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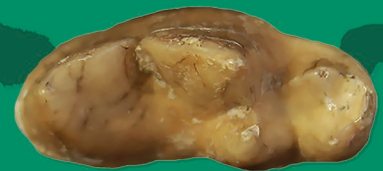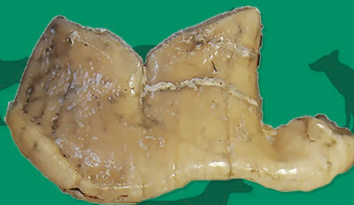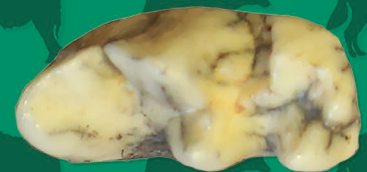
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ABSTRACT

The present paper deals with the ecomorphological characteristics of two sympatric species of ictitheres: *Ictitherium viverrinum* Roth & Wagner, 1854 and *Hyaenictitherium wongii* (Zdansky, 1924) from the Late Miocene of the Eastern Mediterranean. These two species represent different taxonomic groups with allegedly distinct ecological roles. The values of 11 ecomorphological proxies were calculated using cranial and dental elements, in order to make an extensive comparison between them (body mass, bite force, canines' and incisors' bending strength, endocranial volume, relative rostral width, dental mesowear, intercuspid notches and carnassial vs grinding surfaces). The proxies show similar results for both species, pointing out that they had a similar ecological niche in the Late Miocene ecosystems. Carnivorans are usually in the top of the food chain, so the existence of two ecologically similar species in the same spatiotemporal range results in interspecific competition. This explains the geographical distinction of the two species with several localities being dominated by only one of the two (e.g. Samos for *Hyaenictitherium* Kretzoi, 1938 and Pikermi for *Ictitherium* Wagner, 1848). The reason for the prevalence of each genus can be associated with their postcranial morphology, as *Hyaenictitherium* has been proposed to be better adapted to chase hunting, because of its longer limbs, while *Ictitherium* is characterized by shorter and stouter limbs.

KEY WORDS
Hyaenidae,
Ictitherium,
Hyaenictitherium,
Turolian,
Greece.

RÉSUMÉ
Compétition interspécifique chez les ictithères (Carnivora : Hyaenidae) du Miocène supérieur d'Eurasie.
L'article présent traite des caractéristiques écomorphologiques de deux espèces sympatriques d'ictitheres : *Ictitherium viverrinum* Roth & Wagner, 1854 et *Hyaenictitherium wongii* (Zdansky, 1924) du Miocène supérieur de la Méditerranée orientale. Ces deux espèces représentent des groupes taxonomiques différents avec des rôles écologiques prétendument distincts. Les valeurs de 11 proxies écomorphologiques ont été calculées à l'aide d'éléments crâniens et dentaires, afin d'effectuer une comparaison approfondie entre eux (masse corporelle, force de morsure, force de flexion des canines et des incisives, volume endocrânien, largeur rostrale relative, usure dentaire, encoches intercuspidiennes et surfaces de broyage des carnassières). Les proxies montrent des résultats similaires pour les deux espèces, ce qui indique qu'elles avaient une niche écologique similaire dans les écosystèmes du Miocène supérieur. Généralement, les carnivores se sont situés au sommet de la chaîne alimentaire, et l'existence de deux espèces écologiquement similaires dans la même aire temporale entraîne une compétition interspécifique. Ceci explique la distinction géographique des deux espèces, plusieurs localités étant dominées par une seule des deux (par exemple, Samos pour *Hyaenictitherium* Kretzoi, 1938 et Pikermi pour *Ictitherium* Wagner, 1848). La raison de la prévalence de chaque genre peut être associée à leur morphologie postcrânienne, car *Hyaenictitherium* a été proposé comme étant mieux adapté à la poursuite de proies, en raison de ses membres plus longs, tandis qu'*Ictitherium* est caractérisé par des membres plus courts et plus robustes.

INTRODUCTION

The Late Miocene terrestrial faunas of Greece have been studied since the first decades of the 19th century and, ever since, they have added a great amount of data to our knowledge on the fossil record, making them highly valuable for the study of the European Neogene (Gaudry 1862-1867; Woodward 1901; Bernor *et al.* 1996; Roussiakis *et al.* 2019). The best-known Late Miocene localities of Greece are Pikermi (Attica; 7.37-7.11 Ma; Wagner 1839; Roth & Wagner 1854; Gaudry 1862-1867; Woodward 1901; Abel 1922; Bernor *et al.* 1996; Böhme *et al.* 2017; Roussiakis *et al.* 2019) and the several sites of the island of Samos (North-Eastern Aegean; 8.0-6.8 Ma; Bernor *et al.* 1996; Kostopoulos *et al.* 2009; Koufos & Nagel 2009; Koufos 2011; Koufos *et al.* 2011). Palaeoecological studies have pointed out that these sites, based on their faunal assemblage, were part of the "Old World savannah palaeobiome" (Kaya *et al.* 2018). Other authors argue against this term due to disagreements on the plant-based reconstructions (Denk *et al.* 2018). However, for the study and comparison of fossil faunas similar to that of Pikermi, this term seems to be appropriate (Fortelius *et al.* 2019).

Before the establishment of canids in Europe during the Late Miocene/Early Pliocene (Wang & Tedford 2008), their ecological niche was covered by the "ictitheres", a group of hyenas ranging from the size of a Eurasian badger (*Plioviverrops* spp.) to the size of a wolf (*Hyaenictitherium* spp.) (Werdelin & Solounias 1991; Koufos 2021). The taxonomy of ictitheres has suffered a long series of confusions, but during the last decades, a clearer image has been formed concerning their phylogeny and ecology. Four large groups of non-crocutoid hyenas are recognized: the basal opportunistic ictitheres (*Protictitherium* Kretzoi, 1938, and *Plioviverrops* Kretzoi, 1938), the *Ictitherium*-group (*Ictitherium* Wagner, 1848, and *Thalassictis*

Gervais, 1850, ex Von Nordmann), the *Hyaenictitherium*-group (*Hyaenotherium* Semenov, 1989, *Hyaenictitherium* Kretzoi, 1938, and *Miohyaenotherium* Semenov, 1989) and the "transitional, cursorial" forms (*Lycyaena* Hensel, 1862, *Chasmaporthetes* Hay, 1921, and *Hyaenictis* Gaudry, 1861) (e.g. Turner *et al.* 2008). Other genera also occupy intermediate or unresolved positions, but their infrequency and their poor preservation create difficulties concerning their exact phylogeny and ecology (Turner *et al.* 2008).

The most common carnivorans in the Late Miocene of Greece are the ictitheres *Ictitherium viverrinum* Roth & Wagner, 1854, and *Hyaenictitherium wongii* (Zdansky, 1924) and the first bone-cracking hyaenine *Adcrocuta eximia* (Roth & Wagner, 1854) (Koufos & Nagel 2009; Koufos 2011; Kargopoulos 2019; Roussiakis *et al.* 2019). The two former species are morphologically similar to the extant canids, a fact that according to some scholars also points towards a similar ecological role (Werdelin & Solounias 1991; Tseng & Wang 2007; Turner *et al.* 2008; Coca-Ortega & Pérez-Claros 2019, 2020). Their presence in high numbers has been interpreted as an indication of possible social life and perhaps social hunting (Werdelin & Solounias 1991). An interesting fact is that the two species of ictitheres are not found together in great abundance in the same locality. In particular, usually only one of the two dominates every site, e.g. Pikermi is dominated by *I. viverrinum* (e.g. Roussiakis *et al.* 2019; and references therein), while Samos is dominated by *H. wongii* (e.g. Koufos *et al.* 2011; and references therein). Other examples include the dominance of *I. viverrinum* in Vathylakkos 2 (Koufos 2000, 2011) and the dominance of *H. wongii* in Kemiklitepe (de Bonis 1994).

The nomenclature of both species became rather problematic during the 20th century, as it was common to assign *I. viverrinum* to *Thalassictis robusta* Gervais, 1850,

ex Von Nordmann, and *H. wongii* to *Thalassictis hipparionum* (Gervais, 1846). These misunderstandings were solved after the restriction of *T. robusta* to the material from Kishinev (Kurtén 1982; Werdelin 1988; Semenov 1989, 2008) and the consideration of *Palhyaena hipparionum* as *nomen dubium* (Werdelin 1988; Semenov 1989, 2008; Werdelin & Solounias 1991). Another matter of debate is the differentiation of the genus *Hyaenotherium* from the genus *Hyaenictitherium*. Some authors include all the species of the genus *Hyaenotherium* to the genus *Hyaenictitherium* (e.g. Tseng & Wang 2007; Koufos 2009), whereas other retain the name *Hyaenotherium* for some of them (e.g. Semenov 2008; de Bonis *et al.* 2010). The inclusion of at least *H. wongii* to the genus *Hyaenictitherium* is here considered reasonable based on its morphological similarities with *Hyaenictitherium hyaenoides* (Zdansky, 1924) (Tseng & Wang 2007).

This study is referred to a detailed ecomorphological comparison between *I. viverrinum* and *H. wongii* based on cranial and dental material that has been unearthed mainly from Greece. Various ecomorphological proxies were used to make suggestions about the niche overlap of these species and to interpret their spatiotemporal ranges.

MATERIAL AND METHODS

Eleven ecomorphological proxies were used in this study, to integrate a suite of ecomorphological proxies to support a comparison between the two genera. Body mass was estimated using skull length and m1 length based on the equations of Van Valkenburgh (1990) for the canids, which exhibit the most similar morphology to the ictitheres, since no such equation was provided for hyaenids. Bite force was calculated based on the dry-skull method by Thomason (1991), which uses the cross-sectional areas for the temporal and masseter muscles together with the distances of the upper carnassial and the upper canine from the temporomandibular joint. Canine bending strength was estimated based on Van Valkenburgh & Ruff (1987), by measuring the length, width and height of the canine, resulting in Sx for the anteroposterior strength and Sy for the mediolateral strength. A similar methodology was used for the Incisors' bending strength (Biknevicius *et al.* 1996). The endocranial volume was estimated based on the equation of Finarelli (2006), using the maximum length, width and height of the endocranium, whereas the quotient of the volume was calculated based on Damasceno *et al.* (2013). The relative rostrum width was calculated as the palate width in canines' plane divided by the skull length. The dental mesowear patterns were differentiated based on the distinctions made by De Santis *et al.* (2017), but the wear was differentiated into horizontal wear and vertical wear (concerning grinding and slicing functions respectively). The intercuspid notches method was based on Hartston-Rose (2011) by evaluating the number and form of the cusps of p3 and p4. Finally, the methodology of Sacco & Van Valkenburgh (2004) reveals the relative size (length or area) of several ecomorphologically significant structures (m1 trigonid length, m2 area, upper molars' area). Extant members of the family Canidae Fischer von Waldheim, 1817 were used for the comparison since they exhibit very similar skeletal and dental architecture. The species *Canis lupus* Linnaeus, 1758, *Canis latrans* Say, 1823, and *Canis aureus* Linnaeus, 1758, were chosen to represent the niches of a large predator, an intermediate form and an opportunistic feeder respectively (Castelló 2018). Additionally, the species *Crocuta crocuta* (Erxleben, 1777) was used to represent a large, bone-cracking hyena.

All linear measurements were taken with a digital caliper and were rounded to the first decimal point. All area measurements were made by Image J (Schneider *et al.* 2012). Statistical analysis was conducted in PAST3 (Hammer *et al.* 2001). Dental terminology follows Werdelin & Solounias (1991). The term "ictithere" is herein used in its traditional sense (e.g. *sensu* Werdelin & Solounias 1991), in order to describe all the non-bone-crushing hyaenids.

The studied material comes from the localities of Samos (studied at MNHN, NHMA, NHMUK, NHMW and SMNS), Pikermi (studied at AMPG, MNHN, NHMUK and NHMW), Chomateri (studied at NHMW), Kerassia (studied at AMPG) and Maragheh (studied at MNHN and NHMW). Additional comparative data were obtained from the literature.

ABBREVIATIONS

Institutions
AMPG   Athens Museum of Geology and Palaeontolog;
MNHN   Museum national d'Histoire naturelle, Paris;
NHMA   Natural History Museum of the Aegean, Samos;
NHMUK   Natural History Museum of United Kingdom, London;
NHMW   Naturhistorisches Museum Wien;
SMNS   Staatliches Museum für Naturkunde Stuttgart.

Variables
BM   body mass;
BVQ   brain volume quotient (Damasceno *et al.* 2013);
LGR   square root of the summed areas of m1, m2 and m3 divided by dentary length (Sacco & Van Valkenburgh 2004);
m1L   lower carnassial length;
M1BSZ   anteroposterior length of m1 divided by dentary length (Sacco & Van Valkenburgh 2004);
M2SZ   square root of m2 area divided by dentary length (Sacco & Van Valkenburgh 2004);
N   Newtons;
SKL   skull length;
Sx   the maximum anteroposterior bending strength of incisors and canines (Van Valkenburgh & Ruff 1987; Biknevicius *et al.* 1996);
Sy   the maximum mediolateral bending strength of incisors and canines (Van Valkenburgh & Ruff 1987; Biknevicius *et al.* 1996);
UGR   square root of the summed areas of M1 and M2 divided by dentary length (Sacco & Van Valkenburgh 2004).

RESULTS

One important factor while approaching the ecomorphology of an extinct species is the accurate body reconstruction. Unfortunately, not many complete skeletons of ictitheres have been found, so their body plan is not adequately known.
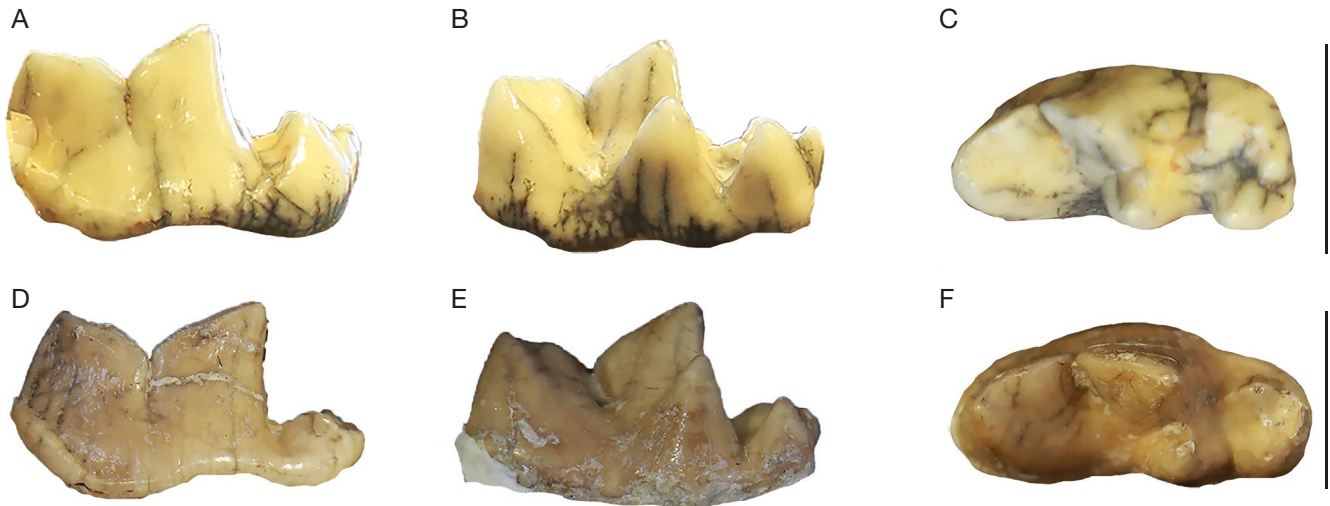
FIG. 1. — Lower carnassial morphology of: **A-C**, *Ictitherium viverrinum* Roth, 1854 (NHMUK-M8989, Pikermi): **A**, lateral; **B**, lingual; **C**, dorsal view; **D-F**, *Hyaenictitherium wongii* (Zdansky, 1924) (NHMA-MTLB-1, Samos) in: **D**, lateral; **E**, lingual; **F**, dorsal view. Scale bars: 10 mm.

TABLE 1. — Body mass comparison (in kg; range, average and number of specimens) between *Ictitherium viverrinum* Roth, 1854 and *Hyaenictitherium wongii* (Zdansky, 1924) based on their skull length and m1 length using the equations given in Van Valkenburgh (1990) for canids. Data for fossil species and *Canis lupus* Linnaeus, 1758 from personal data and Semenov (1989). Data for *Canis aureus* Linnaeus, 1758 from Stoyanov (2012).

	Ictitherium viverrinum Roth, 1854	*Hyaenictitherium wongii* (Zdansky, 1924)	*Canis aureus* Linnaeus, 1758	*Canis lupus* Linnaeus, 1758
BM (SKL)	9.81-28.18	17.54-25.21	10.82-17.16	27.88-49.02
	16.84 (n = 7)	20.78 (n = 5)	13.48 (n = 148)	37.39 (n = 13)
BM (m1L)	9.05-13.01	11.72-17.19	10.80-14.83	15.97-27.61
	11.07 (n = 30)	14.20 (n = 30)	12.81 (n = 148)	22.82 (n = 10)

TABLE 2. — Morphological comparison between the m1 of *Ictitherium viverrinum* Roth, 1854 and *Hyaenictitherium wongii* (Zdansky, 1924).

m1	*Ictitherium viverrinum* Roth, 1854	*Hyaenictitherium wongii* (Zdansky, 1924)
Trigonid	Low	High
Talonid	Long and Wide	Short and Narrow
Cingulum	Restricted	Strong lingually
Metaconid-Paraconid Valley	Deep	Shallow
Metaconid-Entoconid Valley	Smooth	Sectorial
Protoconid	Upright	Bent
Metaconid	Blunt	Sectorial
Entoconid	Very Developed	Reduced
Hypoconid	Developed	Reduced
Hypoconulid	Developed	Reduced

Given their notable resemblance with canids, the equations proposed by Van Valkenburgh (1990) for Canidae are used here to estimate their body mass based on skull length and m1 length (Table 1).

Both fossil species were found to have a body mass range of approximately 10-25 kg, with the mean values of *H. wongii* being nearly 20% larger than those of *I. viverrinum* (Table 1). Additionally, the data exhibited in Table 1 show that the attribution of the fossil species to the jackal's (*Ca. aureus*) or wolf's (*Ca. lupus*) body plan is not very clear. In fact, both fossil species fall between the golden jackal and the grey wolf ranges, being closer to the former. The extant canids with the most similar body masses are the coyote (*Ca. latrans*; 7-20 kg; Bekoff 1977) and the Ethiopian wolf (*Canis simensis*; 11-19 kg; Sillero-Zubiri & Gottelli 1994).

Probably the most informative part of the dentition of the carnivorans from an ecomorphological point of view is the lower carnassial, because it is functionally adapted to complete both sectorial and grinding tasks. Table 2 summarizes the morphological observations based on the comparison of the lower carnassials of *I. viverrinum* and *H. wongii* (Fig. 1).

The morphology of m1 exhibits some differences between the two species. Generally, it is clear that the lower carnassial of *H. wongii* is better equipped to fulfill sectorial functions
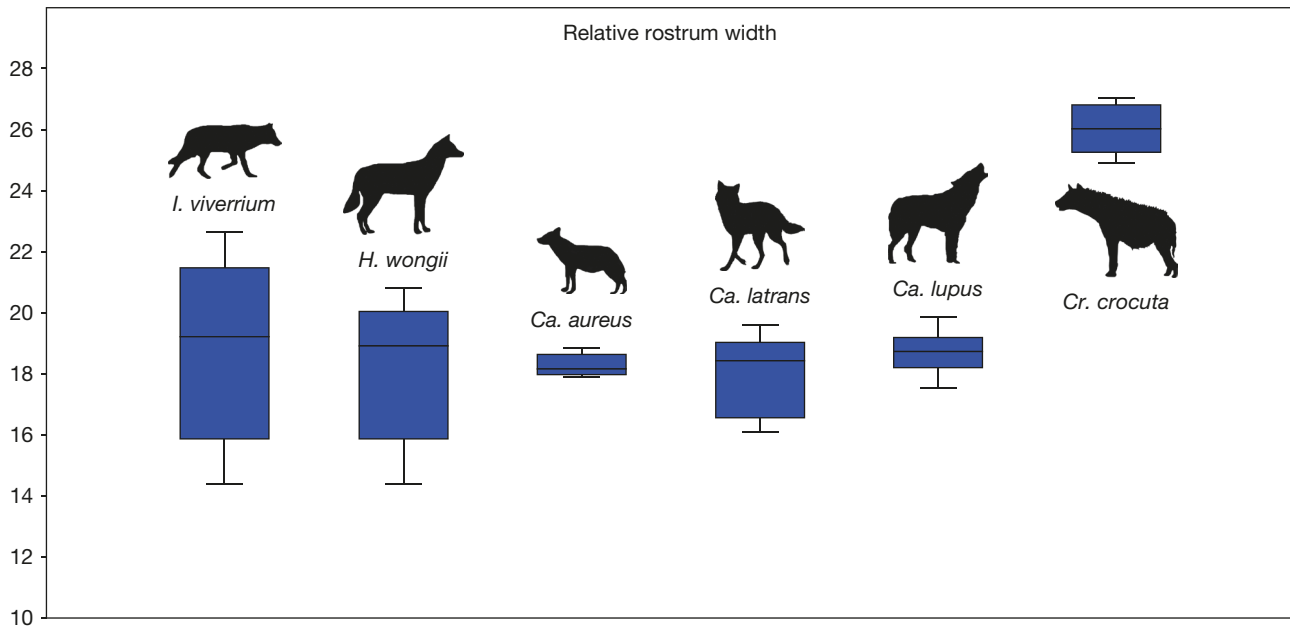
FIG. 2. — Boxplot comparing the relative rostrum width (mm/mm) of *Hyaenictitherium wongii* (Zdansky, 1924) and *Ictitherium viverrinum* Roth, 1854 with that of *Crocuta crocuta* (Erxleben, 1777), *Canis lupus* Linnaeus, 1758, *Canis latrans* Say, 1823 and *Canis aureus* Linnaeus, 1758.

TABLE 3. — Dental wear percentages comparison between *Ictitherium viverrinum* Roth, 1854, *Hyaenictitherium wongii* (Zdansky, 1924) and extant canids belonging to the jackal and wolf group. The levels 1-3 indicate the development of horizontal and vertical wear. The value of the premolars indicates the percentage of specimens that preserved worn premolars.

Species	n	Horizontal			Vertical			Premolars
		1	2	3	1	2	3	
Canis adustus Sundevall, 1847	5	40%	40%	20%	60%	20%	20%	60%
Canis mesomelas Schreber, 1775	4	75%	0	25%	100%	0	0	0
Canis aureus Linnaeus, 1758	4	50%	50%	0	50%	50%	0	0
Canis latrans Say, 1823	5	40%	40%	20%	40%	40%	20%	40%
Speothos venaticus (Lund, 1842)	1	100%	0	0	0	100%	0	0
Cuon alpinus (Pallas, 1811)	1	100%	0	0	0	100%	0	0
Canis lupus Linnaeus, 1758	13	69%	15%	15%	0.69	15%	15%	15%
Lycaon pictus (Temminck, 1820)	4	25%	75%	0	25%	50%	25%	50%
Hyaenictitherium wongii (Zdansky, 1924)	16	25%	44%	31%	31%	31%	38%	75%
Ictitherium viverrinum Roth, 1854	15	40%	33%	27%	40%	47%	13%	57%

(as shown by the higher trigonid, the shorter and narrower talonid, the more pointed metaconid and the reduced talonid cuspids), while that of *I. viverrinum* still retains a great grinding area (as shown by the lower trigonid, the longer and wider talonid, the blunter metaconid and the enlarged talonid cuspids).

The rostrum width at the level of upper canines divided by the total skull length (relative rostrum width) has been connected to dietary habits with wider rostra associated with the hunting of large prey (e.g. Damasceno *et al.* 2013). When comparing this parameter in the two ictitheres and three species of canids (*Ca. lupus*, *Ca. latrans* and *Ca. aureus*), it is clear that there are no significant differences between these groups (Fig. 2). ANOVA test between all the species led to a p-value of 0.72 and the t-test between the two ictitheres to 0.75. Consequently, the two ictitheres do not seem to differ in this parameter. On the contrary, *Cr. crocuta* has a significantly higher relative rostrum width.

Unfortunately, not many I1, I2 or C of the studied ictitheres were available and intact, so the comparison of incisors' and canines' bending strength cannot be considered adequately informative. The S_x parameter for the canines was 19.5 for *H. wongii* (n = 2) and slightly less (19.1) for *I. viverrinum* (n = 2). Again, both species are more similar to *Ca. latrans* (mean 15.0, n = 4), having values higher than *Ca. aureus* (mean 11.0, n = 4) and lower than *Ca. lupus* (mean 28.2, n = 9). A similar correlation is true for the incisors.

Both ictitheres exhibit similar absolute values of endocranial volume, having an average value of 65 ml. A t-test comparison between them resulted in a p-value of 0.12, revealing no significant difference. When the residual BVQ is calculated, the ictitheres have an average value of 86.5, while members of the genus *Canis* have a value of 97.3. Therefore, it is concluded that (according to the present limited sample) these ictitheres had similar endocranial volumes with each other,
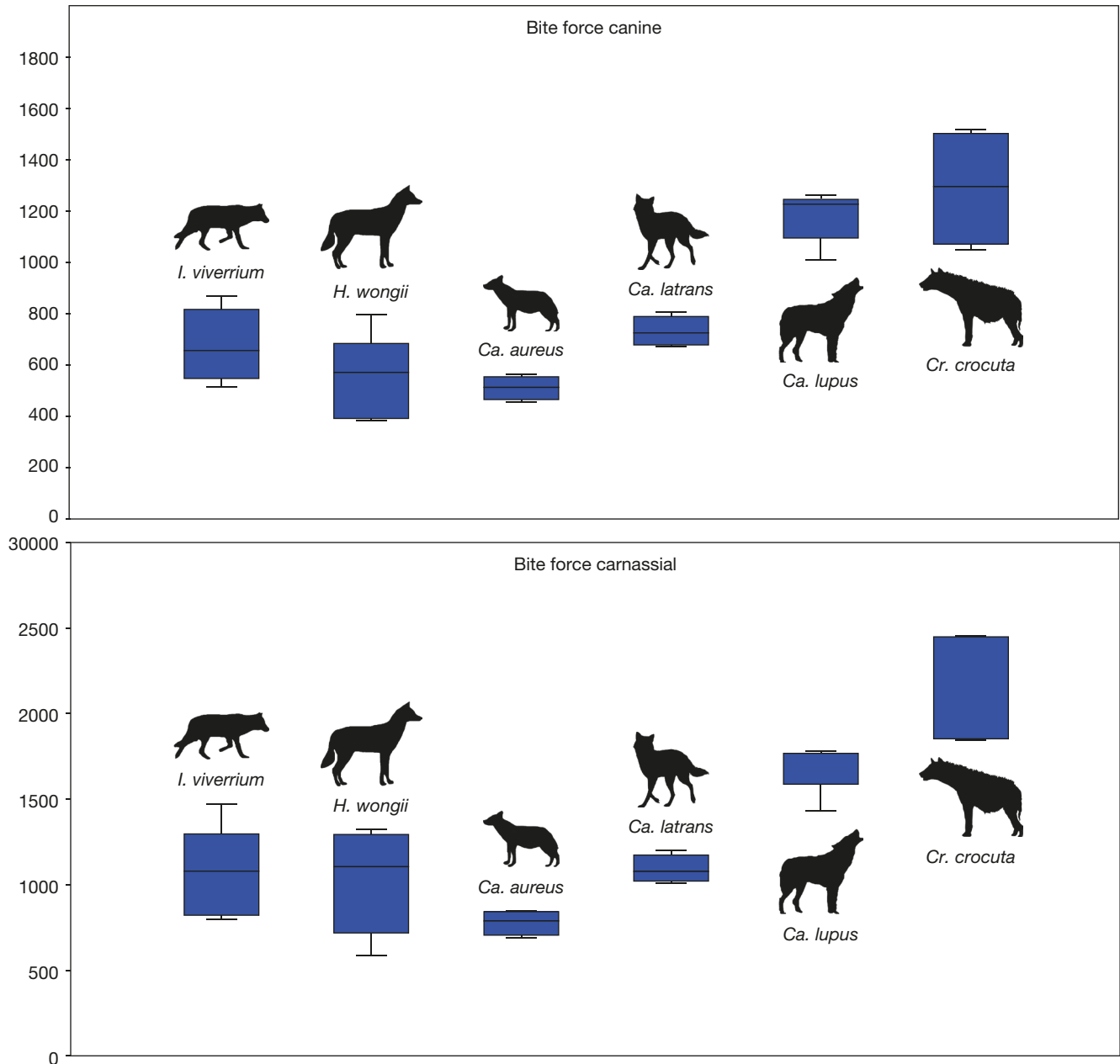
Fɪɢ. 3. — Boxplot comparing the carnassial and canine bite forces (in N) of *Hyaenictitherium wongii* (Zdansky, 1924) and *Ictitherium viverrinum* Roth, 1854 with that of *Crocuta crocuta* (Erxleben, 1777), *Canis lupus* Linnaeus, 1758, *Canis latrans* Say, 1823 and *Canis aureus* Linnaeus, 1758.

but relatively lower values than the canids. The measurements in *Cr. crocuta* are very high, because the method is based on external measurements of the cranium. Therefore, the frontal sinuses are also included. These structures are present also in ictitheres and canids, but they are significantly larger in crocutoid hyenas (Joeckel 1998), biasing the estimations for endocranial volume.

The bite forces of the two ictitheres do not differ significantly in the plane of the canine or the carnassial ($p = 0.29$ and $p = 0.81$ respectively). They both have an average bite force of 1050 N in the carnassial and 600 N in canines (Fig. 3). These values are similar to those resulted in the coyote (1098 N and 736 N respectively, n = 4), higher than those of the golden

jackal (790 N and 517 N respectively, n = 4) and lower than those of the grey wolf (1700 N and 1185 N respectively, n = 5) and *Crocuta crocuta* (2274 N and 1290 N respectively). Other species with similar bite forces to the two discussed ictitheres are *Lynx lynx* (Linnaeus, 1758), *Gulo gulo* (Linnaeus, 1758) and large specimens of *Prionailurus viverrinus* (Bennett, 1833) (Kargopoulos, 2019).

Considering the dental wear of the studied ictitheres, a comparison is made with eight species of canids belonging to the jackal and wolf groups (Table 3). Two types of wear are recognized: horizontal wear, caused by grinding function for the consumption hard material (bones or plants), and vertical wear caused by slicing function for flesh consumption (Fig. 4).
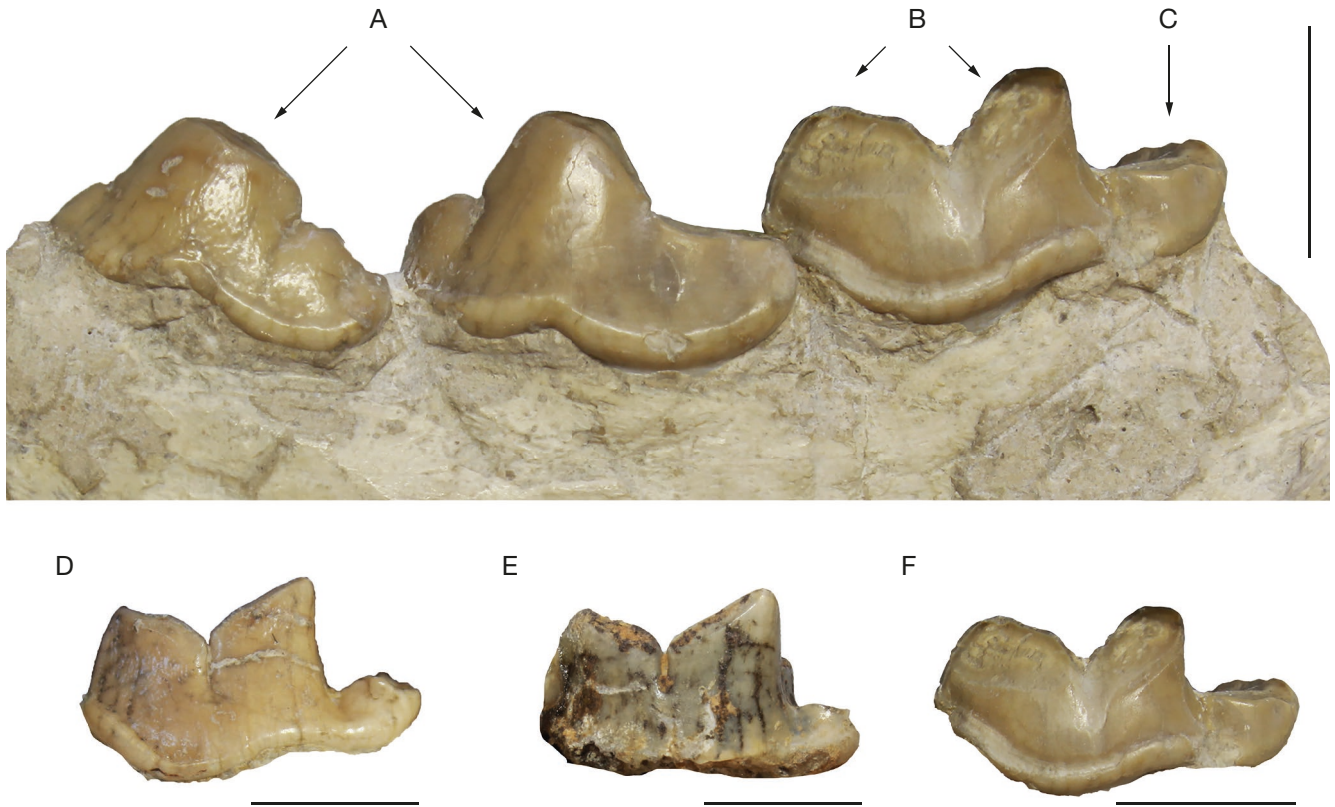
Fig. 4. — **A-C**, The two different types of dental wear in *Hyaenictitherium wongii* (Zdansky, 1924) (NHMW-1911/0005/0778; Samos): **A**, horizontal wear in the premolars; **B**, vertical wear in the m1 trigonid; **C**; horizontal wear in m1 talonid; **D**-**F**, the three wear stages in *Hyaenictitherium wongii*: **D**, no wear (NHMA-MTLB-1; Samos); **E**, moderate wear (NHMW-Mar0015; Maragheh; damaged specimen, flipped horizontally), **F**, extended wear (NHMW-1911/0005/0778; Samos). Scale bars: 10 mm.

The percentage of specimens with worn premolars (a feature connected with durophagy in hyenas; e.g. Werdelin & Solounias 1991) is also mentioned. In general, the variation between the levels of wear is normal, without any extreme values for any of the two species, but the teeth of *H. wongii* are usually more worn than that of *I. viverrinum*, indicating stronger trend to bone consumption.

Unfortunately, most of the studied mandibles of the ictitheres did not possess unbroken distal premolars. Therefore, analysis based on intercuspid notches is highly unsolid. According to the present study, however, both species have some considerably high degree of variability regarding the exact morphology of their accessory cusps in both p3 and p4. Both species exhibit a total notch score of p3 and p4 at approximately 13, which is comparable to that of all three extant canid categories.

Considering the ecomorphological proxies proposed by Sacco & Van Valkenburgh (2004), it is rather difficult to calculate them precisely, since the mandibular condyle is usually destroyed, making the calculation of dentary length impossible. Additionally, most of the skulls do not have associated mandibles. However, some specimens were complete enough to show some trends.

The first proxy based on Sacco & Van Valkenburgh (2004) is M1BSZ: the relative length of trigonid of the lower carnassial. This character has already been mentioned as a difference between the two ictithere species. However, when the trigonid length is divided by the dentary length, this difference is not clear (Fig. 5; t-test p-value = 0.73). Yet, a slight difference between the average values exists. Additionally, all the studied canids have higher values than the ictitheres (p-value <0.01).

The second proxy is the relative area of m2 (M2SZ). Again, there is no significant difference between the two ictitheres (Fig. 6; p = 0.29). Though, the values obtained for *I. viverrinum* seem to be higher. This is probably due to the considerably high variability of *I. viverrinum*. Additionally, the canids have higher values than the ictitheres (p <0.01). This difference probably exists due to phylogenetic constraint of the general trends of the feliforms towards reduced or absent posterior molars. That is the reason that a comparison of the proxy LGR seems irrelevant, since most canids possess m3.

The final proxy based on Sacco & Van Valkenburgh (2004) is the relative area of the upper molars (UGR). This indicator reveals differences between the two ictitheres (p <0.01), with *H. wongii* having smaller molars, and both fossil species having lower values than the canids (p <0.01) (Fig. 7).

DISCUSSION

Summarizing, the ecological distinction of *I. viverrinum* and *H. wongii* is supported by the parameters of body mass, m1 morphology, dental mesowear and UGR, which are showing
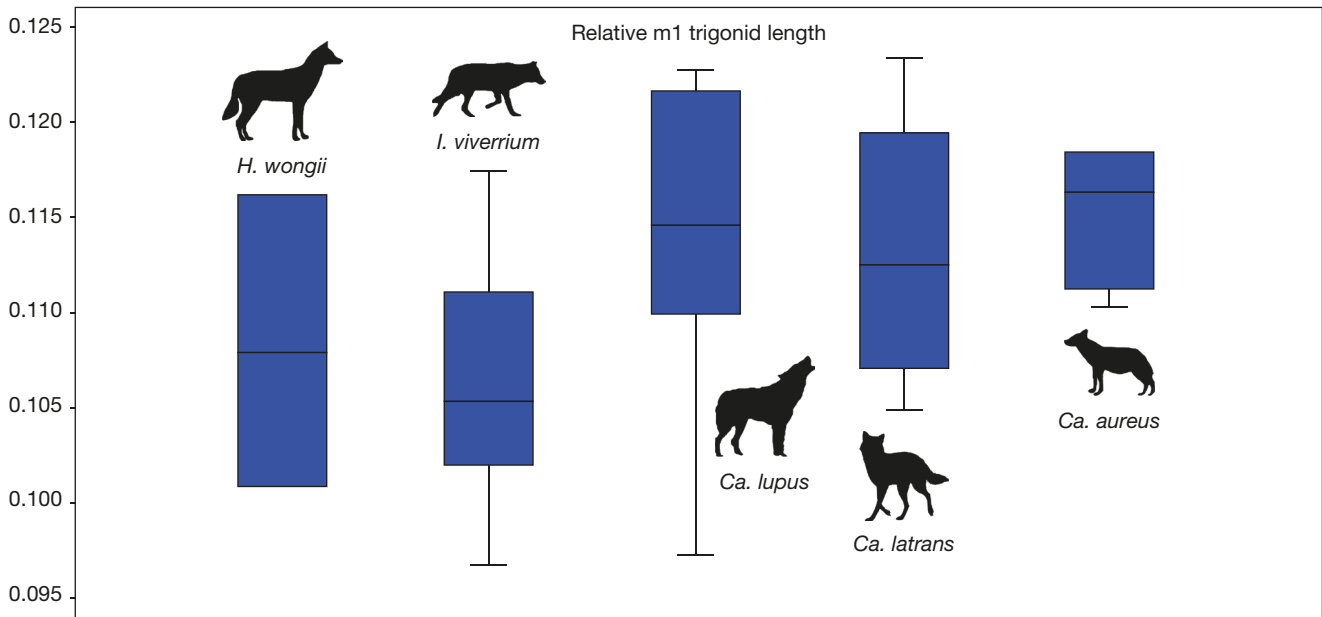
Fɪɢ. 5. — Boxplot comparing the relative trigonid length (M1BSZ in mm/mm) of *Hyaenictitherium wongii* (Zdansky, 1924) and *Ictitherium viverrinum* Roth, 1854 with that of *Canis lupus* Linnaeus, 1758, *Canis latrans* Say, 1823 and *Canis aureus* Linnaeus, 1758.

Tᴀʙʟᴇ 4. — Summary of the t-test statistics for every calculated proxy comparing *Ictitherium viverrinum* Roth, 1854 and *Hyaenictitherium wongii* (Zdansky, 1924).

	Ictitherium viverrinum Roth, 1854		*Hyaenictitherium wongii* (Zdansky, 1924)			
	N	Mean	N	Mean	t	p
Body mass SKL	7	17.603	5	20.908	0.9745	0.3528
Body mass m1	8	10.668	13	14.824	7.4194	<0.0100
Relative rostrum width	5	18.759	5	18.175	0.3295	0.7503
Endocranial volume	7	57.703	5	73.813	1.6970	0.1205
BVQ	6	77.536	4	99.855	2.0222	0.0778
Bite force canines	4	678.82	7	574.97	1.1352	0.2856
Bite force carnassials	5	1068.8	7	1028.9	0.2478	0.8093
M1BSZ	7	0.1066	3	0.1083	0.3593	0.7287
M2BSZ	5	0.0447	3	0.0385	1.1678	0.2872
UGR	4	0.0901	4	0.0722	4.5924	0.0037

a more hypercarnivorous niche for *H. wongii*. However, the parameters of relative rostrum width, canine and incisors' bending strength, endocranial volume, bite force, M1BSZ and M2SZ support that the two species may fill a similar niche. Table 4 depicts the statistical comparison between the two species in the calculated proxies using t-test. This inconsistency of results between the proxies shows that a variety of different methods must be applied in order to make secure suggestions about the ecomorphology of a group.

Both ictitheres are clearly differentiated from the crocutoid ecomorph in every studied proxy, being more similar to the extant canids. However, the attribution of *I. viverrinum* and *H. wongii* to the ecomorphs of jackals and wolves is not verified here. The most similar extant species to both ictitheres in terms of ecomorphology is the coyote (*Ca. latrans*). This correlation shows that both were opportunistic medium-sized carnivorans with a variable diet, probably depending on season and availability. Plant consumption and carrion

scavenging (including the consumption of bone material; Joeckel 1998; Stefen & Rensberger 1999; Tseng 2012) must have occupied a considerable part of their diet, while they could have also hunted their prey, possibly in packs (Werdelin & Solounias 1991).

It has been demonstrated that the two genera share several similarities in terms of ecomorphology. It is therefore considered that they must have been adapted to fill a relatively similar ecological niche. Their high frequency (possibly associated with sociality; Werdelin & Solounias 1991) indicates that both were successful in their environments. It is therefore reasonable that they could have been antagonists. Competitive exclusion (Gause's law; Gause 1934) can lead in either behavioral shift or extinction.

When examining the fossil record of Eastern Mediterranean, it can be observed that in several localities these species have led one another to regional exclusion (Roussiakis 1996; Koufos 2006, 2011). In the localities Ravin
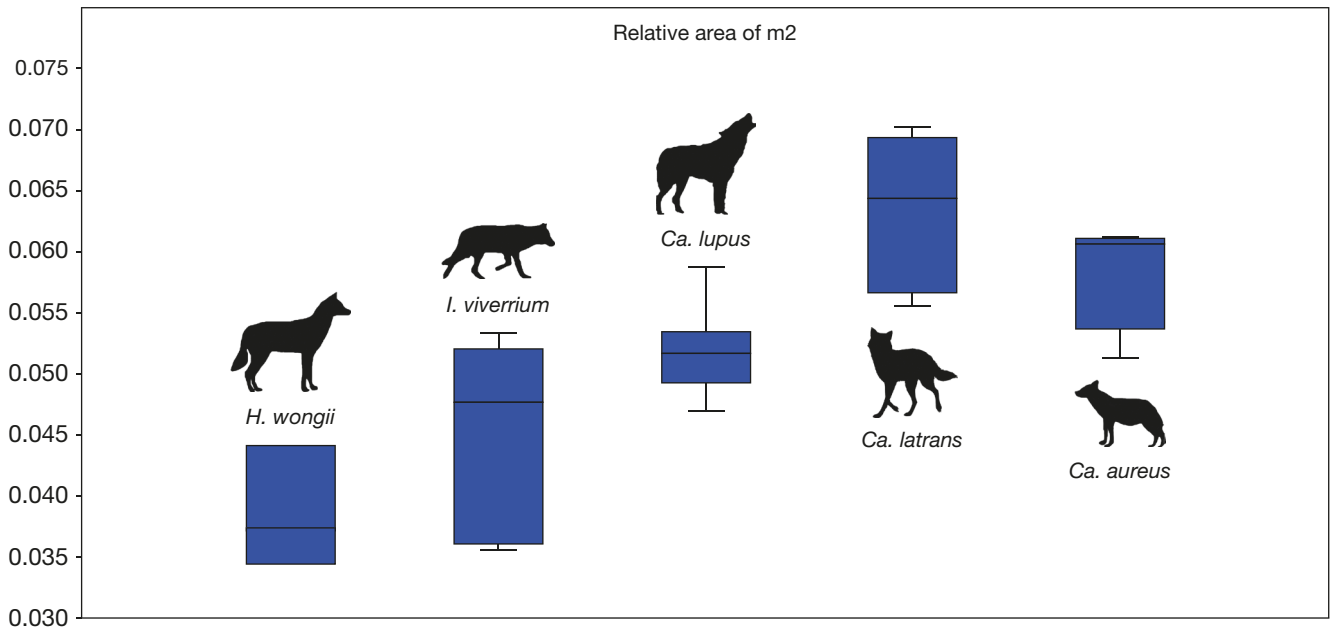
Fig. 6. — Boxplot comparing the relative m2 area (M2SZ in mm²/mm) of *Hyaenictitherium wongii* (Zdansky, 1924) and *Ictitherium viverrinum* Roth, 1854 with that of *Canis lupus* Linnaeus, 1758, *Canis latrans* Say, 1823 and *Canis aureus* Linnaeus, 1758.
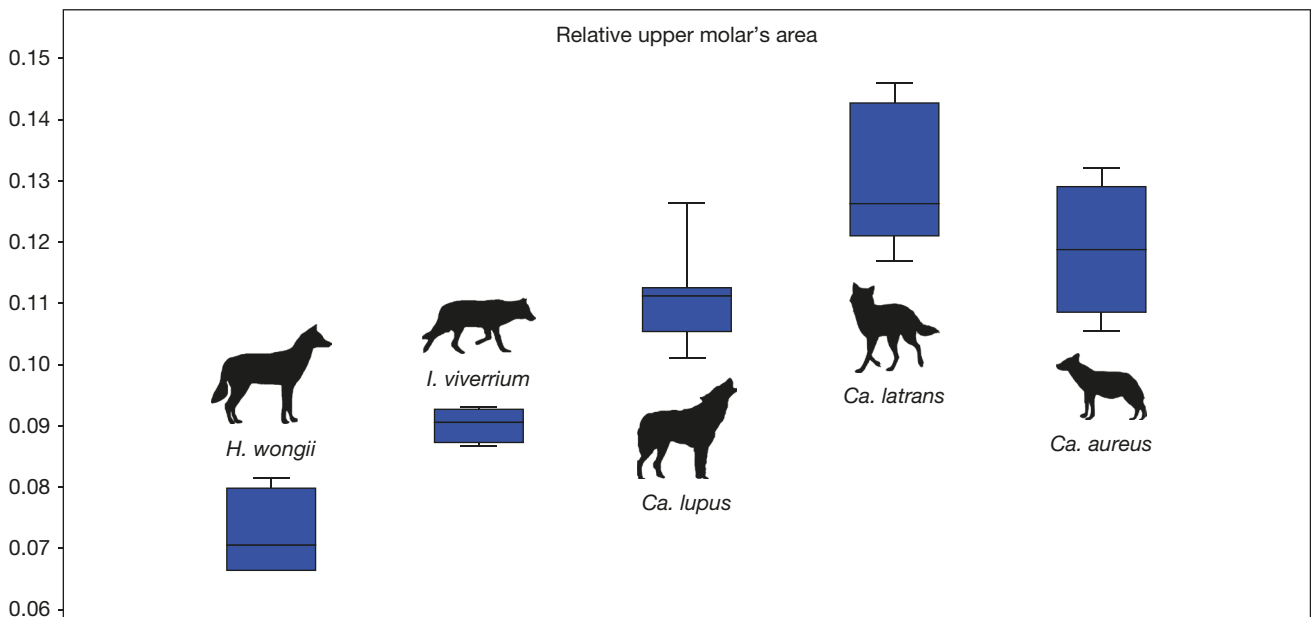

Fig. 7. — Boxplot comparing the relative upper molars' area (UGR in mm²/mm) of *Hyaenictitherium wongii* (Zdansky, 1924) and *Ictitherium viverrinum* Roth, 1854 with that of *Canis lupus* Linnaeus, 1758, *Canis latrans* Say, 1823 and *Canis aureus* Linnaeus, 1758.

des Zouaves 1 (MN 10) and Vathylakkos 2 (MN 11) only *H. wongii* is present (Koufos 2006, 2011). The faunas of the upper horizon of Kerassia (MN 12; Kampouridis *et al.* 2019) and Kemiklitepe (MN 12; de Bonis 1994) also include only *H. wongii* and not *I. viverrinum*. The most interesting difference is spotted during MN 12 between Pikermi and Samos. In these two localities both species have been found, but their relative frequencies are significantly unequal (Koufos *et al.* 2011; Kargopoulos 2019; Roussiakis *et al.* 2019).

Stratigraphic differences between all the aforementioned localities obscure the solidity of the comparison. However, the present knowledge on the spatiotemporal range of these species in Greece indicates a visible differentiation between them. A similar pattern can be seen in other localities in Europe and Asia (NOW Database).

Despite the observed similarities in cranial and dental eco-morphology, these two genera differ in postcranial morphology: the tribe Hyaenotheriini (*sensu* Semenov 2008) is characterized

by long and slender limbs, whereas the genus *Ictitherium* has been found to have relative short and stout limbs (Semenov 1989, 2008; Werdelin & Solounias 1991). This trend differentiates species that are better adapted to open and closed environments respectively, making *H. wongii* a more cursorial form than *I. viverrinum*. This fact is in agreement with the general assumption that the environment of Samos is considered more open than that of Pikermi (e.g. Giaourtsakis *et al.* 2006; Koufos *et al.* 2009; and references therein), thus allowing *H. wongii* to be dominant.

Even though the two forms exhibit a considerable degree of mutual exclusion in several localities, there are other sites where they have been found together, such as Akkaşdaği (de Bonis 2005), Prochoma 1 (Koufos 2021) and Vathylakkos 3 (Koufos 2011, 2021). These cases of coexistence are interpreted as occasions of regional environmental diversity that enabled both species to occupy separate roles in the same ecosystem. Hopefully, future finds from various localities will provide larger samples that will allow us to comprehensively compare the populations' correlations between the two species.

CONCLUSIONS

The majority of the ecomorphological proxies based on cranial and dental material indicates that *I. viverrinum* and *H. wongii* did not have distinct jackal-like and wolf-like ecological roles respectively, as considered before. On the contrary they both seem to occupy a niche similar to that of extant coyote (*Canis latrans*).

However, their postcranial morphology, together with some dental adaptations, indicate that *H. wongii* was more cursorial and less opportunistic than *I. viverrinum*.

Their ecological similarity led to their mutual exclusion, as they are not found as dominant species in the same locality. Their differences led *H. wongii* to fit better in more open (e.g. Samos) and *I. viverrinum* to more closed environments (e.g. Pikermi).

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