii sickenbergii* Kostopoulos, 1997 and *G. meneghinii heintzi* Andrés Rodrigo, 2011), is not possible, since there is no information about the cranium and complete horncores.

Subfamily: Caprinae Gill, 1872

Tribe: Caprini Simpson, 1945

Caprini gen. et sp. indet.

Material

One M1 (KZ1961) and one m3 (KZ3249) (Figure 28).

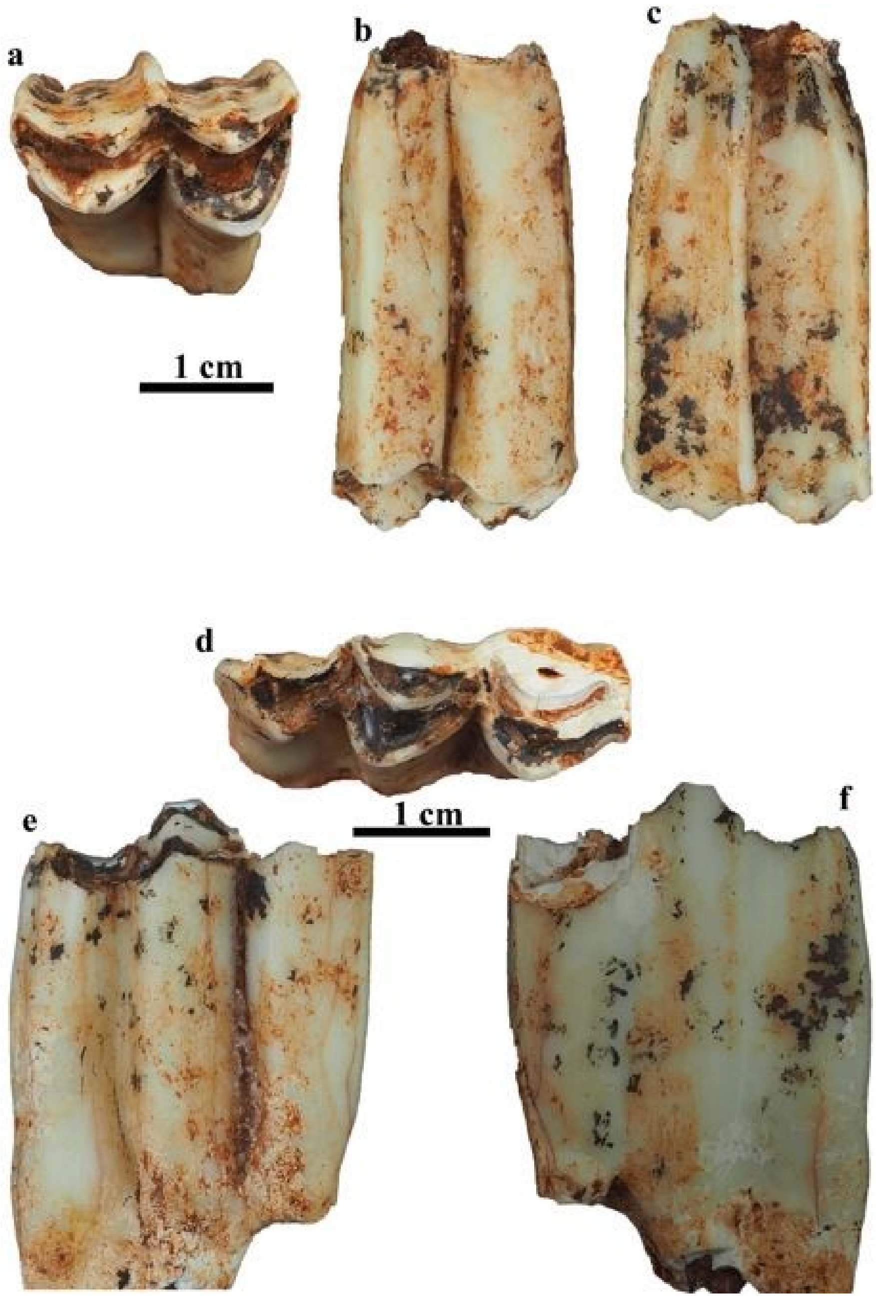

Figure 28: Caprini gen. et sp. indet. Karnezeika. a–c, right M1 (KZ1961), in occlusal (a), lingual (b) and labial (c) view; d–f, right m3 (KZ3249), in occlusal (d), labial (e) and lingual (f) view.

Description

Two specimens. A M1 and a m3, which seem to belong to a bovid of a size in between those of *Gazella* and *Gazellospira*.

The M1 (Figure 28a) is characterised by the presence of columnar lobes with pronounced hypsodonty. The anterior lobe is sub-triangular, while the posterior one is more square shaped. No fossette or metaconule fold are detected occlusally. Lingually, the protocone is slightly displaced anteriorly and protrudes more lingually than the weak and rounded metaconule. In the second lobe, an angular folding is observed along its height in the posterior border. Labially, the paracone and metacone are both extremely weak with the latter being almost absent. The labial styles are similar, strong and generally parallel to each other. However, the mesostyle appears more prominent than the other styles, while the parastyle shows two very gentle curves, one near the base and one near the occlusal surface. The maximum length of the M1 specimen is 17.46 mm, while its maximum width is 11.38 mm.

In m3 (Figure 28(d-f)), all three lobes are straight and parallel to each other near the base of the crown, but the third lobe starts to lean slightly anteriorly from the middle part of the crown towards the occlusal surface. The third lobe also shows a moderately to strongly expressed stylid posterolingually, which creates a small forked structure on the occlusal surface. At its base, the third lobe shows significant swelling. The lingual wall of the tooth appears simple and smooth without any protruding structure. The entostylid is very weak and seems to disappear below the middle point of the crown. Fracture does not allow the mesostylid to be observed along its entire length, but it seems to be moderately expressed. Labially, the protoconid and the hypoconid are relatively pointed, while the hypoconulid is more acute. A moderately expressed anterior cingulid (pli caprin) develops from the middle of the crown towards the occlusal surface. The maximum length of the m3 is 25.87 mm, and its maximum width is 9.06 mm.

Remarks

The two available molars are more hypsodont than the corresponding teeth of *Gazella* from the same site. The upper molar has narrower lobes and a much weaker paracone. The metaconule is also wider and the metastyle is stronger. The lower molar has a triangular instead of a rounded third lobe, which also bears a posterior style. The entostylid is stronger as well. Comparing them with *Gazellospira*, the upper molar has a similar length but both lobes are narrower. The metaconule is wider and both buccal cones appear much weaker than in *Gazellospira*. Furthermore, the lower molar lacks the strong anterior cingulid (pli caprin) seen in *Gazellospira*.

The basic morphology and general size of these teeth does not seem to correspond to any known Antilopini, but they most likely belong to a representative of the Caprini tribe instead. Nevertheless, there is not enough evidence for a more accurate and safe taxonomic determination. The presence of a Caprini is quite common in the Greek Middle Villafranchian bovid assemblages (Koufos and Kostopoulos 2016). However, it usually appears with scarce and isolated remains making it hard to refer to a particular species or genus. *Hemitragus* Hodgson, 1841 would seem to be a suitable candidate taxon. Crégut-Bonnoure (2007) considers that *Hemitragus* was present in Europe's MN17, however, the Karnezeika Caprini cannot be assigned to this genus. An important character of the tahr is, among others, the significant development of the distolingual root of M1 (Crégut-Bonnoure 2020), while the general basal diversion of the distal lobe of m3, along with a columnar entostylid, are typical features for the Villafranchian representative *H. orientalis* (Crégut-Bonnoure and Spassov 2002). These characters are absent from the Karnezeika specimens. Therefore, I refer for the moment the Karnezeika taxon to as Caprini gen. et sp. indet., waiting for more data.

Discussion

Unlike other Lower Pleistocene Greek localities, Karnezeika is vastly dominated by bovids, which comprise up to 90% of the total fauna based on the number of identifiable specimens. The dominant taxa are *G. bouvrainae* and *G. meneghinii*, with numerous dental and postcranial elements.

Gazellospira. torticornis from Karnezeika raises a few concerns, because of its general smaller size, smaller than most known ranges provided by previous authors for other populations (e.g.,, Duvernois and Guérin, 1989; Kostopoulos 1996; Athanassiou 2005; Andrés Rodrigo 2011). However, the metric characteristics of specific skeletal elements (metapodials included) have proved to be subject to sexual dimorphism (Andrés Rodrigo 2011; Hermier et al. 2020). It is not unlikely then, that certain Karnezeika specimens might belong to a female individual, which in combination with the locality's chronology and geographical position may have resulted in these low values.

Gallogoral meneghinii is a common representative in the early Pleistocene mammal assemblages of S. Europe, but it is a rather rare element in the Greek fossil record (Kostopoulos 2022). Karnezeika is an exception, as it has yielded rich, though fragmentary material of this species. The *G. meneghinii* sample in this locality accounts for ~39% of the total number of identified bovid specimens, and corresponds to at least 10 out of the 30 bovid individuals recognized in the assemblage. This strong presence most likely reflects the local rocky environment.

Perissodactyla

Class: Mammalia Linnaeus, 1758
Order: Perissodactyla Owen, 1848.
Family: Equidae Gray, 1821.
Genus: *Equus* Linnaeus, 1758

Equus sp.

Figure 29

Material

Two isolated incisors (KZ1796, KZ1797); three isolated deciduous incisors (KZ1094, KZ3304, KZ1980); a partially preserved upper tooth of the P3-M2 row (KZ1712); two isolated left teeth of the P3-M2 row (KZ1798, KZ1591); two isolated right D4 (KZ2536, KZ3009); one isolated left D4 (KZ574); few fragments of deciduous teeth (KZ2725, KZ1248, KZ2033, KZ2887, KZ1931, KZ2231, KZ1930); a partially preserved cervical vertebra (KZ938); one patella (KZ2959); the proximal part of one metatarsal III (KZ3192); an intermediate phalanx (KZ3097).

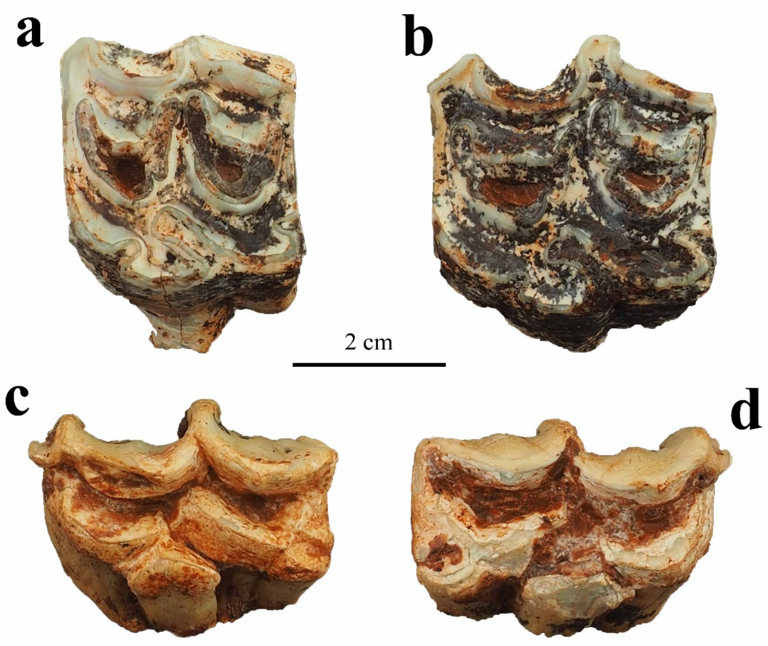

Figure 29: Equus *sp. Karnezeika. a, Tooth of the left P3-M2 row (KZ1591) in occlusal view; b, Tooth of the left P3-M2 row (KZ1798) in occlusal view; c, Left D4 (KZ574) in occlusal view; d, Right D4 (KZ3009) in occlusal view.*

Description

The upper molars have a wide and flat occlusal surface. They show typical equid morphology and advanced stages of wear. The protocone has approximately a triangular/elliptical shape, is fused with the protoloph and corresponds to type 7 by Eisenmann et al., (1988). The paracone appears rounded, while the metacone is more square shaped. A strong parastyle and a strong mesostyle can also be observed. The hypocone is well expressed, it develops parallel to the anteroposterior axis of the tooth and the hypoconal groove is short and forms an acute angle.

The proximal part of the metatarsal is preserved and shows strong taphonomical deformation. The articular surface is trapezoidal in shape. In its center, a round and shallow depression can be observed. On either side of the proximal epiphysis, traces of the fused MtIII and MtIV can be seen which bear residual articular faces.

The intermediate phalanx is short and stout with a square shape. The articular surface is very wide, with the posterior side being higher than the anterior. Posteriorly, two semi-circular ridges can be seen above the distal part. The ridges are a continuation of the border of the distal articular surface which deviate laterally.

Remarks

Isolated Equidae teeth are almost impossible to separate if they are not P2/p2 or M3/m3 due to their identical morphology. Therefore herein, they will be referred to as tooth of the P3-M2/p3-m2 row and will be compared as such (Table 24). The fusion of the protocone with the protoloph confirms that they belong to an *Equus* representative and not an older *Hipaprion* form. As also seen in table 24, the metric characteristics of the teeth cannot be used for their safe determination because of the high similarity in both the size and in morphology, as stated also by Forsten, (1999). Therefore, according to Forsten, (1999), the most suitable skeletal elements for the study of horses are long bones and especially the metapodials.

Table 24. Teeth measurements (in mm) based on (Eisenmann et al., 1988), of the Karnezeika *Equus* and comparison with other common Villafranchian horses. Data by (Athanassiou, 1996, 2018; Garrido, 2008).

		Length	**Width**	**Protocone Length**
Karnezeika	P3-M2	24.97 – 29.84	27.09 – 28.88	7.70 – 8.42
E. stenonis (Sesklo)	P3-M2	23.5 – 36.3	26.2 – 31.6	8 – 14.5
E. altidens (Livakos)	P3-M2	21.5 – 31.9	22.9 – 29.7	7.1 – 11.8
E. stenonis (Saint Vallier)	P3-M2	25 – 33.5	25.5 – 32.5	8 – 12.2
E. senezensis (Senéze)	P3-M2	21.7 – 31.5	24 – 28.1	6.9 – 10
E. cf. major (Fonellas)	P3-M2	27.96 – 34.59	28.16 – 30.78	10.79 – 13.04

Despite the disagreements and suggestions of various researchers about the taxonomy of the different *Equus* species (see Forsten, 1999; Athanassiou, 2001; Eisenmann, 2004; Palombo and Alberdi, 2019), it is a common consensus that when size is the main criterion, the European horse of the Villafranchian appears with three different forms: The "classic" form of *E. stenonis* (Sesklo, Saint Vallier, Upper Valdarno etc.); a smaller and more gracile form mentioned either as *E. senezensis*, *E. stehlini*, *E. s. cf. stehlini* or *E. altidens*, and in this category Forsten, (1999) first included the *Equus* findings from Livakos and then Gkeme et al., (2017) confirmed them as *E. altidens;* and a larger form mentioned as *E. major* – *E. suessenbornensis* line.

The dimensions of the proximal part of the Karnezeika *Equus* metapodial seem to deviate from the smaller and larger forms and fit better with the *E. stenonis* forms of Sesklo and Saint Vallier (Table 25).

Table 25. Measurements of the proximal epiphysis of of the Karnezeika *Equus* metatarsal and comparison with other common Villafranchian horses.

	DTprox	**Mean**	**DAPprox**	**Mean**
KZ3192	52.24	52.24	40.14	40.14
E. stenonis (Sesklo)	45.2 – 53.9	50.4	35.5 – 45.2	40.1
E. altidens (Livakos)	45.2 – 50.8	47.8	36.8 – 43.5	40
E. stenonis (Saint Vallier)	49.5 – 54.5	52.1	40.6 – 43.8	41.8
E. senezensis (Senéze)	45.7 – 51.2	48.1	36.5 – 39.1	43.4
E. cf. major (Fonellas)	50.65 – 56.39	53.8	41.17 – 50.23	44.39

Measurements of the intermediate phalanx (KZ3097) for the Karnezeika *Equus* are provided in Table 26. Comparison with other forms provides different results from those of the metatarsal. As such the phalanx shows a better analogy with the smaller forms (Livakos, Senéze), but with a larger width whatsoever. Nevertheless, the general size appears to be intermediate between the smaller and the "classic" form from Sesklo.

Table 26. Measurements of the intermediate phalanx of the Karnezeika *Equus* and comparison with other common Villafranchian horses. Data as in table 24 with the addition of Bernor et al., (2018).

	Max Length	**Min Length**	**Min Width**	**Max width prox**	**Max length prox**	**Max width dist**
Karnezeika	45.06	32.82	43.99	50.96	32.77	44.97
E. stenonis (Saint Vallier)	45 – 51	-	45.5 – 51.5	53 – 60	32.5 – 38	49 – 55.5
E. senezensis (Senéze)	45.3 – 47.3	32.3 – 35.9	39.5 – 46.2	45.3 – 52.9	31 – 33.7	40.6 – 49.9
E. altidens (Livakos)	43 – 46.6	30 – 34.5	40.1 – 41.1	46.6 – 48.1	28.4 – 32	41.8 – 45.5
E. stenonis (Sesklo)	46.7 – 48	33.6 – 35.9	44.3 – 45	50 – 53.9	33.3 – 35.7	47.4 – 51
E. cf. major (Fonellas)	51.54 – 53.64 (n=2)	-	-	51.74 – 56.99 (n=2)	33.27 – 35.95 (n=2)	44.77–51.97 (n=2)
E. cf. livenzovensis (Montopoli)	54.6 – 56.9 (n=2)	41.8 – 43.6 (n=2)	48.2 – 48.8 (n=2)	58 – 58.4 (n=2)	37.3 – 40.4 (n=2)	45.4–51.3 (n=2)

As Palombo and Alberdi, (2019) mention, even though the genus *Equus* had a dominant role in the Villafanchian ecosystems resulting in an extremely rich fossil record all throughout Europe, their taxonomy is yet under debate, especially for the forms that are not characterised by a significantly larger size (e.g., *E. major*). Furthermore, this difficulty is multiplied in cases such as in Karnezeika where the available material is very poor. Unfortunately, a more precise determination is not currently possible, therefore the Karnezeika horse will be mentioned as *Equus* sp.

Family: Rhinocerotidae Gray, 1821.

Genus: *Stephanorhinus* Kretzoi, 1942

Stephanorhinus etruscus Falconer, 1868

Figure 30

Material

A M3 (KZ3171), a M2 (KZ3090), a P3 (KZ3091), a P2 (KZ2514), a highly fragmented m3 (KZ3100), a fragmented m2 or m3 (KZ2640), a m1 (KZ1908), a p4 (KZ2629), a p2 (KZ3217), a third metatarsal (KZ675), a fourth metatarsal (KZ2708), a third proximal phalanx (KZ677), a fourth proximal phalanx (KZ3109), a fourth intermediate phalanx (KZ1824) and two distal phalanxes (KZ2549, KZ1687).

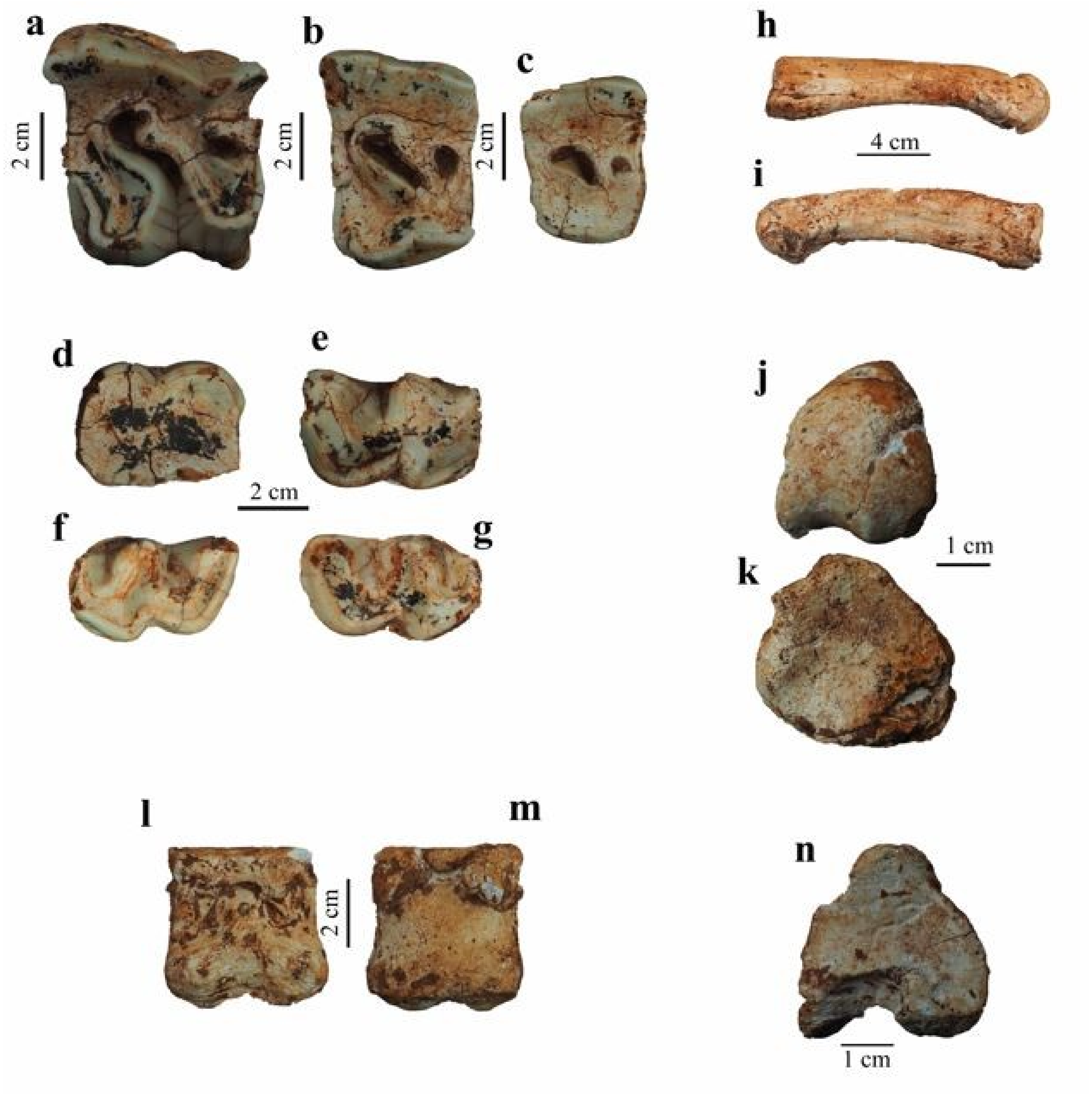

Figure 30: Stephanorhinus etruscus. Karnezeika. a, Left M2 (KZ3090) in occlusal view; left P4 (KZ3091) in occlusal view; left P2 (KZ2514) in occlusal view; d, left p4 (KZ2629) in occlusal view; e, right m1 (KZ1908) in occlusal view; f, left m3 (KZ3100) in occlusal view; g, right m2 (KZ2640) in occlusal view; h-k, fourth metatarsal (KZ278) in medial (h), lateral (i), distal (j) and proximal (k) views; l-m, right third proximal phalanx (KZ677) in posterior (l) and anterior (m) views; n, right third metatarsal (KZ675) in proximal view.

Description

The P2 has a rectangular shape and an extended occlusal surface. The protocone appears fused with the hypocone, while no trace of a lingual valley can be seen. No particular structure is observed in the buccal side of the tooth with the occlusal surface of that side being continuous. In the middle of the occlusal surface a deep and extended fossa is detected as well as a smaller and rounded postfossa.

The P4 is robust and rectangular. The protocone is wide and medially, a small fold appears. The hypocone is equally wide but extends less lingually. The paracone shows no folding and no parastyle is observed, while the metacone is of clear but weak expression. At the center of the occlusal surface an oblong and deep fossa can be seen as well as a smaller and rounded postfossa. A significant lingual cingulum is also present, resulting in a step – like structure.

The M2 is extremely robust and rectangular, retaining the characteristic Π – morphology of the molars. The protocone is strong and has a wide anticrochet behind it. Also wide is the observed constriction of the protocone which is almost parallel to the anteroposterior axis of the tooth. The paracone shows strong folding and close to it an equally strong parastyle is detected resulting in the formation of a forked structure. The hypocone is similar to the protocone but smaller. Above it, on the occlusal surface, an oval shaped postfossa can be seen. The crochet is wide and extends intensively towards the middle fossa giving it a “S” shape. A very small crista is also present. The metacone is strong and inclined inwards. The buccal side of the tooth is higher than the lingual.

All lower teeth (the m1, p4 and p2 that are in good condition) are quite similar in morphology with the only character changing being the size of the lingual valleys. They are robust and retain the characteristic ε – morphology. The metaconid is clearly expressed and the metalophid appears wide and relatively short, while the entoconid is similar but is part of a more oblong hypolophid. The paraconid is weak but the paralophid is relatively strong. The hypoconid appears fairly wide in contrast with the more angular protoconid. The syncline is similar to all specimens and relatively deep and narrow.

The distal end is not preserved in the third metatarsal, while the diaphysis is significantly deformed in its larger part. The proximal epiphysis has an articular surface of a complex morphology but typical for the Rhinocerotidae. In the posteromedial side of the epiphysis, an angular and moderately deep depression can be observed, which ends up in a secondary articular surface in the lateral side. Another secondary articular surface of similar size and shape can be seen in the lateral side as well. In the medial side, two more secondary articular surfaces are present, smaller than the previous ones.

The fourth metatarsal is complete and appears short and robust. The diaphysis is medio-laterally compressed. The articular surface of the proximal epiphysis has an approximately trapezoidal shape. A strong tubercle can be seen in the posterior side. In the medial side, two secondary articular surfaces are present which correspond to the lateral articular surfaces of MtIII.

Remarks

During the study of the Karnezeika material, a small part of it quickly stood out being quite large-sized showing an overall unique morphology, belonging with no doubt to a Rhinocerotidae. The main representative of the family mentioned in the literature during the Villafranchian is *Stephanorhinus etruscus* (Cirilli et al., 2020; Fortelius et al., 1993; Pandolfi et al., 2017). However, the presence of the rarer and larger sized *S. jeanvireti* or *S. elatus*, as Ballatore & Breda, (2016) suggest as a more valid name, has also been confirmed from both Greece and the rest of Europe as well (Cirilli et al., 2020; Guérin & Tsoukala, 2013; Pandolfi et al., 2019).

As mentioned earlier, the morphology of the teeth was examined according to Lacombat, (2006) based on dental observations of the different Pleistocene *Stephanorhinus* species. In the Karnezeika specimens, the crochet of the upper premolars is single while no anticrochet was observed. No crista or anticrochet appears in M2, while a clear protoconal constriction is visible. The middle fossa of M3 is open. Both valleys (anterior and posterior) of the m1 are similarly broad and V-shaped. No lingual cingulum is observed. The above characters point towards the direction of *S. etruscus*. This is further confirmed by their dimensions, as shown in Table 27. The tooth dimensions fit well the ranges of *S. etruscus*, while they are consistently (only with the exception of m1) smaller than the minimum values observed for *S. jeanvireti*.

The fourth metatarsal (KZ2708) seems to fit well with the third metatarsal (KZ675) and probably belongs to the same individual. The teeth also seem to belong to the same individual based on the condition, stage of wear and overall appearance. The morphology of the metatarsal is typical for the Rhinocerotidae, while the comparison of its dimensions (Table 28), further separate them from the large sized *S. jeanvireti*. On the contrary, size is closer to *S. etruscus* and *S. hundsheimensis*. The latter appears in Asia and Europe around the late Villafranchian between 1.3 – 1.1 Ma (Pandolfi & Erten, 2017).

Table 27. Dimensions of the Karnezeika *Stephanorhinus* teeth and comparison with the two known Villafranchian species. In the case of M3, the "absolute" (*sensu* Lacombat, (2006)) dimensions are provided. Data from Guérin, (1980).

		Length	**Width**
KZ2514	P2	28.47	37.49
S. etruscus	P2	29 – 35 (n=10)	32 – 42.5 (n=10)
S. jeanvireti	P2	31 – 37 (n=4)	35 – 39 (n=4)
KZ3091	P3	35.82	48.05
S. etruscus	P3	35 – 41 (n=10)	42 – 54 (n=19)
S. jeanvireti	P3	40 – 42.5 (n=4)	45 – 50.5 (n=5)
KZ3090	M2	47.06	56.82
S. etruscus	M2	45.5 – 57 (n=9)	48 – 65.5 (n=18)
S. jeanvireti	M2	51 – 55.5 (n=7)	51.5 – 61 (n=9)
KZ3171	M3	52.13	47.2
S. etruscus	M3	47 – 59 (n=10)	46 – 56.5 (n=16)
S. jeanvireti	M3	53 – 59 (n=4)	46 – 56 (n=5)
KZ3217	p2	25.26	19.47
S. etruscus	p2	25 – 33 (n=9)	16 – 21.5 (n=10)
S. jeanvireti	p2	27 – 32 (n=8)	16.5 – 21 (n=8)
KZ2629	p4	36.36	26.7
S. etruscus	p4	35 – 39.5 (n=16)	24 – 31 (n=23)
S. jeanvireti	p4	37 – 40.5 (n=10)	24 – 31 (n=10)
KZ1908	m1	42.85	28.34
S. etruscus	m1	37 – 43 (n=17)	26.5 – 33 (n=29)
S. jeanvireti	m1	40 – 47 (n=10)	25 – 34 (n=10)

Table 28. Dimensions (mean values in mm) of the Karnezeika *Stephanorhinus* fourth metatarsal compared with other species. Data from (Fortelius et al., 1993; Guérin, 1980).

	GL	**DT prox**	**DAP prox**	**DT dia**	**DAP dia**	**DT dis**	**DAP dis**
Karnezeika	148.58	35.44	35.67	21.79	29.21	29.06	34.24
S.etruscus	152.32 (n=19)	37.58 (n=25)	36.32 (n=22)	26.25 (n=18)	24.03 (n=18)	33.32 (n=14)	35.93 (n=15)
S. hundsheimensis	158 (n=2)	40.36 (n=5)	39.89 (n=5)	23.2 (n=3)	29 (n=3)	33.25 (n=2)	39.65 (n=2)
S. hemitoechus	152.65 (n=2)	44.4 (n=4)	45.05 (n=4)	27.62 (n=4)	29.25 (n=4)	33.05 (n=2)	37 (n=2)
S. jeanvireti	180.43 (n=7)	49 (n=10)	44.15 (n=10)	35 (n=10)	28.56 (n=9)	41.6 (n=5)	45 (n=7)
D. megarhinus	174.83 (n=9)	49.65 (n=10)	46.92 (n=12)	34.29 (n=12)	31.08 (n=12)	40.22 (n=9)	44.81 (n=8)

The examined dental and metatarsal elements satisfy both the metric and morphological criteria of *S. etruscus*, which is the typical Villafranchian rhinoceros, while they do not seem to correspond to a large-sized representative such as *S. jeanvireti.* Moreover, there are not any other observed elements or characteristics that would imply the presence of a different species. Therefore, the Karnezeika rhinoceros can safely be ascribed to *S. etruscus*.

This species is highly typical for the Villafranchian faunas and its presence in Greece has been certified from several localities (see Giaourtsakis, 2022 for a review). In Karnezeika, as it is also the case for almost all Greek localities, even though *S. etruscus* is recorded, the associated material is scanty and fragmentary, thus making the study of the species in Greece problematic. The best-preserved material comes currently from Aivaliki (Symeonidis et al. 2006). An interesting character concerning the Karnezeika dental specimens is their small size, which is on the lower side of all known compared European populations. The small sized *S. etruscus* populations have already been noted by Mazza et al. (1993) and Fortelius et al. (1993) and also include the specimens from Aivaliki. According to the previous authors, these populations can be regarded as transitional towards the *S. hundsheimensis* form. They could also, however, be considered as a result of local adaptation due to environmental stress.

Palaeoecological interpretations of *Gazella bouvrainae* Kostopoulos & Athanassiou, 1997

As mentioned earlier, *Gazella bouvrainae* Kostopoulos & Athanassiou, 1997, is an interesting bovid species found only in Lower Pleistocene localities of the South part of the Balkan peninsula, which despite being absent from Western Europe, it constitutes a rather common find in Greece, and is the most common species of the genus *Gazella*, replacing the widespread *G. borbonica* in the Greek fossil record. Even though *G. bouvrainae* was an important member of the Middle Villafranchian palaeofauna of Greece, the palaeoecological profile of this taxon has not yet been fully investigated. However, some work has been done in relation to its palaeodiet based on dental mesowear analysis of samples from Gerakarou-1 and Sesklo (Rivals and Athanassiou, 2008).

In this chapter I aim to enrich the palaeoecological profile of *G. bouvrainae* by examining the results of its mesowear analysis in general rather than divided in localities, including also new data from Karnezeika; by estimating its body mass utilizing metric characteristics of specific long bones; and by examining some of its locomotory adaptations based on the morphology of the talus.

Materials and Methods

The studied material includes numerous fossil remains of *G. bouvrainae* from three mainland localities: Gerakarou-1, Sesklo and Karnezeika (Kostopoulos and Athanassiou 1997; Sianis et al. 2022a). Gerakarou-1 and Sesklo provided mainly dental specimens, whereas from Karnezeika we used dental specimens, but also specific postcranial elements such as radii, femora and tali, which were in relative abundance.

The study of dental mesowear as an indicator of a species dietary habits was introduced in 2000 by the pioneering work of Fortelius and Solounias (2000). Since then, a plethora of researchers has utilized this study improving and modifying the original methodology or adapting the method to specific taxa (Rivals and Athanassiou 2008; Valli and Palombo 2008; Winkler and Kaiser 2011; Solounias et al. 2014; Fraser et al. 2014; Strani et al. 2015; Taylor et al. 2016; Stauffer et al. 2019). Herein, for the dental mesowear analysis I follow the extended mesowear technique, utilizing the works of Winkler and Kaiser (2011) and Taylor et al. (2016). This technique was also suggested by the review of Ackermans (2020), because it is easy to produce and is also flexible, since the extended mesowear scores can easily be converted to scores of other techniques such as the first and basic conservative method of Fortelius and Solounias (2000). The necessary measurements can be taken fast and easily, minimizing the error between different studies and thus offering better reproducibility. According to this method we calculated the occlusal relief and the cusp shape of each specimen, which results in 17 different possible combinations, ranging from very high relief with sharp cusps (score 1) to low relief with blunt cusps (score 17). As such, a score of 1 translates to the less abrassion-dominated diet (browsers), whereas a score of 17 to the most abrassion-dominated diet (grazers). As mentioned above, the dental material studied herein comes from the mainland fossiliferous localities of Gerakarou-1, Sesklo and Karnezeika and includes upper first and second molars. Only the sharper of the two buccal cusps was taken under consideration. Specimens of very high or very low wear stage were excluded. More specifically, since the molars were mesodont according to Janis (1988), I used teeth belonging to wear stages 5 to 9 as proposed by Kaiser et al. (2009).

For the body mass estimation I utilized the study of Köhler et al. (2008) and applied their equations to a total of 16 radii and 12 femurs from Karnezeika. These specific long bones were chosen because they were available in relatively large quantity, as well as because according to previous authors (Köhler et al., 2008) they provide the most accurate results. On the contrary, we avoided utilizing dental material for the same purposes of body mass estimation, since the reliability of such results have been disputed in the past (Egi 2001; Millien and Bovy 2010).

For the identification of locomotory adaptations the morphology of 23 talus specimens from adult individuals was studied. Due to the bones’ sturdiness and density, tali are a common find in mammal assemblages. Studies have also shown that they reflect well the animal’s locomotory adaptations, thus being useful in reliably assigning bovid species to habitats (DeGusta and Vrba 2003; Plummer et al. 2008; Barr 2014; Plummer et al. 2015). Herein, we follow the methodology and utilize the comparative material of DeGusta and Vrba (2003). As such, we measured eight linear variables (described and depicted in DeGusta and Vrba (2003) – Fig.2), using digital calipers, recorded to two decimals. All measurements are provided in mm. To eliminate the size factor, all variables of our *G. bouvrainae* material as well as the variables from the comparative material were firstly log-transformed, before a Principal Component Analysis (PCA) was carried out. Statistical analyses were performed in the Rstudio environment (RStudio Team 2020).

Mesowear analysis

Mesowear scores of the examined molars (Table 29), showed values close to the mid-point of the Winkler and Kaiser (2011) calibrated scale, but also towards the browsers group. More specifically, the average mesowear score of G. *bouvrainae* was 7.1, which translates to the most common wear pattern being a combination of very high relief with rounded cusps. Thus, it is safe to conclude that *G. bouvrainae* showed mainly a mixed diet, but with a tendency towards browsing. The highest recorded score (more abrasion-based) was as high as 15, whereas the lowest (more attrition-based) was as low as 2. Specimens from Sesklo and Karnezeika localities showed better correlation in the given scores and the respective teeth showed very similar trends. Comparing the bivariate plot of the hypsodonty index and the mesowear score of extant ungulate taxa with that of *G. bouvrainae*, the latter falls within the overlapping area between leaf browsers and mixed feeders (Fig. 31).

Table 29. Mesowear scores and specimens used in the current study, including a transformation of each score to the original method of (Fortelius and Solounias 2000). The table continues on the next page.

Specimen	**Identifica-tion**	**OR**	**CS**	**Score**	**Average**	**Transformed to classic scores**	**Score**	**Average**
KZ1764	M1	l	rr	15	7.7	l b	3	0.8
KZ2259	M1	hl	r	9		l r	2	
KZ2293	M1	hl	rs	6		l s	0	
KZ2374	M1	hl	rs	6		l s	0	
KZ2750	M1	hl	r	9		l r	2	
KZ2919	M1	hl	r	9		l r	2	
KZ3155	M1	hl	r	9		l r	2	
KZ3156	M1	hl	rs	6		l s	0	
KZ3268	M1	hl	rs	6		l s	0	
KZ400	M1	hl	rs	6		l s	0	
KZ866	M1	hl	s	3		l s	0	
KZ1941	M1	l	rs	13		l s	0	
KZ3277	M2	hl	r	9		l r	2	
KZ760	M2	hl	rs	6		l s	0	
KZ1235	M2	hl	rs	6		l s	0	
KZ1161	M2	hl	rs	6		l s	0	
KZ3321	M2	l	r	14		l r	2	
KZ2368	M2	hl	rs	6		l s	0	

(Continues)

KZ2063	M2	hl	rs	6		l s	0	
KZ3143	M2	hl	s	3		l s	0	
KZ1941	M2	hl	r	9		l r	2	
Σ-98	M1	h	r	8	8.3	h r	1	1.2
	M2 (sin)	h	r	8		h r	1	
	M2(dex)	h	r	8		h r	1	
Σ-393	M1	h	r	8		h r	1	
	M2	h	r	8		h r	1	
Σ-433	M1	h	r	8		h r	1	
	M2	h	r	8		h r	1	
Σ-1014	M1	hl	rr	11		l b	3	
	M2	h	r	8		h r	1	
Gerakarou	M2	hl	rr	11	5.1	l b	3	0.5
Gerakarou	M2	h	rs	5		h s	0	
Gerakarou	M2	h	rr	10		h b	3	
Gerakarou	M2	h	rs	5		h s	0	
Gerakarou	M2	h	s	2		h s	0	
Gerakarou	M2	h	r	8		h r	1	
Gerakarou	M2	h	s	2		h s	0	
Gerakarou	M2	h	s	2		h s	0	
Gerakarou	M2	h	r	8		h r	1	
Gerakarou	M2	h	s	2		h s	0	
Gerakarou	M2	h	rs	5		h s	0	
Gerakarou	M2	h	rs	5		h s	0	
Gerakarou	M1	h	rs	5		h s	0	
Gerakarou	M1	h	rs	5		h s	0	
Gerakarou	M1	h	rs	5		h s	0	
Gerakarou	M1	h	s	2		h s	0	
					7.1			**0.8**

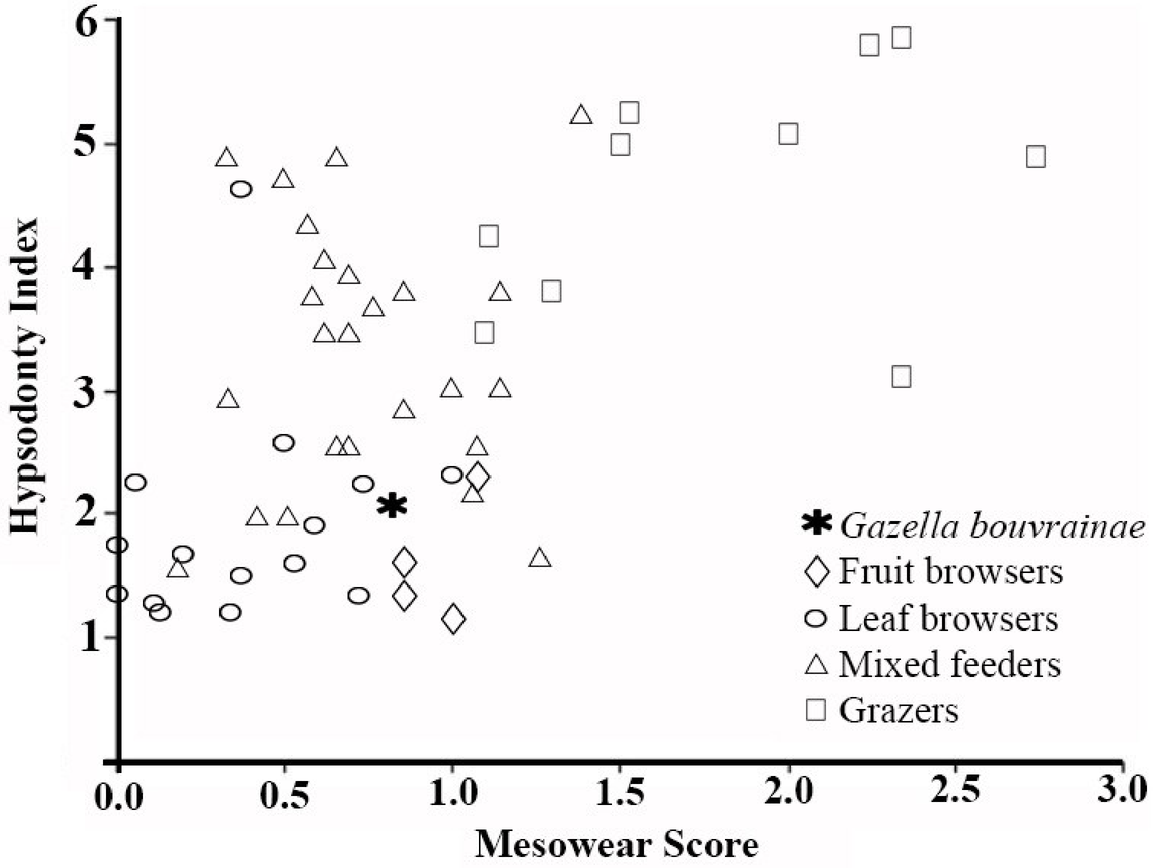

Figure 31: Hypsodonty index vs Mesowear score scatter plot of modern ungulates and G. bouvrainae. *Data for modern taxa from Janis, (1988); Fortelius and Solounias, (2000).*

Mass estimation

Data extracted from the examined radii and femora were homogeneous indicating an average body mass for *G. bouvrainae* of 20.2 kg (Table 30). The lowest recorded body mass value was 15.4 kg, while the highest was 27.7 kg. Since juvenile long bones were excluded from the study, it is possible that low values could correspond to small-sized female individuals, whereas the highest values could correspond to male ones clearly indicating sexual dimorphism.

Table 30. Body mass estimation results for each specimen used in the current study. For information on the methodology and equations see Köhler et al. (2008).

	Specimen	**Fd-t**	**log(Fd-t)**	**b**	**a**	**b(logFd-t) + a**	**Kg**	**Average**
Femur	KZ2393	33.13	1.52	2.92	-3.17	1.27	18.45	19.64
	KZ2013	31.16	1.49	2.92	-3.17	1.19	15.43	
	KZ2972	34.41	1.54	2.92	-3.17	1.31	20.61	
	KZ788	34.53	1.54	2.92	-3.17	1.32	20.82	
	KZ2329	33.95	1.53	2.92	-3.17	1.3	19.81	
	KZ941	34.63	1.54	2.92	-3.17	1.32	21	
	KZ2864	35.57	1.55	2.92	-3.17	1.36	22.7	
	KZ2012	32.56	1.51	2.92	-3.17	1.24	17.54	
	KZ2843	34.52	1.54	2.92	-3.17	1.32	20.8	
	KZ615	33.76	1.53	2.92	-3.17	1.29	19.49	
	KZ3199	32.51	1.51	2.92	-3.17	1.24	17.46	
	KZ2391	34.98	1.54	2.92	-3.17	1.33	21.62	
	Specimen	**Rp-ap**	**log(Rp-ap)**	**b**	**a**	**b(logRp-ap) + a**	**Kg**	**Average**
Radius	KZ2861	13.43	1.13	2.71	-1.84	1.22	16.54	20.77
	KZ2454	15.19	1.18	2.71	-1.84	1.36	23.1	
	KZ822	14.68	1.17	2.71	-1.84	1.32	21.05	
	KZ3023	14.45	1.16	2.71	-1.84	1.3	20.17	
	KZ3233	13.29	1.12	2.71	-1.84	1.21	16.07	
	KZ2950	14.98	1.18	2.71	-1.84	1.35	22.24	
	KZ2736	14.22	1.15	2.71	-1.84	1.29	19.31	
	KZ1554	15.34	1.19	2.71	-1.84	1.38	23.72	
	KZ1952	13.49	1.13	2.71	-1.84	1.22	16.74	
	KZ3258	14.95	1.17	2.71	-1.84	1.34	22.12	
	KZ1923	14.01	1.15	2.71	-1.84	1.27	18.55	
	KZ486	14.67	1.17	2.71	-1.84	1.32	21.01	
	KZ1045	14.52	1.16	2.71	-1.84	1.31	20.44	
	KZ2201	14.86	1.17	2.71	-1.84	1.34	21.76	
	KZ3107	14.89	1.17	2.71	-1.84	1.34	21.88	
	KZ2832	16.25	1.21	2.71	-1.84	1.44	27.74	
								20.2

Locomotory adaptations

The first two components of the PCA, explained up to 99.18% of the variation, with the PC1 explaining 98.79% of it and the PC2 0.39%. The comparative material of DeGusta and Vrba (2003), includes several Bovidae species native to Africa. Despite the overlapping areas, it is possible to identify the main allocation of their four habitat categories (Forest, Heavy cover, Light cover, Open) in the scatter plot (Fig. 32). Bovids adapted to a forested habitat show mostly negative PC1 and PC2 values, while those adapted to a habitat of heavy cover show positive PC1 values and negative PC2 values. Bovids of light-covered habitats occupy the morphospace mostly on the negative side of PC1, but they show both negative and positive values on PC2. Bovids adapted to locomotion in open habitats occupy the largest area in the morphospace, but these values are mainly restricted to the positive side of PC1, showing also both negative and positive values of PC2. Plotting the values resulting from the *G. bouvrainae* measurements, these are restricted to the negative side of PC1, but on both quartiles of PC2. As such, *G. bouvrainae* shows a better correlation with bovids adapted to light-covered and open habitats.

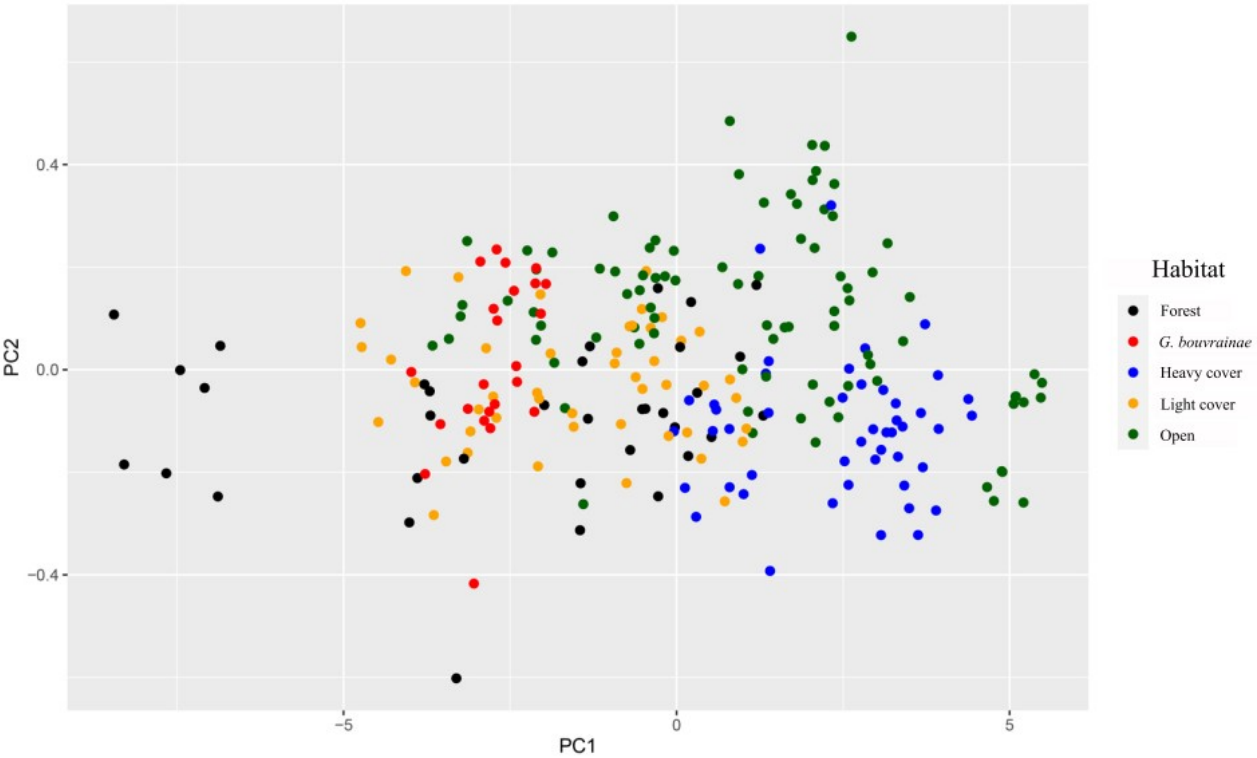

Figure 32: Results of the Principal Component Analysis (PCA) applied on the talus measurements and segregation to habitats. The G. bouvrainae *dataset and loadings plot is provided in the Appendix, see Supplementary Data for PCA and Loadings plot I. Data for modern taxa from DeGusta and Vrba, (2003).*

The values resulting from *G. bouvrainae* measurements were also succumbed to a PCA and were only plotted against other Antilopini or gazelles sensu lato (Fig. 33). The first two components of the second PCA, explained up to 96.82% of the variation, with the PC1 explaining 94.51% of it and the PC2 2.31%. *Antidorcas marsupialis* occupied mostly the morphospace near the axes intersection of both positive and negative PC1 values but only towards positive PC2 values. *Eudorcas thompsoni* shows positive values in both PC1 and PC2 axes. On the contrary, *Ninger granti* shows negative values in both PC1 and PC2 axes. *Litocranius walleri* occupies the morphospace on the negative side of PC1 but on both the negative and positive sides of PC2. *G. bouvrainae* mainly shows positive PC1 values and negative PC2 values.

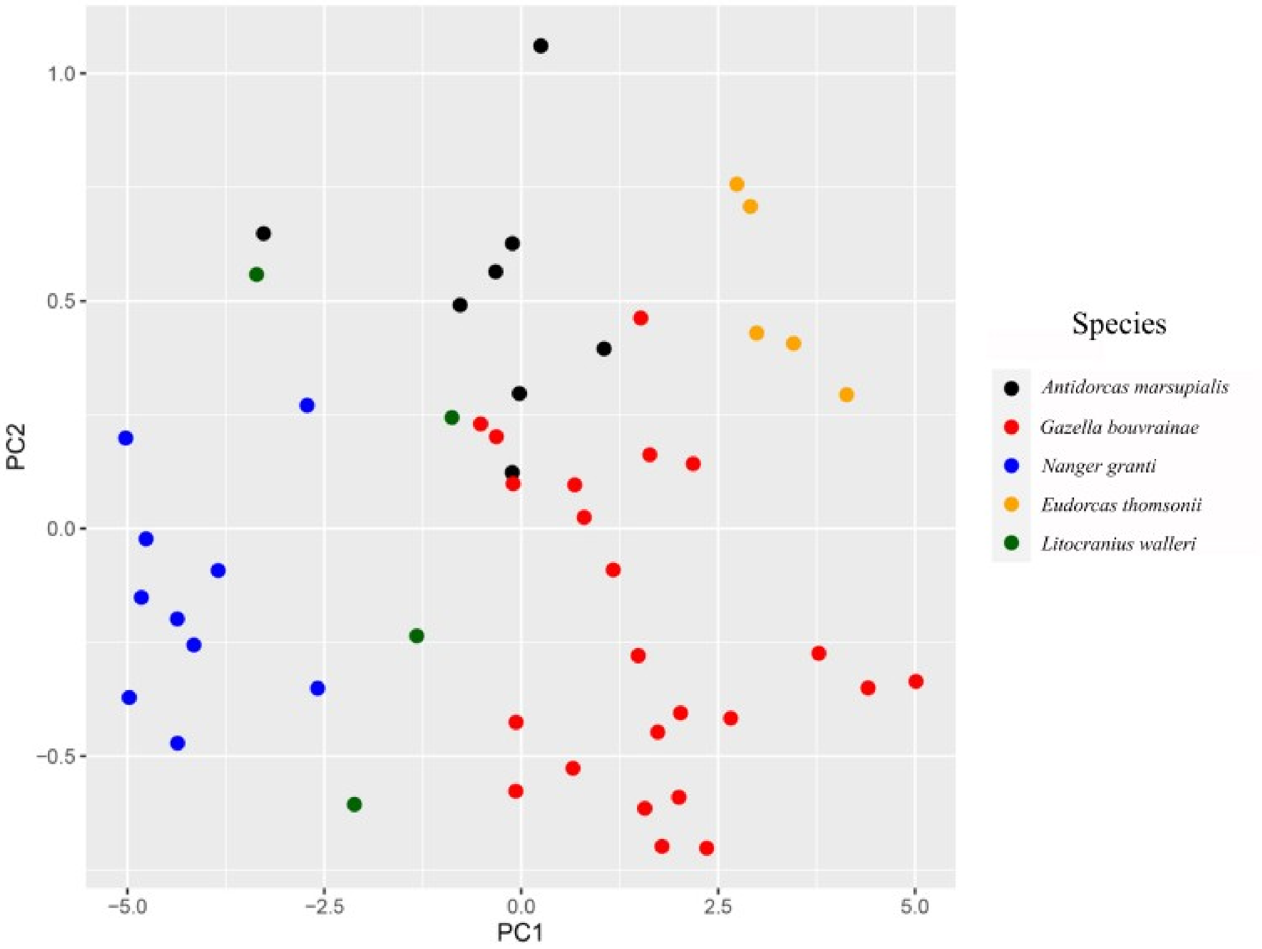

Figure 33: Morphological comparison of the talus of G. bouvrainae *and modern Antilopini through Principal Component Analysis (PCA). The loadings plot is provided in the Appendix, see Loadings plot II. Data for modern Antilopini from DeGusta and Vrba, (2003).*

Discussion

Since plant matter is of low nutritional value, herbivores have developed advanced digestive systems and complex teeth to help minimize the necessary time of feeding and chewing their food and consequently the risk of death by predators. Therefore, the dentition form is directly connected to plant tissue toughness and its arrangement is such to limit food escape and increase capacity (Sanson 2006). Hence, dental mesowear is a useful indicator of an ungulate species' diet. If the plant tissue is soft, as in the case of leaves, then it causes no particular harm to the animal's teeth and wearing is driven mainly by the tooth-to-tooth contact, which is called attrition. This particular wear pattern is commonly observed in browsing species (Fortelius and Solounias 2000). On the contrary, if the plant tissue is hard, such as in the case of grass which contains phytoliths, and which, additionally, is frequently covered by dust and grit due to being close to the ground (Janis and Fortelius 1988), the wearing is mainly driven by these abrasives rather than by tooth to tooth contact, and which is called abrasion. This particular wear pattern is commonly observed in grazing species (Fortelius and Solounias 2000). The results of the mesowear analysis conducted on the studied material revealed a wear pattern for *G. bouvrainae*, intermediate between browsers and grazers, hence indicating a mixed feeding strategy. This type of foraging adaptation is very common between the extant Antilopinae of Africa (see Gagnon and Chew (2000); Louys et al. (2011); Ackermans (2020) – Supplementary data). A mixed feeding strategy is also observed for the Arabian sand gazelle *Gazella marica*, which is native to the Arabian Peninsula (Schulz et al. 2013), and also for *Gazella subgutturosa*, native to Asia (Xu et al. 2012). *Gazella borbonica* Depéret, 1884, which was the dominant gazelle species of Europe during the late Pliocene and early Pleistocene and was partly contemporary to *G. bouvrainae*, has been also characterised as a mixed feeder, based on mesowear and microwear analyses (Rivals and Athanassiou 2008; Strani et al. 2015; Strani et al. 2018). As such, *G. bouvrainae* would have been rather flexible in terms of food acquisition, showing shifts between browsing and grazing diet depending on climatic conditions and seasonality, following the typical practice of most gazelles. As mentioned earlier, the specimens from Gerakarou-1 in general, revealed a more attrition-based wear trend, than those from the other two studied localities. Sesklo is placed within MNQ17 – middle Villafranchian (Athanassiou 2018), and so is Karnezeika (Sianis et al. 2022a, 2023). Gerakarou-1, on the other hand, is younger and along with the other localities of the homonymous formation is placed within the late Villafranchian (Koufos et al. 1995; Konidaris et al. 2015). Nevertheless, we believe this difference consists a random occurrence due to the relatively small number of specimens from the latter site, rather than an indication of a dietary shifting of *G. bouvrainae* during the late Villafranchian.

Comparing the estimated body mass of *G. bouvrainae* (~20 kg) with extant African bovids (Gagnon and Chew 2000), this is comparable with Thomson's gazelle (*Eudorcas thompsonii*), indicating a quite small-sized species with possibly similar foraging strategies, according to previous authors. However, Codron et al. (2007) argued instead, that body mass and diet type are not related, but they do confirm that food quality increases with decreasing body size. This would render *G. bouvrainae* capable to consume smaller quantities of plants, thus decreasing its exposure time to feeding and increasing the likelihood of survival. Due to the small size, *G. bouvrainae* would have avoided too much competition with larger ungulates commonly found in the middle Villafranchian assemblages such as *Gazellospira* or *Gallogoral*, and middle to large-sized cervids, by exploiting the lower vegetation. As such, more serious competition would be imposed by *G. borbonica* which was partly contemporaneous before it got replaced by *G. bouvrainae* (see also Kostopoulos, 2006) and the small-sized cervid *Croizetoceros ramosus* Croizet and Jobert, 1828, typical of the Villafranchian European faunas and present in the studied localities (Kostopoulos and Athanassiou 2005; Athanassiou 2022). However, *C. ramosus*, as the most brachydont deer of the Villafranchian, showed mainly browsing dietary habits (Rivals and Athanassiou 2008; Valli and Palombo 2008; Strani et al. 2018), which would definitely reduce the overlap between the ecological niches of this species and *G. bouvrainae*. *G. borbonica* on the other hand, showed quite similar dietary habits and its gradual replacement by *G. bouvrainae* during the early Pleistocene, indicates that the two species were most likely competing for the same ecological niches. It is not uncommon, however, for two different gezelle species to co-exist in the same fauna. A modern example can be observed in the Tibetan Plateau where the Przewalski's gazelle (*Procapra przewalskii*) and the Tibetan gazelle (*Procapra picticaudata*) co-exist successfully, despite having similar diet and similar feeding hours (see Li et al., 2008). The reason for this, according to the previous authors, most likely is a consequence of occupying different foraging areas. As both *G. borbonica* and *G. bouvrainae* were small-sized gazelles and mixed feeders, they would require small quantities of food and would be flexible in terms of food acquisition. Furthermore, ungulates which occupy mixed habitats (hence, suitable for mixed feeders), are characterised by quite small home ranges (Ofstad et al. 2016). Therefore, the two species would be capable of a successful co-existence, as it is also observed in the locality of Sesklo (Kostopoulos and Athanassiou 1997). Thus, the question of why did *G. bouvrainae* replace *G. borbonica* in the Greek fossil record still remains unanswered.

However, the locomotory adaptation analysis offers some new interesting insights. In Figure 32, we can observe that *G. bouvrainae* shows values intermediate between open and light covered habitats, and better fits the latter group in terms of data allocation. Furthermore, when compared with other Antilopini or gazelles *sensu lato* in Figure 33, we can observe significant discrimination between the different modern taxa and *G. bouvrainae*. It is worth mentioning that all modern taxa in Figure 33, are adapted for locomotion in open habitats. Furthermore, morphological analysis of *G. borbonica* postcranial elements revealed adaptations for clear and open environments as well (Alcalde 2013). As such, it is possible that the different and more flexible locomotory adaptations of *G. bouvrainae*, may have helped it to avoid predation more efficiently than *G. borbonica*, thus prevailing eventually.

Notes on the chronology of the site

As stated in the Introduction, the accidental discovery of the locality by the quarry miners, renders the study of the Stratigraphy practically impossible. Therefore, in order to acquire a more precise picture of the site's chronology, we can only rely on the taxa that are present in the assemblage.

U. etruscus was present in European faunas since the beginning of MN17 (and probably earlier) and until the end of the Villafranchian (Wagner, 2010), therefore its presence in Karnezeika cannot provide useful information concerning the site's stratigraphy. *Felis* sp. also does not offer such information, not only due to the lack of species determination in this case, but because of the general uncertainty in the literature concerning its stratigraphic range as well (Kurtén, 1965). According to Bartolini-Lucenti and Madurell-Malapeira (2020), the European *V. alopecoides* expanded from the late Pliocene to the early Pleistocene, which basically includes the whole Villafranchian. *B. helbingi* is a quite rare taxon, so its absence in Olduvai and post-Oluvai localities cannot safely specify an upper biozone limit. However, the Karnezeika zorilla is very similar to the one from Saint Vallier, which has been correlated with the geomagnetic Chron C2r (1.95 – 2.58 Ma) (Sen, 2004). *M. cultridens* is generally considered a typical predator member in middle Villafranchian faunas, which further implies a middle Villafranchian biochronological context for the locality, but it is also one of the residual species that persisted until the early late Villafranchian, as indicated in the locality of Senèze (MNQ18, 2.21-2.09 Ma according to Nomade et. al., 2014) (Rook and Martínez-Navarro, 2010; Brugal et al., 2020). *P. brevirostris* is frequently considered to mark the beginning of the late Villafranchian with the so-called *P. brevirostris* event (Martínez-Navarro, 2010; Rook and Martínez-Navarro, 2010). Madurell-Malapeira et al. (2014) based on *P. brevirostris* remains from the localities of Fonelas P-1 and Almenara-Casablanca 1 in the Iberian Peninsula, have placed this event before the Olivola Faunal Unit, which serves as the base of the late Villafranchian (Rook and Martínez-Navarro, 2010). Fonelas P-1 is dated around 2 Ma (Arribas, 2008), whereas the stratigraphy of Almenara-Casablanca 1 is rather complex but can be safely correlated with the geomagnetic Chron C2r (Agustí et al., 2011). The typical middle Villafranchian bovid association of Karnezeika, which includes *G. bouvrainae*, *Gazellospira* and *Gallogoral*, and in conjunction with the small size of *G. torticornis*, which is close to that from Fonelas P-1 and to the small-sized specimen from Dafnero, makes possible the chronological correlation with these localities. The presence of the giant hyena *P. brevirostris* in a locality that also yielded fossils of this bovid association further confirms this correlation.

Thus, Karnezeika geochronologically could represent a date similar to that of Dafnero or slightly more recent close to the 2 Ma boundary. Furthermore, the preliminary results concerning the microvertebrate fauna of the site presented by Kokotini et al. (2019), revealed the presence of *Apodemus* cf. *dominans* (the uncertain determination is likely due to the usual difficulty of identifying this particular taxon at the species level; Knitlova and Horacek, 2017). Nevertheless, the stratigraphic range of this small-sized murid does not seem to exceed 2 Ma (Suárez and Mein, 1998), further strengthening the assumption mentioned above.

Mammal structure analysis and palaeoenvironmental discussion

In previous chapters the Systematic Palaeontology of the large mammal fauna from Karnezeika was presented, where 18 different taxa were determined (excluding Rodentia and Lagomorpha mentioned by Kokotini et al, 2019). The assemblage is vastly dominated by bovids, a tendency which is quite unusual for Neogene-Quaternary Greek localities where generally a large number of equid remains occurs instead. Apart from four bovid taxa and an equid, three different cervid species, the giraffe *P. inexpectatus*, the common Villafranchian rhino species *S. etruscus*, seven carnivora taxa were also recognized, as well as scarce remains of a large cercopithecid, rendering Karnezeika as a primate-bearing Villafranchian locality. A complete list of the mammal fauna of the site is provided in Table 31.

Palaeoenvironmental interpretations

The ecological profile of *Par. arvernensis* is yet poorly understood. However, postcranial evidence indicates a large-sized terrestrial monkey supposedly capable of frequent bipedal behavior (see Van der Geer and Sondaar, 2002; Sondaar et al., 2006), while dental microwear analyses suggest a mixed/opportunistic and more abrasive diet with limited grass intake/consumption (see Williams and Holmes, 2011; Plastiras, 2021).

From a palaeoecological aspect, most Quaternary bears were adapted to open or mixed habitats and their scansorial abilities were regulated by their size (Meloro and Marques de Oliveira, 2019), which in the case of the medium sized *U. etruscus* would likely have allowed such an adaptation. Kostopoulos and Vasileiadou (2006) also associate *U. etruscus* with open landscapes during the Early Pleistocene of Greece. Concerning the *Felis* sp. from Karnezeika, if we assume a similar locomotive behavior with the modern European wild cat *Felis silvestris*, then the scansorial adaptation and mixed habitat of the latter (Gálvez-López, 2021) should safely point towards a mixed habitat for the former as well. A mixed habitat also favors the scansorial adaptation of *M. cultridens*, as it exhibits common features in terms of habitat with the modern jaguar *Panthera onca* (Christiansen and Adolfssen, 2007). *P. brevirostris*, even though its shortened limbs disfavor running capabilities (Turner and Antón, 1996), it is usually linked with open landscapes (Croitor and Brugal, 2010). Subsequently, the carnivore association from Karnezeika includes mainly mixed habitat members, while typical open landscape predators such as *H. latidens*, which shows strong cursorial adaptations (Antón et al., 2005) are absent. This comes in contrast with the palaeoecological interpretations based on the carnivore guild of most Greek Early Pleistocene localities that correspond to the Middle Villafranchian, which mainly indicate open grasslands instead (Koufos 2014; Konidaris 2022).

Table 31. The fossil mammal fauna of Karnezeika. Data for Rodentia ad Lagomorpha from (Kokotini et al. 2019).

Artiodactyla	Canidae
Bovidae	*Vulpes alopecoides* Del Campana, 1913
Gazella bouvrainae Kostopoulos & Athanassiou, 1997	
Gallogoral meneghinii (Rütimeyer, 1878)	Hyaenidae
Gazellospira torticornis (Aymard, 1854)	*Pachycrocuta brevirostris* (Gervais, 1850)
Caprini gen. et sp. indet.	
	Felidae
Cervidae	*Megantereon cultridens* Cuvier, 1824
? *Eucladoceros* sp.	*Felis* sp.
cf. *Metacervoceros rhenanus* Dubois, 1904	
Croizetoceros ramosus (Croizet & Jobert, 1828)	**Primates**
	Cercopithecidae
Giraffidae	cf. *Paradolichopithecus* sp.
Palaeotragus inexpectatus (Samson & Radulesco, 1966)	
	Rodentia
Perissodactyla	Arvicolidae
Equidae	*Kislangia* sp.
Equus sp.	
	Muridae
Rhinocerotidae	*Apodemus* cf. *dominans*
Stephanorhinus etruscus Falconer, 1859	
	Gliridae
Carnivora	Gliridae indet.
Ursidae	
Ursus etruscus Cuvier, 1823	**Lagomorpha**
	Leporidae
Mustelidae	*Hypolagus* sp.
Baranogale helbingi Kormos, 1934	
Mustelidae indet.	

Gazellospira torticornis has been observed to show a mixed feeding strategy, easily adaptable between grazing and browsing, depending on seasonal and environmental conditions or resource partitioning (Strani et al. 2015, 2018; Hermier et al. 2020). The study of the dental microwear/mesowear and metapodial morphology of *G. torticornis* from the localities of Sesklo and Dafnero indicate a mainly open environment (Rivals and Athanassiou 2008; Hermier et al. 2020), while the same is true for the Greek *Gazella* species (Rivals and Athanassiou 2008). *G. meneghinii* is also considered a mixed feeder (Strani et al. 2015, 2018). Moreover, based on the morphology of its postcranial skeleton, there is evidence that it occupied rocky areas (Alcalde Rincón 2013), which is compatible with the presence of a Caprini in Karnezeika as well. *G. meneghinii* is a common representative in the early Pleistocene mammal assemblages of S. Europe, but it is a rather rare element in the Greek fossil record (Kostopoulos 2022). Karnezeika is an exception, as it has yielded rich, though fragmentary material of this species. The *G. meneghinii* sample in this locality accounts for ~39% of the total number of identified bovid specimens, and corresponds to at least 10 out of the 30 bovid individuals recognized in the assemblage. This strong presence most likely reflects the local rocky environment.

G. bouvrainae was a mixed feeder, while the locomotory adaptation analysis showed that the taxon was more adapted for a light-covered environment, unlike many modern Antilopini, including *G. borbonica* as well, which are more well adapted for an open habitat.

The mixed feeding capabilities of the other bovids as well, in combination with the striking absence of equids in the assemblage, indicates possibly that open grassland landscapes in the area were rather restricted.

Therefore, based on all of the above, it is more likely that the palaeoenvironment of Karnezeika represented rocky limestone terrains with hills and slopes, carved in the strongly karstified limestones, which consist the dominant background lithology.

Mammal community structure analysis

The mammal community structure analysis technique was developed by Andrews et al. (1979) in order to identify similarities between modern and “palaeo” ecosystems and eventually correlate environments. Although a degree of information can be extracted by studying the ecology of a specific taxon or some taxa, this technique has the advantage of utilizing different ecological aspects such as the animal’s size, diet and locomotor adaptations of many species rather than focusing on one. Thus, it consists a useful tool providing a holistic and composite palaeoenvironmental picture of a site based on all the ecological niches that are present. For more information on the mammal community structure analysis see Kovarovic et al. (2018) and refs therein.

For the mammal community structure analysis, three different niche exploitation profiles were constructed. These include the characterization of each taxon in terms of body mass, locomotor adaptations and dietary adaptations, which are the most common niche profiles used for mammalian species (Andrews et al. 1979; Kovarovic et al. 2002; Kovarovic et al. 2018). Those three profiles were then compared with the profiles of fifteen modern environments, constructed by Kovarovic et al. (2002) utilizing the data by Andrews and Humphrey (1999), in order to find similarities between the Karnezeika ecosystem and the modern ones. Concerning the variables used in each niche profile, I use the categories mentioned in Kovarovic et al. (2002) (see also Tables 32, 33 & 34).

The body mass of *G. bouvrainae* and *G. meneghinii* was estimated through the usage of selected long bones and the equations of Köhler et al. (2008) (see also corresponding chapter herein). *Gazellospira. Torticornis* was included in the *G. meneghinii* mass range since both are often considered of relatively comparable size. The Caprini was included in the size range of most modern wild goats (such as *Capra pyrenaica* and *Hemitragus jemlahicus*). Data for *C. ramosus* and ?*Eucladoceros sp*. were taken from Strani et al. (2018). cf. *Metacervoceros rhenanus* was included in the same category as *C. ramosus* as a small to middle sized cervid. *Palaeotragus inexpectatus*, *E. Stenonis* and *S. etruscus* were included in the larger sized category (>360 kg), as their extant representatives. *Ursus etruscus* was included in the size range of the modern brown bear (*Ursus arctos*), with which shows greater similarity (Koufos and Konidaris 2018). *Felis sp*. was included in the size range of the modern European wild cat (*Felis silvestris*), which most likely consists its descendant (Kurtén 1965; Lewis et al. 2010). *Pachycrocuta brevirostris* was included in the size range of 90-180 kg based on Palmqvist et al. (2011), who estimated an average mass for the species of 108 kg. *Megantereon cultridens* was included in the size range of the modern jaguar (*Panthera onca*) (Christiansen and Adolfssen 2007). *Baranogale helbingi* was included in the size range which covers all modern Ictonychinae. Mustelidae indet. was included in the size range of 1.1-10 kg which covers most members of the family. *Vulpes alopecoides* was included in the size range of the modern red fox (*Vulpes vulpes*). cf. *Paradolichopithecus* sp. was included in the size range that covers all representatives of the *Paradolichopithecus* – *Procynocephalus* group (Kostopoulos et al. 2018). *Kalymnomys* sp., *Apodemus* cf. *dominans* and Gliridae indet. were included in the 0-100 gr size category as their modern representatives. *Kislangia* sp. was included in the 101-1000gr size category as a large sized vole (Tesakov 1998; Mayhew 2012). *Hypolagus* was included in the 1.1-10 Kg size category as a medium to large-sized rabbit (Fostowicz-Frelik 2003).

Concerning the locomotory adaptations of each taxon, all artiodactyls and perissodactyls of the Karnezeika fauna were characterised as terrestrial, since there is no reason to assume a different is type of locomotory adaptation. *Ursus etruscus* was characterised as scansorial, similar to the modern brown bear *U. arctos* (Meloro and de Oliveira 2019). *Felis* sp. was characterised as scansorial similar to the modern European wild cat *Felis silvestris* (Gálvez-López 2021). *Pachycrocuta brevirostris* was characterised as terrestrial, according to Turner and Antón (1996), Palmqvist et al. (2011) and Liu et al. (2021), but also similar to modern hyenas. *Megantereon cultridens* was characterised as scansorial as is reported for the modern jaguar *Panthera onca* (Gálvez-López 2021), with which exhibits the most common features in terms of habitat (Christiansen and Adolfssen 2007). *Baranogale helbingi* was characterised as terrestrial/fossorial which covers the locomotory adaptations of most Ictonychinae (Gálvez-López 2021). Similarly, Mustelidae indet. was characterised as terrestrial/fossorial which covers the locomotory adaptations of most members of the family. *Vulpes alopecoides* was characterised as terrestrial similar to the modern red fox (*Vulpes vulpes*) (Gálvez-López 2021). cf. *Paradolichopithecus* sp. was characterised as terrestrial according to Sondaar and Van der Geer (2002). *Kislangia* sp. was characterised as terrestrial but with aquatic adaptations (Agustí et al. 2010). *Kalymnomys* sp. was characterised as terrestrial/fossorial (Alçiçek et al. 2017), *Apodemus* cf. *dominans* was characterised as terrestrial/fossorial as well, based on the locomotory adaptations of modern wood mice. Gliridae indet. was characterised as arboreal (Striczky and Pazonyi 2014). *Hypolagus* was characterised as terrestrial/fossorial (Lopatin 2019).

Concerning the characterization of each taxon in terms of dietary adaptations, *G. bouvrainae* was included in mixed feeders as resulted from the mesowear analysis presented herein. *Gallogoral meneghinii* was included in mixed feeders based on Strani et al. (2015, 2018). *Gazellospira torticornis* was included in mixed feeders according to Rivals and Athanassiou (2008). The Caprini was included in mixed diet as well, as most Caprinae mentioned in Ackermans (2020). *Croizetoceros ramosus* was included in browser diet based on Rivals and Athanassiou (2008) and Strani et al. (2015). cf. *Metacervoceros rhenanus* was included in browsers as other similar sized cervids (Valli and Palombo 2008). ?*Eucladoceros sp.* was included in browsers according to Strani et al. (2015, 2018). *Palaeotragus inexpectatus* was included in browsers based on Athanassiou (2014) and modern giraffes. *Equus sp.* was included in grazers as most *Equus* species mentioned by Ackermans (2020 – Supplementary data), and also modern horses. *Stephanorhinus etruscus* was included in browsers according to Rivals and Lister (2016). *Ursus etruscus* was supposed of omnivore diet according to Medin et al. (2017). The two Karnezeika felids, as well as *Baranogale helbingi*, Mustelidae indet., *V. alopecoides* and *P. brevirostris* were included in the carnivore diet category as all their modern representatives. *Par. arvernensis* was included in omnivore diet as modern *papio* according to (Williams and Holmes 2011). *Kislangia* sp. was included in mixed feeders as modern water voles (Lee and Houston 1993). *Kalymnomys* was included in the mixed diet category as well, based on its analogue the step-lemming (Alçiçek et al. 2017). *Apodemus* cf. *dominans* was included in omnivores (Vasileiadou et al. 2003; Renaud et al. 2005; van den Hoek Ostende et al. 2015). Gliridae indet. was also characterised as omnivorous (Sarà and Sarà 2007). *Hypolagus* sp. was considered as a grazer based on most modern rabbits.

Following the methodology of Kovarovic et al. (2002), the number of species in each variable was then converted into the percentage of this variable in relation to the total (see also tables 32, 33 and 34). For example, three out the twenty-three taxa in the locality were included to the largest size category (>360 kg), which translates to 13.04% of the Karnezeika mammal fauna belonging to this category. Furthermore, if a species belonged to two categories (e.g., mixed feeders), it was counted half in each.

Body mass profile

Table 32 shows the weight category of each mammal taxon from Karnezeika and the percentage of each category in relation to the total studied fauna. The richest weight categories were the 1.1 – 10 kg and the 46 – 90 kg ranges, each consisting 17.4% of the total fauna, as both contained four taxa. In continuity, the weight ranges of 0 – 100 g, 91 – 180 kg and >360 kg cover 13.04% of the total fauna each, with three taxa per category. Lastly, an equal percentage of 8.7% respectively was covered by the 101 – 1000g, 11 – 45 kg and 181 – 360 kg weight categories, each including two taxa (see also Figure 34).

Table 32. The weight category of each mammal taxon from Karnezeika and the percentage of each category in relation to the total studied fauna.

	Weight category		**Weight category**	**%**
Gazella bouvrainae	11 – 45 kg		0 – 100 g	13.04
Gallogoral meneghinii	91 – 180 kg		101 – 1000 g	8.7
Gazellospira torticornis	91 – 180 kg		1.1 – 10 kg	17.4
Caprini gen. et sp. indet.	46 – 90 kg		11 – 45 kg	8.7
Croizetoceros ramosus	46 – 90 kg		46 – 90 kg	17.4
cf. *Metacervoceros rhenanus*	46 – 90 kg		91 – 180 kg	13.04
?*Eucladoceros* sp.	181 – 360 kg		181 – 360 kg	8.7

(Continues)

Paleotragus inexpectatus	> 360 kg		>360 kg	13.04
Equus stenonis	> 360 kg			
Stephanorhinus etruscus	> 360 kg			
Ursus etruscus	181 – 360 kg			
Felis sp.	1.1 – 10 kg			
Pachycrocuta brevirostris	91 – 180 kg			
Megantereon sp.	46 – 90 kg			
Baranogale sp.	101 – 1000 g			
Vulpes alopecoides	1.1 – 10 kg			
Mustelidae indet.	1.1 – 10 kg			
cf. *Paradolichopithecus* sp.	11 – 45 kg			
Kislangia sp.	101 – 1000 g			
Kalymnomys sp.	0 – 100 g			
Apodemus cf. *dominans*	0 – 100 g			
Gliridae indet.	0 – 100 g			
Hypolagus sp.	1.1 – 10 kg			

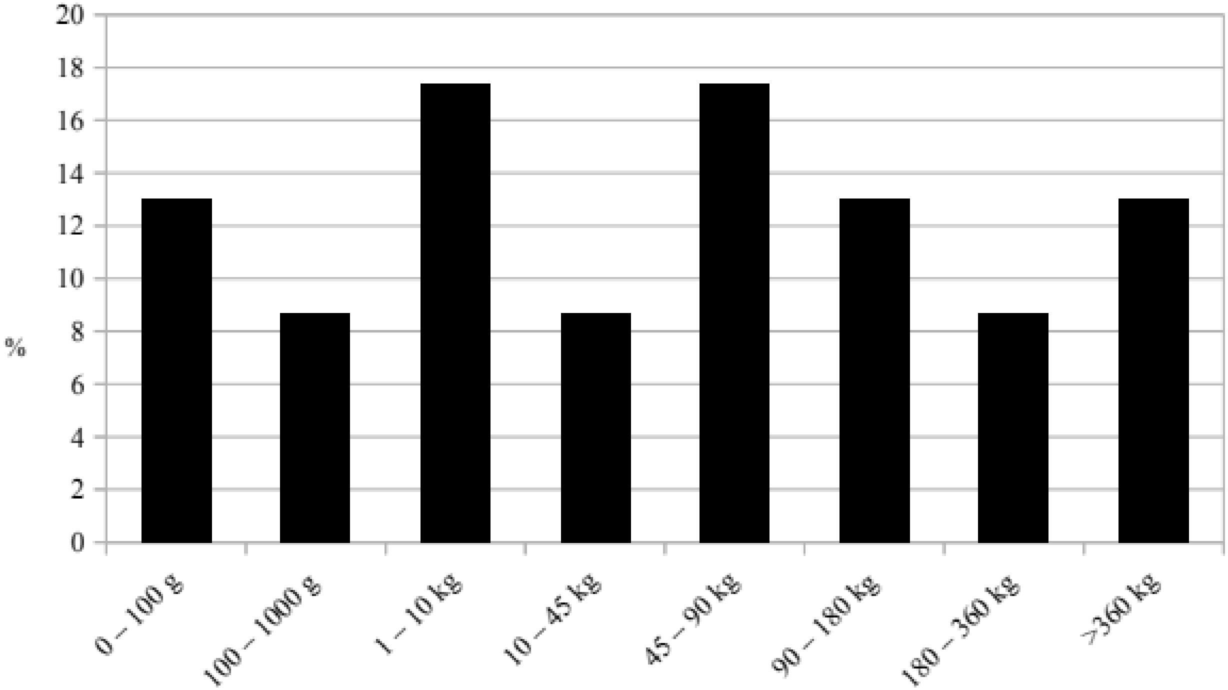

Figure 34: Visualized graph of the percentage of each weight category in relation to the total studied fauna from Karnezeika. Data from table 32.

Locomotory adaptations profile

By far (71.74%) the Karnezeika mammal fauna consisted of taxa which seldomly utilized resources other than those located on the ground (terrestrial), followed by a quite smaller percentage (13.04%) of taxa which could climb trees in order to escape predation or to find food (scansorial). 8.70% of the total taxa were capable of utilizing underground resources, either for food acquisition or nesting (fossorial). 4.35% of the fauna was represented by taxa which spend most of their lives on trees (arboreal), while only 2.17% was adapted to living close to bodies of water (aquatic) (see also Table 33 and Figure 34).

Table 33. The kinetic adaptation of each mammal taxon from Karnezeika and the percentage of each category in the total studied fauna. The table continues on the next page.

	Locomotory patterns		**Locomotory patterns**	**%**
Gazella bouvrainae	Terrestrial		Terrestrial	71.74
Gallogoral meneghinii	Terrestrial		Semi arboreal	0
Gazellospira torticornis	Terrestrial		Arboreal	4.35
Caprini gen. et sp. indet.	Terrestrial		Scansorial	13.04
Croizetoceros ramosus	Terrestrial		Aquatic	2.17
cf. *Metacervoceros rhenanus*	Terrestrial		Aerial	0
?*Eucladoceros* sp.	Terrestrial		Fossorial	8.7
Paleotragus inexpectatus	Terrestrial			
Equus stenonis	Terrestrial			
Stephanorhinus etruscus	Terrestrial			
Ursus etruscus	Scansorial			
Felis sp.	Scansorial			
Pachycrocuta brevirostris	Terrestrial			
Megantereon sp.	Scansorial			
Baranogale sp.	Terrestrial/Fossorial			
Vulpes alopecoides	Terrestrial			
Mustelidae indet.	Terrestrial			
cf. *Paradolichopithecus* sp.	Terrestrial			
Kislangia sp.	Aquatic/Terrestrial			
Kalymnomys sp.	Terrestrial/Fossorial			
Apodemus cf. *dominans*	Terrestrial/Fossorial			
Gliridae indet.	Arboreal			
Hypolagus sp.	Terrestrial/Fossorial			

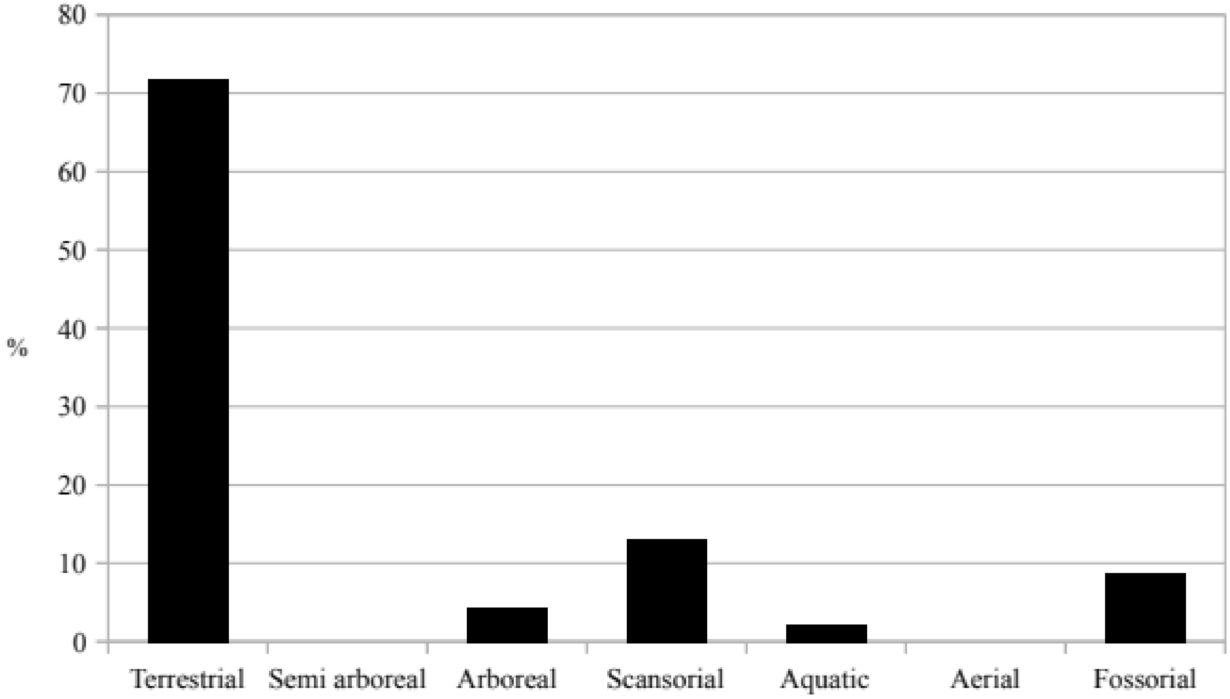

Figure 35: Visualized graph of the percentage of each locomotor adaptation category in relation to the total studied fauna from Karnezeika. Data from table 33.

Dietary adaptations profile

As also shown in Table 34 and Figure 35, most of the Karnezeika mammal taxa were adapted to a browsing diet (34.78%). Carnivores were the second largest category (28.26%), followed by grazers (23.91%). The remaining 13.04% consisted of omnivores.

Table 34. The dietary adaptations of each mammal taxon from Karnezeika and the percentage of each category in the total studied fauna.

	Dietary adaptations		**Dietary adaptations**	**%**
Gazella bouvrainae	Mixed			
Gallogoral meneghinii	Mixed		Insectivore	0
Gazellospira torticornis	Mixed		Frugivore	0
Caprini gen. et sp. indet.	Mixed		Browser	34,78
Croizetoceros ramosus	Browser		Grazer	21.74
cf. *Metacervoceros rhenanus*	Browser		Carnivore	26.09
?*Eucladoceros* sp.	Browser		Omnivore	17.39
Paleotragus inexpectatus	Browser			
Equus stenonis	Grazer			
Stephanorhinus etruscus	Browser			
Ursus etruscus	Omnivore			

(Continues)

Felis sp.	Carnivore			
Pachycrocuta brevirostris	Carnivore			
Megantereon sp.	Carnivore			
Baranogale sp.	Carnivore			
Vulpes alopecoides	Carnivore			
Mustelidae indet.	Carnivore			
cf. *Paradolichopithecus* sp.	Carnivore/Grazer			
Kislangia sp.	Mixed			
Kalymnomys sp.	Mixed			
Apodemus cf. *dominans*	Omnivore			
Gliridae indet.	Omnivore			
Hypolagus sp.	Grazer			

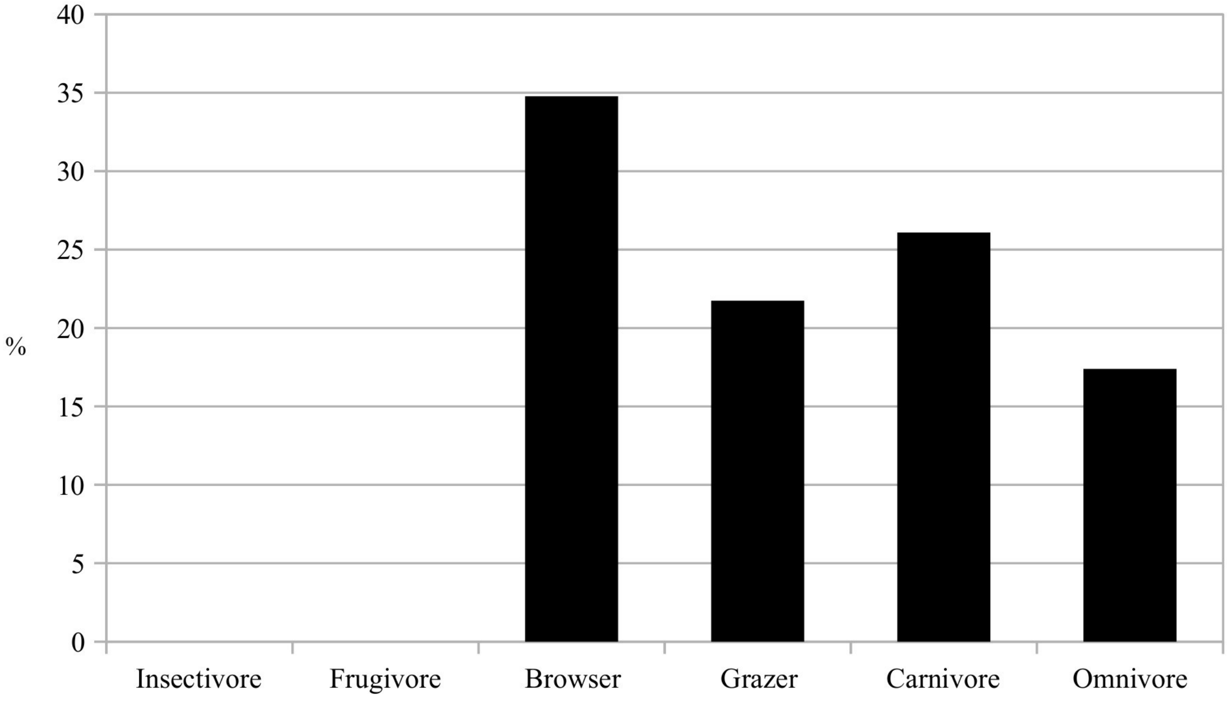

Figure 36: Visualized graph of the percentage of each dietary adaptation category in relation to the total studied fauna from Karnezeika. Data from table 34.

Discussion

Examining the structure of Karnezeika mammal community, I constructed three different profiles based on the characterization of each taxon in relation to their body mass, their locomotor adaptations and their dietary adaptations. As shown in figure 37, possibly due to the lesser number of taxa, the Karnezeika body mass profile looks quite different from the others. Nevertheless, the relatively high percentage of the largest sized taxa (>360 kg), in combination with the significant presence of taxa from the 46 – 90 kg category and the ratio of taxa of the 1.1 – 10 kg to those of the 101 – 1000 g category, reveal a closer correlation to the African bushland, grassland and woodland environments, rather than a forest environment.

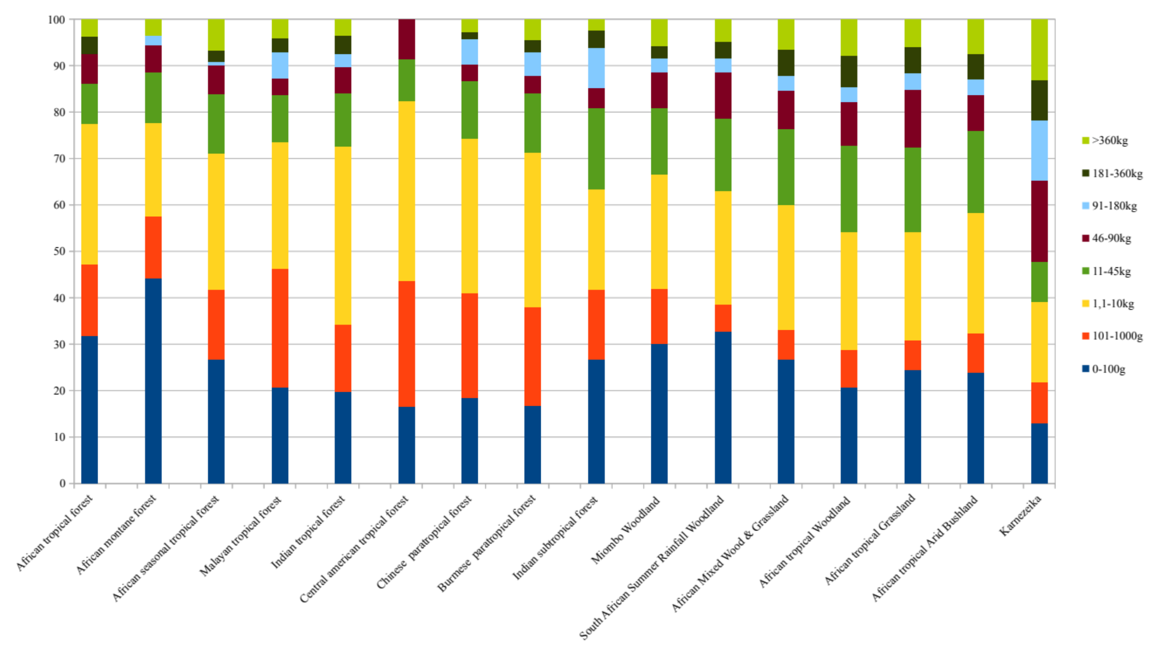

Figure 37: The body mass distributions of taxa from various modern environments and those from Karnezeika. The data of modern environments were taken from Kovarovic et al. (2002).

Concerning the locomotory adaptations profile (Figure 38), the one from Karnezeika differs again from those of modern environments, mainly because of the impressive prevalence of terrestrial taxa. The absence of semi-arboreal taxa might be related to taphonomical factors, which do not favor the preservation of small-sized forms (see also Andrews et al. 1979; Kovarovic et al. 2002), as it is usual for the modern representatives of most of those species. However, the large percentage of terrestrial taxa seems to be indicative, once more, of African bushland, grassland and woodland environments.

As before, the dietary adaptations profile of the Karnezeika taxa was compared to the profiles of modern environments (Figure 39). The absence of insectivores and animals that feed solely on fruit and seeds (frugivores) might be related again to taphonomic factors, which do not favor the preservation of small-sized forms, since there were no large mammal representatives of these dietary adaptations during the lower Pleistocene of Europe (Kurtén 1968). The almost equal ratio of browsers to grazers in combination with the significant presence of carnivores seems to be characteristic of the African bushland and woodland environments.

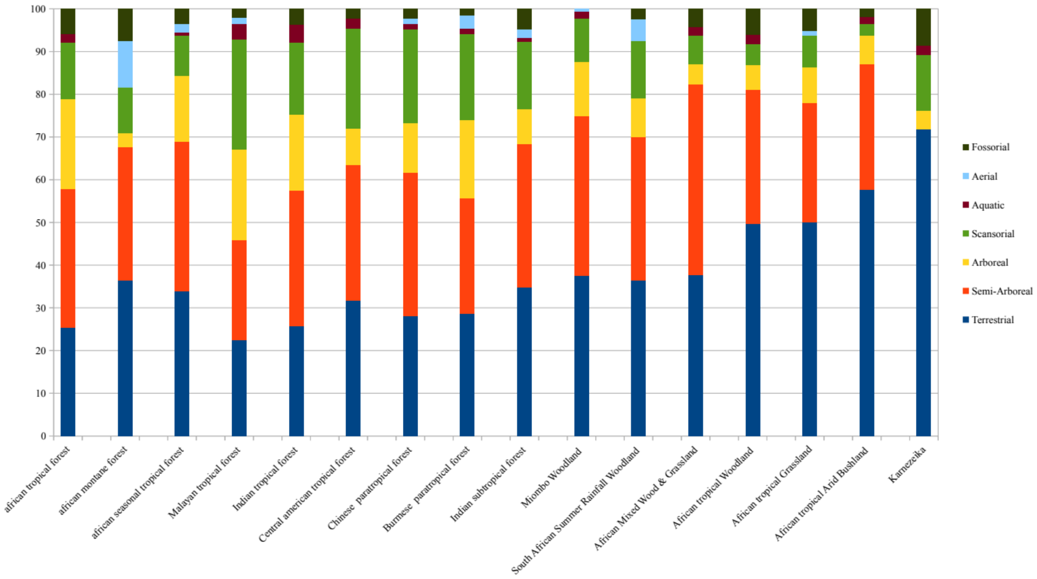

Figure 38: The locomotory adaptation distributions of taxa from various modern environments and those from Karnezeika. The data of modern environments were taken from Kovarovic et al. (2002).

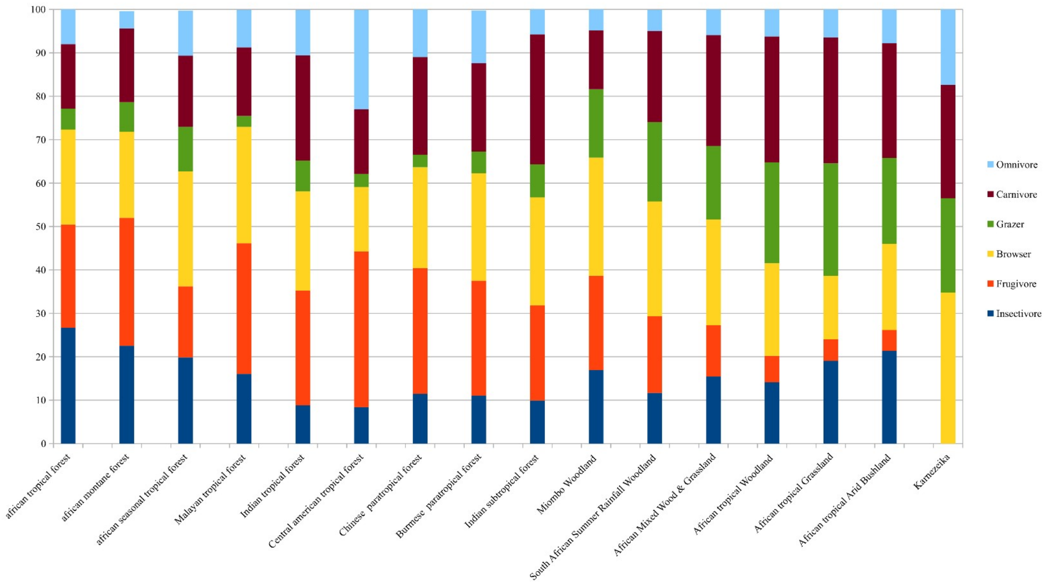

Figure 39: The dietary adaptation distributions of taxa from various modern environments and those from Karnezeika. The data of modern environments were taken from Kovarovic et al. (2002).

As discussed previously, Karnezeika most likely consisted of rocky terrains and rather restricted open areas. The mammal community structure study, which utilizes data from the total mammal fauna for a more holistic view, further revealed a similarity with bushland and woodland environments of an African climate. Therefore, I conclude that Karnezeika was a mountainous area of mixed woodlands and bushlands. This explains the extraordinary prevalence of bovids rather than equids in the locality and also favors most of the carnivoran taxa present there, with the exception of *P. brevirostris* which is usually linked with open landscapes instead (Croitor and Brugal 2010). However, based on its characteristic shortened limbs, which after-all, disfavor running capabilities (Turner and Antón 1996), there is no practical reason for the species to not being able to adapt to a more closed environment, as the one proposed for Karnezeika. As such, the palaeoenvironment of Karnezeika differs from other important Greek Middle Villafranchian sites like Volax, Sesklo, Dafnero and Vatera, which mostly revealed an open and sub-arid landscape (de Vos et al. 2002; Koufos 2014). However, the Karnezeika palaeoenvironment indicates a landscape more similar to that of Saint Vallier with both open and wooded habitats including also a nearby mountainous relief (Valli 2004; Curran 2009).

Taphonomy

According to Lyman, (1994): “*Taphonomy is the science of the laws of embedding or burial. More completely, it is the study of the transition, in all details, of organics from the biosphere into the lithosphere or geological record*”, or according to Behrensmeyer and Kidwell (1985): “*the study of processes of preservation and how they affect information in the fossil record*”. As such, taphonomy is nowadays a fundamental tool that usually accompanies the systematic and palaeoenvironmental study of a fossiliferous locality. Karnezeika is not an exception, hence in this current chapter we provide the taphonomical analysis of the site, in order to acquire more data concerning the formation of the locality.

Material and Methods

In total, 3358 specimens were recorded. Apart from these cataloged and recorded specimens, there were also more than 7000 fragments of all kinds of bone, of quite small size (<2 cm), unsuitable for further utilization other than providing taphonomic data.

NISP is defined as the number of identified specimens per taxon, identified to any taxonomic category (Lyman 1994). In the current study, the NISP is referred to specimens identified at least to the tribe level. For the MNI we utilize the modified version of Klein (1980).

Each specimen, regardless of whether it was identifiable or not, was studied in terms of the various taphonomic variables that can occur, utilizing the works of Behrensmeyer (1978), Villa and Mahieu (1991) Mikuláš et al. (2006), Fernández-Jalvo and Andrews (2016), Maldonado et al. (2016). More specifically there were recorded: the specimens’ completeness, whether it was a complete skeletal element or partially preserved or fragment; the stage of weathering (stages 0-5 of Behrensmeyer (1978); state of abrasion, if there was slight, moderate or great/extreme and also if the abrasion appears on all sides of the bone, on some, or locally. It was also recorded if the abrasion appears before or after other processes; the specimens’ fracture if they are pre-burial or modern. If they were pre-burial we also recorded, wherever possible, the fracture angle, outline and edge; gnawing marks; discoloration; incrustation; deformation, if it was general or local. For the latter case we also recorded if it appeared as a compression point or not.

Results

Based on the calculation of the NISP (Table 35), the large majority of identifiable specimens are attributed to the bovids in general and more specifically to *G. bouvrainae*, including more than 500 specimens. A large quantity of specimens was also attributed to *G. meneghinii* numbering more than 100. The rest of the taxa are represented by a quite smaller number of identifiable specimens, but they were enough for a safe taxonomic attribution. Concerning the MNI, most taxa include up to three individuals with the exception of *G. bouvrainae* which includes at least 16 individuals and *G. meneghinii* which includes 10 (Table 35).

Table 35. The NISP and MNI values of the large mammals from Karnezeika.

	NISP	**MNI**
Gazella bouvrainae	512	16
Gallogoral meneghinii	106	10
Gazellospira torticornis	42	3
Caprini gen. et sp. indet	2	1
Palaeotragus inexpectatum	12	1
Croizetoceros ramosus	6	2
cf. *Metacervoceros rhenanus*	3	1
?Eucladoceros sp.	18	2
Equus stenonis	16	2
Stephanorhinus etruscus	22	1
Ursus etruscus	5	2
Baranogale helbingi	10	3
Mustelidae indet.	2	1
Vulpes alopecoides	7	2
Pachycrocuta brevirostris	1	1
Megantereon cultridens	6	1
Felis sp.	1	1
cf. *Paradolichopithecus* sp.	3	1

Completeness

33% of all recorded skeletal elements were in complete state of preservation. This, however, includes isolated teeth as well, which denotes fragmented mandibles and maxillae. 41% were partially preserved, whereas the remaining 26% were characterised as fragments, but not as small as the 7000 un-recorded fragments mentioned above (<2 cm).

Weathering

The overwhelming majority of the studied specimens (~66%) showed no signs of weathering. The fossils are in good condition and there is no sign that cracking or flaking occurred in the past. They belong to stage 0 of Behrensmeyer (1978). There were also many specimens (~32%) that showed a degree of cracking on their surface, but without signs of flaking and seem to belong to stage 1. Specimens that correspond to later stages are very rare in the Karnezeika fossil material and consist a minimal percentage (~1%) of the total.

Abrasion

Abrasion seems to be an unimportant factor in the taphonomic alteration of the material and polished bones are not expected in the studied collection. Only 14 out of the total 3358 studied specimens showed abrasion, which was also characterised as slight, apart from one specimen which showed a moderate amount. In most cases, abrasion affected the whole bone surface and in all cases it appeared after other processes such as weathering and/or breakage.

Fractures

Since the majority of the studied material was not in a complete state, fractures were very common to observe. More specifically, concerning the long bones, the majority of the fractures showed a curved outline with a right fracture angle and a jagged fracture edge.

Discoloration

Discoloration affected almost all specimens and appeared in the form of black staining. In fact, discoloration is so common that the general appearance of the Karnezeika fossil collection is characterised by a general reddish tinge, due to the red clay present in the locality, stained by black colored dots and/or patches. Furthermore, it was also not uncommon to observe brown-colored patches accompanying the black stains at some areas of the fossil bone.

Incrustation

The majority of the material (71.5%) showed a small degree of incrustation which is included in stage 1 of Maldonado et al. (2016). The incrustation usually appeared in small patches and covered a minute percentage of the total fossil's surface. However, there were also many cases where the fossil bones did not have any incrustations. Cases showing larger degree of incrustation, in which it covered more than 50% of the bone surface, were present but very rare.

Deformation

~31% of the total studied material showed some degree of diagenetic deformation. Cases of extensive deformation which affected the whole fossil were rare, appearing in only 17 specimens. Instead, deformation usually affected parts of the fossil and appeared with impact points and localized cracks.

Other observations

Apart from the main taphonomic processes mentioned above, a few more observations were recorded as well. A few specimens showed a mosaic of scratches and etchings which could be identified as marks due to the action of plant roots spreading upon the bone's surface. Other specimens revealed the presence of one or more small pebbles, which were embedded on the surface of the bone.

Discussion

The majority of the fossil material was broken, while there were also several thousand specimens of complete fragmentation. Taking into account the lack of articulated elements it is safe to assume that the osteological material was transferred to the fossil trap and was not buried *in situ (REFS)*. Judging again from the highly fragmentary state of the fossil material, and also from the large amount of limestone rocks that accompanied the bones, possibly the water acting as a transport agent was characterised by high kinetic energy. This is further suggested by the unusual breakage pattern of curved outline, with a right fracture angle and a jagged fracture edge, which may indicate intense dynamic events (Villa and Mahieu 1991). Concerning the time of transportation, this must have been minimum. The bones show either no weathering at all or an early stage of it, which suggests that they were not subjected to environmental factors for long and were transported fast to the place of burial. Also, the bones in general did not spend much time under the effects of water since the number of specimens showing such an alteration (abrasion) was highly insignificant. Almost a third of the total studied specimens showed some degree of deformation including several cases of local compression points. This could be due to the action of rocks falling into the fossil trap, while the bones were still in an early stage of burial. This agrees with the hypothesis that water under high kinetic energy transferred bones and rocks into the karstic cavity, gathering both of them violently and piling them up. No signs of carnivore action were observed, such as bite or gnawing marks, while the large majority of the specimens showed black-colored discoloration, mainly in the form of spotting. The most common reason for this is manganese oxides (Fernández-Jalvo and Andrews 2016), which indicates either water presence or watery sediments in the place of burial. If there was water in the place of burial (and not just watery sediments), then most likely it was stagnant due to the lack of abrasion on the bones, without them being completely submerged either, since cases of total discoloration were very rare. The small pebbles embedded on the surface of a few of the bones could be explained by the violent way of transportation mentioned earlier, while root marks observed on some other specimens should not come as a surprise. The abundance of sediment and water in the burial place would favor the growth of plant life. The fossils that are present in the studied *oryctocenosis* (Shipman 1993), come from bones with varied values of FTI (Fluvial Transport Index - (Todd and Frison 1986)). Furthermore, the *oryctocenosis* includes fossils of all three groups of Voohries (1969), even though the first two groups are better represented. A lack of any bioclastic sorting is also observed, since there is significant variety in the form and size of the skeletal elements that ended up in the fossil trap. Based on the above and also on the prevalence of non-articulated elements, as well as the absence of signs of abrasion which were mentioned earlier, the studied vertebrate assemblage can be characterised as *peripheral* (Araújo-Júnior 2016). Therefore, I believe that the fossil material derives from animals that died in a close proximity around the karstic cavity and their bones were later transferred and consequently were preserved inside the fossil trap.

Conclusions

Karnezeika is a newly studied Lower Pleistocene locality in Peloponnese, Southern Greece. Despite being a fissure filling, it has yielded rich material of bovids but also other artiodactyl, perrissodactyl, carnivoran taxa as well as a primate, in contrast to other similar Villafranchian assemblages of Peloponnese, such as Vrondamas (Sidiropoulou 1972), Vlachiotis (Symeonidis and Theodorou 1986), Kaiafas (van der Meulen and van Kolfschoten 1986; Villa et al. 2020), Pyrgos (van der Meulen and van Kolfschoten 1986) and Elis (Reimann and Strauch 2008), which are generally poor.

The palaeofauna was rich including eighteen taxa: cf. *Paradolichopithecus* sp.; *Ursus etruscus*; *Baranogale helbingi*; Mustelidae indet.; *Vulpes alopecoides*; *Pachycrocuta brevirostris*; *Felis* sp.; *Megantereon cultridens*; ?*Eucladoceros* sp.; cf. *Metacervoceros rhenanus*; *Croitezoceros ramosus*; *Palaeotragus inexpectatus*; *Gazella bouvrainae*; *Gazellospira torticornis*; *Gallogoral meneghinii*; Caprini gen. et sp. indet.; *Equus* sp.; *Stephanorhinus etruscus*.

Unlike other Lower Pleistocene Greek localities, Karnezeika is vastly dominated by bovids, which comprise up to 90% of the total fauna based on the number of determined specimens. The dominant taxa are *G. bouvrainae* and *G. meneghinii*, with numerous dental and postcranial elements.

The palaeofauna includes some rare taxa not only for Greece but, in general, for European standards. *B. helbingi* is an enigmatic taxon and the very well-preserved specimens described herein provide further useful insights. The presence of *P. brevirostris* marks the first time that there is evidence of this taxon in the current chronological frame from the South-East of Europe. Primate specimens are always valuable especially when they correspond to large-sized and interesting taxa such as *Paradolichopithecus*.

Despite the complex stratigraphy of the site, based on the recorded fauna the locality dates near the 2Ma boundary.

Herein, some further palaeoecological aspects of *G. bouvrainae* are also provided thanks to the abundance of dental and post-cranial material. This unique to Greek localities species was a mixed feeder of quite small size reaching on average ~21 kg. Study of the talus revealed correlations with taxa adapted for life in light-covered habitats.

The mammal structure analysis and comparison with modern ecosystems revealed similarities with the African bushlands and woodlands, rather than open grasslands. Furthermore, based also on the large number of *G. meneghinii* specimens, the relative absence of equids and the geological background of the locality, it is concluded that during the latest part of the Middle Villafranchian (MN17), Karnezeika was a mountainous landscape with a mosaic of mixed woodlands/bushlands and restricted open areas.

The karstified carbonate rocks, which serve as geological background for the wider area, would favor the accumulation of water under high kinetic energy during torrential rains, hence scattered animal remains of the autochthonous fauna were carried fast to the *peripheral* place of burial due to this action. The time of exposure to meteorological agents was short, since the bones show minimum weathering, as also short was the travel distance, as the bones show no abrasion.

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Appendix

Supplementary measurements: *Gazella bouvrainae*

L: length; W: width; DT: Transverse diameter; DAP: Anteroposterior diameter; prox: proximal; diaph: diaphysis; dis: distal. All measurements in mm.

Horncores			
Code (KZ..)	**DT**	**DAP**	
1158	16.06	18.86	Morphotype A
2303	16.34	17.88	
3227	13.38	16.55	
2512	22.41	24.17	Morphotype B

		Lower teeth					
Code (KZ..)	**L**	**W**		**Code (KZ..)**	**L**	**W**	
2113	7.07	3.62	p2	2217	19.83	7.17	m3
872	5.65	2.15	p2	3057	17.76	6.99	m3
1585	8.66	4.49	p2	1970	20.03	7.54	m3
1651	5.07	3.13	p2	2571	19.1	7.5	m3
2798	7.76	3.86	p2	2169	18.66	7.71	m3
2816	5.45	3.42	p2	2781	20.42	8.13	m3
				2061	20.23	7.97	m3
2490	9.19	5.19	p3	3319	19.17	6.66	m3
2491	10.3	5.35	p3	865	18.72	6.79	m3
1653	9.4	5.17	p3	2465	18.05	6.72	m3
1152	9.61	4.56	p3	2820	19.75	7.22	m3
2677	10.34	5.59	p3	1231	18.97	7.58	m3
2000	11.01	5.48	p3	871	19.77	7.03	m3
2816	9.17	5.1	p3	1932	19.05	7.52	m3
2125	10.04	5.95	p3				
2077	9.2	5.2	p3	1932	14.03	7.99	m2
1769	10.03	5.5	p3	2230	14.97	6.94	m2

2456	10.13	4.79	p3	871	13.45	7.81	m2
3322	10.55	5.68	p3	2820	14.91	7.82	m2
2796	9.4	4.59	p3	1231	14.35	7.75	m2
869	9.4	5.28	p3	2216	14.3	6.74	m2
2784	10.56	5.72	p3	2797	13.32	8.25	m2
2382	10.04	6.03	p3	2115	16.54	7.44	m2
1770	9.26	4.7	p3	2672	14.4	6.82	m2
985	9.17	4.74	p3	3159	14.6	6.71	m2
1240	8.94	5.16	p3	2153	13.65	6.74	m2
2121	9.05	4.92	p3	1727	14.23	8.08	m2
2009	9.15	4.85	p3	2573	14.7	7.24	m2
1723	9.41	4.4	p3	1645	13.58	7	m2
1589	9.66	5.1	p3	2803	13.82	6.79	m2
376	9.26	5.06	p3	487	16.28	7.02	m2
1092	9.76	4.56	p3	2375	15.08	6.58	m2
1762	9.24	5.39	p3	3327	14.52	6.95	m2
1063	9.6	4.94	p3				
				376	12.78	5.87	m1
2294	11.14	6	p4	2216	13.47	6.57	m1
1581	10.63	6.29	p4	2466	10.82	8.16	m1
2266	10.42	6.21	p4	2230	12.84	6.91	m1
1721	11.25	6.27	p4	2820	12.8	7.91	m1
2686	11.09	7.98	p4	2098	13.07	7.92	m1
1231	10.45	6.59	p4	1771	11.47	7.42	m1
2466	10.23	6.34	p4	1977	12.94	7.98	m1
871	9.98	6.78	p4	1729	11.79	7.47	m1
1762	9.99	6.19	p4	1827	12.58	7.87	m1
2793	10.29	5.46	p4	2281	12.45	8	m1
3161	10.12	6.14	p4	2118	12.6	6.73	m1
				2588	13.05	7.05	m1
				2679	13.1	8.33	m1
Code (KZ..)	**L**	**W**					
1972	16.31	6.42	d4				
3303	16.91	6.3	d4				

1855	17.71	5.94	d4				
639	16.59	5.71	d4				
1834	18.82	6.51	d4				
864	17.1	5.63	d4				
1891	16.34	5.93	d4				
3160	16.67	5.65	d4				
3313	17.22	5.95	d4				
640	16.98	6.74	d4				
3075	16.7	5.88	d4				
3297	17.42	6.05	d4				
3071	17.11	5.66	d4				
1303	17.43	6.02	d4				
3312	16.51	5.83	d4				
982	17.6	6.13	d4				
2566	17.21	5.69	d4				
1063	18.36	5.64	d4				
1092	18.01	6.03	d4				
376	16.24	6.29	d4				

		Upper Teeth					
Code (KZ..)	**L**	**W**		**Code (KZ..)**	**L**	**W**	
1941	10.28	8.36	P4	903	15.05	9.89	M1
2378	10.13	9.35	P4	2293	14.04	10.89	M1
3139	9.18	9.55	P4	3298	13.06	11.07	M1
3082	8.97	10.73	P4	1764	13.96	11.82	M1
569	9.18	9.17	P4	3146	14.92	10.72	M1
2287	9.02	8.39	P4	866	14.22	10.03	M1
2484	9.38	9.4	P4	400	14.64	10.25	M1
905	8.95	9.06	P4	2259	14.64	10.44	M1
2485	9.02	8.35	P4	2919	14.27	11.88	M1
				1838	14.31	11.78	M1

1726	8.76	9.94	P3	3268	14.31	11.65	M1
1994	9.09	9.62	P3	2750	14.09	10.04	M1
2926	8.8	10.37	P3	2374	14.89	9.48	M1
2127	8.89	10.23	P3	3269	14.51	9.8	M1
1301	8.41	8.1	P3	3084	12.14	10.31	M1
2278	9.7	9.55	P3	3156	14.28	10.84	M1
2147	9.86	9.85	P3	3155	13.2	11.34	M1
3083	9.14	10.07	P3	1941	14.96	10.44	M1
1301	8.66	7.51	P2	1941	16.14	10.25	M2
2957	8.97	8.02	P2	3143	15.32	9.99	M2
1235	8.63	6.5	P2	2063	15.47	11.3	M2
345	9.75	8.38	P2	3277	15.73	11.71	M2
				3036	15.77	10.56	M2
				735	15.51	13.54	M2
Code (KZ..)	**L**	**W**		1161	14.91	11.65	M2
845	8.5	7.89	D2	1234	15.39	14.08	M2
1238	9.71	7.03	D2	1235	16.39	12.86	M2
989	8.54	6.47	D2	760	15.57	11.62	M2
1305	9.28	7.1	D2	984	14.79	13.34	M2
1313	8.8	6.81	D2	2568	16.28	11.35	M2
2148	8.36	5.68	D2	2241	16.29	10.73	M2
1966	8.55	5.54	D2	3321	15.18	12.83	M2
3079	11.11	7.44	D3	2442	16.12	10.22	M3
1307	12.84	7.06	D3	1936	15.87	10.34	M3
1097	11.34	7.51	D3	3293	15	9.6	M3
2377	12.1	7.55	D3	2918	15.4	10.08	M3
2143	12.85	7.92	D3	1812	15.95		M3
1966	10.84	7.02	D3	2462	15.12	10.78	M3
2148	10.87	6.75	D3	3046	14.79	10.14	M3
				1792	15.5	10.48	M3
1842	13.01	8.58	D4	2111	14.79	9.26	M3
638	13.44	8.71	D4	1188	15.21	11.06	M3

1991	12.87	8.8	D4	3157	14.35	9.5	M3
1793	12.15	8.98	D4				
2696	12.93	8.71	D4				
581	12.26	8.39	D4				
2891	12.65	8	D4				
1096	12.74	9	D4				
2379	13.31	8.97	D4				
867	13.46	9.4	D4				
1237	12.57	8.44	D4				
2297	11.97	8.82	D4				
2912	14.46	9.89	D4				
1966	12.69	7.81	D4				
2376	14.07	9.37	D4				
983	12.41	8.87	D4				

Humerus			
Code (KZ..)	**DT dist**	**DAP dist**	
1082	27.11	22.22	
1289	28.02	23.18	
2825	27.75	23.87	
1803	29.69	25.12	
1778	28.36	23.75	
2726	26.82		
3117	29.04	23.01	
434	27.41		
3252	26.42		
2813	26.02	22.39	
1182	27.08	22.79	
1807	27.26		
2200	28.13		
2873	26.56	22.09	

1802	28.03	22.88	
1183	29.40		
1672	26.32	22.89	

Radius		
Code (KZ..)	**DT prox**	**DAP prox**
2736	28.13	14.07
2861	26.81	15.04
3023	27.27	14.36
1923	26.25	14.14
2201	29.04	15.11
3107	27.68	15.09
1554	29.03	15.59
2454	28.60	15.12
1952	28.67	13.4
486	28.85	14.75
3258	27.67	15.06
1045	28.04	14.57
2950	28.13	15.19
822	27.66	15.02
2832	29.41	16.26

Metacarpal				
Code (KZ..)	**DT prox**	**DAP prox**	**DT dis**	**DAP dis**
357	21.51	17.16		
2877	19.78	16.45		
823	21.67	16.99		
474	21.13	15.52		
2317	19.71	16.23		
952	21.04	16.88		
3175	21.51	16.69		

1902	20.88	15.33		
1734	21.09	17.65		
1840			21.51	15.37
2632			21.64	15.6
2526			21.83	15.29
2224			20.75	14.33
2883			21.23	14.41
2242			21.83	14.3
2472			21.57	15.1
1780			21.02	14.06
1387			21.86	13.85
1606			22	14.88
2136			22.31	14.52

Tibia		
Code (KZ..)	**DT dist**	**DAP dist**
435	23.81	20.07
2975		20.98
519	23.42	17.8
2836	21.55	16.24
3028	21.78	17.65
1831	22.87	18.08
1164	25.79	18.17
2339	26.05	16.82
2748	23.56	19.64
1061	24.28	18.37
2183	24.82	16.62
1937	23.45	
3131		18.20
2762	23.42	18.25
761	23.95	18.00

Metatarsal				
Code (KZ..)	**DT prox**	**DAP prox**	**DT dis**	**DAP dis**
3272			20.91	14.25
2068			22.18	15.16
2530			22.91	16.06
2983			22.1	15.53
1779			20.69	15.32
2727			22.22	15.14
2988			21.95	15.55
1949			22.28	15.34
2553			20.96	15.23
2083	19.45	21.66		
2410	21.65	22.35		
2334	18.33	19.75		
1817	20.5	22.58		
2974	19.25	21.47		
1962	20.14	21.58		
1782	20.36	20.75		
3180	20.2	21.95		

Talus				
Code (KZ..)	**L medial**	**DAP max**	**L lateral**	**DT dis**
1882	26.09	16.22	27.89	15.80
3035	27.25	16.48		16.57
3223	26.03	16.16	28.60	16.3
2221	26.51	15.61	27.77	15.41
2049		15.18		16.24
2546	25.93	14.36	26.31	15.12
686	26.45	15.42	28.19	15.81
2226	27.21	16.21	29.62	17.6
892	28.02	16.93	30.56	18.27
2431	25.53	14.86	27.92	15.58

1449	26.32	16.01	29.13	16.25
3243	28.91	16.68	30.31	17.55
1917	27.81	16.8	29.77	17.33
2057	26.29	14.97	28.65	16.62
3324	26.73	15.44	27.92	16.79
2534	27.39	16.14	29.48	17.17
2060	27.57	15.86	29.38	16.85
1448	27.96	16.64	30.65	18.42
2155	26.68	16.59	28.48	16.95

Supplementary measurements: *Gallogoral meneghinii*

L: length; W: width; DT: Transverse diameter; DAP: Anteroposterior diameter; prox: proximal; diaph: diaphysis; dis: distal. All measurements in mm.

Horncore		
Code (KZ..)	**DAP**	**DT**
880	45.7	45.2

Lower teeth							
Code (KZ..)	**L**	**W**		**Code (KZ..)**	**L**	**W**	
2476	15.97	10.21	p4	2752	22.67	12.67	m1
3015	17.39	10.9	p4	2369	23.48	12.01	m1
3022		10.31	p4	1457	22.04	9.03	m1
2439	16.16	10.65	p4	448	23.46	10.26	m1
2572	17.83	10.93	p4	1091	23.73	9.68	m1
691	18.4	9.86	p4	2876	22.16	11.52	m1
				2282	22.65	11.73	m1
1863	17.65	8.48	p3	2985	22.66	11.24	m1

692	15.76	8.98	p3	2728	24.85	11.79	m1
3045	15.11	10.54	p3				
1302	14.83	10.48	p3	2367	25.65	11.28	m2
399	16.26	7.19	p3	3020	23.32	13.57	m2
2575	14.45	9.08	p3	2777	18.61	12.75	m2
1095	14.95	7.99	p3	3220	25.33	12.55	m2
3074	16.31	7.87	p3	527	26.5	11.13	m2
346	14.82	7.73	p3	326	25.69	12.26	m2
2929	15.43	9.99	p3	2862	28.98	13	m2
2580	14.69	8.53	p3				
1236	14.75	9.36	p3	2982	32.16	12.08	m3
2086	14.59	8.51	p3	2370	31.19	11.53	m3
2461	14.61	8.02	p3	2979	30.34	11.63	m3
3042	15.95	7.83	p3	2548	33.3	13.11	m3
2569	16.7	9.71	p3	2531	34.33	13.24	m3
2503	16.02	8.71	p3	1763	32.44	12.06	m3
750	15.91	7.45	p3	2915	32.36	12.65	m3
				3111	33.76	12.97	m3
750	9.5	6.82	p2	2422	33.46	12.62	m3
2665	10.76	7.41	p2				
1304	10.95	6.94	p2				
2381	10.23	6.23	p2				
2380	9.85	5.89	p2				
2467	11.91	8.54	p2				
1093	10.62	6	p2				
2273	9.95	6.19	p2				
2675	9.58	5.8	p2				
2914	9.66	6.09	p2				
2657	10.33	6.41	p2				
2279	9.87	5.29	p2				
2920	10.31	6.98	p2				
2486	10.28	6.35	p2				
3086	9.39	5.44	p2				
401	9.88	5.35	p2				

			Upper teeth				
Code (KZ..)	**L**	**W**		**Code (KZ..)**	**L**	**W**	
2731	15.14	13.37	P3	2234	21.78	14.85	M1
2778	12.71	16.65	P3	2433	23.8	14.35	M1
2767	14.07	14.04	P3	2630	21.42	15.58	M1
3281	14.77	15	P3	490	22.8	14.79	M1
902	13.66	14.03	P3	901	22.65	14.46	M1
				1420	22.85	14.63	M1
2917	15.24	13.21	P4	3247	23.36	15.77	M1
2996	15.04	12.95	P4	1919	19	14.3	M1
2625	15.08	13.47	P4	2889	21.03	18.36	M1
2731	15.62	13.49	P4	2758	20.2	15.33	M1
				2567	19.98	17.53	M1
				1455	26.87	17.9	M2
				3257	24.25	16.69	M2
				2933	26.17	16.65	M2
				1459	24.41	20.52	M2
				2624	25.17	17.03	M2
				3003	24.98	17.76	M2
				2388	27.36	17.9	M2
				2432	26.86	16.75	M3
				3121	27.24	18.53	M3

Metacarpal							
Code (KZ..)	**DT prox**	**DAP prox**	**DT diaph**	**DAP diaph**	**DT dist**	**DAP dist**	**L**
2647	45.8	28.17	28.13	20.33	50.02	26.9	183.2
1411	42.69	27.42	28.13	19.56		27.46	180.9
485	48.73	30.36	32.47	20.47			
1440					49.55		

787					52.6		
2953					46.29		
3099					51.99		
2389					52.65		
535					52.53		
1739					54.39		
1134					50.99		
3200					46.05		

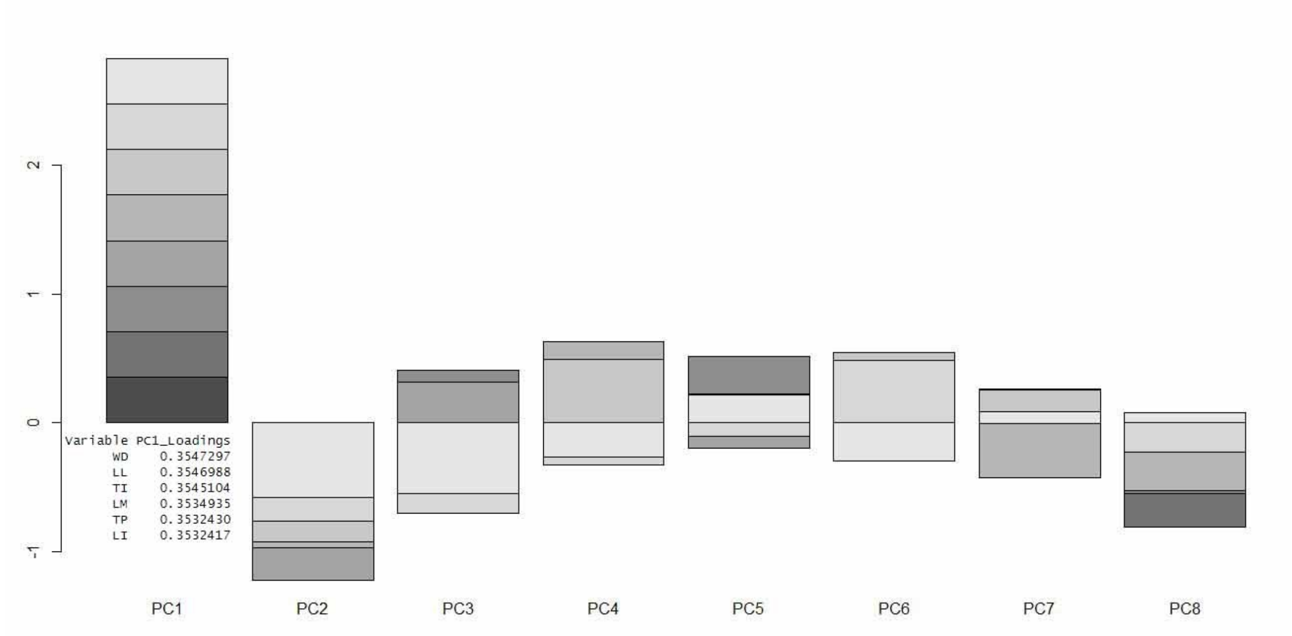
Metatarsal							
Code (KZ..)	**DT prox**	**DAP prox**	**DT diaph**	**DAP diaph**	**DT dist**	**DAP dist**	**L**
2811	40.91	33.34	23.59	22.81	45.6	25.63	185.6
2938	41.65	36.6	25	26.32			
3193	33.15	35.29	24.48	23.04			
1504	36.26	31.97	22.49	21.53			
2392					43.83		

Supplementary Data for PCA

The dataset used in Figure 32. Measurements are described and depicted in DeGusta and Vrba (2003) – Fig.2.

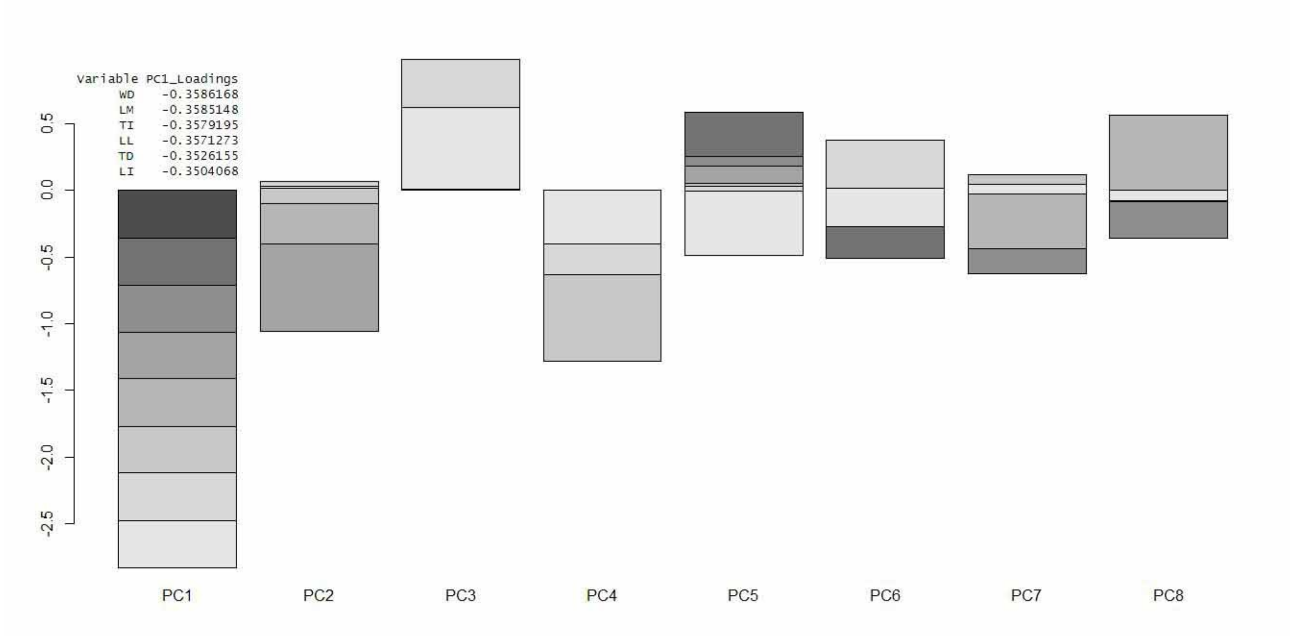
Specimen	**LL**	**LI**	**LM**	**WI**	**WD**	**TP**	**TI**	**TD**
KZ1448	30.53	24.15	27.93	17.89	18.43	11.47	15.11	13.65
KZ2431	27.85	22.55	25.63	15.26	15.36	10.18	14.09	12.01
KZ1613	25.03	20.7	23.5	14.11	14.2	8.46	12.48	9.99
KZ633	23.58	19.83	22.69	13.54	13.95	7.68	12.49	10.77
KZ3276	24.56	21.62	25.78	15.52	16.05	10.21	14.3	12.49
KZ1917	29.76	24.28	27.79	16.21	17.52	11.06	15.99	14.55
KZ1938	24.68	20.92	24.47	14.13	14.66	9.46	12.55	10.62
KZ2546	26.47	21.85	25.92	14.7	15.37	9.75	13.15	11.68
KZ2060	29.4	24.32	27.59	16.22	16.98	10.21	14.75	13.38
KZ2451	28.45	22.91	26.94	14.93	15.62	9.9	13.21	10.34
KZ2155	28.52	22.85	26.71	16.46	16.94	10.87	15.14	13.17
KZ686	28.24	23.09	26.45	15.65	15.78	8.9	13.71	12.49
KZ3324	27.72	22.45	26.72	15.45	16.82	9.82	14.33	13.23
KZ1549	27.41	21.42	25.16	15.99	16.99	11.26	14.3	12.49
KZ3223	28.45	22.49	25.98	16.1	16.32	10.26	15.15	13.51
KZ2534	29.58	24.35	27.37	17.96	17.45	10.98	15.43	14.22
KZ3243	30.22	25.12	28.9	16.61	17.45	11.03	15.39	13.32
KZ2226	29.75	23.03	27.22	16.85	17.3	11.22	14.3	12.49
KZ3035	28.01	20.87	27.21	15.97	16.43	10.21	14.3	12.49
KZ2221	27.76	23.24	26.43	15.11	15.34	10.02	14.7	12.14
KZ2057	28.68	22.87	26.26	15.13	16.55	10.17	13.72	11.99
KZ1449	29.02	22.95	26.33	15	16.24	9.98	14.61	12.37
KZ892	30.56	24.09	28.05	18	18.38	11.64	15.72	13.92

Loadings plot I



Variable	PC1_Loadings
WD	0.3547297
LL	0.3546988
TI	0.3545104
LM	0.3534935
TP	0.3532430
LI	0.3532417

Loadings plot II



Variable	PC1_Loadings
WD	-0.3586168
LM	-0.3585148
TI	-0.3579195
LL	-0.3571273
TD	-0.3526155
LI	-0.3504068