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Plioviverrops faventinus reloaded: the last survivor of a successful genus

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ABSTRACT - The taxonomic and systematic conundrum of Middle to Late Miocene small-sized hyaenids includes several taxa generally ascribed to the genera Protictitherium *and* Plioviverrops*. Especially the latter was often related to the extant aardwolf,* Proteles cristatus*, although a recent study suggests the new genus* Gansuyaena *as being the plausible ancestor of the African* Proteles*. In general terms, few studies have concentrated specifically on these small hyaenids, and little is known with regard to their systematics and phylogenetic relationships. Rather, they were ecomorphologically divided in civet-like and mongoose-like hyaenids based on their morphological and metric features. Often overlooked in literature,* Plioviverrops faventinus *was originally described by Danilo Torre, who was the first to recognise the peculiarity of the most recently established species of the genus* Plioviverrops*. In the present paper, we revise the sample from the type locality of Cava Monticino (Brisighella, Ravenna, Italy) clarifying the affinities and differences with other species of* Plioviverrops *as well as of* Protictitherium *and* Gansuyaena*. Moreover, we focus on dentognathic features to test the ecological preferences of* P. faventinus *and other small-sized hyaenids, compared to a sample of extant Herpestidae and Viverridae. Our ecological results suggest the marked hypocarnivorous/invertebrivorous specialisation of* P. faventinus *similar to some extant herpestids.*

INTRODUCTION

The family Hyaenidae is nowadays represented by only four species living in sub-Saharan Africa and southwestern Asia: *Crocuta crocuta* Erxleben, 1777, *Hyaena hyaena* Linnaeus, 1758, *Parahyaena brunnea* (Thunberg, 1820) and *Proteles cristatus* (Sparrman, 1783). All these species, except for the aardwolf (*Pt. cristatus*), are bone-cracker carnivores specialised in consuming meat and bones (Nowak, 2005), displaying several craniomandibular characteristics adapted to this diet such as buccolingual wide cheek teeth and a strong cranial and mandibular muscular structure (see hyaenid ecomorphotypes in Werdelin & Solounias, 1991, 1996). During most of the Miocene and specially during the second half of this epoch, hyaenids exhibited a huge ecological and specific diversity occupying several ecological niches todays restricted to canids and mustelids (Wang et al., 2008; Tseng & Wang, 2011). At least 70 species of extinct hyaenas are known today, and due to the impossibility to reconstruct their exact phylogeny for the sometimes-scarce fossil record, Werdelin & Solounias (1991, 1996) classified these taxa using their ecological role and their morphology. Six ecomorphotypes were identified (Werdelin & Solounias, 1996): civet-like, mongoose-like, jackal- and wolf-like meat and bone-eaters, cursorial meat and bone-eaters, transitional bone-crackers and fully developed bone-crackers (groups 1 to 6, respectively). Though these groups well represent the variability of adaptations in the Miocene fossil hyaenas, it is not always easy to allocate the various fossil species to one group or to another (see Werdelin & Solounias, 1991). Recently even this reasonable scheme has proven its plausible limits (Coca-Ortega & Pérez-Clarós, 2019; Pérez-Clarós & Coca-Ortega, 2020). Within the group of most basal hyaenas, *Plioviverrops* Kretzoi, 1938 was one of the most successful genera with a fossil record which encompassed most of the Miocene and beyond (Turner et al., 2008). This genus is defined sometimes as mongoose-like and sometimes as civet-like hyaenas. There are at least four species of *Plioviverrops* characterised by small dimensions (i.e., a body-mass range between 2 and 7 kg) and ecological adaptations somewhat in between those of modern insectivores and hypocarnivores. Despite the long-spanning time range from the Early Miocene to the Early Pliocene (MN4-MN15; Turner et al., 2008), *Plioviverrops* spp. are mostly represented and diversified in European Tortonian-Messinian faunal assemblages (MN11-MN13; following Hilgen et al., 2012), with remains found in France, Spain, Italy, Greece and Bulgaria, showing very effective ecological adaptations. Furthermore, this taxon is one of the few Hyaenidae genera that survived the Mio-Pliocene boundary, when a drastic reduction on hyaenid ecological diversity and relative abundance took place, possible due to various causes such as climate changes and the arrival into Eurasia and Africa of canids from North America (Sotnikova & Rook, 2010; Tseng & Wang, 2011).

Systematic and taxonomic tangle of Plioviverrops

Plioviverrops is among the oldest taxa of Hyaenidae to appear, together with *Protictitherium* and *Tungurictis*, in the late Early Miocene (MN4-MN5, ca. 17 Ma; see Hilgen et al., 2012 and references therein) of Europe (for *Protictitherium* and *Plioviverrops*) and East Asia (for *Tungurictis*) (Werdelin & Solounias, 1991; Turner et al., 2008; Wang et al., 2020). Despite their relative primitiveness, these taxa are all characterised by showing a high specific diversity (Werdelin & Solounias, 1991;

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Reference	**Family**	**other ranks**	**Taxon**				
			gervaisi	***gaudryi***	***orbignyi***	***guerini***	***faventinus***
			MN4-5	*MN7-8*	*MN7-12 ->MN14*	*MN12*	*MN13-MN14*
Gaudry & Lartet, 1856	Viverridae				*Viverra orbignyi*		
Trouessard, 1897	Viverridae	Ictitheriinae			*Ictitherium*		
Dietrich, 1927	Viverridae				*Ictitherium*		
Kretzoi, 1938	Hyaenidae sensu lato = Viverridae	Ictitheriinae			*“Ictitherium” d’orbignyi* but *Plioviverrops*		
De Villalta-Comella & Crusafont-Pairó, 1943	Viverridae		-			*Herpestes* cf. *crassus*	-
De Villalta-Comella & Crusafont-Pairó, 1948	Viverridae		-			*Herpestes guerini* (Piera+Concud)	-
Viret, 1951	Viverridae		-		“*Ictitherium*”		-
Mein, 1958	pars Viverridae & pars Hyaenidae		pars *J. grivensis* & pars *Progenetta* cf. *praecurrens*				
Thenius, 1966					*Ictitherium*		
de Beamont, 1967	Hyaenidae						
Crusafont-Pairó & Petter, 1969			-			*Plioviverrops* (?) (Los Mansuetos)	-
de Beamont, 1969	Hyaenidae		-		*Plioviverrops*		-
de Beamont & Mein, 1972	?Hyaenidae		*Plioviverrops* (*Protoviverrops*) *gervaisi* (Vieux-Collonges)	*Plioviverrops* (*Mesoviverrops*) *gaudryi* (La Grive de Saint-Alban)	*Plioviverrops* (*Plioviverrops*)	*Plioviverrops* (*Mesoviverrops*)	-
Schmidt-Kittler, 1976	Hyaenidae		*Plioviverrops* (*Protoviverrops*) (related to *Protictitherium intermedium*)		*Plioviverrops* (*Plioviverrops*)		
Petter, 1976	Hyaenidae		?*Plioviverrops* (*Protoviverrops*)		*Plioviverrops*		
Torre, 1989	Hyaenidae		*Plioviverrops*	*Plioviverrops*	*Plioviverrops*	*Plioviverrops*	*Plioviverrops*
Semenov, 1989	Viverridae	Ictitheriinae	*Plioviverrops*	*Plioviverrops*	*Plioviverrops*	*Plioviverrops*	
Hunt & Solounias, 1991	Hyaenidae				*Plioviverrops*		
Werdelin & Solounias, 1991	Hyaenidae		*Plioviverrops*	*Plioviverrops*	*Plioviverrops*	*Plioviverrops*	
de Bonis, 1994	Hyaenidae						
Ginsburg, 1999	Hyaenidae	Ictitheriinae	*Plioviverrops*	*Plioviverrops*	*Plioviverrops*	*Plioviverrops*	*Plioviverrops*
Turner et al., 2007	Hyaenidae		*Plioviverrops* (maybe =*gaudryi*)	*Plioviverrops* (maybe =*gervaisi*)	*Plioviverrops*	*Plioviverrops*	‘*Plioviverrops*’
Semenov, 2008	Viverridae	Ictitheriinae					
Sen & Sarac, 2017	Hyaenidae				*Plioviverrops*		
Spassov et al., 2019	Viverridae	Ictitheriinae			*Plioviverrops*		
Galiano et al., 2022	Hyaenidae	Protelinae	*Protoviverrops* (not in Protelinae) and including *Protictitherium intermedium* as *Protoviverrops intermedium*	*Mesoviverrops*	*Plioviverrops*	*Gansuyaena*	*Plioviverrops*

Turner et al., 2008; Wang et al., 2020). Their taxonomy and phylogenetic affinities have been a hotly debated topic among scholars nearly since their description (de Beaumont & Mein, 1972; Werdelin & Solounias, 1991; Turner et al., 2008; Galiano et al., 2022).

Starting with the authorship of the generic name, the first to propose it was Kretzoi (1938) for *Viverra orbignyi* Gaudry & Lartet, 1856 from Pikermi (Greece; Gaudry, 1862). In this work, Kretzoi included the taxon "*Ictitherium*" *d'orbignyi* (Kretzoi, 1938, p. 114) in Ictitheriinae Trouessart, 1897, one of the two phyletic groups of his "Hyaenidae sensu lato" ("Die in diesem weiteren Sinn aufgefaßten Hyaeniden"; cf. Kretzoi, 1938, p. 112). On the one side, he maintained plausible the attribution to Viverridae (evidently included in this "Hyaenidae sensu lato") and, on the other, considering the impossibility of associating the morphological features of the Greek specimens to those of *Ictitherium* Wagner, 1848 or with those of living Viverridae, Kretzoi proposed the new generic attribution of *Plioviverrops*.

Second issue is that of the familial identity of *Plioviverrops*, as well as *Protictitherium* and other taxa originated in the Early Miocene. Although apparently easy to solve, the matter remained open in the literature for a long time (e.g., de Beaumont, 1969) and periodically re-emerges (Semenov, 1989, 2008; Spassov et al., 2019; Tab. 1). Nowadays, a fairly wide consensus has established in considering these taxa and their lineages as hyaenids (among others Turner et al., 2008; Coca-Ortega & Pérez-Claros, 2019; Wang et al., 2020; Galiano et al., 2022; Tab. 1). Genetic evidence has clearly pointed out that the sister group to the whole family Hyaenidae are the Herpestidae and Eupleridae (Koepfli et al., 2006; Agnarsson et al., 2010; Eizirik et al., 2010; Zhou et al., 2017; Westbury et al., 2019; Hassanin et al., 2021), and Viverridae stems at the base of the clade Hyaenidae + Herpestidae + Eupleuridae (see also Gaubert & Cordeiro-Estrela, 2006; Hassanin et al., 2021). Estimation of divergence between the latter three families (Hyaenidae and Herpestidae + Eupleuridae) suggests the arise of two clades during the Oligocene, generally with a mean age of divergence around 29 Ma (Koepfli et al., 2006; Zhou et al., 2017), although older (32.5 Ma; Eizirik et al., 2010) and younger estimations (24.5 Ma; Hassanin et al., 2021) have been proposed. Despite the uncertainties, these ages are far older than the oldest recognised hyaenid (ca. 17-16 Ma; see below). In the past, there was a fairly generalised consensus among scholars on which of the many earliest Miocene (Aquitanian, MN2; Hilgen et al., 2012) taxa of Europe could be among the ancestor of the whole Hyaenidae. Among these, *Herpestides antiquus* (de Blainville, 1841) particularly sparked the interest of scholars. This basal aelouroid taxon was often considered as the first member of a lineage leading to all hyaenids (de Beaumont, 1967), especially relevant for the genus *Plioviverrops* (de Beaumont & Mein, 1972) or to *Proteles* and its lineage (Thenius, 1966; Galiano et al., 2022). Nevertheless, nowadays, *H. antiquus* is recognised as a viverrid (Hunt, 1991; Turner et al., 2008) and Werdelin & Solounias (1991) discouraged its use as a stem hyaenid due to the poor phylogenetic significance of its features. Regarding the earliest occurrence of hyaenids, there is still debate. de Bonis (1994) proposed "*Herpestides*" *collectus* de Bonis, 1973 from the MN2b (early Burdigalian) locality of Laugnac (France) as the earliest hyaenid of the fossil record. Indeed, de Bonis (1994) redescribed the specimens and ascribed them to *Plioviverrops*, as *Plioviverrops collectus*. Turner et al. (2008) recognised the distinction of "*H.*" *collectus* from the genus *Herpestides* de Beaumont, 1967 but pointed out the lack of sufficient support for an attribution to either *Plioviverrops* or even to a Hyaenidae. We share Turner et al. (2008) doubts on, at the very least, de Bonis (1994)'s generic attribution. Unchallenged attribution of hyaenids comes from European deposits of the MN4-MN5 and are attributed to *Protictitherium* and *Plioviverrops*. Here we briefly but exhaustively review the known-knowns and the known-unknowns on the species historically ascribed to *Plioviverrops* (see Tab. 1). A list of known occurrences is reported in Tab. 2 and in Fig. 1.

The earliest taxon attributed to the genus in study herein is *Plioviverrops gervaisi* de Beaumont & Mein, 1972, described from the locality of Vieux Collonges, France (see Mein, 1958; correlated between MN4-MN5; de Bruijn et al., 1992; Mein, 1999; Steininger, 1999). The hypodigm of the species includes only few and isolated dental specimens (de Beaumont & Mein, 1972) that were initially ascribed in pars to *Progenetta* cf. *praecurrens* Dehm, 1950 and in pars to *Journanictis grivensis* Viret, 1951 by Mein (1958). *Plioviverrops gervaisi* is known from the type locality and reported also from Calatayud (Spain, MN6; Petter, 1976). In their hypothesis of the lineage of the early hyaenid *Plioviverrops*, de Beaumont & Mein (1972) identified *P. gervaisi* as the oldest and the most primitive of the lineage. This led them to propose the new subgenus *Protoviverrops* de Beaumont & Mein, 1972 to accommodate this primitiveness. Schmidt-Kittler (1976) retained this vision and pointed out the similarity between *P. gervaisi* and his new species *Protictitherium intermedium* Schmidt-Kittler, 1976 (Paşalar, Turkey, late MN5-MN6; Mayda et al., 2015), although the latter is somewhat more derived (i.e., towards other *Protictitherium* species). Werdelin & Solounias (1991) ignored the subgeneric distinction of de Beaumont & Mein (1972) and suggested instead the possible synonymy of *P. gervaisi* with *Plioviverrops gaudryi* de Beaumont & Mein, 1972 (see below), considering the similarity, the scarcity of specimens and limited diagnostic differences between them. Recently, Galiano et al. (2022) reproposed the use of *Protoviverrops* elevating it to generic rank. In their work, they use it for *Protoviverrops gervaisi* and *Prot. intermedium*. In the phylogenetic analysis proposed in the same work, these taxa were a priori included in a single operational taxonomic unit (OTU) that stems at the base of the clade of other Hyaenidae (apart from *Tungurictis*) (Galiano et al., 2022). Despite the clear primitiveness of both these taxa, their congenericity might need additional evidence and a deeper discussion.

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Tab. 1 - Summary of attribution and interpretations of *Plioviverrops* spp. (in terms of taxonomy and phylogenetic affinities) available in literature. See text for additional details.

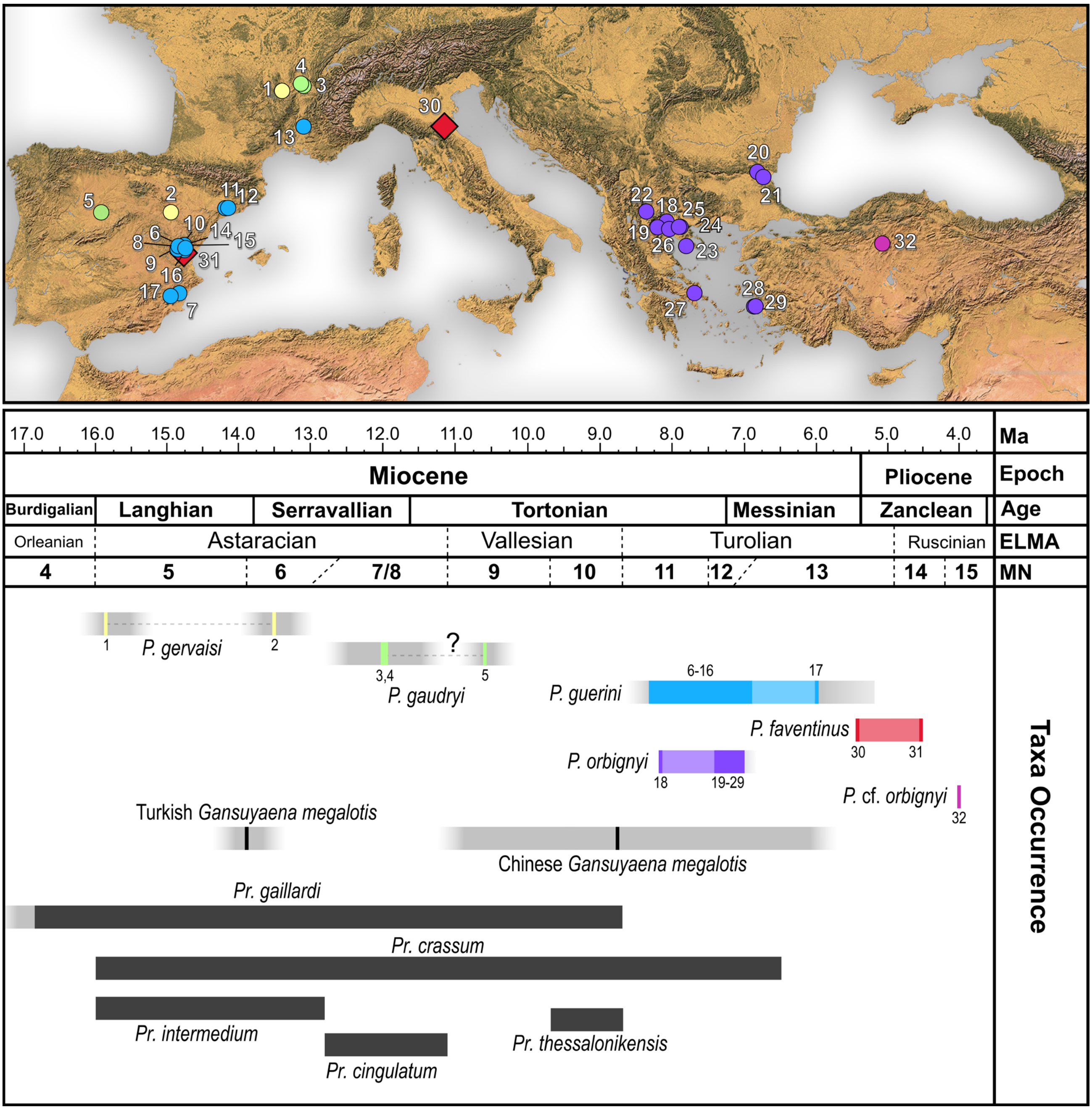


Fig. 1 - (color online) Spatial and temporal distribution of *Plioviverrops* species, with number of localities the same as in Tab. 2. At the bottom, the chronological distribution of taxa discussed in the text, i.e., *Gansuyaena megalotis* from Turkey (Schmidt-Kittler, 1976; Galiano et al., 2022) and China (Galiano et al., 2022); *Protictitherium cingulatum* (Schmidt-Kittler, 1976; Fraile, 2015; Mayda et al., 2015); *Protictitherium crassum* (Fraile, 2015, 2017); *Protictitherium gaillardi* (Koufos, 2012b; Fraile, 2015); *Protictitherium intermedium* (Schmidt-Kittler, 1976; Kaya et al., 2003; Fraile, 2015; Mayda et al., 2015); *Protictitherium thessalonikensis* (Koufos, 2012b). Abbreviations in the figures: *P.*, *Plioviverrops*; *Pr.*, *Protictitherium*.

The second species, in terms of chronology of its localities (Tab. 2 and Fig. 1), is *P. gaudryi* described from the MN7/8 French site of La Grive-Saint Alban (de Beaumont & Mein, 1972). As in the case of *P. gervaisi*, *P. gaudryi* is known almost exclusively from dental material. Again similarly to *P. gervaisi*, the authors describing it proposed a the new subgeneneric distinction, *Plioviverrops* (*Mesoviverrops*) de Beaumont & Mein, 1972, accounting for the dental features intermediate between *Protoviverrops* and true *Plioviverrops*, i.e., *Plioviverrops orbignyi* (Gaudry & Lartet, 1856). It should be noted that the type specimen of *P. gaudryi* (the maxillary fragment with P4-M1 MdC.LGr.1360) was originally part of the hypodigm of *Jourdanictis grivensis* Viret, 1951. In his revision of carnivorans from La Grive, Viret (1951) created this new viverrid taxon while also noting a plausible similarity with *Plioviverrops*, especially for upper teeth (Viret, 1951). Following authors supported this plausible relationships (de Beaumont, 1967, 1969; Crusafont-Pairó & Petter, 1969) until de Beaumont &

	Locality	Country	Chronology	Species	Ref.
1	Vieux Collonges	France	MN5 (16.0-13.7 Ma)	*P. gervaisi*	a
2	Calatayud	Spain	MN6 (13.7-12.75 Ma)	*P. gervaisi*	a
3	La Grive 1	France	MN7/8 (ca. 12.75-11.1 Ma)	*P. gaudryi*	a
4	La Grive 2	France	MN7/8 (ca. 12.75-11.1 Ma)	*P. gaudryi*	a
5	Los Valles de Fuentidueña	Spain	MN9 (11.1-9.7 Ma)	*Plioviverrops* cf. *gaudryi*	b
6	Puente Minero	Spain	MN11 (8.3 Ma)	*P. cf. guerini*	c
7	Crevillente 2	Spain	MN11 (ca. 8.16 Ma)	*P. guerini*	d
8	Viveros de Pinos	Spain	MN11 (8.7-7.5 Ma)	*P. guerini*?	e
9	Los Aguanaces	Spain	MN11 (~8.1 Ma)	*P. cf. guerini*	c
10	Los Aljezares-Aljezar B	Spain	MN12 (7.87 Ma)	*P. guerini*	c
11	Piera - Torrentet de Traginers	Spain	MN12 (ca. 7.6-7.1 Ma)	*P. guerini*	f
12	Torrent del Gall Mullat	Spain	MN12 (ca. 7.6-7.1 Ma)	*P. guerini*	g
13	Les Mistrales III	France	MN12 (ca. 7.6-7.1 Ma)	*P. guerini*	This work
14	Los Mansuetos	Spain	MN13 (6.9-6.8 Ma)	*P. guerini*	h
15	Concud-Cerro de la Garita	Spain	MN13 (6.9-6.8 Ma)	*P. guerini*	f
16	Las Casiones	Spain	MN13 (6.8 Ma)	*P. guerini*	i
17	La Alberca	Spain	MN13 (7.1-5.3 Ma)	*P. guerini*	j
18	Ravin des Zouaves 5	Greece	MN11 (ca. 8.2 Ma)	*P. orbignyi*	k
19	Prochoma-1	Greece	MN12 (ca. 7.6-7.1 Ma)	*P. orbignyi*	l
20	Kalimantsi 2	Bulgaria	MN12 (ca. 7.6-7.1 Ma)	*P.* cf. *orbignyi*	m
21	Kalimantsi 4	Bulgaria	MN12 (ca. 7.6-7.1 Ma)	*P. orbignyi*	m
22	Kiro Kuchuk	Northern Macedonia	MN12 (ca. 7.6-7.1 Ma)	*P. orbignyi*	n
23	Kryopigi	Greece	MN12 (ca. 7.6-7.1 Ma)	*P. orbignyi*	o
24	Vathylakkos-2	Greece	MN12 (ca. 7.3 Ma)	*P. orbignyi*	p
25	Vathylakkos-3	Greece	MN12 (ca. 7.3 Ma)	*P. orbignyi*	q
26	Perivolaki	Greece	MN12 (ca. 7.3-7.1 Ma)	*P. orbignyi*	r
27	Pikermi	Greece	MN12 (ca. 7.1 Ma)	*P. orbignyi*	p
28	Samos	Greece	MN12 (ca. 7.1 Ma)	*P. orbignyi*	p
29	Mytilinii-1 B	Greece	MN12 (ca. 7.1-7.0 Ma)	*P. orbignyi*	l
30	**Brisighella**	**Italy**	**MN13 (5.4 Ma)**	***P. faventinus***	
31	La Gloria 4	Spain	MN14 (4.54 Ma)	*P. faventinus*	e
32	Çalta-1	Turkey	MN15 (4.0 Ma)	*P. orbignyi?*	s

Tab. 2 - List of occurrences of *Plioviverrops* spp. known in literature. The number on the left refers to the localities of Fig. 1. References: [a] de Beaumont & Mein (1972); [b] Ginsburg et al. (1981); [c] Van Dam et al. (2001); [d] Montoya (1994); [e] Alcalá (1994); [f] De Villalta-Comella & Crusafont-Pairó (1948); [g] Golpe-Posse (1974); [h] Crusafont-Pairo & Petter (1969); [i] Salesa et al. (2012); [j] Piñero et al. (2017); [k] de Bonis & Koufos (1991); [l] Koufos et al. (2009); [m] Spassov et al. (2006); [n] Spassov et al. (2019); [o] Lazaridis (2015); [p] Koufos (2009); [q] Koufos (2000); [r] Koufos (2006); [s] Sen & Saraç (2018).

Mein (1972) erected *P. gaudryi* on the very same maxillary fragment. In the same paper the latter authors reinforced the idea that, although MdC.LGr.1360 is a *Plioviverrops*, the mandibles MNHL.LGr.1361 and MNHL.LGr.1362 are clearly different in dental morphology (especially in comparison to the m1 NMB Ga 2113, the other specimens from La Grive-St. Albain; see de Beaumont & Mein, 1972) and belong to the viverrid *Jourdanictis*. Thus, the latter remains a valid viverrid taxon described from the same locality. This complex but straightforward attribution is followed by numerous authors (e.g., Kargopoulos et al., 2021) although some have synonymised *P. gaudryi* and *J. grivensis* (e.g., Galiano et al., 2022). The generic distinction of *P. gaudryi* was retained by Galiano et al. (2022) as *Mesoviverrops gaudryi*. Nevertheless, the correspondent OTU in the phylogeny ("*Mesoviverrops* sp."; see Galiano et al., 2022) clusters with *P. orbignyi*, decreasing the support to the generic distinction between these taxa (Galiano et al., 2022). The only additional occurrence of *P. gaudryi* is that of Los Valles de Fuentidueña reported by Ginsburg et al. (1981).

The species *P. orbignyi* is the most renowned and the best characterised of the genus, thanks to an abundant record of cranial and postcranial specimens (unlike many species of the genus) and rich history of taxonomic classification and study (since Gaudry, 1862). As mentioned above, Kretzoi (1938) chose it as the genotype species of *Plioviverrops* and de Beaumont & Mein (1972) reinforced this with the nominotypical subgenus. The majority of the occurrences of *P. orbignyi* comes from southeastern Europe, mainly located in Greece and in the Balkan area (see Fig. 1) and principally dated to the Turolian (MN12, see Tab. 2). The attribution to this species of the material from Gorna Sushitsa (Spassov et al., 2019) is doubtful (for the morphology of the p4 more similar to *Protictitherium*) and we prefer not including it. Similarly, occurrences reported outside the Greco-Balkan region (Koufos, 2009; Robles, 2014) remain doubtful and should be disregarded. Additionally, the occurrence of a small ictitheriine in the Early Pliocene locality of Çalta-1 (MN15, 4.0 Ma; Bernor & Sen, 2017), similar in size and dental features to *P. orbignyi*, challenges previous understanding of the evolution of *Plioviverrops*. If the provenance from Pliocene layers remained confirmed (since Turolian beds and fossils also crop out in the area; see Sen & Saraç, 2018), the presence of *Plioviverrops* in Çalta-1 would suggest a complex chronological setting that may indicate the presence of closely related species or a continuation of the lineage, once limited to the Miocene, into the Pliocene (Sen & Saraç, 2018). It is indeed uncertain if this taxon is conspecific with the Turolian species or rather a new taxon (Sen & Saraç, 2018).

Historically considered as the end term of the generic tendency towards hypocarnivory (de Beaumont & Mein, 1972; Werdelin & Solounias, 1991), *P. orbignyi* has been the subject of extensive discussion especially in relation to the extant aardwolf (the only living non-durophagous hyaenid). The morphology of *P. orbignyi* points out a certain degree of affinity with *Proteles*, e.g., its primitive auditory bullae are comparable to those of the aardwolf (Werdelin & Solounias, 1991). Thenius (1966) indeed identified this species as the ancestor of *Proteles*. Yet it could be argued that these similarities are symplesiomorphies and other features shown by *P. orbignyi* cannot be found in *Proteles*, e.g., the presence of an alisphenoid canal, a primitive character state for Hyaenidae (Werdelin & Solounias, 1991). Aside from the relationship with *Proteles* (see also below), nowadays *Plioviverrops faventinus* Torre, 1989 is considered the taxon of the lineage of *Plioviverrops* in which the derived morphology towards omnivory/insectivory culminates (Torre, 1989; Turner et al., 2008; Coca-Ortega & Pérez-Clarós, 2019).

Late Miocene deposits of western Spain yielded on of the youngest species of *Plioviverrops*, described as *Plioviverrops guerini* (De Villalta-Comella & Crusafont-Pairó, 1948) from the sites Torrentet de Traginers (Piera, MN12) and Concud-Cerro de la Garita (MN12) (Werdelin & Solounias, 1991; Alcalá, 1994; Montoya, 1997). The species is confidently confined to the MN11-MN12 of the Iberian Peninsula and France (Fig. 1), as older occurrences (Koufos, 2009; Robles, 2014) or records outside this area are dubious (e.g., Koufos, 2011) and should be disregarded. Dental features of *P. guerini* are comparable to those of *P. gaudryi*, despite the difference in age between the two occurrences (Fig. 1) and the larger size of the Iberian taxon (de Beaumont & Mein, 1972; Werdelin & Solounias, 1991). Indeed, the “primitiveness” of its features in comparison to the coeval *P. orbignyi* is striking, as Werdelin & Solounias (1991) noted. Interestingly, de Beaumont & Mein (1972) suggested a direct relationship with *P. gaudryi* so included it in the subgenus *Mesoviverrops*: in their view *P.* (*Mesoviverrops*) *guerini* represented a parallel lineage of this small-sized hyaenids which maintained “neutral” features unlike *P.* (*Plioviverrops*) *orbignyi*, which derived towards more omnivorous diet (de Beaumont & Mein, 1972). In their recent study, Galiano et al. (2022) attribute *P. guerini* to the new genus *Gansuyaena* Galiano et al., 2022. According to these authors, “*G.*” *guerini* differs from the genotypical species, *Gansuyaena megalotis* Galiano et al., 2022, for the larger size, the stouter premolars (especially the p4 for the buccolingually large talonid) and the proportionally short m1 talonid with more developed entoconid (see Galiano et al., 2022). The generic re-attribution apparently relies on “the overall cusp development”, “the uncrowded premolar series”, and the “weak anterior cusp of p4” (Galiano et al., 2022, p. 104). Phylogenetically, Werdelin & Solounias (1991) proposed *P. guerini* as sister taxon of *P. orbignyi*, whereas Turner et al. (2008) reported an unresolved polytomy between *P. gaudryi*, *P. guerini* and *P. faventinus*. In their phylogeny, Galiano et al. (2022) grouped *Gansuyaena* in a single OTU and the retrieved topology supports their interpretation as the closest relative of *Proteles*. The origin of the extant *Proteles* from a basal group of hyaenids is well established in literature, and surely the *Plioviverrops* lineage was regarded as the plausible one from which the aardwolf derived (as mentioned above and confirmed by molecular and morphological interpretations; among others Werdelin & Solounias, 1991; Westbury et al., 2019). The estimations of divergence of *Proteles* from the lineage of other extant hyaenid are currently suggesting a Late Miocene age: 7.2 Ma according to Eizirik et al. (2010) and 10 Ma according to Hassanin et al. (2021). Considering that the earliest records of fossil *Proteles* come from Gelasian sites like Swartkrans, Kromdraai Member 2, Cooper’s Cave and Sterkfontein Member 5 (whose “East” layers are dated to ca. 2.18 Ma by Granger et al., 2015, and not 3.67 Ma as reported by Galiano et al., 2022, the estimations of divergence fit with both the interpretations of a descendance from *Plioviverrops* and/or from *Gansuyaena*, and do not allow a resolution of this debate.

The last species of the genus to be discussed is, of course, *Plioviverrops faventinus*. It was described by Danilo Torre in 1989 using the abundant cranial and postcranial material from Cava Monticino (Brisighella, Italy, 5.53-5.33 Ma; Marabini & Vai, 1989; Torre, 1989; Vai, 1989). This form shows dental morphologies typical of a hypocarnivorous species such as crushing-puncturing cusps on the molars (Ferretti, 2007; Bartolini-Lucenti et al., 2022) and reduced body size. Compared to the other species previously described, in literature it has often been overlooked or poorly considered. Torre (1989) considered its feature more similar to *P. orbignyi* than to *P. guerini*, although he recognised, correctly, that *P. faventinus* was more derived than the Greek taxon. He proposed a possible phylogenetic relationship between *P. faventinus* and *P. orbignyi*, with the former as the result of a westward dispersal during the Messinian of the Greco-Balkan species (Torre, 1989). Such an hypothesis is consistent considering the latest record of the species at La Gloria 4 (Spain, MN14; Alcalá, 1994). This occurrence makes *P. faventinus* one of the last species of *Plioviverrops* to survive in Eurasia. From the ecomorphological point of view, the derived dental features retained by *P. faventinus* led Werdelin & Solounias (1996) to regard it as a mongoose-like taxon, rather similar to modern insectivores.

The confused and complex systematic and taxonomic states of *Plioviverrops*, as well as of the genus *Protictitherium*, might suggest that these genera are paraphyletic. Resolving the present taxonomic conundrum of these species is a daunting task and surely not something we are willing to endeavour in the present paper. The aim of this study is to review and update the taxonomic status of *P. faventinus*, redescribing and expanding the comparison of the original material by Torre (1989) and the one preliminary described by Bartolini-Lucenti et al. (2022), with other species of *Plioviverrops* in the light of new research and to refine the palaeoecological interpretation of this small Messinian hyaenid.

MATERIALS AND METHODS

Considered specimens and comparative sample

The analysed material includes cranial and dentognathic specimens recovered from the site of Cava Monticino (Brisighella, Ravenna, Italy). The fossils are housed at the Dipartimento di Scienze della Terra of the Università di Firenze and at the Museo Civico di Scienze Naturali Malmerendi (Faenza, Italy). Regarding the analyses, we focused on a morphological and morphometrical comparison with fossil taxa of the genera *Plioviverrops* and *Protictitherium* and with modern species of small carnivores of the suborder Feliformia, particularly Herpestidae and Viverridae. During the morphological comparison, special attention was given to identify similar dental morphologies hinting comparable food habits between the studied taxon and the comparative sample. This is helpful to outline the possible composition of food resources in the diet of *P. faventinus* and its palaeoecology. Among the specific features in the postcanine dentition considered in this analysis there are: the length of the metastylar blade of P4, the morphology of m1 trigonid and the presence of cingula/cingulids (as expressed also in literature; e.g., Crusafont-Pairó & Truyols-Santonja, 1956; Werdelin & Solounias, 1991; Ferretti, 2007; Coca-Ortega & Pérez-Clarós, 2019). For the comparison with fossil taxa, direct observation of both samples and digital materials has been used. As fossil comparison material we used specimens of: *P. gaudryi*, MN7/8-MN9, from La Grive-St. Alban (NMB GA 2113; MdC LGR 1360) and Los Valles de Fuentidueña (Ginsburg et al., 1981); *P. gervaisi*, MN5-MN6, from Vieux-Collonges (e.g., UCBL FSL 65565, UCBL FSL 65566) and Catalayud (de Beaumont & Mein, 1972); *P. guerini*, MN11-MN13, from Los Mansuetos (IPS2056), Les Mistrales III (UCBL FLS 295052) and other Spanish localities of Tab. 2 (see Montoya, 1994); *P. orbignyi* from Pikermi and Samos (e.g., MNHN-PIK-3032; MB.Ma.29580) and other Greek-Balkan localities of Tab. 2 (see Koufos, 2012a; Lazaridis, 2015). We also revised relevant literature on fossil taxa (De Villalta-Comella & Crusafont-Pairó, 1948; Crusafont-Pairó & Petter, 1969; de Beaumont, 1969; Petter, 1976; Schmidt-Kittler, 1976; Ginsburg et al., 1981; de Bonis & Koufos, 1991; Werdelin & Solounias, 1991; Alcalá, 1994; Montoya, 1997; Koufos, 2006, 2009, 2011, 2012b; Sen & Saraç, 2018; Coca-Ortega & Pérez-Clarós, 2019; Galiano et al., 2022). Additional fossil comparison material includes taxa of *Protictitherium* and *Gansuyaena*, directly studied by us or taken from literature. These are: *Gansuyaena megalotis* Galiano et al., 2022, MN6-?, from the Linxia Hui province and Paşalar (Galiano et al., 2022); *Protictitherium cingulatum* Schmidt-Kittler, 1976, MN6-MN7/8, from Yeni Eskisihar (Schmidt-Kittler, 1976) and Paşalar (Mayda et al., 2015); *Protictitherium crassum* (Depéret, 1892), MN7/8-MN12, from Batallones-1 (Fraile, 2015), Can Mata (ICP), La Grive-St. Alban (MdC, UCBL); *Protictitherium gaillardi* (Forsyth Major, 1903), MN7/8-MN10, from La Grive-St. Alban (MdC), Castell de Barberà (ICP), San Miquel del Taudell (Fraile, 2015); *Protictitherium intermedium* Schmidt-Kittler, 1976, MN6, from Çandir (Schmidt-Kittler, 1976; Mayda et al., 2015), Mordoğan (Kaya et al., 2003) and Paşalar (Schmidt-Kittler, 1976; Mayda et al., 2015); *Protictitherium thessalonikensis* Koufos, 2012b, MN10, from Ravin de la Pluie (Koufos, 2012a).

Comparative extant species material include the following taxa (see Supplementary Online Material [SOM] 1: Tab. S1 for the catalogue numbers): Herpestidae: *Atilax paludinosus* (Cuvier, 1829); *Bdeogale crassicauda* Peters, 1852; *B. nigripes* Pucheran, 1855; *Crossarchus alexandri* Thomas & Wroughton, 1907; *C. ansorgei* Thomas, 1910; *C. obscurus* Cuvier, 1825; *C. platycephalus* Goldman, 1984; *Cynictis penicillata* (Cuvier, 1829); *Galerella sanguinea* (Rüppell, 1835); *Helogale hirtula* Thomas, 1904; *Hel. parvula* Sundevall, 1846; *Herpestes brachyurus* Gray, 1837; *He. ichneumon* Linnaeus, 1758; *He. pulverulentus* Wagner, 1839; *Ichneumia albicauda* Cuvier, 1829; *Mungos mungo* (Gmelin, in Linnaeus, 1788); *Paracynictis selousi* (de Winton, 1896); *Suricata suricatta* Schreber, 1776; *Urva edwardsii* (Geoffroy Saint-Hilaire, 1813); *U. javanica* (Geoffroy Saint-Hilaire, 1813); *Xenogale naso* (de Winton, 1901); Viverridae: *Civettictis civetta* (Schreber, 1776); *Genetta genetta* Linnaeus, 1758; *Ge. tigrina* Schreber, 1776; *Ge. victoriae* Thomas, 1901; *Paradoxurus hermaphroditus* (Pallas, 1777); *Pa. jerdoni* Blandford, 1885; *Viverra megaspila* Schreber, 1776; *V. zibetha* Linnaeus, 1758; *Viverricula indica* (Geoffroy Saint-Hilaire, 1803).

Body-mass reference and calculation methods

The body masses of *P. faventinus* and of fossil species used in the analyses were estimated using the regression formula provided by Legendre & Roth (1988) based on length and width of the m1 (SOM 1: Tab. S2). Despite the known problematics affecting any body-mass estimation based on tooth measures (e.g., Van Valkenburgh, 1990), our resulting values for the fossil taxa (SOM 1: Tab. S3) are in line with those obtained, independently, by other researchers (e.g., Coca-Ortega, 2019). The estimated average body weight of *P. faventinus* is circa 5.3 kg, with a maximum of 6.5 kg and a minimum of 4.3 kg (SOM 1: Tab. S2). These body masses were then used to calculate the RPS ratios for the fossil taxa (see below and SOM 1: Tab. S3). Regarding the extant comparative sample, body-mass values were taken from literature. Details are reported in SOM 1: Tab. S3, along with the ecological ratios described in the following paragraph.

Metric procedures and morphometric analyses

The morphometric comparison involved specific dental measurements and body-mass estimation, commonly used in taxonomical and ecological determination of carnivorans. For linear measurements, we used standardised measurements proposed by von den Driesch (1976) and Werdelin & Solounias (1991) with slight modifications (Fig. 2). The measurements were taken directly on the samples using a digital caliper to the nearest 0.1 mm. In the limited cases of missing measures to characterise specimens taken from literature, we used ImageJ (v. 1.52a; Schneider et al., 2012) on digital images to improve the database. When 3D scans were available instead of photos, we used the measuring tool of Artec Studio 17 Professional (v. x64 17.12.2.15; Artec3D, 2024) to take linear measurements.

We performed two Principal Component Analyses (PCA) on selected variables of P4 and m1 in the attempt of discriminating between different taxa while taking into consideration several dental parameters. Particularly, we considered six measurements on the P4 (Fig. 2) and five measurements on the m1 (Fig. 2). These measurements are: the buccal length of the P4; the maximum buccolingual width of the P4; the buccolingual width of the carnassial blade; the mesiodistal lengths of the parastyle, of the paracone and of the metastylar blade; the mesiodistal lengths of m1, of the trigonid and of the talonid, and the maximum buccolingual width of the carnassial and of its talonid (Fig. 2). The raw measurements were used to perform the PCA. In those analyses we included species of *Protictitherium* as comparison taxa (see above). The complete datasets for the two analyses are available on Zenodo at the following link: https://doi.org/10.5281/zenodo.14671672. We also ran a correlation test between each of the first three principal components and body mass of the fossil taxa. We used the software RStudio (v. 2023.12.1+402 "Ocean Storm" Release 4da58325ffcff29d157d9264087d4b1ab27f7204, 2024-01-28; RStudio Team, 2024) in R environment (v. 4.3.2, R Core Team, 2024) to perform analyses and produce graphs. PCAs on upper and lower tooth measurements were carried out using the function *prcomp()* ("*stats*" package v.4.3.2; R Core Team, 2024); the correlation test was performed via the function *cor.test()* ("*stats*" package v.4.3.2; R Core Team, 2024). The plots were obtained with *ggplot()* ("*ggplot2*" package v.3.4.0; Wickham et al., 2016) and *pch3D()* ("rgl" v. 1.2.1; Adler et al., 2003).

Considering the established characterisation of early hyaenids (namely *Plioviverrops* and *Protictitherium*) as mongoose-like and civet-like taxa (Werdelin & Solounias, 1991), we decided to test the possible ecomorphological affinities of these fossil hyaenids (see SOM 1: Tab. S3), especially in comparison to extant herpestids and viverrids. We thus included in the analysis 24 extant species and nine fossil hyaenids. In addition to *P. faventinus*, we considered *P. guerini*, *P. orbignyi*, *G. megalotis*, *Pr. cingulatum*, *Pr. crassum*, *Pr. gaillardi*, *Pr. intermedium* and *Pr. thessalonikensis*. Dental parameters used for the construction of the ecomorphological graph were established in literature for palaeoecological investigations of fossil carnivores and discussed by Van Valkenburgh (1989). For each considered species (both fossil and modern species mentioned above) two parameters were calculated using the formulae given in Van Valkenburgh (1989). These parameters are: 1) the relative blade length (RBL), i.e., the ratio between length of the trigonid blade and the length of the m1; 2) the relative premolar size (RPS), i.e., the ratio between the width of the p4 and the cubic root of the body mass. For the fossil taxa, the body mass was estimated as described in the previous paragraph. In general terms (see Van Valkenburgh, 1989), RPS gives information on the relative portion of hard material consumed and RBL on the percentage of meat. These parameters have proved valuable for inferences on the composition of diet of carnivores, especially in terms of carnivory grade (sensu Crusafont-Pairó & Truyols-Santonja, 1956) and relative durophagy of the taxa (among others Coca-Ortega & Pérez-Claros, 2019; Tarquini et al., 2020; Bartolini-Lucenti & Rook, 2021; Landry et al., 2021). The data were standardised following Van Valkenburgh (1989), in order to be comparable with the results in literature. See SOM 1: Tab. S3 for values of the extant taxa used in the analysis. We then performed a discriminant function analysis on the same variables using a priori dietary groups for the extant species and then plotted the fossil taxa a posteriori. This was done to further test the possible dietary inferences for the considered fossil species. The used groups for the extant species are: 1) carnivores, when meat is the key element in the diet of the taxon; 2) frugivores, when fruits compose more than any other income in the taxon's diet; 3) insectivores, for the taxa that feed on insects and chitinous-shelled invertebrates; 4) omnivores, when no particular item dominates the diet of the considered taxon. See SOM 1: Tab. S3 for the list of taxa, referred dietary group and bibliographic reference of the reported information. The analysis was performed in RStudio using the function *lda()* ("MASS" v. 7.3-60; Ripley et al., 2013).

Genus abbreviations

B., *Bdeogale*; *C.*, *Crossarchus*; *G.*, *Gansuyaena*; *Ge.*, *Genetta*; *H.*, *Herpestides*; *He.*, *Herpestes*; *Hel.*, *Helogale*; *P.*, *Plioviverrops*; *Pa.*, *Paradoxurus*; *Pc.*, *Paracynictis*; *Pr.*, *Protictitherium*; *Prot.*, *Protoviverrops*; *Pt.*, *Proteles*; *U.*, *Urva*; *V.*, *Viverra*.

Measurement abbreviations

AP1-P4 L, alveolar length of the upper premolar row; GPW, greatest width of the palate measured at the level of P4-M1 interalveolar space; HPrac, height between the angular process and the mandibular condyle; HR, height of the mandibular ramus, between the angular process and the dorsal tip of the coronoid process; L, mesiodistal length; Ll, mesiodistal length on the lingual side of the tooth (in the P4 is the maximum length from the protocone to the end of the metastylar blade; in the M1-M2, is the mesiodistal length of the lingual portion of the trigon);

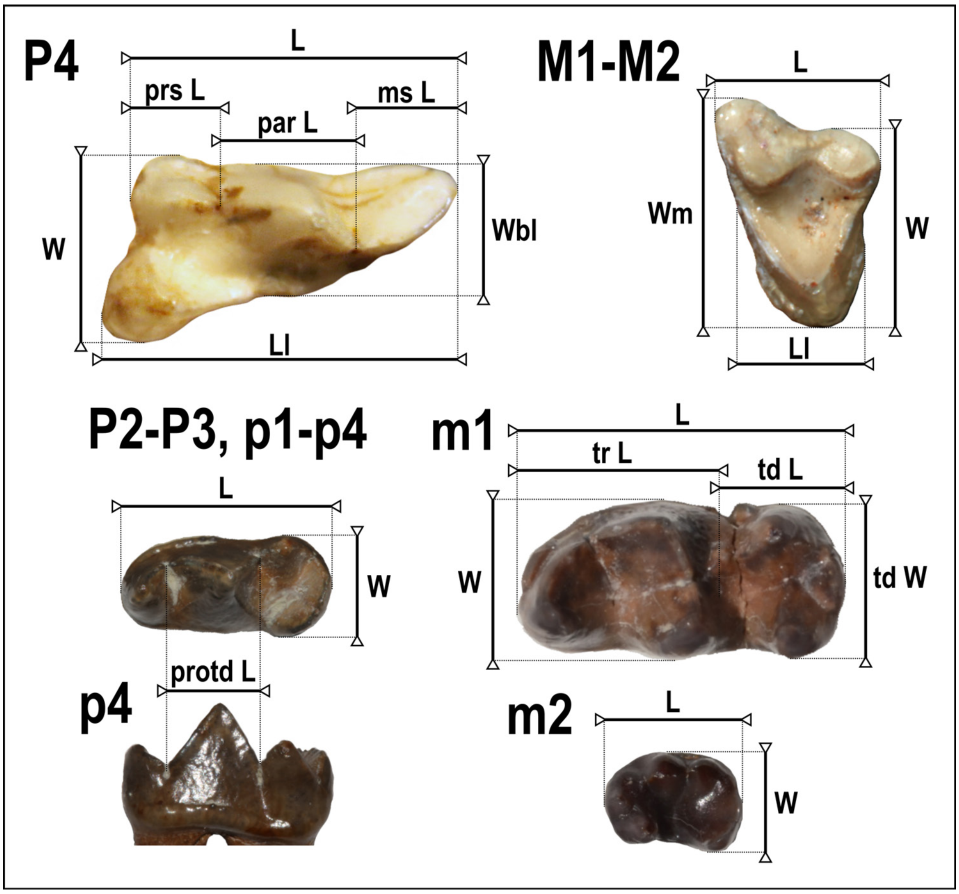


Fig. 2 - (color online) Schematic representation of the dental measurements taken on the considered sample of *Plioviverrops* and on the comparison specimens. Abbreviations, in alphabetical order: L, mesiodistal length; Ll, mesiodistal length on the lingual side of the tooth (in the P4, it is the maximum distance from the protocone to the end of the metastylar blade; in the M1-M2, it is the mesiodistal length of the lingual portion of the trigon); par, P4 paracone; protd, protoconid; protd L, mesiodistal length of the p4 protoconid (measured only for the p4); prs, P4 parastyle; ms, P4 metastylar blade; td, m1 talonid; tr, m1 trigonid; W, buccolingual width; Wbl, buccolingual width of the P4 blade; Wm, mesial buccolingual width of the M1-M2.

MdiastH, height of the mandible corpus at the diastema between canine and first premolar; Mm1B, breadth of the mandible corpus below the midpoint of the m1; Mm1H, height of the mandible corpus distal to the m1; Mp3p4B, breadth of the mandible corpus between the p3 and p4; Mp4H, height of the mandible corpus distal to the p4; ms, P4 metastylar blade; par, P4 paracone; protd, protoconid; protd L, mesiodistal length of the p4 protoconid (measured only for the p4); prs, P4 parastyle; PwP1, width of the palate at the level of the lingual side of the P1; PWP2, width of the palate at the level of the lingual side of the P2; td, m1 talonid; tr, m1 trigonid; W, buccolingual width; Wbl, buccolingual width of the P4 blade; Wm, mesial buccolingual width of the M1-M2; WR, maximum rostrocaudal width of the mandibular ramus.

Institutional abbreviations

BRS, Cava Monticino site, Brisighella, Ravenna (Italy); CBL, Collezione Borzatti, Museo di Antropologia e Etnologia di Firenze, Università degli Studi di Firenze, Florence (Italy); DSTUNIFI, Dipartimento di Scienze della Terra, Università di Firenze, Florence (Italy); ICP, Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès (Spain); MB, Museum für Naturkunde Berlin, Berlin (Germany); MdC, Musée des Confluences, Lyon (France); MNHN, Muséum national d'Histoire naturelle, Paris (France); MSF, Museo Civico di Storia Naturale Malmarendi, Faenza (Italy); MZUF, Collezione Zoologica "La Specola", Museo di Storia Naturale, Università degli Studi di Firenze, Florence (Italy); NMB, Basel Naturhistorisches Museum, Basel (Switzerland); UCBL, Université Claude Bernard Lyon-1, Lyon (France); UMMZ, University of Michigan Museum of Zoology, University of Michigan (US).

SYSTEMATIC PALAEONTOLOGY

Order Carnivora Bowdich, 1821
Family Hyaenidae Gray, 1821

Genus *Plioviverrops* Kretzoi, 1938

Type species - *Plioviverrops orbignyi* (Gaudry & Lartet, 1856).

Included species - *Plioviverrops gaudryi* de Beaumont & Mein, 1972, *Plioviverrops guerini* (De Villalta-Comella

& Crusafont-Pairó, 1948), *Plioviverrops gervaisi* de Beaumont & Mein, 1972, *P. orbignyi* (Gaudry & Lartet, 1856), *Plioviverrops faventinus* Torre, 1989.

Plioviverrops faventinus Torre, 1989
(Figs 3-5; Tabs 3-6)

Holotype - MSF 92 and MSF 92.1 (both BRS 5/34), respectively right mandible fragment with p3-m2 and left mandible fragment with p4-m2.

Referred Material from Cava Monticino - MSF 62, fossiliferous block containing two fragmentary skulls of *Plioviverrops* and postcranial fragments of Carnivora indet. cf. *Plioviverrops* in anatomical connection.

Cranial material (field numbers in parentheses): DSTUNIFI BRS 25, right maxillary with P4; MSF 408 (BRS 5/33), palate with left and right P4; MSF 430 (BRS 19/5), left maxillary fragment with P3-P4.

Upper dentition (isolated teeth): DSTUNIFI BRS 3, left C; DSTUNIFI BRS 24, right C; MSF 423_1 (BRS 5/294), right C; MSF 411 (BRS 5/ 61), right C; MSF 417_2 (BRS 5/278), right P2; MSF 423_1 (BRS 5/279), left P2; MSF 424_1 (BRS 5/279), left P2; MSF 424_2 (BRS 5/ 279), left P2; DSTUNIFI BRS, right P3; DSTUNIFI BRS 9/4, left P3; DSTUNIFI BRS 9/5, right P3; DSTUNIFI BRS 27_1, right P3; DSTUNIFI BRS 27_2, right P3; MSF 418 (BRS 5/300), right P3; MSF 425_1 (BRS 5/ 64), right P3; MSF 425_2 (BRS 5/65), left P3; MSF 425_3 (BRS 5/ 301), right P3; MSF 425_4 (BRS 5/281), left P3; DSTUNIFI BRS 25, right P4; DSTUNIFI BRS 3/34, right P4, erratic; DSTUNIFI BRS 25/CP3_1, left P4; MSF 415 (BRS 5/165), right P4; MSF 426_1 (BRS 5/ 63), left P4; MSF 426_2 (BRS 5/ 297), right P4; MSF 426_3 (BRS 5/162), left P4; DSTUNIFI BRS 16/5 right M1, erratic; DSTUNIFI BRS 25/CP3_2, left M1; MSF 413 (BRS 5/ 313), left M1; MSF 428_1 (BRS 5/310), right M1; MSF 428_2 (BRS 5/56), right M1; MSF 428_3 (BRS 5/sn), right M1; DSTUNIFI BRS 25/CP3_3, M2; DSTUNIFI BRS 1/26, left M2; MSF 414_1 (BRS 5/57), right M2; MSF 414_2 (BRS 5/312), right M2.

Mandible: DSTUNIFI BRS 1/19, left hemimandible fragment with c; DSTUNIFI BRS 5/179, right edentulous hemimandible fragment; DSTUNIFI BRS 2/5, right edentulous mandible; MSF 93 (BRS 5/30), left mandible fragment with c and p3; MSF 94 (BRS 19/6), right edentulous mandible fragment; MSF 407 (BRS 5/ 158), right hemimandible fragment with p3-m2; MSF 448, right hemimandible fragment with p4; MSF 449, left edentulous hemimandible fragment.

Lower dentition (isolated teeth): DSTUNIFI BRS 27_1, right c; MSF 412 (BRS 5/sn), left c; MSF 423_1 (BRS 5/16), left c; MSF 423_2 (BRS 5/293), right c; MSF 423_3 (BRS 5/62), right c; MSF 423_4 (BRS 5/279), right c; DSTUNIFI BRS 26_1 left p2; DSTUNIFI BRS 9/5, right p3; DSTUNIFI sn, left p3, erratic; DSTUNIFI BRS 9/6, right p3; MSF 409 (BRS 5/167), right p3; DSTUNIFI BRS 24, left p4; DSTUNIFI BRS 25/CP3_4, right p4;

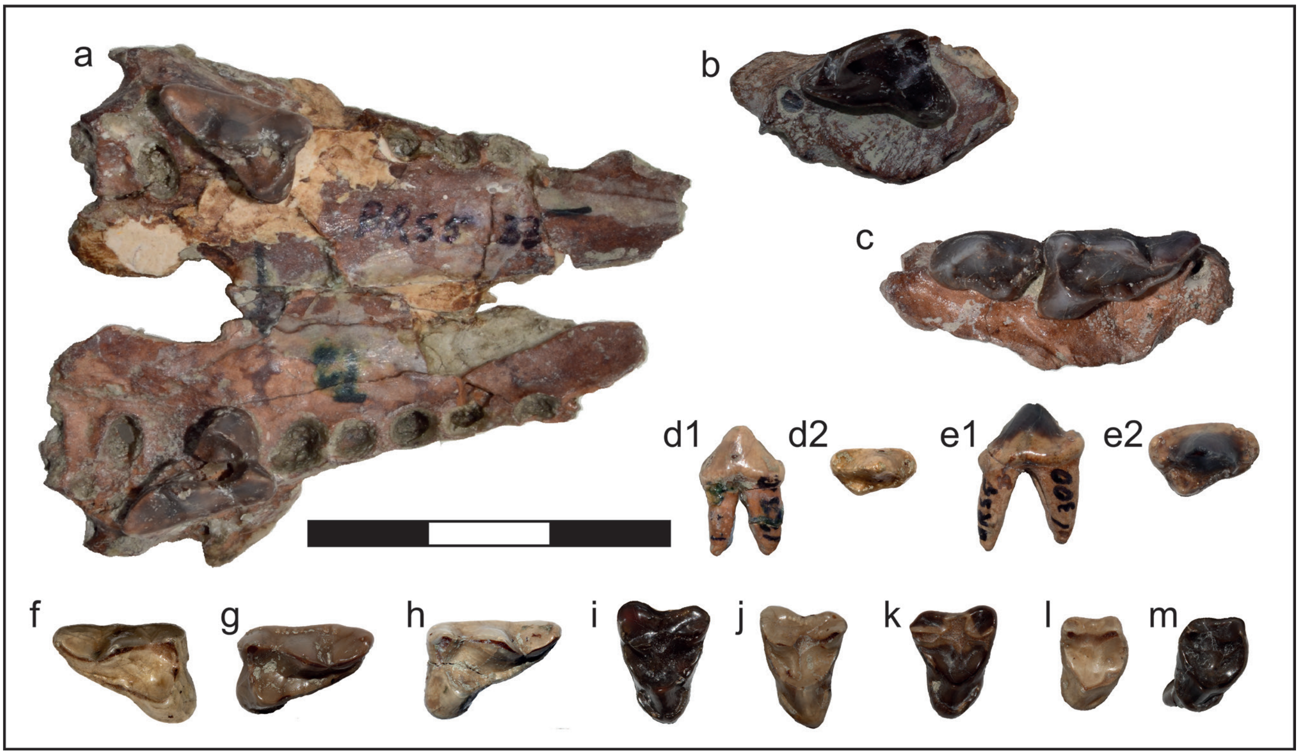


Fig. 3 - (color online) Cranial fragments and upper teeth of *Plioviverrops faventinus* from Cava Monticino (Brisighella, Italy). a) MSF 408 (BRS 5/33), cranial fragment with P4 in ventral view. b) DSTUNIFI BRS 25, right maxillary fragment with P4 in ventral view. c) MSF 430 (BRS 19/5), left maxillary fragment with P3-P4 in ventral view. d) MSF 417 (BRS 5/271), right P2 in buccal (d1) and occlusal (d2) views. e) MSF 418 (BRS 5/300), right P3 in buccal (e1) and occlusal (e2) views. f) MSF 415 (BRS 5/165), right P4 in occlusal view. g) MSF 424 (BRS 5/162), left P4 in occlusal view. h) MSF 426 (BRS 5/63), left P4 in occlusal view. i) DSTUNIFI BRS25/CP3_2, left M1 in occlusal view. j) MSF 413 (BRS 5/313), left M1 in occlusal view. k) MSF 428 (BRS 5/310), right M1 in occlusal view. l) MSF 414 (BRS 5/67), left M2 in occlusal view. m) DSTUNIFI BRS25/CP3_3, left M2 in occlusal view. Scale bar equals 3 cm.

MSF 410 (BRS 5/168), right p4; DSTUNIFI BRS 4/5, right m1; DSTUNIFI BRS 27_2, right m1; DSTUNIFI BRS 16/6, left m1; DSTUNIFI BRS 3, right m1, erratic; DSTUNIFI BRS 25, left m1; MSF sn (BRS 27_), left m1; MSF 416 (BRS 5/54), left m1; MSF 417_1 (BRS 5/169), right m1; MSF427_1 (BRS 5/314), left m1; MSF 427_2 (BRS 5/sn), right m1; MSF 427_3 (BRS 5/67), right m1; MSF 427_4 (BRS 5/68), right m1; DSTUNIFI BRS 4/10, left m2; DSTUNIFI BRS 26_2, left m2; DSTUNIFI BRS 27_4, right m2; MSF 429_1 (BRS 5/sn), left m2; MSF

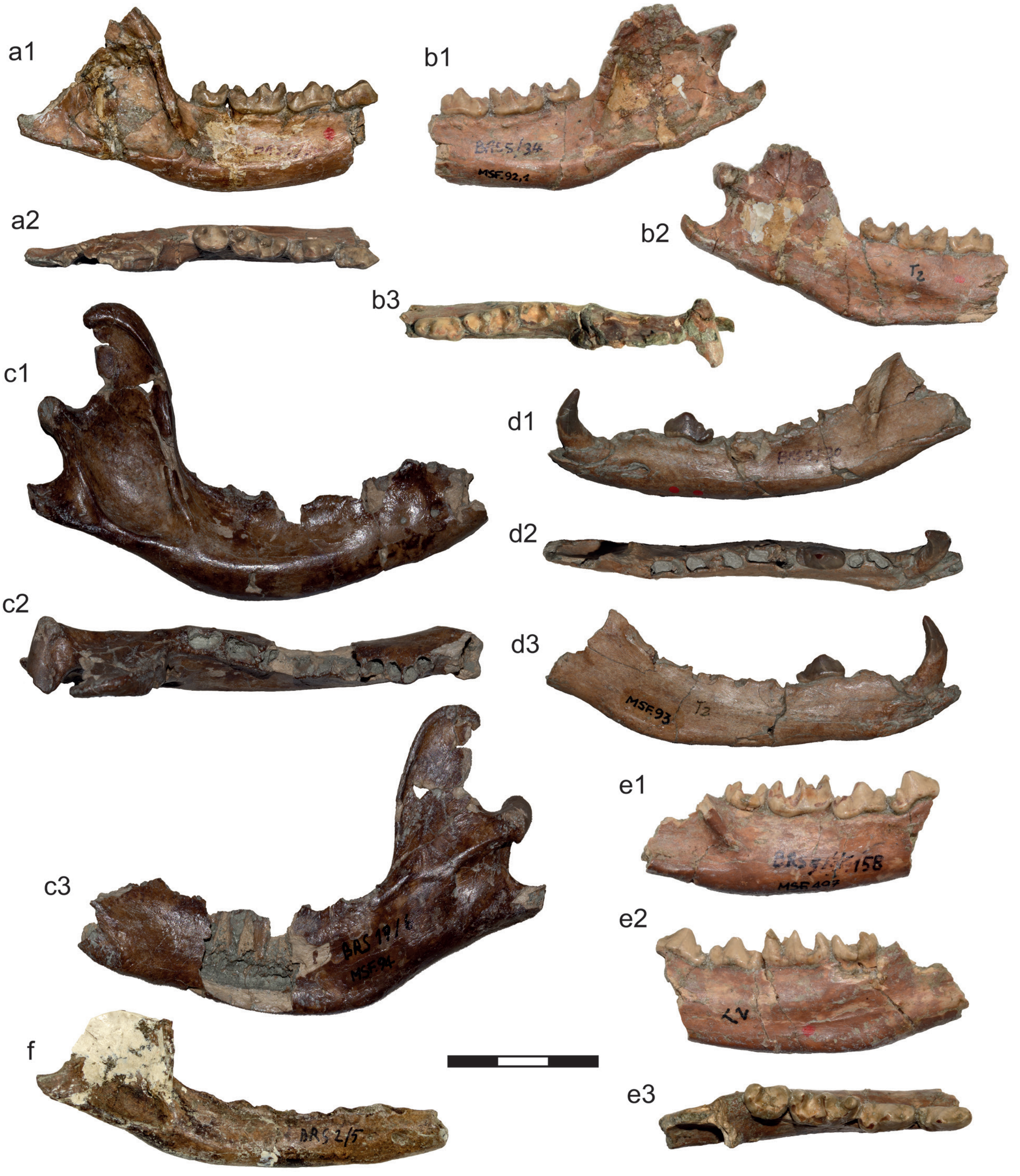


Fig. 4 - (color online) Mandibular fragments of *Plioviverrops faventinus* from Cava Monticino (Brisighella, Italy). a) MSF 92 (BRS 5/34), right mandible fragment with p3-m2 in buccal (a1) and occlusal (a2) views. b) MSF 92.1 (BRS 5/34), left mandible fragment with p4-m2 in buccal (b1), lingual (b2) and occlusal (b3) views. c) MSF 94 (BRS 19/6), right edentulous mandible fragment in buccal (c1), lingual (c2) and occlusal (c3) views. d) MSF 93 (BRS 5/30), left mandible fragment with c and p3 in buccal (d1), lingual (d2) and occlusal (d3) views. e) MSF 407 (BRS 5/ 158), right hemimandible fragment with p3-m2 in buccal (e1), lingual (e2) and occlusal (e3) views. f) DSTUNIFI BRS 2/5, right edentulous mandible. Scale bar equals 3 cm.

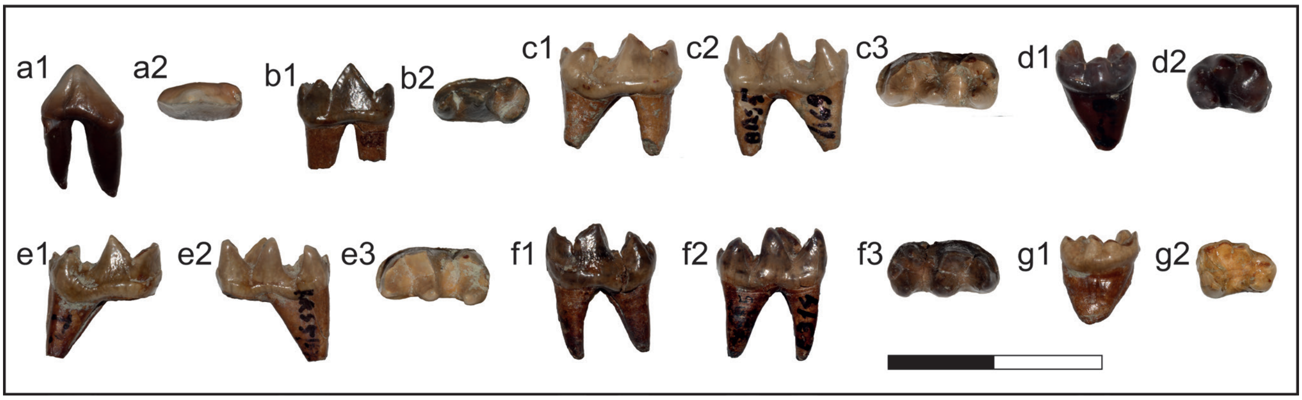


Fig. 5 - (color online) Detailed view of the lower teeth of *Plioviverrops faventinus* from Cava Monticino (Brisighella, Italy). a) DSTUNIFI BRS 26, left p2 in buccal (a1) and occlusal (a2) views. b) DSTUNIFI BRS 25/CP3_4, right p4 in buccal (b1) and in occlusal (b2) views. c) MSF 417_1 (BRS 5/169), left p2 in buccal (c1), in lingual (c2) and in occlusal (c3) views. d) DSTUNIFI BRS 26_2, left m2 in buccal (d1) and in occlusal (d2) views. e) MSF 427_3 (BRS 5/67), right p2 in buccal (e1), in lingual (e2) and in occlusal (e3) views. f) MSF427_1 (BRS 5/314), left m1 in buccal (f1), in lingual (f2) and in occlusal (f3) views. g) MSF 429_4 (BRS 5/170), right m2 in buccal (g1) and in occlusal (g2) views. Scale bar equals 2 cm.

429_2 (BRS 5/sn), right m2; MSF 429_3 (BRS 5/sn), left m2; MSF 429_4 (BRS 5/170), right m2; MSF 429_5 (BRS 5/286), right m2.

Referred material from La Gloria 4 - See Alcalá (1994).

Description - The reduced number of cranial specimens, and their deformation, makes difficult to describe their morphologies properly. The general structure of the muzzle is narrow and tapered in its rostral portion (Fig. 3). In ventral view, the palate is relative narrow. In fact, MSF 408 has a tapered and triangular morphology that tends to widen slightly and gradually at the height of the P4. The maxillary increases in height laterally at the level of P4. The upper canines are marked by a curved and high crown. Dentally, the premolars, upper and lower are moderately compressed buccolingually and with an oval occlusal outline. The P1 is present and single-cusped. The P2 is larger than the P1, two-rooted and has a small distolingual expansion marked by an evident accessory cusp. The P3 protocone is larger than that of P2, especially mesiodistally. The P3 has two accessory cusps: a small one distal to the protocone, and a larger second one on the lingual expansion. This cusp connects to the distal and mesial crests of the protocone with an evident cuspule-like cingulum, as visible in MSF 418, MSF 424 and MSF 425. In buccal view, the P4 (e.g., MSF 424_3 and MSF 426_1) shows a well-developed and pointed paracone, slightly projected in distal direction. The parastyle instead is shorter but still fairly pointed. The metastylar blade is rather shortened mesiodistally, especially in comparison to the other P4 cusps. In occlusal view, the protocone is considerably enlarged, expanded in comparison to mesiodistal length of the tooth and not particularly sharp. It projects mesiolingually. On the lingual side of the P4, an evident cuspule-like cingulum extends distally from the protocone to the base of the metastyle. The protocone and the cingulum give the tooth an odd subtriangular occlusal shape, especially clear in MSF 424_3. The M1 has three main cusps and a three-sided occlusal shape. Buccally, the paracone is smaller than the metacone, especially mesiodistally, and both are bounded by a wide buccal cingulum marked by a medial notch between the buccal cusps. MSF 413 exemplifies this. Lingually, a large-based and pointed protocone identifies a wide trigon basin bounded by a the pre- and postprotocrista. The latter shows a small but evident cuspule, possibly a feeble metaconule. The lingual side of the protocone there is marked by a cingulum. It is generally particularly developed on the mesial and the distal side of the protocone, e.g., MSF 413, but it can almost coalesce into a continuous cingulum in some specimens (e.g., DSTUNIFI BRS5/CP3_2). In addition, M1 has a slight distal curvature.

The M2 recalls M1 in occlusal shape and features, e.g., MSF 414_1 and MSF 414_2 both possess a slight distal curvature, a prominent buccal cingulum, an accessory

ID	Element	Side	P3 L	P3 W	P4 L	P4 Ll	P4 W	P4 Wbl	P4 prs L	P4 par L	P4 ms L	GPW	PwP1	PWP2	AP1-P4 L
DSTUNIFI BRS 25	maxillary fr.	R	-	-	-	-	7.8	5.5	3.1	5.0					
MSF 408 (BRS 5/33)	palate	R	-	-	11.8	12.9	8.1	5.4	3.5	4.3	5.1	36.4	18.4	20.6	33.6
MSF 430 (BRS 19/5)	maxillary fr.	L	9.3	5.6	12.4	13.8	7.2	6.1	3.2	5.0	5.0	-	-	-	-

Tab. 3 - Measurements (mm) of maxillary fragments of *Plioviverrops faventinus* from Cava Monticino. Abbreviations in Materials and Methods.

ID	Tooth	Side	L	W	Wbl	prs L	par L	ms L	Ll	Wm
DSTUNIFI BRS 3	C	L	5.7	4.5	-	-	-	-	-	-
MSF 411 (BRS 5/61)	C	R	6.5	5.0	-	-	-	-	-	-
MSF 423_1 (BRS 5/294)	C	R	6.6	4.3	-	-	-	-	-	-
MSF 417_12 (BRS 5/278)	P2	R	7.1	3.9	-	-	-	-	-	-
MSF 424_1 (BRS 5/279)	P2	L	7.2	3.9	-	-	-	-	-	-
MSF 424_2 (BRS 5/279)	P2	L	7.4	4.9	-	-	-	-	-	-
DSTUNIFI BRS	P3	R	8.2	5.5	-	-	-	-	-	-
DSTUNIFI BRS 9/4	P3	L	8.5	5.5						
DSTUNIFI BRS 9/5	P3	L	9.5	6.1						
DSTUNIFI BRS 27_2	P3	R	9.2	5.9	-	-	-	-	-	-
MSF 418 (BRS 5/300)	P3	R	9.2	5.9	-	-	-	-	-	-
MSF 425_1 (BRS 5/64)	P3	R	8.6	5.4	-	-	-	-	-	-
MSF 425_2 (BRS 5/65)	P3	L	8.3	5.5	-	-	-	-	-	-
MSF 425_3 (BRS 5/301)	P3	R	9.8	6.0	-	-	-	-	-	-
MSF 425_4 (BRS 5/281)	P3	L	8.4	5.6	-	-	-	-	-	-
MSF 426_1 (BRS 5/63)	P3	L	11.2	8.0	5.5	3.1	4.9	4.1	12.1	-
DSTUNIFI BRS 3/34	P4	L	12.4	9.0	6.6	3.4	4.8	4.3	14.8	-
DSTUNIFI BRS 25/ CP3_1	P4	L	11.6	7.9	6.1	3.4	5.0	4.6	14.0	-
MSF 415 (BRS 5/165)	P4	R	11.3	8.3	6.1	3.4	4.0	3.8	12.1	-
MSF 424_2 (BRS 5/297)	P4	R	11.6	8.5	5.9	3.6	4.1	4.4	12.3	-
MSF 424_3 (BRS 5/162)	P4	L	11.5	7.3	5.6	3.7	4.7	4.4	13.1	-
DSTUNIFI BRS 16/5	M1	R	6.7	9.1	-	-	-	-	4.7	9.8
DSTUNIFI BRS 25/ CP3_2	M1	L	7.7	9.8	-	-	-	-	5.4	10.4
MSF 413 (BRS 5/313)	M1	L	7.2	10	-	-	-	-	4.9	10.3
MSF 428_1 (BRS 5/310)	M1	R	7.1	8.8	-	-	-	-	4.7	9.2
MSF 428_2 (BRS 5/56)	M1	R	7.3	9.9	-	-	-	-	2.9	10.5
MSF 428_3 (BRS 5/sn)	M1	R	7.5	10.1	-	-	-	-	5.0	10.4
DSTUNIFI BRS 25/ CP3_3	M2	R	5.7	7.6	-	-	-	-	5.0	8.1
MSF 414_1 (BRS 5/57)	M2	R	5.5	7.7	-	-	-	-	4.9	7.8
MSF 414_2 (BRS 5/312)	M2	R	5.5	8.4	-	-	-	-	4.6	8.4

Tab. 4 - Measurements (mm) of isolate upper teeth of *Plioviverrops faventinus* from Cava Monticino. Abbreviations in Materials and Methods.

cuspule on the postprotocrista (metaconule), and the lingual cingulum on the base of the protocone. In contrast to the M1, however, the M2 is more squared, especially in its buccal side. The M2 protocone is proportionally more developed than paracone and metacone. The lingual cingulum is proportionally developed as it is in M1.

In lateral view, the mandible is tapered and with a slightly curved shape with a dorsal concavity and tending to thin in the rostral portion (Fig. 4). If observed in section, the mandible corpus is ovoidal, with a slight thickening in its ventral part. In occlusal view, the tooth row is gently arched laterally, especially at the level of the p4. There are no diastemata in the postcanine dentition, except for a small one between c and p1 (Fig. 4). There can be one or two mental foramina on the lateral side of the corpus. The rostral one is the largest and is located at the level of the distal side of p1 or mesial root of p2; when the second is present, it is smaller and located below the distal root of the p2 or mesial side of p3. The coronoid process does not show evident development in vertical direction remaining slightly inclined compared to the mandibular body (Fig. 4). The angular process, visible in MSF 92.1, has a thin, elongated and dorsally arched hook morphology. The condyle is slightly shorter mesiodistally than the angular process (Fig. 4). The masseteric fossa is marked and deep and almost reached the distal side of m2. Its ventral margin is sharp, and the insertion of the masseteric muscle is evident (e.g., in MSF 92.1) (Fig.

ID	Side	c L	c W	p3 L	p3 W	p4 L	p4 W	p4 protd L	m1 L	m1 W	trm1 L	tdm1 L	tdm1 W	m2 L	m2 W
DSTUNIFI BRS 1/19	L	5.7	5.0	-	-	-	-	-	-	-	-	-	-	-	-
MSF 407 (BRS 5/158)	R	-	-	9.1	4.1	9.6	4.9	4.1	11.8	5.5	6.5	5.3	5.7	7.5	5.4
MSF 92 (BRS 5/34)	R	-	-	8.6	4.2	9.8	4.6	4.0	11.5	5.6	6.1	5.4	5.7	7.3	5.6
MSF 92.1 (BRS 5/34)	L	-	-	-	-	9.9	4.8	4.0	10.9	5.8	6.4	4.5	5.6	7.4	5.4
MSF 93 (BRS 5/30)	L	5.0	4.5	9.8	4.6	-	-	-	-	-	-	-	-	-	-

ID	Side	MdiastH	Mp4H	Mm1H	Mp3p4B	Mm1B	HPrac	HR	WR
DSTUNIFI BRS 1/19	L	12.2	-	-	-	-	-	-	-
DSTUNIFI BRS 2/5	R	11.3	12.7	14.1	6.0	5.7	-	-	-
DSTUNIFI BRS 5/179	R	-	-	16.1	-	7.2	-	-	20.5
MSF 407 (BRS 5/158)	R	-	13.5	14.2	6.8	6.8	-	-	-
MSF 92 (BRS 5/34)	R	-	15.1	16.6	6.9	6.6	-	-	-
MSF 92.1 (BRS 5/34)	L	-	14.1	16.7	6.5	7.1	18.7	-	18.6
MSF 93 (BRS 5/30)	L	9.6	14.0	16.5	7.2	6.7	-	-	-
MSF 94 (BRS 19/6)	R	-	-	18.5	-	8.4	19.8	38.6	17.5

Tab. 5 - Measurements (mm) of mandibular fragments of *Plioviverrops faventinus* from Cava Monticino. Abbreviations in Materials and Methods.

4). The mandible corpus is characterised by a marked subangular region, that in some specimens can be fairly high (e.g., DSTUNIFI BRS2/5, MSF 92.1, MSF 94) but milder in other (e.g., MSF 93) (Fig. 4).

The lower canine is smaller and shorter than the upper one, on average (Fig. 5). It has an oval cross-section with a lingual surface less convex than the buccal one. The crown is more curved distally compared to the upper canine. In dorsal view, the crown seems to diverge slightly laterally. The p1 has a single main cusp rather higher than mesiodistally elongated, with no accessory cuspulids (Fig. 5). The p2 is similar to P2, but simpler with no accessory cuspulids (Fig. 5). The p3 is characterised by a short protoconid, two accessory cuspulids, one mesial and another distal to the protoconid (Fig. 5). Moreover, distally there is a cingulid that extends lingually and is marked by a cuspulid-like structure. The p4 is characterised by a peculiar morphology (e.g., MFS 92.1, DSTUNIFI BRS25/CP3_4) (Fig. 5): the molarisation is markedly advanced as we can recognise a sharp mesial cuspid (a paraconid), a pointed protoconid and a developed distal accessory cuspulid (a hypoconid), as high as the mesial one. Distal to this cuspid, a cuspulid-like cingulid extends lingually from the buccal side, bounding the whole distal margin of p4 and identifying a talonid basin. The lingual end of the cingulid seems enlarged in the shape of a cuspulid. Buccally a basal cingulid bounds the mesial half of p4 (Fig. 5).

The m1 is marked by high and pointed cuspids, especially in unworn specimens (e.g., MSF 427_1 and MSF 427_3) (Fig. 5). In buccal view, the mesiodistal shortening of the m1 and the height of the cuspids are striking: the protoconid and metaconid are the highest cuspids but the height difference with paraconid and entoconid is really reduced (Fig. 4). The m1 of *P. faventinus* has a well-developed trigonid with the three tips of cusps arranged to form a three-sided trigonid basin, in occlusal view, and are almost of similar size. In occlusal view, the five-pointed cuspids morphology is evident (Fig. 5). The talonid is characterised by entoconid and hypoconid, which are comparable in size at their base but the second is slightly shorter. On the distal margin of the tooth there is an evident hypoconulid. Lingually, the trigonid and talonid basins are open. Buccally, m1 is characterised by a high and sharp cingulid that bounds the buccal side of the trigonid, and in some specimens uninterruptedly as in MSF 427_1. The m2 is characterised

ID	Tooth	Side	L	W	p4 protd L	trm1 L	tdm1 L	tdm1 W
DSTUNIFI BRS 27_1	c	R	5.4	3.9	-	-	-	-
MSF 412 (BRS 5/sn)	c	L	5.7	4.3	-	-	-	-
MSF 423_1 (BRS 5/160)	c	L	7.1	5.0	-	-	-	-
MSF 423_2 (BRS 5/293)	c	R	6.2	4.4	-	-	-	-
MSF 423_3 (BRS 5/62)	c	R	6.0	5.0	-	-	-	-
MSF 423_4 (BRS 5/279)	c	R	5.6	5.0	-	-	-	-
DSTUNIFI BRS 26_1	p2	L	7.9	3.6	-	-	-	-
DSTUNIFI BRS 9/5	p3	R	8.2	4.0	-	-	-	-
MSF 409 (BRS 5/167)	p3	R	9.8	4.2	-	-	-	-
DSTUNIFI BRS 25/CP3_4	p4	R	9.0	4.2	3.6	-	-	-
MSF 410 (BRS 5/168)	p4	R	10.5	5.0	5.0	-	-	-
DSTUNIFI BRS 4/5	m1		11.6	5.0	-	7.6	4.0	5.1
DSTUNIFI BRS 5/158	m1	L	11.3	4.9	-	7.5	3.8	5.5
DSTUNIFI BRS 16/6	m1	L	-	5.6	-	-	5.4	5.5
DSTUNIFI BRS 25	m1	L	11.6	5.2	-	8.2	3.4	5.5
DSTUNIFI BRS 27_3	m1	R	11.1	4.7	-	7.6	3.5	4.8
MSF sn (BRS 27_)	m1	L	11.5	5.6	-	7.4	4.1	5.1
MSF 416 (BRS 5/54)	m1	L	11.6	5.2	-	6.5	5.1	5.1
MSF 417_1 (BRS 5/169)	m1	R	11.5	5.3	-	6.4	5.1	5.4
MSF 427_2 (BRS 5/sn)	m1	R	10.6	5.1	-	6.1	4.5	5.2
MSF 427_3 (BRS 5/67)	m1	R	11.3	5.4	-	6.4	4.9	5.5
MSF 427_4 (BRS 5/68)	m1	R	10.1	5.5	-	6.2	3.9	5.5
MSF427_1 (BRS 5/314)	m1	L	10.4	4.8	-	7.0	3.4	4.9
DSTUNIFI BRS 4/10	m2	L	7.5	5.1	-	-	-	-
DSTUNIFI BRS 26_2	m2	L	7.7	5.5	-	-	-	-
DSTUNIFI BRS 27_4	m2	R	6.9	5.0	-	-	-	-
MSF 429_1 (BRS 5/sn)	m2	L	7.5	5.5	-	-	-	-
MSF 429_2 (BRS 5/sn)	m2	R	7.4	5.4	-	-	-	-
MSF 429_3 (BRS 5/170)	m2	R	7.4	5.3	-	-	-	-
MSF 429_4 (BRS 5/286)	m2	R	7.5	5.4	-	-	-	-

Tab. 6 - Measurements (mm) of isolate lower teeth of *Plioviverrops faventinus* from Cava Monticino. Abbreviations in Materials and Methods.

by a subrectangular occlusal shape (Fig. 5), marked by three buccal cuspulids (mesial to distal: a small mesial paraconid, large protoconid and hypoconid, and an evident hypoconulid, placed distobuccally) and two large lingual cuspids (the mesial metaconid and the distal entoconid). The latter two are higher than the others, and visible in buccal view, with the metaconid highest of all. In lingual and occlusal views the lingual opening of the m2 talonid basin is clear (Fig. 5).

RESULTS

Morphological comparison

Cranial fragments and upper dentition - Although the cranial specimens of *P. faventinus* consist only of an incomplete and deformed partial skull, it is possible to make some comparisons with the others fossil species, in particular with *P. orbignyi* (Gaudry, 1862; de Beaumont, 1969; Koufos, 2011; Lazaridis, 2015) of which there are almost complete cranial specimens, and with *G. megalotis* (Galiano et al., 2022). As for the neurocranium, the samples found (MSF 62) are too fragmented and deformed to identify specific cranial morphologies. In comparison to *P. orbignyi*, the fragment of palate (MSF 408) is slightly wider proportionally in the rostral portion, as *P. orbignyi* has a more marked narrowing at the level of P2. The premolar dentition of *P. faventinus* is stouter, in general terms, than the other fossil species considered (Fig. 6). Moreover, premolars are marked by a considerable degree of molarisation, visible especially on P3 and p4, not present in older taxa (i.e., *P. gervaisi* and *P. gaudryi* or *G. megalotis*). In particular *G. megalotis* has very narrow and mesiodistally elongated premolars. Nevertheless, such a molarisation is not so developed neither in taxa coeval of *P. faventinus*, i.e., *P. guerini* and *P. orbignyi* (Fig. 6). On both P2 and P3 there is a cingulum and an accessory cusp in the lingual portion of the teeth. This cusp on P2 is not possessed by any other fossil species. Some fossil species show a lingual expansion on P3, e.g., *G. megalotis* and *Pr. cingulatum* (see Schmidt-Kittler, 1976; Galiano et al., 2022), or even a evident lingual cingulum, e.g., *P. orbignyi* (see de Beaumont, 1969; Lazaridis, 2015) (Fig. 6), none of them show the degree of development nor the cuspule-like morphology of *P. faventinus*. The P3 of *P. faventinus* is the widest of the fossil species included in this comparison. The P4 is characterised by greater buccolingual enlargement compared to the other comparative species, which are marked by the reduction of the mesiodistal length of the whole tooth; the enlargement of the paracone and parastyle parallel to reduction of its metastylar blade; height, prominence and cuspule-like lingual cingulum; and the development of the protocone, both in width and length. This morphology of P4 is markedly different especially from *Protictitherium* spp. and *G. megalotis* which instead have mesiodistally elongated P4, with generally sharp and long blades (Fraile, 2015; Galiano et al., 2022). Moreover, the protocone of these taxa is proportionately less developed than in *P. faventinus*. An exception is *Pr. thessalonikensis* which has shorter P4, unlike other *Protictitherium* (Koufos, 2012b). In comparison with other *Plioviverrops*, P4 of *P. faventinus* is shorter mesiodistally compared to *P. gervaisi* from Vieux-Collonges (de Beaumont & Mein, 1972), *P. gaudryi* from La Grive-St. Alban (de Beaumont & Mein, 1972), *P. guerini* from Crevillente 2 (Montoya, 1997), *P. orbignyi* from Pikermi, Samos and Kryopigi (Koufos, 2011; Lazaridis, 2015) and also *P.* cf. *orbignyi* from Çalta-1 (Sen & Saraç, 2018), and definitely wider buccolingually (see also Fig. 6). The P4 parastyle in *P. faventinus* is large at its base, in a way similar to *P. guerini* and *P.* cf. *orbignyi*, more than *P. gervaisi* but also of *P. gaudryi* and *P. orbignyi* (Fig. 6). The P4 protocone of *P. faventinus* is enlarged and lingually projected, similarly to *P. gaudryi*, *P. guerini*, *P. orbignyi*, and *P.* cf. *orbignyi* although proportionally larger, in occlusal view (Fig. 6). Although in *P. orbignyi*, the protocone is generally more advanced mesially. *Plioviverrops gervaisi* has a reduced, poorly expanded protocone. In the other fossil taxa, the lingual cingulum is variably developed, from *P. gervaisi* with almost no cingulum if not distolingually to *P. orbignyi* in which the cingulum is continuous but less expanded lingually and without cuspule-like features on it (Fig. 6). On the contrary, in *P. faventinus* the cingulum is enlarged and show evident accessory cuspules on it; some specimens of *P. orbignyi* possess feeble cuspules on their lingual cingulum but smaller than those of *P. faventinus*. On the contrary, the specimen from Çalta-1 has a large additional cuspule distally to the protocone and a cuspule-like lingual cingulum.

In comparison to *Protictitherium* spp. and *G. megalotis*, the M1 of *P. faventinus* shows a reduction of the mesiobuccal cingulum around the paracone (cf. the lobed and buccally extended condition of e.g., *Pr. gaillardi* from various localities in Koufos, 2012b; *Pr. crassum* from Batallones-1 in Fraile, 2015, 2017); and buccolingual enlargement of the lingual portion of the M1, characterised in *P. faventinus* of a large-based protocone bounded by a developed shelf-like cingulum, unlike *Gansuyaena* or *Protictitherium* (whose species seldomly develop this cingulum but way less expanded or prominent, cf. *Pr. cingulatum*). Furthermore, neither *Protictitherium* nor *Gansuyaena* possess the enlarged M1 protocone of *P. faventinus*, which expands towards the centre of the tooth, shortening the trigon basin. The latter is wide and elongated lingually in *Protictitherium* spp. and *Gansuyaena*. In comparison to other *Plioviverrops* spp., similarities are obviously higher. For instance, the mesiobuccal cingulum tends to be reduced in these taxa, as *P. orbignyi* from Samos, Pikermi and Kryopigi (de Beaumont, 1969; Koufos, 2011; Lazaridis, 2015) and *P.* cf. *orbignyi* from Çalta-1 (Sen & Saraç, 2018) testify to. It should be noted that *P. gaudryi* from La Grive-St. Alban and *P. guerini* from Concud (Fig. 6; Alcalá, 1994; Montoya, 1997) possess a developed buccal expansion, more so in comparison to the former species of *Plioviverrops*. The upper molars described by Alcalá (1994) from Vivero de Pinos and ascribed to *P. guerini* are considerably different from that of the locality of Concud (site where the paratype of De Villalta-Comella & Crusafont-Pairó, 1948 comes from). Particularly the specimens from Vivero de Pinos are considerably elongated buccolingually, mesiodistally short, with a conspicuous mesiobuccal expansion of cingulum and a large trigon basin. All these morphologies resemble the condition of *Protictitherium* species, e.g., *Pr. gaillardi* from various Spanish localities (Robles, 2014 and S. B.-L. unpublished data), or *Gansuyaena megalotis* from Paşalar (n.b., Schmidt-Kittler, 1976 described these very same specimens as *Pr.* aff. *gaillardi*), and contrast with the buccolingually short and mesiodistally enlarged M1 from Concud (see Alcalá, 1994). Considering this uncertainty, we prefer to exclude the specimens from Vivero de Pinos from the hypodigm of *P. guerini* but retain the record with doubts on it (Tab. 2), since we were not able to study in person the other specimens, upper and lower premolars, attributed to *P. guerini* by Alcalá (1994). In general terms, the occlusal morphology of M1 of *P. faventinus* has a squared-like buccal margin compared to the rounded or lobed one respectively of *P. gaudryi* and *P. guerini* (rounded) and *P. orbignyi* and *P.* cf. *orbignyi* (lobed) (Fig. 6). Other relevant features are the development of the metacone in *P. faventinus*, which is almost as developed as the paracone similar to some specimens of *P. orbignyi* (e.g., from Kyopigi and Pikermi; Koufos, 2011; Lazaridis, 2015), *P. guerini* from Concud (Alcalá, 1994) and *P.* cf. *orbignyi* (see Sen & Saraç, 2018). On the contrary *P. gaudryi* from La Grive-St. Alban and *P.* cf. *gaudryi* from Los Valles de Fuentidueña (Ginsburg et al., 1981) have a smaller metacone compared to the paracone. The M1 protocone of *P. gaudryi*, *P.* cf. *gaudryi*, *P. orbignyi* and *P.* cf. *orbignyi* is somewhat smaller in occlusal view, in comparison to that of *P. faventinus*, and often placed lingually and with a reduced height. The position of the M1 protocone in such species identifies a proportionally buccolingually longer trigon compared to *P. faventinus*, but still mesiodistally wider than the condition of *Protictitherium* spp. and *Gansuyaena*. *Plioviverrops guerini* have a buccolingually short M1, with a protocone fairly similar to that of *P. faventinus* although the cingulum surrounding this lingual cusp is less developed, especially distally. The lingual cingulum bounding the protocone on both mesial and distal side (even uninterruptedly), is a distinctive feature of *P. faventinus* (Fig. 6). Indeed, the extent of development reached in this species is not present in any other, despite its presence in all other *Plioviverrops* spp. (n.b., the M1 of *P. gervaisi* is unknown).

The M2 does not seem to be particularly variable in the comparative sample. We might note a tendency in *Protictitherium* spp. and *G. megalotis* to have rounded M2 whereas in *Plioviverrops* the M2 is more elongated buccolingually and with a squared occlusal shape. There are no evident differences in the morphology of the M2 between *Plioviverrops* spp., except for, possibly, a lingual cingulum, which is present both mesially and distally in *P. faventinus* unlike other taxa, in which the lingual cingulum, if present, is limited to the mesial side of the protocone.

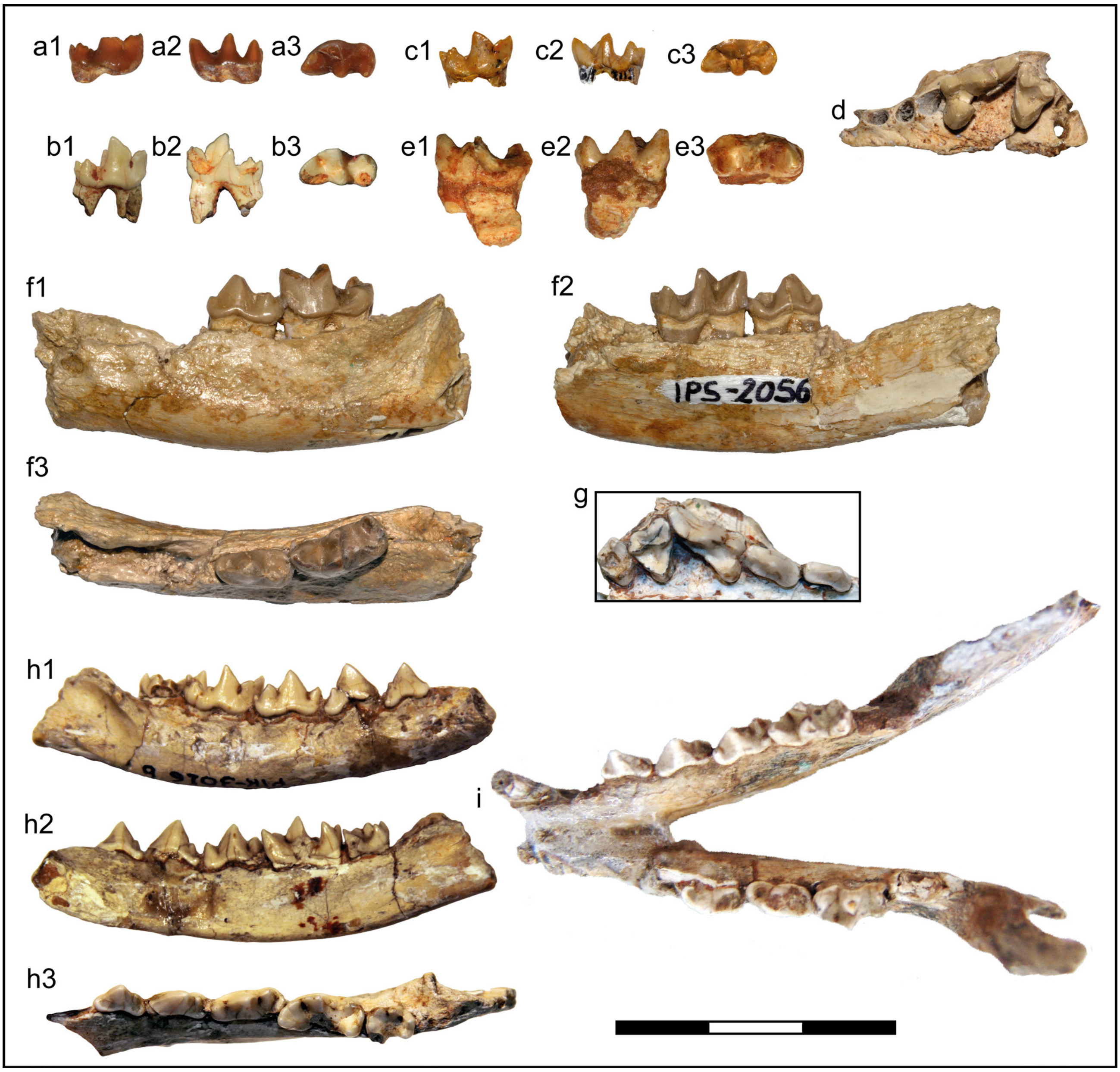


Fig. 6 - (color online) Types, paratype and other material of *Plioviverrops* spp. used as comparison in the analyses. a-b) *Plioviverrops gervaisi* from Vieux-Collonges (France, see Fig. 1 and Tab. 2). a) UCBL FSL 65566 (VxC 113a), right m1, type of *P. gervaisi* (in de Beaumont & Mein, 1972), in buccal (a1), lingual (a2) and occlusal (a3) views. b) UCBL FSL 65565 (VxC 113b), right m1 (figured in de Beaumont & Mein, 1972) in buccal (b1), lingual (b2) and occlusal (b3) views. c-d) *Plioviverrops gaudryi* from La Grive-Saint Alban (France; see Fig.1 and Tab. 2). c) NMB GA 2113, right m1 (figured in de Beaumont & Mein, 1972) in buccal (c1), lingual (c2) and occlusal (c3) views. d) MdC LGr.1360, left maxillary fragment with P4-M1, type of *P. gaudryi* (in de Beaumont & Mein, 1972), in occlusal view. e-f) *Plioviverrops guerini* from France and Spain (see Fig. 1 and Tab. 2). e) UCBL FSL 295052, left m1 from Les Mistrales III (France) in buccal (e1), lingual (e2) and occlusal (e3) views. f) IPS2056, left hemimandible with m1-m2 from Los Mansuetos (figured in Crusafont-Pairó & Petter, 1969; see Fig.1 and Tab. 2) in buccal (f1), lingual (f2) and occlusal (f3) view. g-i) *Plioviverrops orbignyi* from Pikermi (Greece; see Fig. 1 and Tab. 2). g-h) MNHN-F-PIK3016, detailed occlusal view (g) of the right upper P2-M2 (figured in, e.g., Koufos, 2009), and right hemimandible (h) with p2-m2 in buccal (h1), lingual (h2) and occlusal (h3) views. i) MNHN-F-PIK3022, mandibles with left p3-m1 and right c, p2-m1 from the type of *P. orbignyi* (in Gaudry & Lartet, 1856 and figured in Gaudry, 1867) in occlusal view. Scale bar equals 3 cm.

Mandible and lower dentition - The corpus of *P. faventinus* is distinguished from that of *Protictitherium* spp. (e.g., *Pr. crassum* or *Pr. gaillardi* from Spain; see Fraile, 2015) and *G. megalotis* from Gansu for the development of a more or less marked bending in the subangular region, giving a peculiar salient lateral shape to its mandible. Generally, the mandibular corpus of *P. orbignyi* from Pikermi and Kryopigi (Koufos, 2011; Lazaridis, 2015) (Fig. 6) do not show this lateral morphology, but some specimens from Perivolaki (e.g., PER-1; see Koufos, 2006) do possess a curvature of the ventral margin of the corpus and of the subangular region of comparable morphology to that observed in *P. faventinus*. Thus, it is possible that this feature is variable (even at a low degree) in the Greek-Balkan species. The mandibular specimens of *P. guerini* currently known, i.e., from Los Mansuetos (IPS2056; Fig. 6f) and Concud (De Villalta-Comella & Crusafont-Pairó, 1948), are broken rostrally to the subangular region, making impossible to compare the region with that of *P. faventinus*. The species from Cava Monticino shows a variability in number and position of the mental foramina, much like *P. orbignyi* from Kryopigi (see Lazaridis, 2015) or *P. guerini* from Los Mansuetos and Concud (De Villalta-Comella & Crusafont-Pairó, 1948) (Fig. 6). Whereas *Gansuyaena* seems to have only one mental foramen, the description is on a single specimen. Unlike *Protictitherium* spp. (e.g., *Pr. crassum* or *Pr. gaillardi* from Spain; see Fraile, 2015), *G. megalotis* from Gansu and *P. orbignyi* from Kryopigi, Perivolaki and Pikermi (Koufos, 2006, 2011; Lazaridis, 2015), *P. faventinus* has a more vertical coronoid process and a markedly deeper masseteric fossa compared to that of *P. orbignyi*. The same can be said for *G. megalotis*, whose masseteric fossa seems weaker than in *P. faventinus*. Like in the upper teeth, the lower cheek teeth of *P. faventinus* are characterised by shorter mesiodistal length and proportionately increased buccolingual width, especially in p2-p3, and for their molarisation. This is more evident in comparison to *Protictitherium* spp., e.g., *Pr. intermedium* and *Pr. cingulatum* from Turkey (Mayda et al., 2015) or *Pr. gaillardi* from La Grive-St. Alban. But this is also true for *P. orbignyi* (e.g., from Kryopigi; Lazaridis, 2015) and for *P. guerini* (e.g., from Concud; De Villalta-Comella & Crusafont-Pairó, 1948), in which p2 and p3 are more slender (Fig. 6). The two species share with *P. faventinus* the presence of a small mesial accessory cuspulid on p3 and a distal cingulid bounding p3 from the buccal to the lingual side. The distal accessory cuspulid on p3 is present in some specimens of *P. orbignyi* from Kryopigi, Perivolaki and Pikermi (Koufos, 2006, 2011; Lazaridis, 2015), but apparently missing in *P. guerini* (Fig. 6). Yet neither *P. orbignyi* nor *P. guerini* seem to possess a distolingual accessory cuspulid on p3, which is evident in *P. faventinus*. In terms of cuspulids, p4 of *P. faventinus* differs from those of *Protictitherium* spp. (e.g., *Pr. crassum* from Batallones-1; Fraile, 2015, or *Pr. gaillardi* from La Grive-St. Alban) and of *G. megalotis* from Gansu and Paşalar (Schmidt-Kittler, 1976; Galiano et al., 2022) for the relative size of the mesial cuspulid, the presence of a distolingual cuspulid and the marked buccal cingulid bounding p4. *Plioviverrops orbignyi* have a molarised p4 with distolingual cuspulid but with a slender p4, unlike the shortened and stout morphology of *P. faventinus* (Fig. 6). The degree of development of the accessory cuspulids in *P. guerini* is most similar to that in *P. faventinus*, but the two distal accessory cusps are shorter in buccal view and the mesial cuspulid is much slender and buccolingually narrower in occlusal view (Fig. 6). The morphology of the m1 trigonid cuspids of *P. faventinus* contrasts greatly with the condition of *Protictitherium* spp. (see e.g., *Pr. cingulatum* and *Pr. intermedium* in Schmidt-Kittler, 1976 and Mayda et al., 2015; *Pr. crassum* in Fraile, 2015; *Pr. gaillardi* and *Pr. thessalonikensis* in Koufos, 2012b) and *G. megalotis* (see Schmidt-Kittler, 1976; Galiano et al., 2022), in which the paraconid and the protoconid are the largest cuspids of the trigonid, and the metaconid is evidently smaller in comparison with the former. Moreover, these hyaenids differ from *P. faventinus* for the mesiodistally elongated m1, the slender and long talonid, and for the arrangement of the cuspids (Fig. 6). If observed in buccal and lingual view, the unworn paraconid, protoconid and metaconid tips of *P. faventinus* are located at the same height. In *Protictitherium* spp. and *G. megalotis* the protoconid is higher than the other trigonid cuspids (see among others, Schmidt-Kittler, 1976; Koufos, 2012b; Mayda et al., 2015; Galiano et al., 2022). Similarly, on the talonid of *P. faventinus*, the hypoconid is slightly lower than the entoconid, although similar at their base. The arrangement of the talonid cuspids in *Protictitherium* spp. and *G. megalotis* is different with the hypoconid shallow or reduced in comparison to the entoconid (see among others, Schmidt-Kittler, 1976; Koufos, 2012b; Mayda et al., 2015; Galiano et al., 2022). The lower carnassial of *P. gervaisi* from Vieux-Collonges (de Beaumont & Mein, 1972) (Fig. 6) has a slender trigonid, like *Protictitherium* spp., but with the talonid almost as wide as the trigonid. Moreover, the m1 metaconid of *P. gervaisi* is much smaller compared to the paraconid and protoconid, as evident in occlusal view; lastly, *P. gervaisi* shows an evident difference in height between the paraconid and protoconid, in buccal view (Fig. 6). The trigonid cuspids of *P. gaudryi* from La Grive-St. Alban are more similar in their sizes but their arrangement differs from those of *P. faventinus*. Particularly, *P. gaudryi* possesses a well-developed and long blade of the paraconid that projects mesially, unlike *P. faventinus* (Fig. 6). *Plioviverrops guerini* shows placement of the trigonid cuspids comparable to that of *P. faventinus*, although its metaconid is smaller and the paraconid is more elongated mesiodistally, similarly to *P. gaudryi* (Fig. 6). The most similar morphology to *P. faventinus* of trigonid cuspids is that of *P. orbignyi*, although in the latter the paraconid is yet slightly longer than the protoconid and metaconid (in some specimens e.g., from Kryopigi; Lazaridis, 2015) in comparison to *P. faventinus* (Fig. 6). The talonid of *P. faventinus* has the same width of the trigonid, a condition comparable to that of *P. guerini* and *P. orbignyi* but not of *P. gaudryi* and *P. gervaisi*, and it is proportionately shortened buccolingually compared to other *Plioviverrops* (cf. the distal elongation of e.g., *P. orbignyi* or *P. guerini* despite its relative width). Also the height of the talonid cuspids in *P. faventinus* are unmatched by other *Plioviverrops*, as even in derived taxa like *P. orbignyi* from Samos (de Beaumont, 1969) or *P. guerini* from Concud (De Villalta-Comella & Crusafont-Pairó, 1948) the unworn hypoconid and entoconid never reach the height of the trigonid cuspids (Fig. 6). Distally, a cuspulid-like cingulid and even a hypoconulid are often present in *Plioviverrops* spp. (from *P. gervaisi* from Vieux-Collonges; de Beaumont & Mein, 1972, to *P. orbignyi* from Greece; Koufos, 2011, 2012a), in a way comparable to *P. faventinus*. The m1 of *P. faventinus* shows a high and marked buccal cingulid larger than other species of the genus (Fig. 6). The m2 of *P. faventinus* is almost as buccolingually wide as the m1, unlike *Protictitherium* spp. (see e.g., Fraile, 2015) or *G. megalotis* (see Galiano et al., 2022) in which the m2 is elongated distally. Moreover, compared to *P. faventinus*, these taxa do not possess majority of the accessory cuspulids *P. faventinus* has. *Plioviverrops orbignyi* has a smaller m2 compared to the m1, characterised, in occlusal view, by a large-based hypoconid with and evident buccal projection (see Lazaridis, 2015) (Fig. 6). Although this cuspid is enlarged compared to that of *P. faventinus*, it is rather low in buccal view unlike the m2 hypoconid of *P. faventinus* that is higher and lies in line with the protoconid. Furthermore, the m2 talonid is reduced in comparison to that of *P. faventinus*, giving the m2 a distal thin occlusal outline. The entoconid of *P. orbignyi* is stouter and enlarged compared to that of *P. faventinus* (Fig. 6).

Morphometric comparison

The results of the PCA on the P4 are reported in Fig. 7 and SOM 1: Tab. S4. The PC1 accounts for 81.7% of the variability, whereas the PC2 and PC3 for a comparable portion of the total variability (i.e., respectively for the 8.3% and 5.7%). The PC1 is positively loaded by length and width of the upper carnassial, whereas the minimum width of the carnassial blade negatively influences the PC1. This axis is strongly and negatively correlated with body mass (*p*-value <<1). Along this axis, *Protictitherium* spp. with available material here reported (i.e., *Protictitherium crassum*, *Pr. gaillardi*, *Pr. intermedium* and *Pr. thessalonikensis*) occupy the majority of the morphospace, with *Pr. crassum* with negative values, *Pr. intermedium* and *Pr. thessalonikensis* with positive values and *Pr. gaillardi* with a wide range. *Gansuyaena* has high positive values of PC1. Along the axis, the basal *P. gaudryi*, *P. gervaisi* and the derived *P. orbignyi* are characterised by positive values of PC1, whereas *P. faventinus* have low positive values of PC1; *P. guerini*, unfortunately represented only by two specimens, is located across the center of the axis. The PC2 is positively influenced by the length of the paracone and of the metastylar blade, whereas the minimum width of the carnassial blade has strong negative loading on this axis. There is no correlation with body mass of the PC2 (*p*-value= 0.524). Along this axis, several species show a wider variability. This is particularly the case of *Pr. crassum* (Fig. 7), but also other taxa have a board range, e.g., *Pr. gaillardi*, *P. faventinus* and *P. orbignyi*. The only taxa separated along the PC2 are *P. gaudryi*, *P. gervaisi* and *G. megalotis*. *Plioviverrops faventinus* is the taxon with lowest values of PC2, and its variability in general is all located in the negative part of the PC2. The PC3 is positively influenced by the length of the metastylar blade and the width of the P4 at the carnassial blade, whereas the length of the parastyle negatively influences the PC3. There is no correlation with body mass of the PC3 (*p*-value = 0.678). Along this axis (Fig. 7), the taxa are almost all concentrated close to zero. Thus, there is little separation between taxa. Despite this, in the 3D plot we can see a good degree of distinction between species, and especially of *Plioviverrops* ones (Fig. 7 and the interactive plot in SOM 2 and SOM 3).

The results of the PCA on m1 measurements are reported in Fig. 8 and SOM 1: Tab. S5. The PC1 accounts for 75.2% of the variability, whereas the PC2 and PC3 for a comparable portion of the total variability (i.e., respectively for the 12.2% and 10.6%). The PC1 is positively loaded by length and width of the m1, and negatively by the width and length of the talonid. The PC1 is also strongly and positively correlated to body mass (*p*-value <<1). Regarding *Protictitherium* we notice an evident segregation of species, especially of *Pr. crassum* from *Pr. cingulatum* and *Pr. intermedium*. Along this axis it is possible to observe a clear division between *Plioviverrops* species. The most basal species *P. gaudryi* and *P. gervaisi* and the derived *P. orbignyi* are characterised by negative values of PC1, whereas *P. faventinus* and *P. guerini* mainly have low positive values of PC1. The specimens of *G. megalotis* are fairly separated from one another along this axis, although in a range of variability of other taxa e.g., *Pr. crassum*. The PC2 is positively influenced by the length of the trigonid and, to a lesser extent, by the width of the tooth; the length of the talonid and its width have strong negative loadings on this axis. No correlation between PC2 and body mass was retrieved (*p*-value = 0.333). Along this axis, the segregation of taxa is less evident, as species apparently experience a certain degree of intraspecific variability. This is particularly evident considering *Pr. crassum* and *Pr. gaillardi* (Fig. 8). The only taxa separated along the PC2 are the two basal species of *Plioviverrops* (*P. gaudryi* and *P. gervaisi*) and *Pr. cingulatum*. *Plioviverrops faventinus* and *P. guerini* show a degree of variability almost comparable to that of *Pr. crassum*. The PC3 is positively influenced by the width of the talonid and to a lesser extent, by the length of the trigonid, whereas negatively by the length of the talonid. Even in the case of PC3, no correlation between this axis and body mass was retrieved (p-value =0.203). As in the case of upper teeth, along this axis all taxa are clustered together with no distinction among them. The 3D plot using the first three axes shows better discrimination between species especially regarding *Pr. crassum* and *P. orbignyi*, whose 3D convex hull are separated from any other (Fig. 6 and the interactive plots in SOM 2 and SOM 3). The convex hull of *P. guerini* intersects that of *P. faventinus*, despite only a single specimen of *P. guerini* is close to the tridimensional variability of *P. faventinus* (Fig. 8).

Analysis of ecomorphological parameters

The plot of the ecomorphological indices RPS (relative size of the largest premolar expressed as width of p4 divided by the cubic root of the body mass) and RBL (relative length of the blade of m1 resulted from the ratio between m1 trigonid length and mesiodistal length of m1) on extant herpestids and viverrids and fossil hyaenids is reported in Fig. 9a. We see a partial overlap between the two extant families (dash-lined convex hull for Herpestidae and dot-lined convex hull for Viverridae in Fig. 9), but they differ as to which ecomorphological parameter is the

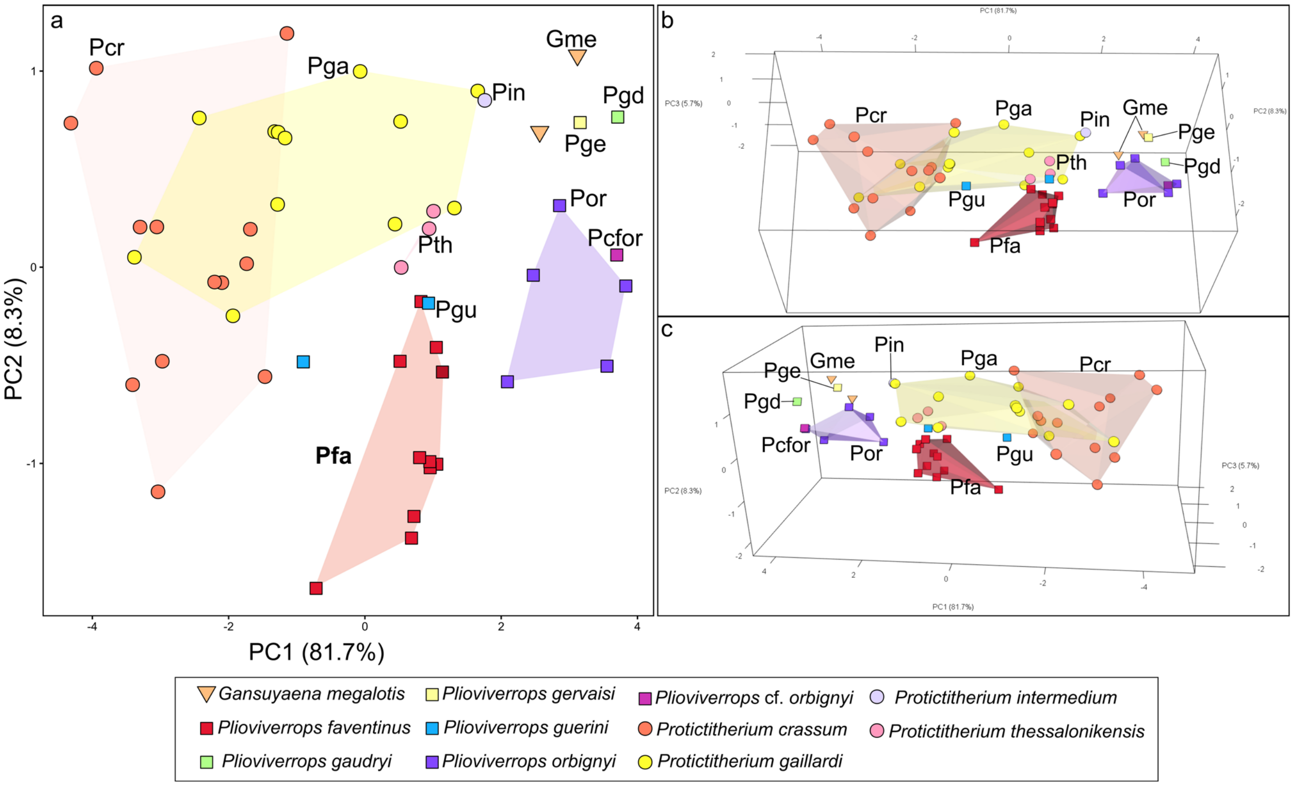


Fig. 7 - (color online) a) Biplot of the two first components of the Principal Components Analysis (PCA) based on the upper carnassial measurements of fossil hyaenids referred to *Gansuyaena*, *Plioviverrops* and *Protictitherium*. b-c) 3D plot of PC1-PC3 showing additional variability (see SOM 2 and SOM 3). Symbols and colors are explained in the legend. Notice the high degree of separation between taxa, especially *Plioviverrops* spp. from *Protictitherium* spp. and *P. faventinus* from *P. orbignyi*. Abbreviations: Gme, *G. megalotis*; Pcr, *Pr. crassum*; Pcfor, *P.* cf. *orbignyi*; Pfa, *P. faventinus*; Pga, *Pr. gaillardi*; Pgd, *P. gaudryi*; Pge, *P. gervaisi*; Pgu, *P. guerini*; Pin, *Pr. intermedium*; Por, *P. orbignyi*; Pth, *Pr. thessalonikensis*.

most variable. Viverrids show a greater variability in the values of RPS and a lower one in RBL, although there is some degree of difference in RBL especially considering the position of *Civettictis civetta*. On the contrary, herpestids have very wide range of values of RBL and a smaller range of RPS. Considering fossil taxa, we notice that almost all of them have relatively wide range of RBL and RPS. Among *Protictitherium*, *Pr. crassum* have the relative lowest RBL and *Pr. intermedium* the lowest RPS index, whereas the highest values of both indices are those of *Pr. cingulatum* from MN7/8 of Turkey. *Plioviverrops guerini* and *G. megalotis* are within the variability of other *Protictitherium* species, and particularly *G. megalotis* is very close to *Pr. intermedium*. Indeed, all the three taxa have relatively low RBL (among *Protictitherium* spp.) and together with *Pr. crassum*, they fall in the proximity of *Genetta cristata* and *Viverra megaspila*. *Protictitherium gaillardi* and *Pr. thessalonikensis* have high values of RBL, far from extant species (Fig. 9a). All these species fall in the variability of the extant omnivores (Fig. 9a). *Protictitherium cingulatum* is separated from all the other extinct taxa both for RBL and RPS and falling well outside any dietary groups (Fig. 9a). The last two species of *Plioviverrops* are well separated from the rest of the extinct species. *Plioviverrops orbignyi* has a rather low RBL value (lower than *Pr. crassum*) but a high RPS value, close to that of *P. faventinus* and lower only to *Pr. cingulatum* (Fig. 9a). Its position is right close to those of *Herpestes ichneumon* and *Urva edwardsii* in the area of overlap between extant omnivores and insectivores (Fig. 9a). Lastly, *P. faventinus* has a high RPS value but an outstandingly low RBL value. These parameters include it in the variability of insectivores (Fig. 9a). Although no living carnivore is close to its position, *Pc. selousi* is the nearest to *P. faventinus* (Fig. 9a). The results of the discriminant function analysis are reported in Fig. 9b and SOM 1: Tab. S6. Axis 1 accounts for 74.8% of the variability and is positively influenced by both variables. Axis 2 accounts for a quarter of the variability (25.2%) and is mainly negatively influenced by the RBL. The resulting graph substantially confirms the pattern observed in the biplot (Fig. 9b). The two major groups, i.e., omnivores and insectivores, have some overlap. The extant families share a portion of the morphospace. Regarding the fossil taxa, most of them are included in the variability of extant omnivores. The relative positions of the fossil taxa are also maintained, with *G. megalotis*, *P. guerini*, *Pr. crassum* and *Pr. intermedium* clustered close together; *Pr. gaillardi* and *Pr. thessalonikensis* separated from other extant and fossil taxa but within the omnivore hull. Lastly, *P. orbignyi* lies again close to *He. ichneumon* and *U. edwardsii* in the overlapping area of omnivore and insectivore convex hulls. The exceptions in the fossil taxa are *Pr. cingulatum*, well outside any a priori group, and *P. faventinus* falling in the convex hull of insectivores. The a posteriori prediction matrix (Tab. 7) classifies most of the taxa as omnivores whereas *P. faventinus* is classified as insectivore and *Pr. cingulatum* as frugivore.

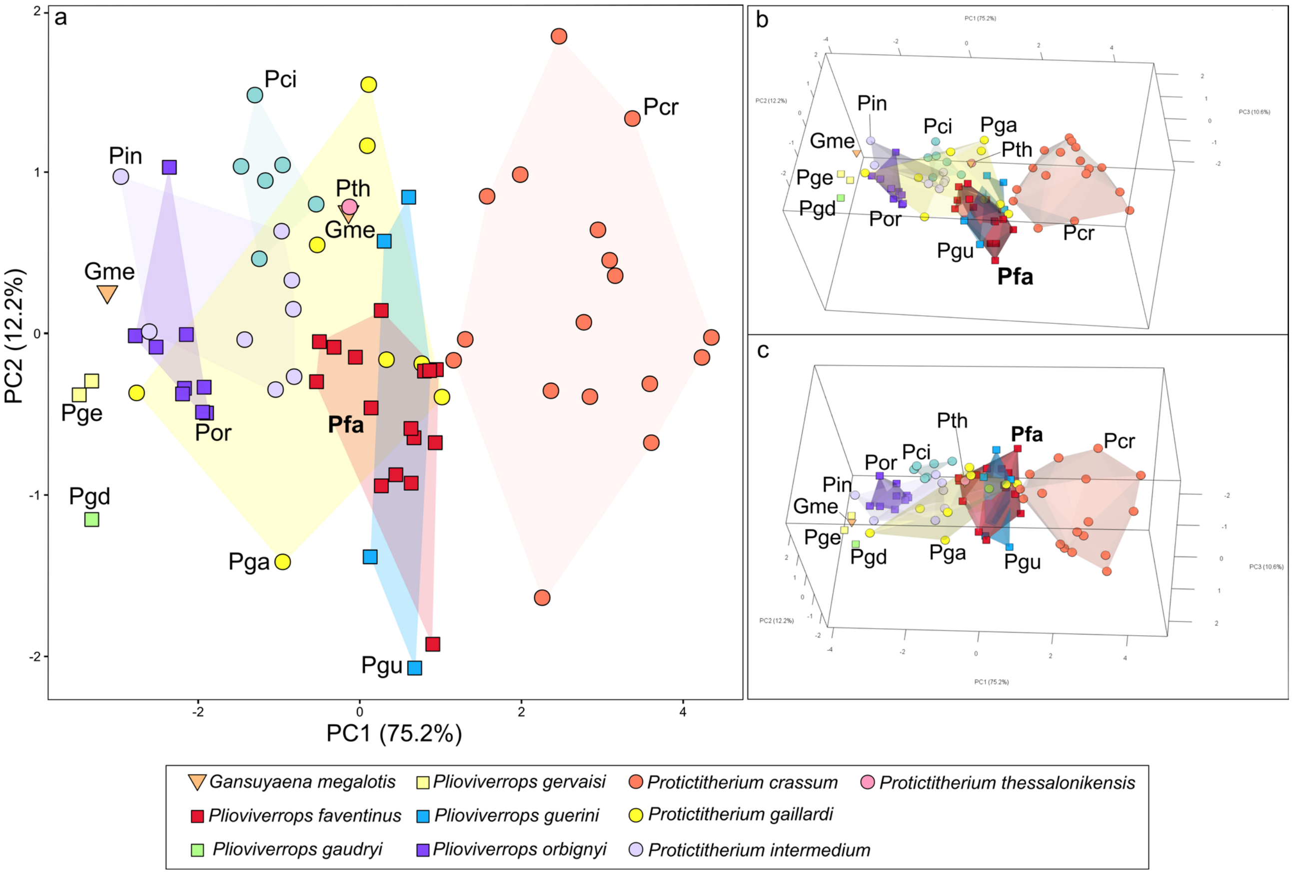


Fig. 8 - (color online) a) Biplot of the two first components of the Principal Components Analysis (PCA) based on the lower carnassial measurements of fossil hyaenids referred to *Gansuyaena*, *Plioviverrops* and *Protictitherium*. b-c) 3D plot of PC1-PC3 showing additional variability (see SOM 2 and SOM 3). Taxa are less separated from one another compared to Fig. 7, although if we consider *Plioviverrops* spp., we see that taxa are well distinguished with the exception of *P. faventinus* and *P. guerini*. Unlike *P. guerini*, whose variability is greatly scattered, specimens identified as *P. faventinus* form a consistent cluster, as evident in panels (b-c). Symbols and colors are explained in the legend. Abbreviations: Gme, *G. megalotis*; Pcr, *Pr. crassum*; Pcfor, *P.* cf. *orbignyi*; Pfa, *P. faventinus*; Pga, *Pr. gaillardi*; Pgd, *P. gaudryi*; Pge, *P. gervaisi*; Pgu, *P. guerini*; Pin, *Pr. intermedium*; Por, *P. orbignyi*; Pth, *Pr. thessalonikensis*.

DISCUSSION

Plioviverrops faventinus*: the last representative of a long-lasting genus*

The morphological and morphometric characteristics of *P. faventinus* clearly distinguish it from the other small-sized hyaenids known in the fossil record, confirming the description made by Torre (1989). The attribution to the genus *Plioviverrops* proposed by Torre (1989) seems the most parsimonious considering the features possessed by the taxon from Cava Monticino and La Gloria 4. Among these: 1) the enlargement of the subangular region on the mandible; 2) the molarisation of the premolars, especially p4; 3) the mesiodistal shortening of the shearing surface of the P4 trigon and the m1 trigonid; 4) the enlargement of lingual cuspids/cuspulids of the upper and lower molars (e.g., M1 protocone; m1 entoconid). Despite remarking some degree of uncertainty, Turner et al. (2008) stressed the affinity of *P. faventinus* with *Plioviverrops*. It is nonetheless true that some of the features that are normally considered highly diagnostic are missing in the specimens from Cava Monticino, such as the morphologies of the auditory bulla (Hunt, 1991; Hunt & Solounias, 1991; Werdelin & Solounias, 1991; Galiano et al., 2022), as this region is not preserved in any of the specimens recovered either in Cava Monticino nor in La Gloria 4. Several authors used these features to support the primitiveness of *Plioviverrops* (de Beaumont, 1969; Werdelin & Solounias, 1991), with many similarities to the extant *Proteles* (de Beaumont, 1969; Hunt, 1987; Hunt & Solounias, 1991; Werdelin & Solounias, 1991) or the fossil *Gansuyaena* (Galiano et al., 2022) and *Protictitherium* (Fraile, 2015). Although such similarities might represent symplesiomophies rather than actual valuable phylogenetic features, they have been used (along with others craniodental ones) to link *Plioviverrops* to the *Proteles* lineage (e.g., Thenius, 1966). However, it should be noted that *Proteles* lacks the alisphenoid canal that all these fossil taxa retain (as evident from de Beaumont, 1969 for *Plioviverrops*; from Hunt & Solounias, 1991 for *Tungurictis*; from Fraile, 2015 for *Protictitherium*, particularly *Pr. crassum*; and from Galiano et al., 2022 for *Gansuyaena*). This retention is the exemplification of the primitive state of these fossil taxa (Wozencraft, 1989; Goswami & Friscia, 2010). Although not present in the hypodigm of *P. faventinus*, the morphologies of the auditory bulla are relevant to the discussion on the relation of *Plioviverrops* and other hyaenids. Moreover, the recent erection of *Gansuyaena*, with the ascription of *P. guerini* to this genus and the possible close relationship with *Proteles*

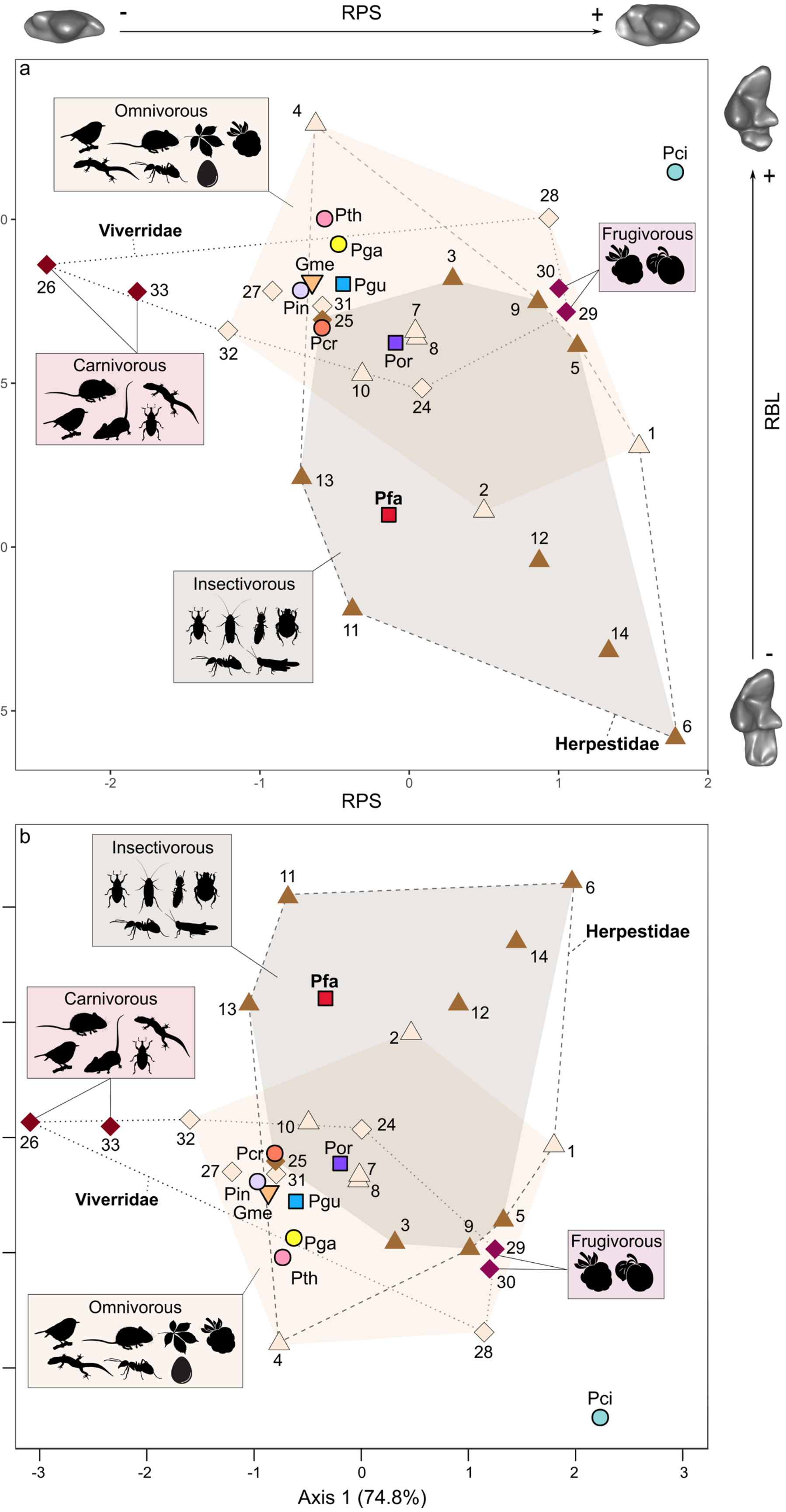
(Galiano et al., 2022), make the issue of *Plioviverrops* affinities of a certain relevance. According to Galiano et al. (2022), the reattribution of *P. guerini* to *Gansuyaena* is apparently relying on "the overall cusp development", "the uncrowded premolar series" and the "weak anterior cusp of p4" (Galiano et al., 2022: p. 104). In this sense we fail to see the distinction of the genus *Gansuyaena* from both *Protictitherium* and *Plioviverrops*, but also, for the same reason, we fear that numerous *Protictitherium* and/or *Plioviverrops* species could potentially be included in "*Gansuyaena*". The age uncertainty of the Chinese specimens and the geographic distance with the supposed Turkish one (Galiano et al., 2022) (Fig. 1), complicates the interpretation. It is true, that the most reliable diagnostic auditory features of "*G.*" *megalotis*, i.e., the hypertrophy of the ectotympanic and the bilaminar bullar septum, may be plausibly still interpreted as specific discriminants although cranial specimens with basicranial region preserved are lacking, especially of *Protictitherium* spp. (e.g., *Pr. cingulatum*; *Pr. gaillardi*; *Pr. intermedium*; *Pr. thessalonikensis*) and *Plioviverrops* spp. (all apart from *P. orbignyi*). Thus, both the distinction and the conspecificity are difficult to test. *Plioviverrops guerini*, thus, remains a peculiar taxon with limited hypocarnivorous adaptations especially in relation to other coeval small-sized hyaenids, as *P. orbignyi* (see Koufos, 2006, 2011; Lazaridis, 2015) (Fig. 6). The ascription to a distinct group might not be too far reached. This fits with the initial proposal by de Beaumont & Mein (1972) of including *P. guerini* in the subgenus *Mesoviverrops* and was followed by Galiano et al. (2022), who included it in *Gansuyaena*. Despite these reasonable hypotheses, we deem hard at the moment to support the choice of a different generic name among the available taxa, considering the fragmentary nature of reliable specimens attributable to *P. guerini*, composed almost entirely of dental remains. We share Beaumont & Mein (1972)'s view of a resemblance of *P. guerini* to *P. gaudryi* (Fig. 6) but fail to see the remarkable similarities with "*G.*" *megalotis* in their teeth. At present, we prefer to maintain the generic attribution of *P. guerini* to *Plioviverrops*, bearing in mind its possible different nature. Regarding the species *P. faventinus*, we can plausibly exclude a relationship with "*G.*" *megalotis* considering the remarkably different tooth morphology of the former in comparison to the latter (Figs 3-5 in comparison to those in Galiano et al., 2022). The morphometric and morphological comparison with other taxa showed that *P. faventinus* undoubtedly shares a high number of dentognathic features with other members of *Plioviverrops*, and particularly with *P. gaudryi* and *P. orbignyi* (Fig. 6). We believe that the phylogenetic and ecological interpretations of previous authors (mainly Werdelin & Solounias, 1996; Werdelin & Turner, 1996; Turner et al., 2008), of a tendency towards hypocarnivory culminating with *P. faventinus*, still finds supports in the morphological and morphometric evidence currently available (see also the following section).

Summing up on the tangle of the most basal genera of hyaenids, their taxonomy and phylogenetic relationships are far from being resolved and will need deep research in the close future. Firstly, it will be necessary to check the validity of some of the current taxa ascribed to *Protictitherium* and test them to exclude possible instances of synonymy with other small-sized hyaenids, chiefly *Plioviverrops* and/or *Tungurictis*. This, hopefully, will resolve the long-expressed concern of paraphyly or even polyphyly of these genera, thus clarify the evolutionary scenario of basal hyaenids. Secondly, although we are conscious of the problematic nature of the issue, there is the need of a shared understanding of phylogenetically relevant characters to be used to build robust and supported phylogenetic reconstructions, which will guide the just-mentioned resolution of Hyaenidae affinity. At the same time, the current chronological scenario of these taxa needs also to be substantially improved, particularly with more robust stratigraphic constraints compared to biochronological interpretations. The present work represents a drop in this wide ocean, on a very peculiar and fairly easily defined taxon. We clarified the taxonomic validity and the plausible affinities of *P. faventinus*, reinforcing the ideas expressed by other scholars (Torre, 1989; Turner et al., 2008).

Ecomorphology of early hyaenids and inference on the dietary preferences of Plioviverrops

An established tradition in literature has ecomorphologically regarded *Plioviverrops* spp. as mongoose-like hyaenids (Ecomorph Group 2 of Werdelin & Solounias, 1991, 1996; see also Turner et al., 2008). This definition distinguishes them from *Protictitherium* spp., considered instead as civet-like hyaenids (Ecomorph Group 1 of Werdelin & Solounias, 1991, 1996). This ecomorphological classification helped picturing the specialisation and the niches occupied by these early hyaenids in Miocene environments (Werdelin & Turner, 1996). In this general view, the phylogenetically primitive *Protictitherium* (at least as normally understood) maintained a generalised carnivore dentognathic morphology, similar to certain extant Viverridae. Conversely, *Plioviverrops* specialised toward hypocarnivory, maybe invertebrivory/insectivory (and even more if considering them in the lineage of extant

Fig. 9 - (color online) a) Morphospace of dietary preferences of extant Herpestidae and Viverridae and extinct small-sized Hyaenidae of the genera *Gansuyaena*, *Plioviverrops* and *Protictitherium* obtained by the relative premolar size (RPS) and relative length of the trigonid blade (RBL). On the top and the right side the 3D of a p4 and of a m1 (respectively) visually show what the two indices express in terms of ecomorphological characteristics of the lower teeth. b) Discriminant function analysis on the same variables and the a priori dietary ecological groups (SOM 1 Tab. S3 for the references) fitting a posteriori the fossil taxa. List of taxa as expressed by numbers: Herpestidae: 1, *Atilax paludinosus*; 2, *Crossarchus obscurus*; 3, *Cynictis penicillata*; 4, *Galerella sanguinea*; 5, *Helogale hirtula*; 6, *Helogale parvula*; 7, *Herpestes ichneumon*; 8, *Urva edwardsii*; 9, *Urva javanica*; 10, *Xenogale naso*; 11, *Ichneumia albicauda*; 12, *Mungos mungo*; 13, *Paracynictis selousi*; 14, *Suricata suricatta*. Viverridae: 24, *Civettictis civetta*; 25, *Genetta cristata*; 26, *Genetta genetta*; 27, *Genetta tigrina*; 28, *Genetta victoriae*; 29; *Paradoxurus hermaphroditus*; 30, *Paradoxurus jerdoni*; 31, *Viverra megaspila*; 32, *Viverra zibetha*; 33, *Viverricula indica*. Abbreviations: Gme, *G. megalotis*; Pcr, *Pr. crassum*; Pcfor, *P.* cf. *orbignyi*; Pfa, *P. faventinus*; Pga, *Pr. gaillardi*; Pgd, *P. gaudryi*; Pge, *P. gervaisi*; Pgu, *P. guerini*; Pin, *Pr. intermedium*; Por, *P. orbignyi*; Pth, *Pr. thessalonikensis*.


a
RPS
-
+
RBL
Omnivorous
Frugivorous
Carnivorous
Insectivorous
Viverridae
Herpestidae
Pci
Pth
Pga
Gme
Pgu
Pin
Pcr
Por
Pfa
1
2
3
4
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6
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9
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12
13
14
24
25
26
27
28
29
30
31
32
33
0.00
-0.05
-0.10
-0.15
-2
-1
0
1
2
b
Axis 1 (74.8%)
Axis 2 (25.2%)
2
1
0
-1
-2
-3
3

Proteles; as Galiano et al., 2022), and progressively so during the Late Miocene (as suggested by de Beaumont & Mein, 1972 and followed by subsequent authors e.g., Torre, 1989; Werdelin & Solounias, 1991; Turner et al., 2008). Coca-Ortega & Pérez-Clarós (2019) updated this interpretation using dental parameters to fine-tune the ecomorphological interpretation at a specific level, rather than at a generic/grade one. Their results show that some *Protictitherium* are reconsidered as mongoose-like forms, i.e., *Pr. intermedium* and *Pr. thessalonikensis*. Similarly, *P. guerini* should actually be considered as civet-like taxon, while confirming that *P. faventinus* and *P. orbignyi* have dentognathic proportions comparable to the Herpestidae. Our results on lower tooth ecomorphological parameters (Fig. 9) show a significant variability in the extant taxa. This is particularly true in terms of relative length of the carnassial blade for herpestids and relative size of the largest lower premolar for viverrids. Yet it is clear that unlike herpestids, whose variance along the y-axis is great, the majority of Viverridae are clustered in a limited morphospace region (Fig. 9). Regarding fossils, we notice that "*G.*" *megalotis* from China and Turkey (Galiano et al., 2022), *P. guerini* from Spain (De Villalta-Comella & Crusafont-Pairó, 1948; Montoya, 1997) and *Pr. intermedium* from Çandir (Schmidt-Kittler, 1976; Mayda et al., 2015) have very similar parameters. *Protictitherium crassum* from various European localities (Fraile, 2015) share similar RPS values by having a proportionally shorter carnassial blade compared to the latter three taxa. Similarly, although to a lesser extent, *Pr. gaillardi* and *Pr. thessalonikensis* have comparable RPS and RBL values with one another. In general terms we can say, following previous authors (Van Valkenburgh, 1989; Van Valkenburgh et al., 2003; Friscia et al., 2007) that the closer in morphospace the extant species are to the studied fossil species, the more probable their similarity as extant ecological analogues. In the case of "*G.*" *megalotis*, *P. guerini* and *Pr. intermedium* the closest taxa are *V. megaspila* (the Asian large-spotted civet) and *Genetta tigrina* (the Cape genet), whereas *Pr. crassum* is close to *Genetta victoriae* (the giant forest genet). This suggests that these fossil species could have been opportunistic mesocarnivores (Van Rompaey & Colyn, 2013; Jennings & Veron, 2022). *Protictitherium gaillardi* and *Pr. thessalonikensis* are within the variability of omnivores but no extant species is close in terms of RBL and RPS indices. Therefore, it is difficult make further dietary inferences. *Protictitherium cingulatum* from Yeni Eskisihar (Schmidt-Kittler, 1976) is considerably separated from the other fossil species, but also from extant ones (Fig. 9). It is difficult to suggest a possible ecological affinity with any of the considered living species, although the discriminant analysis suggests a possible affinity with frugivorous taxa (Tab. 7). In our sample, frugivorous species are only represented by the Asian palm civet *Paradoxurus hermaphroditus* (Bartels, 1964; Su & Sale, 2007; Kwan, 2016; Zaki et al., 2018) and the brown palm civet *Pa. jerdoni* (Grzimek et al., 2004; Mudappa et al., 2010) so this classification needs further testing. Moreover, without dental wear analyses and study of possible scansorial/arboreal adaptations eventually present in all these early hyaenids (as suggested by some authors, e.g., Semenov, 1989) it is difficult to make further inference on the preferences of this taxon. Despite difficulties, following the previously mentioned ecomorphological classification, our results would suggest classifying these taxa as "civet-like" hyaenids. *Plioviverrops orbignyi* has the second lowest RBL value, for the proportionate reduction of the trigonid length, and the highest relative size of the premolar of *Plioviverrops* (although slightly more than *P. faventinus*). This might suggest a diet composed of tougher food items in comparison to the other taxa of the genus. Moreover, it is interesting to notice that *P. orbignyi* has RBL and RPS values very close to those of the Egyptian mongoose *He. ichneumon* and the Indian grey mongoose *U. edwardsii*. Both these taxa are opportunistic mesocarnivorous taxa but with a great variety of meat, invertebrates and plant food items in the diet (Palomares, 2013; Hussain & Mahmood, 2016). Thus, the classification of *P. orbignyi* as an omnivore taxon does not seems too farfetched. Additionally, the ecomorphological similarity is not in sharp contrast with the morphological dentognathic features of these taxa (see e.g., Rasouli & Yousefi, 2023). It is moreover interesting to note the distinction between the coeval *P. guerini* and *P. orbignyi* (see Fig. 1), with the first one plausibly more carnivorous (and "civet-like" as noticed above) whereas the latter more of an opportunist with varied diet (and "mongoose-like"). *Plioviverrops faventinus* is the most peculiar taxon here analysed, and this peculiarity is also reflected in ecomorphological parameters. The reduction of the trigonid characterised the reduction of RBL value but also of the premolar size itself considering its fairly large body mass (comparable to *P. guerini* and more than double of *P. orbignyi*), locate *P. faventinus* in an area of the morphospace predominantly occupied by herpestids, confirming the "mongoose-like" interpretation (Werdelin & Solounias, 1996), and particularly in the range of

		Fossil Species								
		"G." megalotis	*P. faventinus*	*P. guerini*	*P. orbignyi*	*Pr. cingulatum*	*Pr. crassum*	*Pr. gaillardi*	*Pr. intermedium*	*Pr. thessalonikensis*
Predicted	**CARN**	0	0	0	0	0	0	0	0	0
	FRU	0	0	0	0	1	0	0	0	0
	OMNI	1	0	1	1	0	1	1	1	1
	INSE	0	1	0	0	0	0	0	0	0

Tab. 7 - Predicted attribution of the fossil taxa to the a priori defined ecological groups in the discriminate function analysis of Fig. 9. Abbreviations: CARN, carnivores; FRU, frugivores; INSE, insectivores; OMNI, omnivores. Groups defined in Materials and Methods.

variance of insectivores (Fig. 9, Tab. 7). What was its diet composition like? As for other fossil taxa, there is no extant taxon which is easily relatable to *P. faventinus*: the only species closer to the Messinian taxon is the extant Selous's mongoose *Pc. selousi* (Fig. 9), although the former has proportionally shorter trigonid and more robust premolar. This small-sized herpestid is principally invertebrivorous, and particularly insectivorous, with seldom income of small-vertebrate meat (Smithers, 1971; Smithers & Wilson, 1979; Stuart & Stuart, 2013). This ecomorphological closeness between *P. faventinus* and *Pc. selousi* might be confirmation of the long-hypothesised shift of the species of *Plioviverrops* towards hypocarnivory (etymologically) and invertebrivory. The values of RBL and RPS of *P. faventinus* (and its dentognathic morphology) seem to confirm this hypothesis. New analysis, especially of its dental wear, could indeed help support or correct this interpretation.

CONCLUDING REMARKS

The taxonomic and systematic status of the genus *Plioviverrops* continues to remain problematic after nearly a hundred years of research. The scarce and scattered record, the difficulty in the interpretation of possible diagnostic characters and the complex relationship with other Miocene hyaenids and carnivorans hinder the general understanding of the old and long-ranged genus (Turner et al., 2008). We reported in Tab. 1 a summary of the hypotheses proposed in literature in order to understand the evolution of ideas on this group of hyaenids and, hopefully help clarifying its systematics. At least five taxa have generally been associated with this genus, spanning from the Early-Middle Miocene to the Pliocene (Fig. 1 and Tab. 2). The taxonomic status of some of these remains debated, e.g., *P. guerini* that was referred to "*P.* (*Mesoviverrops*)" or to "*Gansuyaena*". Although plausible, a distinct generic attribution for this taxon is at present difficult to confirm. Other species of *Plioviverrops* are far more characterised thanks to their relatively more abundant record, e.g., *P. orbignyi* from the Late Miocene of the Greek-Balkan area is the most renowned species of the genus. Within this picture, *P. faventinus* is a key taxon in the evolutionary scenarios of the small-sized hyaenids. It represents one of the last (if not the last) of this group of hyaenid that arose in Eurasia. Apart from its outstanding record in the type locality (here redescribed after the work of Torre, 1989), dated around 5.4 Ma, the only other certain occurrence of the taxon is that of the Spanish La Gloria 4, reported by Alcalá (1994).

Plioviverrops faventinus is also easily distinguished by other *Plioviverrops* for its diagnostic dentognathic features, like the high and angulate mandible corpus, sharp and pointed cusps/cuspids and reduced carnassial blades. These special dentognathic features indicate hypocarnivorous/invertebrivorous adaptations unlike any other known taxon of *Plioviverrops* or *Protictitherium*. They are comparable to those of some extant herpestids. This fits with the previous ecomorphological interpretations (e.g., Werdelin & Solounias, 1991; Coca-Ortega & Pérez-Claròs, 2019) regarding the group and, particularly, *P. faventinus* as a "mongoose-like" hyaenid. Considering their record, from the earliest forms of the MN4-MN5 (i.e., *P. gervaisi* and *P. gaudryi*) to *P. faventinus*, and through *P. orbignyi*, the interpretation of de Beaumont & Mein (1972) of a tendency towards the hypocarnivory in the lineage remains justified. Less clear are the relationships of *Plioviverrops* with other hyaenids and particularly with *Proteles*. The fossil record of this African hyaenid is known only from the Early Pleistocene (Turner, 1997; Werdelin & Peigné, 2010), about 2 Ma after the last occurrence of *Plioviverrops*, and these occurrences already showed the peculiar dentognathic features that typify the aardwolf (Werdelin & Solounias, 1991). Historically, in literature, a relationship between *Plioviverrops* and *Proteles* has been proposed on the basis of the small-size and the hypocarnivorous/insectivorous adaptations (Thenius, 1966; Werdelin & Solounias, 1991). Similar but alterative hypotheses have been suggested, e.g., the affinity with "*Gansuyaena*" (Galiano et al., 2022), although none of them can be excluded nor confirmed, even using molecular evidence (Eizirik et al., 2010; Westbury et al., 2019; Hassanin et al., 2021). The phylogenetic issues of *Plioviverrops* remains open. Among them, *P. faventinus* has been often overlooked in scientific literature, possibly for the limited publications centered on it. The present paper offers a new overview on the craniodental features of this hyaenid after the pioneering work of Danilo Torre (Torre, 1989), updating and clarifying its morphometric and morphological features and, for the first time, its ecomorphology.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data generated and analysed in this contribution are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-641/

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