The Fossil Record of Hyaenids (Mammalia: Carnivora: Hyaenidae) in Greece

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1 Introduction

Hyaenidae is a carnivoran family known with several taxa since the Miocene to the present. Extant hyaenids include four species: the hunting and scavenging large hyaenas *Parahyaena brunnea* (brown hyaena), *Hyaena hyaena* (striped hyaena), and *Crocuta crocuta* (spotted hyaena), as well as the aardwolf *Proteles cristata*, which is feeding on termites. The family is characterized by narrow and low-to-short and broad cranium, moderately elongated and bony auditory meatus, expanded ectotympanic and semi-recumbent to recumbent septum bullae, massive canines without cutting edges or grooves, upper carnassial with elongated parastyle, blade-like metastyle and sometimes reduced protocone, blade-like lower carnassial with metaconid in the primitive forms which decreases and disappears in the later forms and with relatively small talonid, sometimes absence of the P1 and p1, decrease in size and disappear of the M1 and M2, and absence of the m2 in the later forms (Orlov 1968; Myers 2000). In *Proteles*, the teeth are simple and uniform, like flattened cones, except the canines which are strong for protection. The limbs are elongated with the forelegs being longer than the hinder ones; the legs are usually tetradactyls (except in *Proteles*) with nonretractile claws. The hyaenas are generally considered as scavengers but they can hunt and kill large animals, especially if they are hunting as a group. They can cover long distances to find carrions or in other cases, they follow other predators (lions, cheetahs) to find food (Orlov 1968; Myers 2000).

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2 Historical Overview

The hyaenids were relatively common in the first collections from the various Greek Miocene localities. Some taxa were originally recognized in the first collections from Pikermi and Samos. Several articles on the Greek hyaenids have been published by various Greek and foreign authors as early as the nineteenth century (e.g., Gaudry 1862–1867; Arambourg and Piveteau 1929; Pilgrim 1931; Melentis 1967; Sickenberg 1968; Tsoukala 1989; Roussiakis 1996; Koufos 2000, 2011).

3 Phylogenetic Relationships

The hyaenids originated from the viverrids and arrived in the Old World during the beginning of the Miocene. The early Miocene hyaenids include small-sized and arboreal forms very similar to the modern *Hemigalus derbyanus* ("banded civet"). The genus *Plioviverrops* is one of the earliest hyaenids and occurred in Southern Europe since the early Miocene. It is considered as the ancestral form of the large hyaenids appeared later in the Miocene–Pleistocene (MacDonald 1992). The family reached its maximum diversity in the middle Miocene (~15.0 Ma) with more than 30 species, which are dog-like, nimble, and similar to wolves or jackals (e.g., *Ictitherium viverrinum*). The bone-cracking hyaenids appeared at the end of middle–beginning of late Miocene, and they are common in the late Miocene faunas. The bone-cracking hyaenids survived the different climatic changes from the Miocene to the Pleistocene. *Adcrocuta eximia*, the predominant species in the late Miocene, was replaced in the Pliocene by *Pliocrocuta*, and later by *Pachycrocuta*, which was a large-sized bone-cracking hyaena scavenging on large herbivore carcasses. The decline of the large herbivores at the last Ice Age causes the disappearance of *Pachycrocuta* and its replacement by *Crocuta*, which is still living. The modern aardwolf *Proteles* is directly related with the evolutionary line of *Plioviverrops*, representing a living dog-like hyaenid (MacDonald 1992).

4 Distribution

The family Hyaenidae is widely distributed in the whole Old World; some taxa have a wide distribution and can be used as biostratigraphic markers, e.g., *Adcrocuta eximia*, *Hyanectitherium wongii*, and *Pachycrocuta brevirostris*. In Greece, the hyaenids are well known from the middle Miocene to the Pleistocene with several taxa. They are very common in the late Miocene faunas of Greece with a lot of ictitheriines and hyaenines. The most common species is *Adcrocuta eximia* in the late Miocene and *Crocuta crocuta* in the Pleistocene. They were recognized in several localities all over the country (see Fig. 1 and the Appendix). Besides the referred

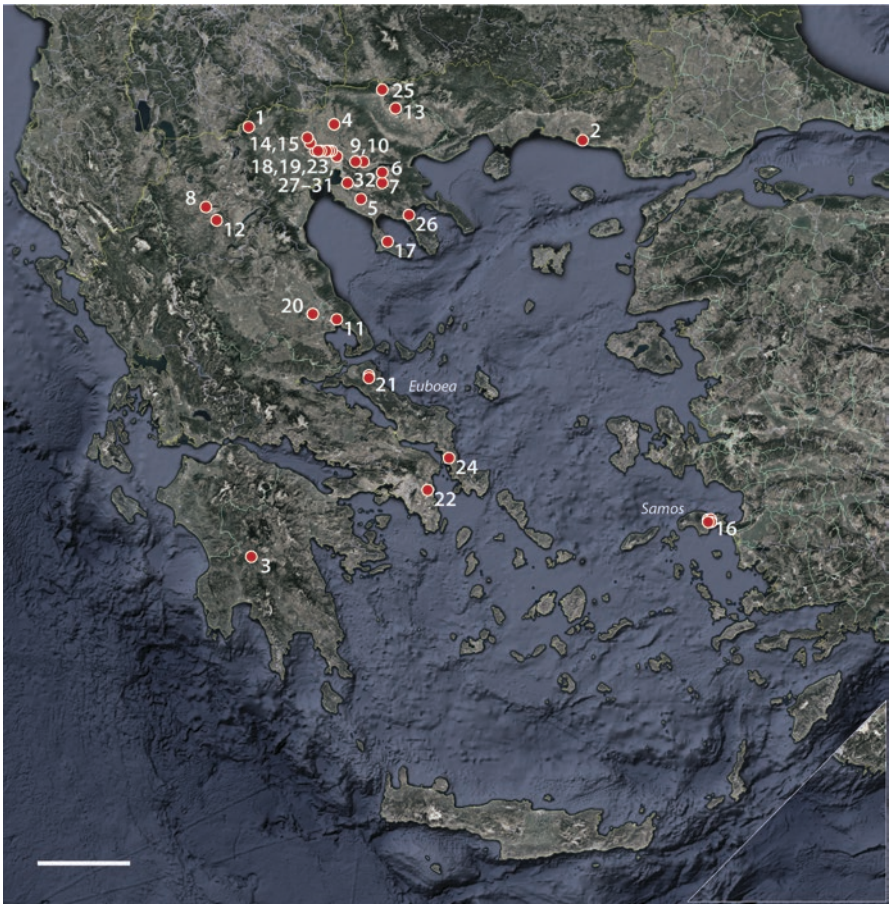

Fig. 1 Map of Greece showing the geographic distribution of the most important localities with hyaenid fossils. **1**, Loutra Almopias Cave; **2**, Maronia Cave; **3**, Megalopolis basin; **4**, Agios Georgios Cave; **5**, Petralona Cave; **6**, Tsiotra Vrissi; **7**, Kalamoto; **8**, Libakos; **9**, Apollonia 1; **10**, Gerakarou 1; **11**, Sesklon; **12**, Dafnero 1; **13**, Maramena; **14**, Dytiko 1; **15**, Dytiko 3; **16**, various localities in Samos Island; **17**, Kryopigi; **18**, Vathylakkos 2; **19**, Vathylakkos 3; **20**, Perivolaki; **21**, Kerassia localities; **22**, Pikermi; **23**, Prochoma 1; **24**, Halmyropotamos; **25**, Thermopigi; **26**, Nikiti 2; **27**, Ravin des Zouaves 5; **28**, Ravin X; **29**, Ravin de la Pluie; **30**, Ravin des Zouaves 1; **31**, Pentalophos 1; **32**, Antonios. See Appendix for more information. Image exported from Google Earth Pro © 2019, map data from US Dept. of State Geographer, SIO, NOAA, U.S. Navy, NGA, GEBCO, image from Landsat/Copernicus. Scale bar equals 80 km, North faces upward

fossiliferous sites in the description of each species, hyaenid remains are referred from some other sites but their material is poor and the specific determinations are doubtful.

5 Systematic Paleontology

Hyaenidae Gray, 1821

Ictitheriinae Trouessart, 1897

Protictitherium Kretzoi, 1938

Type Species *Herpestes crassus* Depéret, 1892.

Remarks A small protictithere is known by two fragments of m1 from the locality Antonios in Chalkidiki. Despite their similarities with *P. crassum,* it cannot be definitely attributed to this species as the material is too scarce and fragmentary and thus it was attributed as *P*. cf. *crassum* (Koufos 2008). The genus is also present in the locality Pentalophos 1; although its similarity with *P. crassum*, it differs from it displaying slightly smaller size, more molarized premolars, long talonid in the m1, higher and stronger metaconid in the m1, and more robust teeth, thus it is referred to as *P.* cf. *crassum* (de Bonis and Koufos 1991). In the material from Ravin de la Pluie, there is an m1 displaying similar morphology and size to that of *P. intermedium* but the limited material cannot allow a definite attribution; therefore, it is identified as *P.* cf. *intermedium* (Koufos 2000).

Protictitherium crassum (Depéret, 1892)

Nomenclatural and Taxonomical History *Herpestes crassus* in Depéret 1892 (new species); *Progenetta crassa* in Forsyth Major 1903 (new combination and mandatory change); *Protictitherium crassum* in Kretzoi 1938 (new combination and mandatory change).

Type Material Specimen number unknown (holotype), some mandibular remains and an isolated P4 (Depéret 1892: p. 31; pl. 1, figs 14–17).

Type Locality La Grive, France, middle Miocene, MN7 + 8.

Distribution The species is recognized in the Greek localities Xirochori 1, and Dytiko 3 in Axios Valley, and Mytilinii 4 in Samos Island. Besides its type locality in France, it is also referred from Spain, Germany, and Turkey.

Remarks The first occurrence of this species in Greece was from Dytiko 3, based on a hemimandible (Koufos 1980) (Fig. 2a), and later in Xirochori 1 and Mytilinii 4 (Koufos 2000, 2009). It is characterized by relatively deep and thin mandibular corpus, large mental foramen below the anterior root of the p2, elongated and narrow symphysis roughly inclined backward, slightly curved ventral margin of the mandibular corpus, small, single rooted and monocuspid p1, elongated and narrow p2 and p3 without anterior and small posterior accessory cuspid, p4 with anterior

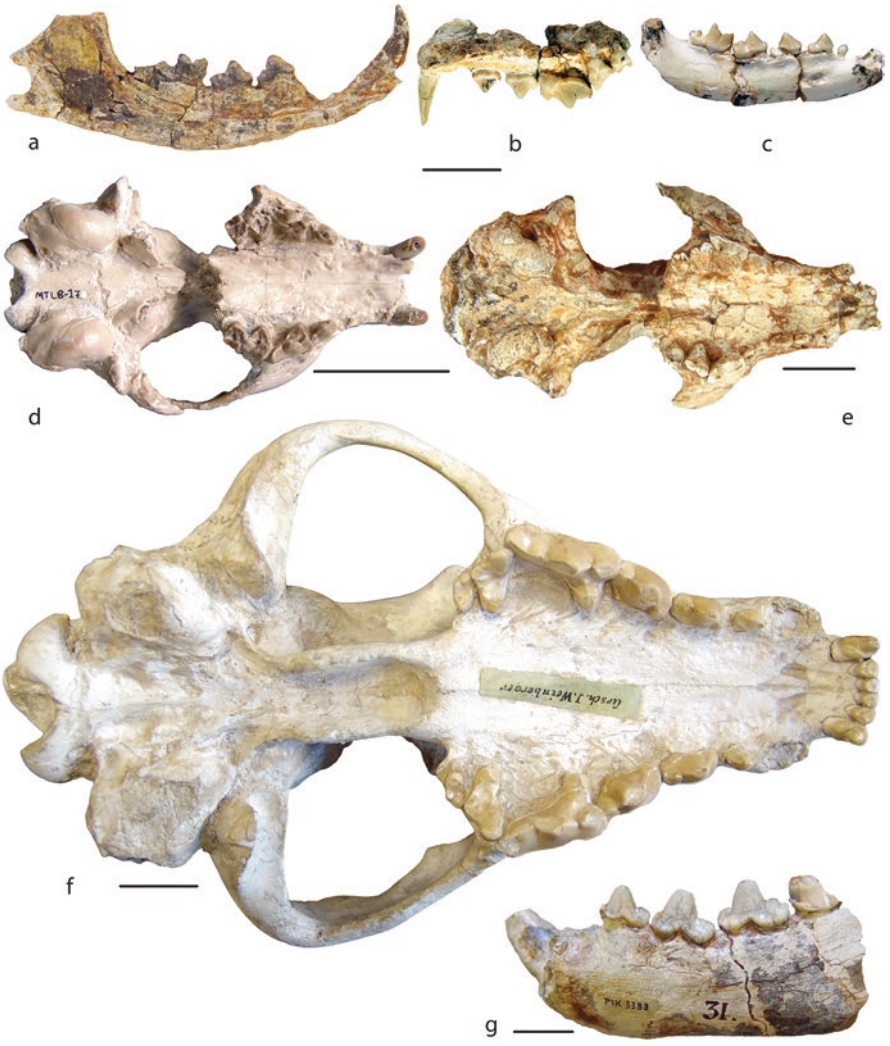

Fig. 2 Selected specimens of Ictitherinae (Hyanidae) from Greece. (**a**) *Protictitherium crassum*, LGPUT-DKO-20, hemimandible with c, p3–m1 from Dytiko 3 in buccal view; (**b**, **c**) *Protictitherium thessalonikensis* from Ravin de la Pluie; (**b**) LGPUT-RPl-69, right maxillary fragment with C–M2 (holotype) in lingual view; and (**c**) LGPUT-RPl-68, left mandibular fragment with c–m1 in buccal view; (**d**) *Plioviverrops orbignyi*, NHMA-MTLB-170, cranium from Mytilinii 1B in palatal view; (**e**) *Ictitherium viverrinum*, MNHNP-PIK-3022, cranium from Pikermi in palatal view; (**f**) *Hyaenictitherium wongii*, NHMW-SAM-A.4746, cranium from an unknown locality of Samos Island in palatal view; (**g**) *Lycyaena chaeretis*, MNHNP-PIK-3383 (holotype), left mandibular fragment with c, p2–p4 from Pikermi in buccal view. Scale bar equals 2 cm

accessory cuspid and talonid-like posterior part, short and wide lower carnassial with clear metaconid and large tricuspid talonid (Koufos 2000, 2009).

Protictitherium gaillardi (Forsyth Major, 1903)

Nomenclatural and Taxonomical History *Herpestes crassus* in Gaillard 1899 (initial identification); *Progenetta gaillardi* in Forsyth Major 1903 (new species); *Protictitherium gaillardi* in Schmidt-Kittler 1976 (new combination).

Type Material Lgr-1352–1353 (holotype) maxilla and associated mandible, housed in Natural History Museum of Lyon (Gaillard 1899: 60; pl. II, figs 1, 3).

Type Locality La Grive, France, middle Miocene, MN7+8.

Distribution This species is also known from the Miocene of Spain and Turkey, and the early/middle Miocene (MN 4/5) locality of Antonios, Greece.

Remarks The type material of this species is characterized by slender upper premolars with developed cingulum, strong protocone in the P4 situated in front of the parastyle and a triangular-shaped M1 (Gaillard 1899). The generic attribution of this species has been subject to several changes until its current referral to *Protictitherium* (Schmidt-Kittler 1976). A maxillary fragment with M1–M2 and a mandibular fragment with p4 are only known from Greece. A number of characters support the attribution of the Greek material to this species, including the strongly projected buccally paracone of M1, the small metacone and the well-developed protocone (higher than the other two cusps on M1), the elongated p3 with a strongly projected distally distal cingulum, the strong posterior accessory cuspid on p4, the high main cuspid, the well-defined metaconid, and the bicuspid talonid on m1 (Koufos 2008).

★*Protictitherium thessalonikensis* Koufos, 2012

Nomenclatural and Taxonomical History *Plioviverrops orbignyi* in Koufos 1980 (initial identification); *Protictitherium* aff. *gaillardi* in de Bonis and Koufos 1991 (new identification); *Protictitherium thessalonikensis* in Koufos 2012 (new species).

Type Material LGPUT-RPl-69 (holotype), right maxillary fragment with C–M2 (Fig. 2b, c).

Type Locality Ravin de la Pluie, Axios Valley, Macedonia, late Miocene, MN10.

Remarks The initial poor material from Ravin de la Pluie did not allow the distinction from the other taxa, though some differences have been observed. During the continuous excavations, the enrichment of the collection allowed the recognition of this new species. The main characters of this species are: small size; low cusps(-ids) in the teeth; protocone of the P4 aligned with the mesial border of the parastyle; large molars, especially M2; slight buccal projection of the paracone in the M1;

strongly molarized p4; strong metaconid; and large talonid with high entoconid on the m1 (Koufos 2012).

Plioviverrops Kretzoi, 1938

Type Species *Viverra orbignyi* Gaudry and Lartet, 1856.

Remarks A few dental remains of a small ictithere are known from the locality Vathylakkos 3 in Axios Valley. The relatively large size, the high and narrow p2 and p3 without accessory cuspids, and the less molarization suggest similarities with *P. guerini* and thus they are identified as *P.* cf. *guerini* (de Bonis and Koufos 1991). New material of *Plioviverrops* from other Greek localities indicates that there is a variation in the size and the presence of the accessory cuspids. Therefore, it is important to reexamine the taxonomy of this species (Koufos 2006, 2009). Some postcranial remains of *Plioviverrops*, known from the fossiliferous site Kerassia-3 in Euboea Island, have similar dimensions to *P. orbignyi* from Pikermi. However, the limited comparative material and the absence of dental remains cannot certify the presence of the species and thus the postcrania is referred to as *Plioviverrops* sp. (Roussiakis and Theodorou 2003).

★*Plioviverrops orbignyi* (Gaudry and Lartet, 1856)

Nomenclatural and Taxonomical History *Viverra orbignyi* in Gaudry and Lartet 1856 (new species); *Thalassictis orbignyi* in Gaudry 1861 (new combination); *Ictitherium orbignyi* in Gaudry 1862–1867 (new combination); *Plioviverrops orbignyi* in Kretzoi 1938 (new combination).

Type Material MNHN-PIK-3022 (holotype), skull associated with the mandible, stored in the Museum national d'Histoire naturelle of Paris and described by Gaudry and Lartet (1856: 273).

Type Locality Pikermi, Attica, Greece, late Miocene, MN12.

Distribution The species is known from the Greek localities Ravin des Zouaves 5, Prochoma 1 and Vathylakkos 2, 3 in Axios Valley, Perivolaki in Thessaly, Mytilinii 1B, Samos Q1, A in Samos Island, and Kryopigi in Chalkidiki. Besides Greece, it is also known from Bulgaria and possibly from Turkey.

Remarks The main characters of the species are: the oval narial opening, the large elliptical orbits, the large auditory bullae, the short and wide palate, the very long postorbital processes, the long-narrow and roughly inclined backward symphysis, the pointed cusps in the teeth, the absence or the rudimentary accessory cusps on the P2 and P3, the elongated upper carnassial with relatively large protocone situated in front of the parastyle's mesial margin, and the long talonid, the high and equal-sized metaconid and protoconid, and the high entoconid of the m1 (Pilgrim 1931; Koufos 2006, 2009) (Fig. 2d).

Ictitherium Wagner, 1848

Type Species *Ictitherium viverrinum* Roth and Wagner, 1854.

Remarks A right mandibular ramus with c, p3–m1 (AMPG-KER-K3/204 from Kerassia 3 in Euboea Island displays larger p3, m1, m3, and more robust p3 than those of *I. viverrinum*, as well as an m2 similar to that of *I. pannonicum*. Besides this similarity, the poor material and its bad preservation cannot allow its definite attribution to this species and thus it is referred to as cf. *I. pannonicum* (Roussiakis and Theodorou 2003). There is also a single p2 from the locality Perivolaki in Thessaly, which has similar morphology and size to *I. viverrinum*, but it is reported as *Ictitherium* sp. because of the poor material (Koufos 2006).

★*Ictitherium viverrinum* Roth and Wagner, 1854

Nomenclatural and Taxonomical History *Galeotherium* sp. in Wagner 1840 (initial identification); *Ictitherium* sp. in Wagner 1848 (new genus); *Ictitherium viverrinum* Roth and Wagner 1854 (new species).

Type Material BSPM-PIK-AS II.66 (holotype), the right mandibular fragment with p2–m1 and the left mandibular fragment with c–p4, housed in the Bayerische Staatssammlung für Paläontologie und Geologie, München, described and figured by Roth and Wagner (1854:49; taf. 8, figs 3, 5).

Type Locality Pikermi, Attica, Greece, late Miocene, MN12.

Distribution Besides the type locality, *I. viverrinum* is widespread in Greece, found in the localities Ravin des Zouaves 5, Prochoma 1, Vathylakkos 3 of Axios Valley, Kryopigi in Chalkidiki, and Q1 and A in Samos Island. The species is also known from Slovakia, Moldova, Ukraine, Turkey, Iran, and China.

Remarks The species is characterized by medium size, infraorbital foramen above the P2, short and relatively wide palate, oval-shaped and hyaenid-like auditory bullae with their anterior border behind the post-glenoid processes, high mandibular corpus with almost straight ventral margin, short angular process, shallow masseteric fossa with its anterior margin situated below the mesial one of the m2, absence of anterior accessory cusp on P2 and P3 but with strong posterior one situated on a distal cingular projection, short and robust P4 with weak protocone aligned mesially with the parastyle, long and narrow M1, long M2 relative to the M1, absence of anterior accessory cuspid in the p2 and p3, small posterior accessory cuspid on a strong distal cingular projection of the p2 and p3, small anterior and large posterior accessory cuspids on the p4, pointed cuspids on the m1, low shearing blade (paraconid + protoconid blade) on the m1, high metaconid relative to the protoconid, and large and oval-shaped m2 (Kurtén 1982; Koufos 2000) (Fig. 2e).

Hyaenictitherium Kretzoi, 1938

Type Species *Ictitheriun hyaenoides* Zdansky, 1924.

Remarks An isolated tooth from the locality Mytilinii 4 of Samos Island is similar to that of *Hyaenictitherium wongii* and therefore it was identified as *H.* cf. *wongii*, indicating its possible presence in the older levels of Samos fossiliferous deposits (Koufos 2009).

Hyaenictitherium wongii (Zdansky, 1924)

Nomenclatural and Taxonomical History *Hyaena hipparionum* in Gervais 1846, 1850 (initial identification); *Ictitherium hipparionum* in Gaudry 1862–1867 (new combination); *Palhyaena hipparionum* in Kittl 1887 (new combination); *Ictitherium wongii* in Zdansky 1924 (new species); *Palhyaena wongii* in Howell and Petter 1980 (new combination); *Thalassictis wongii* in Solounias 1981 (new combination); *Hyaenotherium wongii* in Semenov 1989 (new combination); *Hyaenictitherium wongii* in Andersson and Werdelin 2005 (new combination).

Type Material Although, several skulls and mandibles from China were described by Zdansky (1924:73; taf. 14, figs. 3–6, taf. 15, figs. 1–4, taf. 16, figs. 1, 2), he did not define a holotype. Solounias (1981) defined the cranium and mandible from Locality 109, figured in plate 15 of Zdansky (1924) and housed in the Palaeontological Institute of Uppsala, as the lectotype of the species.

Type Locality Locality 109, Yushe, Shansi, China, MN11–13.

Distribution The species is widely distributed in the whole Eurasia, from Spain to China. In Greece, it is referred from Pikermi in Attica, Ravin des Zouaves 1, Ravin des Zouaves 5, Vathylakos 2, 3 in Axios Valley, and Mytilinii 1A, B, C, Q1, Q4, Q5, and S3 in Samos Island.

Remarks It is a medium-sized ictithere quite common in Eurasia (Fig. 2f). It differs from *Ictitherium* by displaying an elongated metastyle-blade and a large protocone in the P4, reduced molars and relatively short talonid on the m1. The elongated metastyle-blade of the P4, the less high protoconid of the m1, the weak talonid with lower cuspids of the m1, and the smaller size separate it from *Thalassictis*.

Lycyaena Hensel, 1862

Type Species *Hyaena chaeretis* Gaudry, 1861.

★*Lycyaena chaeretis* (Gaudry, 1861)

Nomenclatural and Taxonomical History *Hyaena chaeretis* in Gaudry 1861 (new species); *Lycyaena chaeretis* in Hensel 1862 (new combination).

Type Material MNHNP-PIK-3383 (holotype), mandibular fragment with c–p2 (right) and p2–m1 (left) (Fig. 2g), housed in the Museum national d'Histoire naturelle of Paris, described and figured by Gaudry (1861:534; pl. 11, figs 3–6).

Type Locality Pikermi, Attica, Greece, late Miocene, MN12.

Distribution The taxon is relatively scarce in Eurasia; in Greece, besides the type locality, it is known from the locality A of Samos Island.

Remarks The main characters of the species are: the absence of the anterior and the presence of a strong posterior accessory cusp on the P2 and P3, the elongated and narrow upper carnassial with strong and well separated protocone, the large m1, the well-developed posterior accessory cuspid in the lower premolars situated on a distal cingular projection, the strong anterior accessory cuspid of the p4, and the rudimentary anterior accessory cuspid (like a cingular projection) of the p2 and p3 (Pilgrim 1931) (Fig. 2g).

Hyaeninae Gray, 1821

Hyaenictis Gaudry, 1861

Type Species *Hyaenictis graeca* Gaudry, 1861.

Remarks A right P3 from the locality Ravin de la Pluie of Axios Valley is morphologically and metrically similar to that of *Hyaenictis graeca* but it is referred to as *Hyaenictis* sp. because of the single and not well-preserved tooth (Koufos 2012).

★*Hyaenictis graeca* Gaudry, 1861

Nomenclatural and Taxonomical History *Hyaenictis graeca* in Gaudry 1861 (new species).

Type Material MNHNP-PIK-3002 (lectotype), left mandibular ramus with dP2–dP4 and P4–M1 (Fig. 2b), described and figured by Gaudry (1861:527; pl. 11, figs 1–2), defined by Pilgrim (1931), and housed in the Museum national d'Histoire naturelle of Paris.

Type Locality Pikermi, Attica, Greece, late Miocene, MN12.

Distribution Except the type locality, the species is referred from Spain, where another species is also referred (*H. almerai*). The genus *Hyaenictis* is recognized in Africa (Kenya, Ethiopia and South Africa) by different species.

Remarks Except the type mandible, one maxillary fragment, housed in the Museum national d'Histoire naturelle of Paris, and one maxillary fragment and one mandibular fragment in the Natuhistorisches Museum, Wien (Fig. 3a), belonging possibly to the same individual, are the only known material of *H. graeca*. The main

characters of the species are the moderately long slender and shallow mandibular corpus, the large protocone of the upper carnassial which is aligned with the mesial border of the parastyle, the long shearing blade of the P4 with its distal end directed buccally, the large M1, the slender p2 and p3 with strong posterior accessory cuspid and absence of anterior one, the large anterior and posterior cuspids on the p4, the relatively short m1 without metaconid, the short talonid with large entoconid and hypoconid of the m1 (pers. observations). The large protocone of the upper carnassial, as well as the narrow and slender premolars distinguish *H. graeca* from *Adcrocuta eximia*.

Chasmaporthetes Hay, 1921

Type Species *Chasmaporthetes ossifragus* Hay, 1921.

Remarks Some dental remains from the locality Maramena in Serres Basin have been described as *Chasmaporthetes* sp. because they are morphologically closer to this taxon (Schmidt-Kittler 1995:85, fig. 9–13).

★*Chasmaporthetes bonisi* Koufos, 1987

Type Material LGPUT-DTK-126 (holotype), left mandibular ramus with p2–m1, housed in the Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki, described and figured by Koufos (1987:918; pl. 1, figs 1, 2, 3c).

Type Locality Dytiko 1, Axios Valley, Greece, late Miocene, MN13.

Distribution Besides the type locality, it is known from the locality Ravin des Zouaves 5 of Axios Valley.

Remarks *Chasmaporthetes bonisi* represents a primitive form of hunting hyaenas recognized for the first time in Greece by Koufos (1987) (Fig. 3c). It is characterized by relatively narrow palate, moderately developed P1, large protocone in the P4, well-developed M1, curved and imbricated lower tooth row, oval distal margin in the lower premolars, absence or rudimentary anterior accessory cuspid on the p2 and p3, absence of metaconid on the m1, and small-bicuspid talonid with reduced entoconidon in the m1 (Koufos 1987; de Bonis and Koufos 1994).

Chasmaporthetes lunensis (del Campana, 1914)

Nomenclatural and Taxonomical History *Lycyaena lunensis* in del Campana 1914 (new species); *Hyaena honannesis* in Zdansky 1924 (new species); *Lycaenops lunensis* in Kretzoi 1938 (new genus); *Euryboas bielawski* in Schaub 1941 (new species); *Euryboas lunensis* in Viret 1954 (new combination); *Chasmaporthetes kani* in Galiano and Frailey 1977 (new species); *Chasmaporthetes lunensis* in Kurtén and Werdelin 1988 (new combination).

Fig. 3 Selected specimens of Hyaeninae (Hyaenidae) from Greece. (**a**, **b**) *Hyaenictis graeca* from Pikermi; (**a**) NHMW-PIK- A4715, left maxillary fragment with P3–M1 in lingual view; (**b**) MNHNP-PIK-3002, left mandibular fragment with p2–m2 and dp2–dp4 (lectotype) in buccal view; (**c**) *Chasmaporthetes bonisi* from Ravin des Zouaves 5, LGPUT-RZO-125, maxilla with I2–M1 (right side) and I2, I3, P2–P4 (left side) in palatal view; (**d**) *Chasmaporthetes lunensis* from Dafnero 1, LGPUT-DFN-75, left mandibular fragment with i1–p4 in buccal view. Scale bar equals 2 cm

Type Material IGF 4377 (holotype), partial cranium with the upper dentition, stored in the Museum of Florence, described and figured by del Campana (1914: p. 87; pl. 11).

Type Locality Olivola, Val di Magra, Italy, Early Pleistocene (MNQ17).

Distribution The species is dispersed in Eurasia known from Spain, France, Italy, Ukraine, Russia, Tajikistan, Turkey, China, and Mongolia. In Greece, it is only known from Dafnero 1 in Western Macedonia.

Remarks The known material from Greece includes two mandibular fragments (Fig. 3d) and some isolated teeth, characterized by elongated and slender upper carnassial with strong protocone aligned with the mesial margin of the parastyle, elongated and narrow lower premolars, presence of both accessory cuspids in the lower premolars, m1 short and narrow without or with vestigial metaconid, short bicuspid talonid with a large hypoconid and a small entoconid; all these characters allow its attribution to *C. lunensis* (Koufos 1993).

Adcrocuta Kretzoi, 1938

Type Species *Hyaena eximia* Roth and Wagner, 1854.

★*Adcrocuta eximia* (Roth and Wagner, 1854)

Nomenclatural and Taxonomical History *Hyaena eximia* in Roth and Wagner 1854 (new species); *Crocuta eximia* in Pilgrim 1931 (new combination); *Adcrocuta eximia* in Kretzoi 1938 (new genus).

Type Material BSPM-PIK-105 (holotype), right mandibular ramus with i3–m1 (Fig. 4a, b), stored in the Bayerische Staatssammlung für Paläontologie und Geologie, München (Roth and Wagner 1854: 396; tab. 8, fig. 6).

Type Locality Pikermi, Attica, late Miocene, MN12.

Distribution *Adcrocuta eximia* was widely distributed in Eurasia, from Spain to China. In Greece, besides Pikermi, it is known from Xirochori 1, Ravin de la Pluie, Ravin des Zouaves 1, Ravin des Zouaves 5, Ravin X, Prochoma 1, Vathylakkos 3 in Axios Valley, Nikiti 2 and Kryopigi in Chalkidiki, Mytilinii 1A, Q1, Q4, Q5, A, and S3 in Samos Island, Perivolaki in Thessaly, Thermopigi in Serres Basin, Halmyropotamos and Kerassia 4 in Euboea Island.

Remarks It is a common hyaenid and easily recognizable in the late Miocene mammal faunas of Eurasia. The main characters of the species are: elongated and wide cranium, strong zygomatic arches projecting laterally, large nasal cavity, wide palate, large and flattened laterally auditory bullae with their anterior border at the level of the posterior wall of the post-glenoid fossa, elongated and narrow occipital condyles, large foramen magnum (Fig. 4c), high and thick mandibular corpus with convex ventral margin, relatively low ascending ramus, elongated and narrow mandibular condyle, oval and deep masseteric fossa with its anterior margin below the distal end of the m1, two mental foramens below the p2 and p3 and robust teeth. The P2 and P3 have rather elliptical occlusal outline and lack anterior accessory cusp while the posterior one is large and packed on the main cusp. The upper carnassial is elongated and slender with strongly reduced protocone situated well behind the mesial margin of the parastyle. The M1 is very small and situated vertically to the P4. The p2 is small and oval-shaped without anterior but with large posterior accessory cuspid packed on the main one. The p3 is rectangular more robust than the p2 with only posterior accessory cuspid and the p4 bears anterior and posterior accessory cuspids. The lower carnassial is long and relatively narrow lacking metaconid (in some cases there is a small metaconid) and bearing a small, low, and bicuspid talonid (pers. observations). Two subspecies have been recognized in Greece: *A. e. leptoryncha* de Bonis and Koufos, 1981 in the Vallesian (MN10) and *A. e. eximia* in the Turolian (MN11–13). *A. e. leptoryncha* differs from the nominal subspecies displaying longer snout, narrower palate, less compressed jugal tooth row, and slenderer premolars (de Bonis and Koufos 1981; Koufos 2000).

Pliocrocuta Kretzoi, 1938

Type Species *Hyaena perrieri* Croizet and Jobert, 1828.

Fig. 4 Selected specimens of derived Hyaeninae (Hyaenidae) from Greece. (**a–c**) *Adcrocuta eximia* from Pikermi; (**a**, **b**) BSPM-PIK- AS II105 (holotype), right hemimandible with i3–m1 in (**a**) lingual and (**b**) occlusal views; (**c**) MNHNP-PIK-3000, cranium in palatal view; (**d**) *Pliocrocuta perrieri* from Gerakarou 1, LGPUT-GER-150, right mandibular fragment with i3–m1 in lingual view; (**e, f**) *Pachycrocuta brevirostris* from Gerakarou 1; (**e**) LGPUT-GER-156, left maxillary fragment with DP3–DP4 and erupting P4 in buccal view; (**f**) LGPUT-GER-157, right mandibular fragment with p4–m1 in lingual view. Scale bar equals 2 cm

Pliocrocuta perrieri (Croizet and Jobert, 1828)

Nomenclatural and Taxonomical History *Hyaena perrieri* in Croizet and Jobert 1828 (new species); *Hyaena (Pliohyaena) arvernensis* in Kretzoi 1938 (new combination); *Pachycrocuta perrieri* in Howell and Petter 1980 (new combination); for details about synonymy, see Werdelin and Solounias (1991).

Type Material MNHNP coll. Croizet no. 834 (holotype), mandible, housed in the Museum national d'Histoire naturelle of Paris.

Type Locality Les Étouaires, France, late Pliocene, MN17.

Distribution The species has a wide distribution covering whole Eurasia; it is recognized in Spain, France, Italy, Netherlands, Germany, Austria, Slovakia, Bulgaria, Turkey, Georgia, Ukraine, Russia, Tajikistan, China, and India. In Greece, it is known from Gerakarou 1 in Mygdonia Basin, Petralona Cave in Chalkidiki, and possibly from Sesklon in Thessaly.

Remarks *Pliocrocuta perrieri* is poorly represented in the Greek fossil record, known certainly from Gerakarou 1 (Fig. 4d) and Petralona Cave. Though the species is mentioned from Sesklon (Symeonidis 1992), the material is lost and thus its presence in this locality is questionable (Athanassiou 1998). The main characters of the species are the robust and high mandibular corpus, the presence of a large mental foramen below the p2, the small or rudimentary accessory cuspids on the p2 and p3, the very broad p3, the large accessory cuspids on the p4, and the short lower carnassial relative to the p4 (Koufos 1992). Baryshnikov and Tsoukala (2010) noted that the size of *P. perrieri* is close to that of *Crocuta crocuta* but the previous taxon differs displaying elongated P2, shorter carnassial (smaller metastyle-blade in the upper and enlarged talonid in the lower carnassial), and a well-developed metaconid versus a weak or absent on the m1 of *C. crocuta*.

Pachycrocuta Kretzoi, 1938

Type Species *Hyaena brevirostris* Gervais, 1850.

Pachycrocuta brevirostris (Gervais, 1850)

Nomenclatural and Taxonomical History *Hyaena brevirostris* Aymard in Anonymous 1856 (nomen nudum); *Hyaena brevirostris* in Gervais 1850 (new species); *Pachycrocuta brevirostris* in Kretzoi 1938 (new genus). The species has a long nomenclatural history, referred under various names for the material of the different localities from Eurasia (Werdelin and Solounias 1991). It is also referred with wrong authorship and date for more than 100 years; recently it was corrected and the right name is given (Alba et al. 2015).

Type Material Gervais (1848–1852) mentioned two cranial fragments in the Museum of Le Puy, but he did not define a holotype (specimen number unknown).

Type Locality Sainzelles, Polignac pres de Puy, France, Early Pleistocene, MNQ 20 (Palombo and Valli 2003–04).

Distribution Besides France, where is the type locality of the species, it is recognized in the entire Eurasia from Spain to China. In Greece, it is mentioned from Gerakarou 1, Apollonia 1, Kalamoto, Tsiotra Vrissi in Mygdonia Basin, Libakos in Western Macedonia, and Petralona Cave in Chalkidiki.

Remarks *Pachycrocuta brevirostris*, although present in Greece, its known material is scanty, including a partial cranium of a young individual, some maxillary or mandibular fragments with one or two teeth or with deciduous ones and some isolated teeth (Fig. 4e–f). The species is characterized by large and robust upper carnassial with relatively reduced protocone, elliptical and broader distally p2 with small anterior and large posterior accessory cuspids, elliptical-shaped p3 and p4 with small anterior and larger posterior accessory cuspids, elongated and broad lower carnassial without metaconid and with short talonid in comparison to the trigonid (Koufos 1992; Koufos and Kostopoulos 1997; Tsoukala and Chatzopoulou 2005).

⊙*Crocuta* Kaup, 1828

Type Species *Canis crocuta* Erxleben, 1777.

⊙*Crocuta crocuta* (Erxleben, 1777)—the Spotted Hyena

Nomenclatural and Taxonomical History *Canis crocuta* in Erxleben 1777 (new species); *Crocuta crocuta* in Kaup 1828 (new combination). See Werdelin and Solounias (1991) for information on synonymy.

Distribution The species is dispersed in the whole Old World from the Early Pleistocene-to the present. In Greece, it is traced from Petralona Cave in Chalkidiki.

Remarks *Crocuta crocuta* is the modern spotted hyaena. The main characters modified from the description of the Petralona cave material (Tsoukala 1989; Baryshnikov and Tsoukala 2010) are: short and broad cranium with high occipital crest; triangular occipital bone; convex ventral margin of the mandibular corpus; elongated and relatively narrow symphysis; large masseteric fossa with its anterior margin below the distal end of the m1; the premolars, except the upper carnassial, are situated close to each other and sometimes imbricated; weak posterior accessory cusp on the P2; elongated and strong upper carnassial; well-developed protocone situated in front of the mesial parastyle's margin; p2 and p3 with weak anterior and strong posterior accessory cuspids; p4 with strong anterior accessory cuspid from which starts a crest running across the mesial margin of the main cuspid; posterior

accessory cuspid stronger than that of the p3; elongated and relatively narrow lower carnassial; no metaconid; small talonid with tendency to disappear; a small cuspid can only be distinguished on the talonid.

Crocuta crocuta spelaea (Goldfuss, 1823)—the Spotted Cave Hyena

Nomenclatural and Taxonomical History *Hyaena spelaea* in Goldfuss 1823 (new species); *Crocuta spelaea* in Ewer 1954 (new combination); *Crocuta crocuta spelaea* in Cardoso 1993 (new combination). See Sauqué et al. (2017) for further information on synonymy.

Type Material M2609 (holotype), incomplete cranium, housed in the Goldfuss-Museum Bonn (Diedrich 2008: fig. 3).

Type Locality Zoolithen Cave No. D 106, Geilenreuth, Bavaria, Germany, Upper Pleistocene, Weichselian/Würmian (probably OIS 3; Diedrich 2008).

Distribution It is well distributed in Eurasia ranging from Northern China to Iberian Peninsula and British Isles. In Greece, it is known from Agios Georgios Cave, Loutra Almopias Cave, and Haliakmon Basin in northern Greece, Maronia Cave in Thrace, as well as from Ktisti Cave, Ermionis in Peloponnese.

Remarks The main characters of *C. c. spelaea*, as given by Sauqué et al. (2017), are the larger size compared to that of *C. c. crocuta*, the extremely high-crowned P1, the short diastema between C and P1, the absence of diastema between P1 and P2, the disposition of the premolars in the tooth row clearly curved, and the relative shortening of the distal parts of the extremities.

Appendix

List of the Greek localities containing hyaenid fossils. Type localities are marked with bold. Locality numbers refer to the collection numbers of the PaleoBiology Database (PBDB)

Localities[PBDB No]	Age (MN; GPTS in Ma)	Taxon
Loutra Almopias Cave[203847]	Late Pleistocene	*Crocuta crocuta spelaea*[1]
Maronia Cave	Late Pleistocene	*Crocuta crocuta spelaea*[2]
Megalopolis Basin	Late Pleistocene	*Crocuta crocuta spelaea*[3]
Ktisti Cave Ermionis	Late Pleistocene	*Crocuta crocuta spelaea*[4]
Agios Georgios Cave[207192]	Late Pleistocene	*Crocuta crocuta spelaea*[5]
Petralona Cave[183123]	Late M. Pleistocene	*Crocuta crocuta*[6] *Pachycrocuta brevirostris*[7] *Pliocrocuta perrieri*[8]

(continued)

Localities[PBDB No]	Age (MN; GPTS in Ma)	Taxon
Tsiotra Vrissi[192004]	Late Villafranchian (MNQ18; 1.78–1.50)	*Pachycrocuta brevirostris*[9]
Kalamoto[200084]	Late Villafranchian	*Pachycrocuta brevirostris*[10]
Libakos[34764]	?Late Villafranchian	*Pachycrocuta brevirostris*[11]
Haliakmon Basin	Villafranchian	*Crocuta crocuta spelaea*[12]
Apollonia 1[197942]	Epivillafranchian (MN20)	*Pachycrocuta brevirostris*[13]
Gerakarou 1[134617]	Late Villafranchian (MNQ18)	*Pachycrocuta brevirostris*[14] *Pliocrocuta perrieri*[14]
Sesklon[34614]	Middle Villafranchian (MNQ17)	*Pliocrocuta perrieri*[15]
Dafnero 1[34594]	Middle Villafranchian (MNQ17; 2.4–2.3)	*Chasmaporthetes lunensis*[16]
Maramena[32189]	Miocene/Pliocene (MN13/14)	*Chasmaporthetes* sp.[17]
Dytiko 1[32374]	**Late Turolian (MN13; 7.0–6.0)**	***Chasmaporthetes bonisi*[18]**
Dytiko 3[32376]	Late Turolian (MN13; 7.0–6.0)	*Protictitherium crassum*[19]
Samos Q5[95690]	Late Turolian (MN13; 6.9–6.7)	*Adcrocuta eximia*[20] *Hyaenictitherium wongii*[20]
Kryopigi[157582]	Middle–Late Turolian (MN12–13; 7.3–6.4)	*Adcrocuta eximia*[21] *Ictitherium viverrinum*[21] *Plioviverrops orbignyi*[21]
Samos A[206461]	Middle Turolian (MN12)	*Adcrocuta eximia*[20]
Mytilinii 1A[202215]	Middle Turolian (MN12; ~7.1)	*Adcrocuta eximia*[23] *Hyaenictitherium wongii*[23]
Mytilinii 1B[202216]	Middle Turolian (MN12; ~7.1)	*Hyaenictitherium wongii*[23] *Plioviverrops orbignyi*[23]
Mytilinii 1C[202217]	Middle Turolian (MN12; ~7.1)	*Hyaenictitherium wongii*[23]
Samos Q1[95691]	Middle Turolian (MN12; 7.3–7.1)	*Adcrocuta eximia*[20] *Hyaenictitherium wongii*[20] *Ictitherium viverrinum*[20] *Plioviverrops orbignyi*[20]
Samos S3[205351]	Middle Turolian (MN12; ~7.3)	*Hyaenictitherium wongii*[20] *Adcrocuta eximia*[20]
Vathylakkos 2[202703]	Middle Turolian (MN12; ~7.3)	*Hyaenictitherium wongii*[23] *Plioviverrops orbignyi*[23]
Vathylakkos 3[182750]	Middle Turolian (MN12; ~7.3)	*Adcrocuta eximia*[24] *Hyaenictitherium wongii*[24] *Ictitherium viverrinum*[24] *Plioviverrops orbignyi*[24] *Plioviverrops* cf. *guerini*[24]
Perivolaki[194879]	Middle Turolian (MN12; 7.3–7.1)	*Adcrocuta eximia*[26] *Plioviverrops orbignyi*[26] *Ictitherium* sp.[26]
Kerassia 3[195435]	Middle Turolian (MN12)	*Plioviverrops* sp.[27] cf. *Ictitherium pannonicum*[27]
Kerassia 4[195435]	Middle Turolian	*Adcrocuta eximia*[27]

(continued)

Localities[PBDB No]	Age (MN; GPTS in Ma)	Taxon
Pikermi[182754]	**Middle Turolian (MN12; 7.33–7.29)**	***Adcrocuta eximia*[28]** ***Hyaenictis graeca*[29]** ***Ictitherium viverrinum*[28]** ***Lycyaena chaeretis*[30]** *Hyaenictitherium wongii*[31] ***Plioviverrops orbignyi*[32]**
Prochoma 1[202222]	Middle Turolian (MN12; ~7.4)	*Ictitherium viverrinum*[33] *Plioviverrops orbignyi*[24] *Adcrocuta eximia*[33]
Samos A[206461]	Middle Turolian (MN12)	*Lycyaena chaeretis*[20] *Ictitherium viverrinum*[20] *Plioviverrops orbignyi*[20]
Halmyropotamos[202213]	?Middle Turolian (?MN12)	*Adcrocuta eximia*[34]
Thermopigi[73553]	?Middle Turolian (?MN12)	*Adcrocuta eximia*[35]
Samos Q4[95689]	Early Turolian (MN11; ~7.5)	*Adcrocuta eximia*[20] *Hyaenictitherium wongii*[20]
Mytilinii 4[202219]	Late Early Turolian (MN11; ~7.5)	*Protictitherium crassum*[26] *Hyaenictitherium* cf. *wongii*[26]
Nikiti 2[73869]	Early Turolian (MN11; 8.7–8.2)	*Adcrocuta eximia*[36]
Ravin des Zouaves 5[195489]	Early Turolian (MN11; ~8.2)	*Adcrocuta eximia*[23] *Chasmaporthetes bonisi*[37] *Hyaenictitherium wongii*[23] *Ictitherium viverrinum*[33] *Plioviverrops orbignyi*[38]
Ravin X[182745]	?Early Turolian (?MN11)	*Adcrocuta eximia*[22]
Ravin de la Pluie[191070]	**Late Vallesian (MN10; ~9.3)**	*Adcrocuta eximia leptoruncha*[24] ***Protictitherium thessalonikensis*[38]** ?*Hyaenictis* sp.[38] *Protictitherium* cf. *intermedium*[33]
Xirochori 1[195490]	Late Vallesian (MN10; ~9.6)	*Adcrocuta eximia*[34], *Protictitherium crassum*[33]
Ravin des Zouaves 1[182746]	Late Vallesian (MN10)	*Adcrocuta eximia*[33] *Hyaenictitherium wongii*[34]
Pentalophos 1[202119]	Early Vallesian (MN9)	*Protictitherium* cf. *crassum*[24] *Dinocrocuta gigantea*[39]
Antonios[73861]	Early/Middle Miocene (MN4/5)	*Protictitherium gaillardi*[40] *Protictitherium* cf. *crassum*[40]

GPTS Geomagnetic Polarity Time Scale

[1]Tsoukala et al. (2006), [2]Pavlides et al. (2005), [3]Melentis (1964), [4]Mitzopoulos (1960), [5]Tsoukala (1991), [6]Kanellis (1962), [7]Baryshnikov and Tsoukala (2010), [8]Sickenberg (1971), [9]Konidaris et al. (2015), [10]Tsoukala and Chatzopoulou (2005), [11]Steensma (1988), [12]Melentis (1966), [13]Koufos and Kostopoulos (1997), [14]Koufos (1992), [15]Athanassiou (1998), [16]Koufos (1993), [17]Scmidt-Kittler (1995), [18]Koufos (1987), [19]Koufos (1980), [20]Solounias (1981), [21]Lazarides (2015), [22]Koufos (2009), [23]de Bonis et al. (1973), [24]Arambourg and Piveteau (1929), [25]de Bonis and Koufos (1991), [26]Koufos (2006), [27]Roussiakis and Theodorou (2003), [28]Roth and Wagner (1854), [29]Gaudry (1846–50), [30]Gaudry (1861), [31]Gaudry (1862–67), [32]Gaydry and Lartet (1856), [33]Koufos (2000), [34]Melentis (1967), [35]Geraads et al. (2007), [36]Koufos (2016), [37]de Bonis and Koufos (1994), [38]Koufos (2012), [39]Koufos (1995); [40]Koufos (2008)

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