

A complete skull of *Chasmaporthetes lunensis* (Carnivora, Hyaenidae) from the Spanish Pliocene site of La Puebla de Valverde (Teruel)

M. Antón¹, A. Turner², M. J. Salesa¹, J. Morales¹

ABSTRACT

A remarkably complete, well-preserved skull of the Pliocene hunting hyaena *Chasmaporthetes lunensis* from La Puebla de Valverde (Teruel) is described. This exceptional find allows us to define more clearly the cranial morphology of this taxon, and to put its morphological features into evolutionary and functional perspective. Compared with the sympatric hyaenid *Pliocrocota perrieri*, *C. lunensis* has a higher and wider rostrum, cheek teeth placed more anteriorly in relation to the orbits, a lower zygoma and a dorsally concave sagittal crest, all pointing to a lesser development of the muscle *temporalis* and a greater emphasis on canine bite over premolar crushing bite. Horizontal wear on the premolars, caudal extension of the frontal sinus and other features indicate that scavenging or at least complete utilization of carcasses was a behavioural trait of the hunting hyaena. Overall, the available evidence suggests that *C. lunensis* was an active, group hunting predator of medium-sized ungulates, able to fully utilize carcasses but less dedicated to scavenging than the contemporary species *P. perrieri*.

Key words: Carnivora, Hyaenidae, *Chasmaporthetes*, Pliocene, La Puebla de Valverde.

RESUMEN

Describimos un cráneo prácticamente completo y bien preservado de la hiena cazadora del Plioceno, *Chasmaporthetes lunensis*, proveniente de La Puebla de Valverde (Teruel). Este hallazgo excepcional nos permite definir más claramente la morfología craneal de este taxón, y poner sus rasgos morfológicos en perspectiva funcional y evolutiva. Comparado con el hienido simpátrico *Pliocrocota perrieri*, *C. lunensis* muestra un hocico más alto y ancho, dientes post-caninos situados en posición más anterior respecto a las órbitas, arcos zigomáticos más bajos y una cresta sagital con un perfil dorsal cóncavo, todo lo cual apunta a un desarrollo menor del músculo temporal y un mayor énfasis en la mordida a nivel de los caninos respecto a la mordida trituradora de los premolares. El desgaste horizontal en los premolares, la extensión caudal de los senos frontales y otros rasgos indican que el carroñeo, o al menos la utilización a fondo de los cuerpos de las presas, sería un rasgo del comportamiento de las hienas cazadoras. En conjunto, la evidencia disponible sugiere que *C. lunensis* era una cazadora activa y grupal de ungulados medianos, capaz de utilizar a fondo las presas pero menos estrictamente carroñera que *P. perrieri*.

Palabras clave: Carnívora, Hyaenidae, *Chasmaporthetes*, Plioceno, La Puebla de Valverde.

Introduction

The genus *Chasmaporthetes* Hay, 1921 includes several species of medium to large sized hyaenids of Pliocene and Pleistocene age, which reached a remarkably wide distribution, from South Africa to China in the Old World, eventually becoming the

only hyaenid taxon to enter into North America (Berta, 1981). Often referred to as the “hunting hyaenas”, species of *Chasmaporthetes* differ from all other large Pliocene and Pleistocene hyaenids in a series of morphological features indicative of a more hypercarnivore diet and more active hunting (Kurtén & Werdelin, 1988). These features include

¹ Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, C/José Gutiérrez Abascal, 2. 28006 Madrid, Spain.

² School of Biological and Earth Sciences, Byrom Street, Liverpool John Moores University, Liverpool, L3 3AF, United Kingdom.

a broad rostrum, a more trenchant and less crushing post-canine dentition than that of the more typical scavenging hyaenas, and long, slender limbs adapted for high speed running.

In spite of its wide distribution, fossils of *Chasmaporthetes* are nowhere abundant, and the species *C. lunensis* in particular disappears from the fossil record in the early Pleistocene, while several species of more purely scavenging hyaenas survived into the Ice Ages, with three of them surviving in the present, concretely the brown hyaena (*Parahyaena brunnea*), striped hyaena (*Hyaena hyaena*), and spotted hyaena (*Crocuta crocuta*), together with the termite-eating aardwolf (*Proteles cristatus*), the only other extant member of the Hyaenidae.

In many of the fossil sites where it is found, *C. lunensis* coexisted with another hyaenid species of similar size, but with more marked adaptations for bone-crushing: *Pliocrocuta perrieri*. Localities where this association has been recorded include Perrier (Schaub, 1941), Saint Vallier (Viret, 1954), Sénèze (Schaub, 1943), Villarroya (Villalta, 1952), Layna (Crusafont & Aguirre, 1971), La Puebla de Valverde (Kurtén & Crusafont, 1977) and Upper Valdarno (Schaub, 1941). Usually *P. perrieri* is the more abundant of the two, a pattern that may reflect a real prevalence in the past ecosystems, or it may be a consequence of a preservational bias. The coexistence of these two hyaenid species in the Villafrankian of Europe poses interesting paleoecological problems, regarding the way they shared the available resources, but in order to infer the role of each species in their environments, detailed assessment of their functional morphology is necessary.

In order to gain insights into the paleobiology of these animals, relatively complete fossils are necessary, but, since the original description of *C. lunensis* on the basis of a partial, damaged skull from Valdarno, Italy (Del Campana, 1914) not a single complete skull was described in nearly a century, until in 2003 a cranium was found in the classic site of St. Vallier. Unfortunately the French skull as figured (Argant, 2004) is contained in hard matrix, which precluded complete cleaning and observation of fine detail, in spite of the essentially undistorted state of the fossil.

The specimen from la Puebla de Valverde was originally described by Dolores Soria as part of her doctoral thesis (Soria, 1979), which has remained unfortunately unpublished. Thanks to its excellent



Fig. 1.—Map showing the situation of La Puebla de Valverde fossil site.

preservation, the fossil permits for the first time precise observation of all anatomical details, from cranial sutures to general proportions, allowing us to provide a morphological description, functional interpretation, and evolutionary assessment of the skull in this significant taxon.

The Site of La Puebla del Valverde

The fossil site of La Puebla de Valverde (Teruel, Spain) (fig. 1) is one of the most relevant mammal-bearing deposits of the European middle Villafrankian. General information about the site is provided by Crusafont *et al.* (1964), Gautier & Heintz (1974) and Adrover *et al.* (1974), while Heintz (1970); Heintz *et al.* (1971); Guerin & Heintz (1971) and Kurtén & Crusafont (1977) deal with the systematics of fossils discovered in excavations prior to 1974. The latter authors described the carnivores from the site, but back then the only material assigned to *Chasmaporthetes* was a heavily worn P4. In the spring of 1974, Professor Emiliano Aguirre from the Museo Nacional de Ciencias Naturales de Madrid led a fruitful excavation campaign in the western section of the site, making several interesting finds (Aguirre & Soto, 1974; 1978; Heintz & Aguirre, 1976; Heintz, 1978). Among the results from Aguirre's excavation, one of the most noteworthy was the beautiful skull of *Chasmaportetes lunensis*, which we describe here.

Material and Methods

The skull studied in this paper, MNCN-67100, is housed at the paleontological collections of the Museo Nacional de Ciencias Naturales-CSIC of Madrid (Spain). Smaller measurements were taken with a digital calliper, and large skull measurements were taken with a stainless steel vernier calliper.

We took the following measurements of the skull (fig. 2):

MBC, maximum breadth at the level of the canines; BI, rostrum breadth between the infraorbital foramina; BIO, interorbital breadth; BPO, breadth between the postorbital processes of the frontal; BPC, breadth at the level of the postorbital constriction; MBB, maximum breadth of the braincase; MBZ, maximum breadth between zygomatic arches; mHZ, minimum height of the zygomatic arches; MHZ, maximum height of the zygomatic arches; MLO, maximum length of the orbits; HBI, height from basion toinion; LJT, length of jugal tooth row from P1-M1; LP, length of jugal tooth row from P2-M1; LCB, condylo-basal length; LBP, length from basion to prosthion; LPO, length from prosthion to the most anterior point of the palatine opening; LBC, length of basicranium from most anterior point of the palatine opening to basion; BIA, breadth of the incisor arch; BC, breadth between the lingual sides of the canines; MBP, maximum breadth of the palate; MBPO, maximum breadth between the pterygoids; MBOC, maximum breadth at the occipital condyles; LCM, length of tooth row from C-M1; LTF, length from the carnassial notch to the approximate centre of the glenoid fossa.

We took the following measurements of the dentition:

L, mesiodistal length; B, buccolingual breadth; LPa, length of the paracone; LMts, length of the metastyle; BMts, breadth at the level of the metastyle.

We conducted a CT Scan of the skull using a computerized axial tomography (CAT). This is a non-destructive methodology, very useful to study the inner cavities of the skull. The skull was scanned with a YXLON MU 2000-CT scanner at the Universidad de Burgos (Burgos, Spain), making coronal sections with the following parameters: 225 kV and 2,8 mA of energy, 0,5 mm thick slice, and slices interval of 0,5 mm. The field of vision was 299,97 mm. The distance emitter-object was 258,80 mm and object-detector was 741,20 mm, obtaining 529 slices with a image size of 1024 x 1024 pixels, and a pixel size of 0,21 mm, both in 16 bit BMP and 32 bit Float formats. We used Mimics 8.0 software (Materialise N. V.) to create 3D-images.

Systematic Paleontology

Order Carnivora Bowdich, 1821

Family Hyaenidae Gray, 1869

Genus *Chasmaporthetes* Hay, 1921

Chasmaporthetes lunensis Del Campana, 1914

Type locality: Olivola, Val di Magra (MN 17, Italy).

Holotype: IGF 4377, maxilla.

Other localities: Layna (MN 15, Spain), Puebla de Valverde (MN 17, Spain), Villarroya (MN 16, Spain), Etouaires (MN 16, France), Roccaneyra (MN 17, France), Pardines (MN 17, France), Saint Vallier (MN 17, France), Sènèze (MN 18, France),

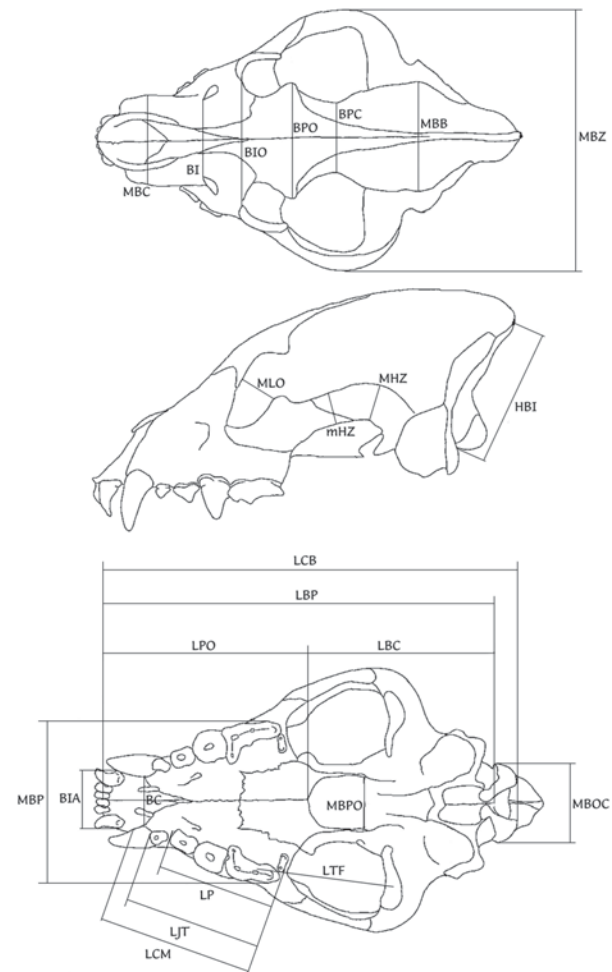


Fig. 2.—Schematic view of a hyaenid skull in dorsal (top), lateral (middle) and ventral (bottom) views, showing the cranial measurements (modified from Argant, 2004).

Inferno (MN 18, Italy), Erpfinger Höhle (MN 18, Germany) and Gülyazi (MN 16, Turkey).

Stratigraphic Range: latest Ruscinian (latest Early Pliocene) to late Villafrankian (late Early Pleistocene).

Diagnosis: Moderately large hyaenid with long and slender limbs. Skull with broad rostrum, frontal profile variably stepped, cheek teeth slender, trenchant; dental formula I3/3, C1/1, P3-4/3-4, M1/1; P1 large but tending to be shed early in life; anterior premolars with strong posterior accessory cusps; P4 with large protocone, short paracone, and elongated metastyle; m1 without metaconid and with talonid bearing a single bladelike cusp.

New material described: MNCN 67100, skull from La Puebla de Valverde with Cs alveoli, all

Table 1.—Measurements in mm of the skull MNCN-67100 of *C. lunensis* from La Puebla de Valverde. Approximate measurements are in *italics*

Number	Species	MBC	BI	BIO	BPO	BPC	MBB	MBZ	mHZ	MHZ
MNCN-67100	<i>Chasmaporthetes lunensis</i>	63.8	70.2	72.0	74.2	43.1	70.0	<i>176.0</i>	18.7	24.6
		MLO	HBI	LCM	LJT	LP	LCB	LBP	LPO	
		36.0	79.0	98.4	<i>80</i>	71.0	225.0	214.5	112.0	
		LBC	BIA	BC	MBP	MBPO	MBOC	LTF		
		102.5	34.6	35.2	104.3	27.8	45.0	87.4		

Table 2.—Measurements in mm of the dentition of the skull MNCN-67100 of *C. lunensis* from La Puebla de Valverde. For each measurement, the first number is the right side and the second the left side; approximate measurements are in *italics*

Number	Species	L I3	B I3	L P2	B P2	L P3	B P3	
MNCN-67100	<i>Chasmaporthetes lunensis</i>	8.2/8.5	6.7/6.8	16.5/17.0	10.2/10.3	19.4/–	<i>12.1/–</i>	
		L P4	B P4	L P4 Pa	L P4 Mts	B P4 Mts	L M1	B M1
		29.9/30.3	16.0/–	10.2/9.9	13.6/–	10.0/–	6.0/–	14.9/–

incisors present; P1 alveoli, right P2-M1 present, left P2 present, left P3 broken post-mortem, P4 damaged, M1 roots.

Description of the new material

Throughout the following description, we remark on features that differ noticeably from the condition observed in the modern true hyaenas of the genera *Crocuta*, *Hyaena* and *Parahyaena*.

The specimen is relatively small compared to other known cranial material of *C. lunensis* and it is similar in size to members of the extant species *Parahyaena brunnea*. Its excellent preservation allows detailed observations of morphological details, including sutures, structure of the bullae and basicranial anatomy. Overall, the specimen is similar to the partial St. Vallier *Chasmaporthetes* specimen QSV 53, but the teeth are much larger in the French fossil (fig. 3; tables 1 and 2).

Dorsal view

The nasals are sub-rectangular and the nasal opening is wide and square (fig. 3A). There is a

considerable distance (around 1.5 cm) between the premaxilla-nasal contact and the frontal-nasal contact. The muzzle is wide and lacks a marked post-canine constriction. The postorbital processes of the frontal are relatively smooth and with hardly any lateral projection. The angle that marks the position of the mastoid process is relatively shallow, lacking the indentation seen just above the external auditory meatus in extant hyaenas. The temporal lines are smoother than in extant hyaenas.

Ventral view

The tooth rows are straight with slight imbrication (fig. 3B). The palate is wide at the rear, the result of the strong divergence of the tooth rows. The anterior margin of the choane develops a blunt nasal spine, as in *P. brunnea*, and unlike *H. hyaena* and *C. crocuta*, in which this border is gently concave. Both palatine fissures seem to have been relatively smaller than those of extant hyaenids. The zygomatic arch is triangle-shaped, due to the marked angle between the posterior and lateral part, as in *H. hyaena* and *P. brunnea*; in *C. crocuta* this arch is more inflated in ventral view. The postglenoid process is less antero-ventrally projected than

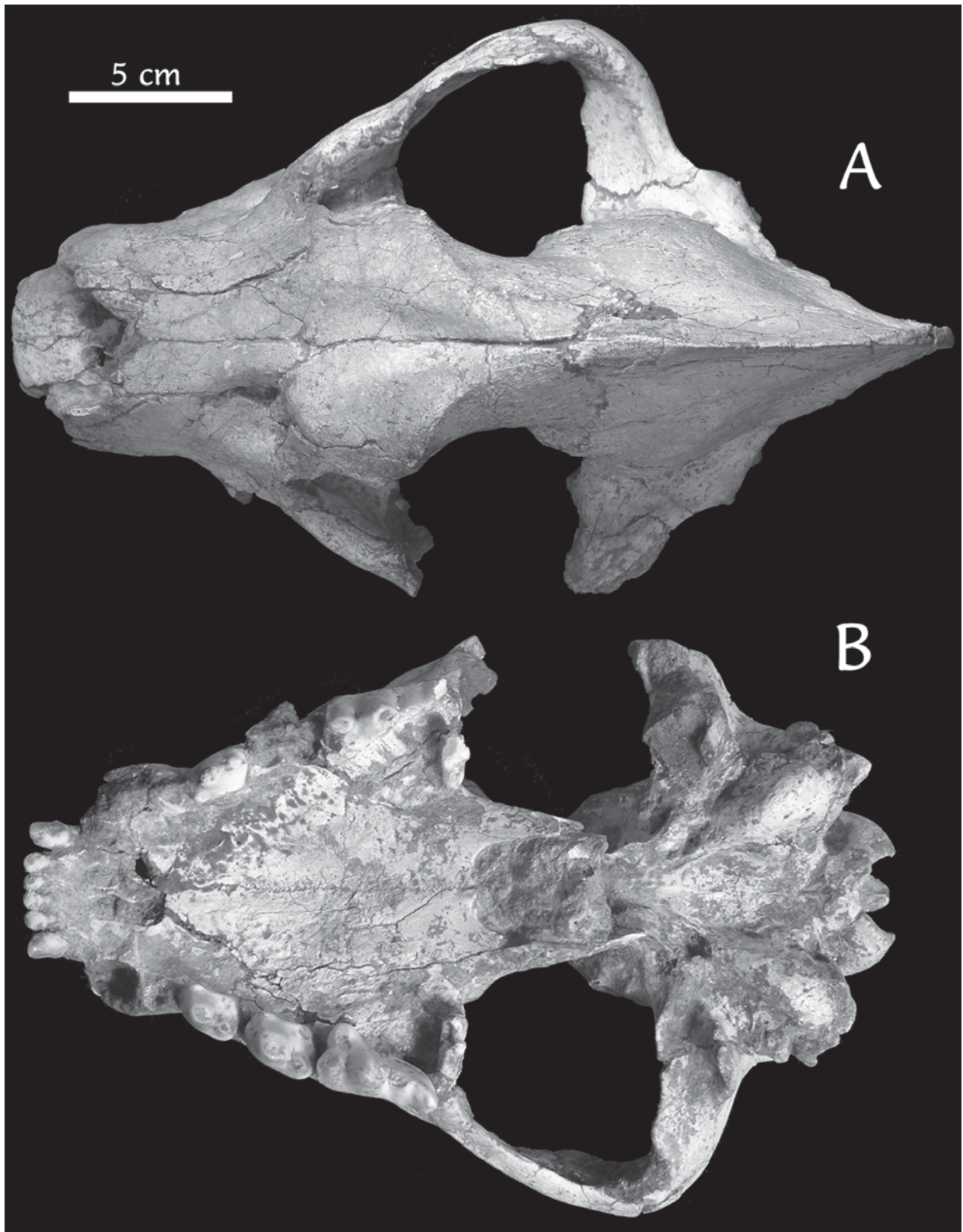


Fig. 3.—Photographs of the skull of *Chasmaporthetes lunensis* from La Puebla de Valverde, MNCN-67100: A) dorsal view; B) ventral view.

in the extant species, being ventrally developed. The basioccipital shows a slight central ridge, flanked by two large and marked scars for the attachment of the muscle *longus capitis*; the anterior border of these two surfaces reaches the level of the posterior border of the foramen ovale, thus being placed more anteriorly than in *C. crocuta*, in which the anterior border of the scars does not surpass the middle point of the tympanic bullae. The opening of the external carotid foramen and foramen ovale are similarly placed as in extant hyaenids.

Lateral view

The dorsal outline of the temporal region is relatively straight instead of being regularly convex as in extant hyaenas (figs. 4A and 4B). The rostrum is relatively high above the canine and premolars. The infraorbital foramen is placed at the level of the space between P3 and P4, instead of being above the mesial root of P3, as in extant hyaenas. The anterior margin of the orbit is located at the level of the parastyle of P4, whilst in extant hyaenas it is placed above P3. The postorbital processes of the frontal and of the zygomatic are very reduced. The posterior part of the zygomatic arch is less high.

Frontal view

The most striking features seen in frontal view are the relatively wide nasal opening and nasal bones of *C. lunensis* in relation to the extant species, the relatively smaller I3, and the proportionally smaller postorbital processes (fig. 5A). Also noticeable is the rounded infraorbital foramen of *C. lunensis* in contrast with the elliptical shaped one of the extant species.

Nuchal view

The outline of the skull (fig. 5B) is triangle shaped, with a marked nuchal crest. Overall, this nuchal view is very similar to that of extant hyaenids, although a detailed view shows a lesser development, in *C. lunensis*, of the strongly marked occipital external crest seen in the extant species; this is because in the former the most dorsal portion of this crest is not ridged, but flat, whereas in the

latter the crest is equally posteriorly projected in its whole length. In this view is also noticeable that the bullae of *C. lunensis* are lightly less inflated, and the zygomatic arches are less dorsally curved than those of extant hyaenids.

Frontal sinuses

As revealed by the CT Scan imagery, the frontal sinuses of *C. lunensis* (fig. 6) show considerable caudal elongation. As shown by Joeckel (1998) extant hyaenid species (excluding the insectivorous *Proteles cristatus*) display the most caudally elongated frontal sinuses of any carnivoran, but fossil hyaenids already show varying degrees of caudal elongation. Compared with the sample of fossil and extant hyaenids illustrated in Joeckel's study, the frontal sinuses of *C. lunensis* show a greater caudal extension than those of *Ictitherium viverrinum*, *Hyaenotherium wongii* and *Palinhyaena reperta*, and is second only to the extant hyaenines in this respect.

Dentition

The teeth are small and rather elongated (fig. 7; table 2), but P2 and P3 are well-developed, with hypsodont anterior cusps, and there is some posterior or lingual bulging on both. P4 is quite gracile, with a turned-out metastyle and high paracone, and the protocone is very well developed but not well separated from the rest of the tooth, with a more felid-like morphology. There is a poorly developed internal cingulum. M1 is large, with 3 cusps, and shows evidence of wear. The incisors are small, and I1 and I2 seem to lack the typical tri-cusped crown with two small cusps behind the main one, although this may be due to wear. I3 in particular is very small compared with that of other hyaenid species.

Compared with the *C. lunensis* maxilla from Perpiñán, the teeth of the Puebla de Valverde specimen are much smaller. The former has a well-developed and separated protocone on P4 and anterior portions of P2 and P3 are well developed also.

Comparison with *Pliocrocuta perrieri*

In this section we compare the skull morphology of *C. lunensis* with that of the sympatric hyaenid *P. perrieri*, but we also take as a reference the morphology

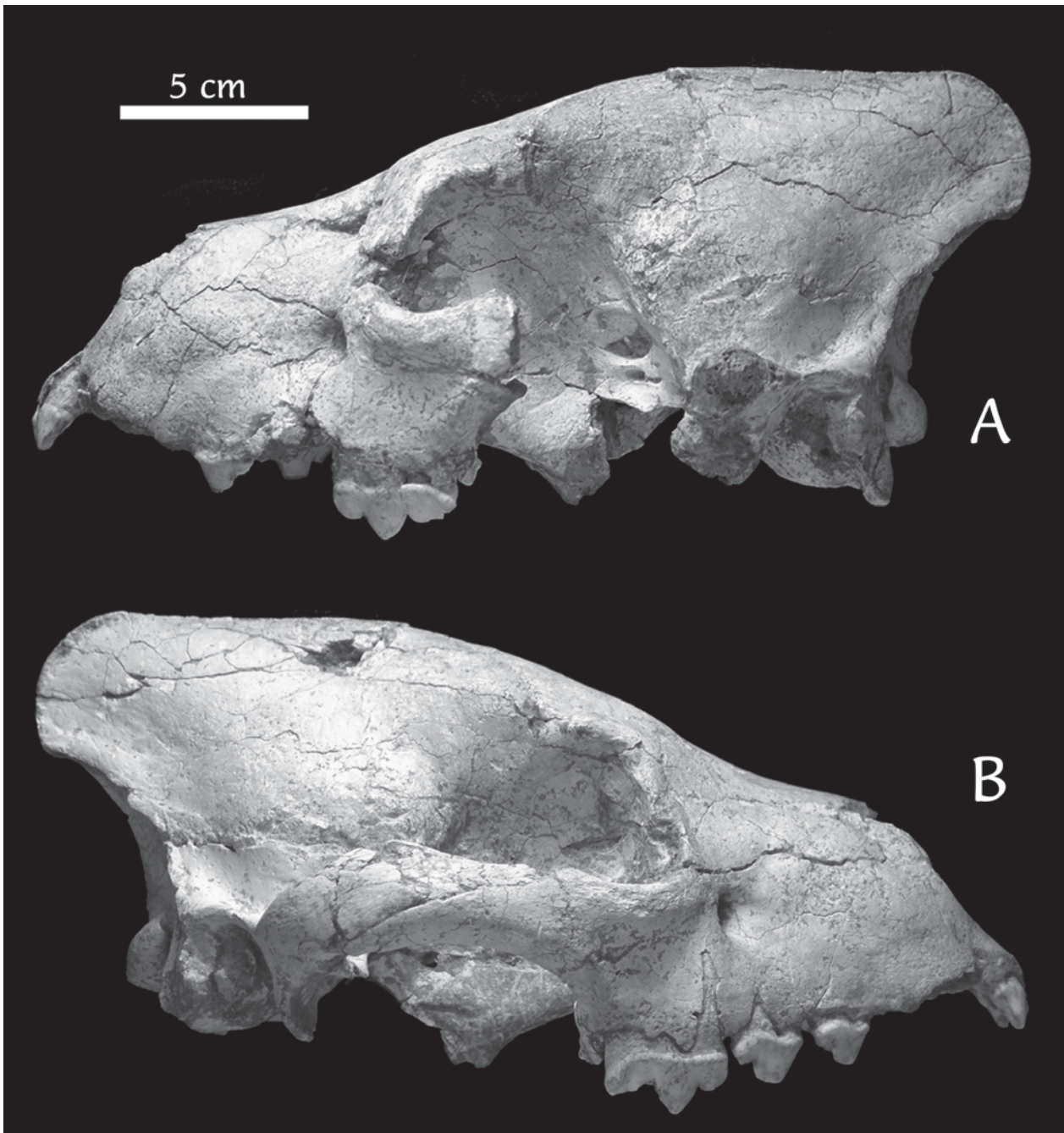


Fig. 4.—Photographs of the skull of *Chasmaporthetes lunensis* from La Puebla de Valverde, MNCN-67100: A) right lateral view; B) left lateral view.

of the Turolian hyaenid *Hyaenotherium wongii*, both because it is considered a suitable primitive taxon from which the more specialized morphologies of the Pliocene hyaenids can be derived (Werdelin & Solnias, 1991), and because it is known on the basis of complete, well-preserved skulls.

In lateral view (figs. 4 and 8), the dorsal outline of the sagittal crest in *C. lunensis* is straight, and slightly concave in the posterior half, resembling *Hyaenotherium wongii* and the wolf, instead of regularly convex as in *P. perrieri* and the other bone-crushing hyaenids. In *P. perrieri* and the other scavenging hyaenids the

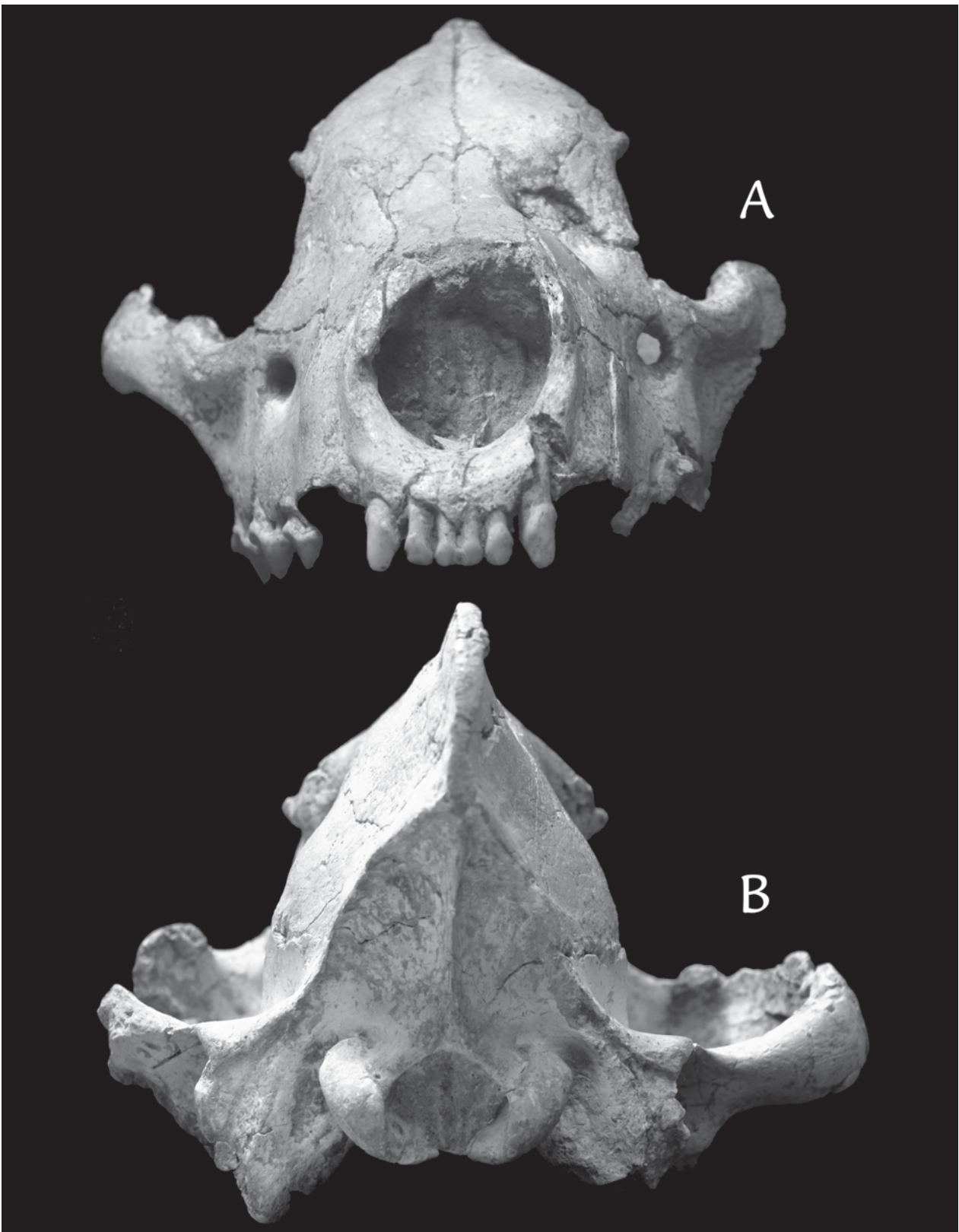


Fig. 5.—Photographs of the skull of *Chasmaporthetes lunensis* from La Puebla de Valverde, MNCN-67100: A) anterior view; B) nuchal view.

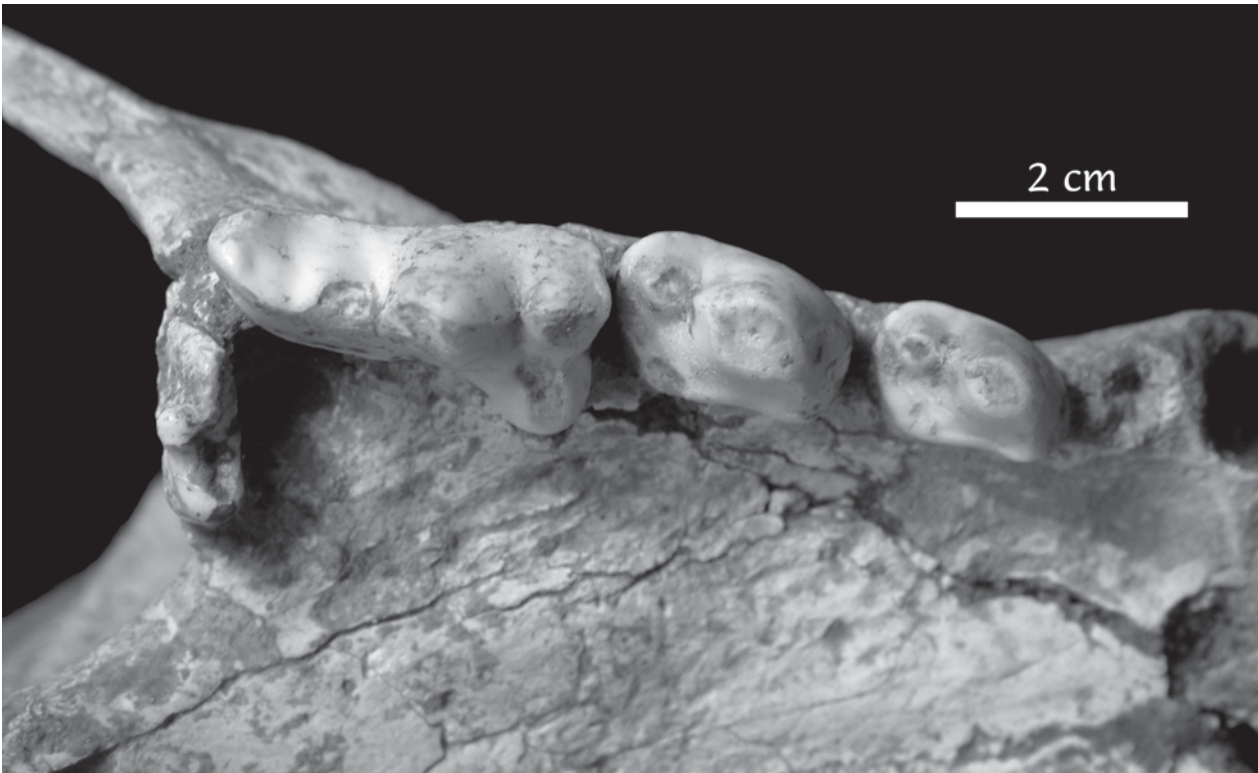


Fig. 7.—Occlusal view of the right P2, P3, P4 and M1 of the skull of *Chasmaporthetes lunensis* from La Puebla de Valverde, MNCN-67100.



Fig. 6.—Schematic drawing of a sagittal section of the skull of *C. lunensis*, based on CT scan imagery, and showing position and development of frontal sinus (shown in grey).

orbits occupy a more antero-ventral position relative to the tooth row, and the infraorbital foramen opens above the anterior root of P3, while in *C. lunensis* the orbits retain a more posterior position and the infraorbital foramen is just above the anterior margin of P4. The postorbital processes are much less marked in *C. lunensis*, and the posterior section of the zygomatic arch is relatively low as in *H. wongii* and the wolf, while in *P. perrieri* and in modern hyaenas it is high and with a strong dorsal curvature.



Fig. 8.—Comparison of outline drawings in lateral view of the skulls of *Chasmaporthetes lunensis* (black line) and *Pliocrocota perrieri* (grey line). Skulls are shown to the same size, with overlap of the two outlines at the level of the carnassial teeth. Notice the more posteriorly placed orbit, higher muzzle and dorsally concave sagittal crest in *C. lunensis*.

The mastoid and paroccipital processes of *C. lunensis* resemble those of *P. perrieri* and modern hyaenas in being close to each other, sub-parallel and ventrally projected below the level of the occipital condyles, while in *H. wongii* the paroccipital process retains a more posterior inclination, diverg-

ing, in lateral view, from the more anteriorly oriented mastoid process, and with its tip remaining above the level of the occipital condyles in lateral view.

In dorsal view, the rostrum of *C. lunensis* is broader. Indeed, in many respects the snout of *Chasmaporthetes* seems to resemble that of the African wild dog, *Lycaon pictus*, a voracious pursuit predator (although the third upper incisor is not as reduced in the canid), and may suggest the need in both species for a wide nasal opening allowing a high volume of air to be obtained. The nasal bones of the Spanish hyaena are distinctive, as in the anterior skull from St. Vallier (Viret, 1954), and differ from those of *P. perrieri* and modern hyaenas in their sub-rectangular, rather than triangular shape. Also distinctive is the large distance separating the contact of the frontal and the premaxilla along the lateral margins of the nasals, while in *P. perrieri* and modern hyaenas these two bones actually contact each other where they join the nasals. In *H. wongii* the nasals are triangular but there is some distance between the frontal and premaxilla.

The dorsal surface of the posterior root of the zygomatic arch, where the muscle *temporalis pars zygomatica* inserts, is relatively smooth in our specimen of *C. lunensis*, but in modern hyaenas it bears marked ridges, as appears to do in *P. perrieri* judging from photographs of the specimens from St. Vallier (Viret, 1954) and Lunel-Viel (Bonifay, 1971), and as it does in all modern hyaenas.

In ventral view, the posterior nasal opening of *C. lunensis* opens just a short distance behind the carnassials, while in *P. perrieri* and modern hyaenas the opening is farther behind. In the dentition, the most obvious differences are the relatively narrower premolars and lesser relative development of P3, and the relatively smaller I3.

Functional and evolutionary implications

Temporal fossa

Several of the cranial features that distinguish *C. lunensis* from *P. perrieri* and the modern hyaenas appear to be associated with the greater development of the temporal musculature in the latter. The great height and strong dorsal curvature of the posterior zygomatic arch observed in modern hyaenas are indicative of a strongly developed *pars zygomatica* of the *temporalis* muscle. In a study of the masticatory muscles of extant carnivores, Gaspard (1971)

concluded that the muscle *zygomaticomandibularis* was extremely well developed in hyaenas, more so than in any other members of the Carnivora, but a review of the anatomical literature suggests that the muscle identified by Gaspard as the *zygomaticomandibularis* is in fact the *temporalis pars zygomatica* of other authors such as Turnbull (1970). The latter author acknowledges the existence of a muscle *zygomaticomandibularis*, but he refers to a muscle originating on a more anterior section of the inner side of the zygomatic arch, and extending vertically to the ascending ramus of the mandible. This muscle would correspond with the one identified by Gaspard (1971) as the *maxillomandibularis*.

The presence in the scavenging hyaenas of strongly sculpted ridges in the area where the *pars zygomatica* attaches is consistent with its great development, while the lesser height of the arch, and the smooth surface of the insertion area in *C. lunensis*, resembles the condition in canids, and indicates a more moderate development of this muscle in the hunting hyaena.

Other osteological correlates of the development of the muscle *temporalis* in modern hyaenas, and in the giant panda (Davis, 1964), are the smoothly convex curvature of the dorsal outline of the sagittal crest, and the slight antero-ventral displacement of the orbits, as if the latter were "pushed" by the expanding temporals (Davis, 1964). In these features *C. lunensis* resembles the more primitive hyaenids and the canids, indicating a lesser development of the *pars profunda* and *pars superficialis* of the muscle *temporalis*. In contrast with these indications of a relatively moderate development of the *m. temporalis*, the marked caudal elongation of the frontal sinus in *C. lunensis* is comparable with that in modern hyaenas, indicating a similar adaptation of the skull walls to resist strong loads produced during mastication.

Mastoid region

The distinctive mastoid morphology that *C. lunensis* shares with modern hyaenas has implications for the function of the muscles that insert on the mastoid and paroccipital processes (figs. 4, 5B and 9). The main muscles involved are the *digastricus*, which stretches from the ventral side of the mandible to the tip of the paroccipital process, and the *obliquus capitis anterior*, with origin on the ventral side of the atlas and insertion on the mastoid and on the surface between the latter and the paroccipital. Compared to

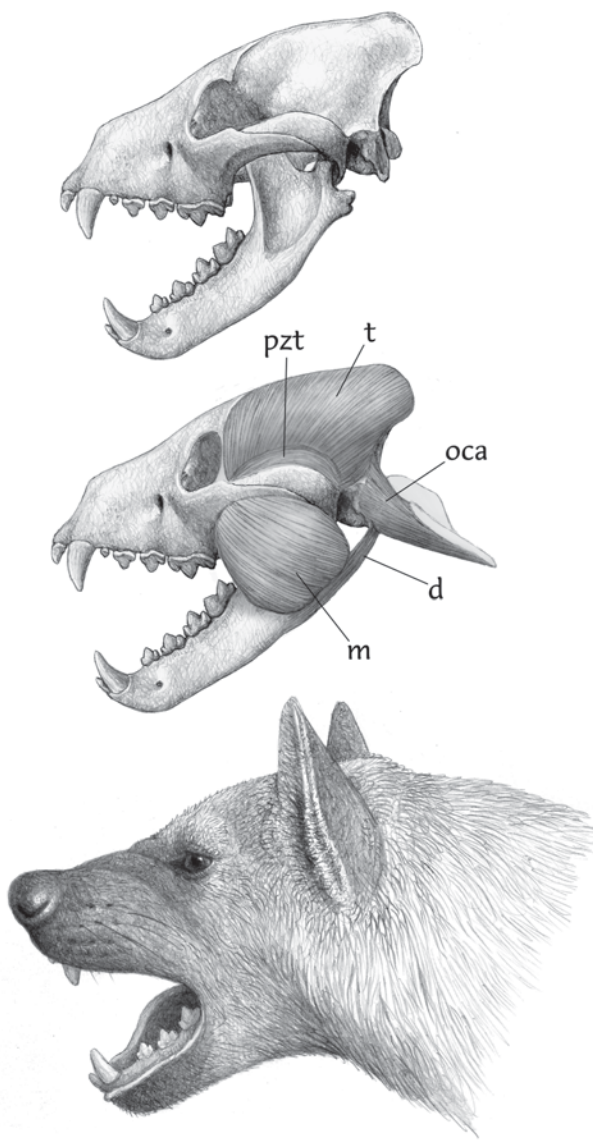


Fig. 9.—Anatomical reconstruction of the head of *Chasmaporthetes lunensis*: top, skull and mandible based on skull MNCN-67100 from La Puebla de Valverde. Upper P1 inferred from the alveoli, upper canine, mandible and lower dentition reconstructed on the basis of fossils from Perrier and St. Vallier (Schaub, 1941; Viret, 1954); middle, reconstruction of deep muscles including *masseter* (m), *temporalis* (t) pars zygomatica of the *temporalis* (pzt), *digastricus* (d) and *obliquus capitis anterior* (oca). Muscle shape and insertion areas based on our own dissection of a striped hyaena (*Hyaena hyaena*) and on Spoor & Badoux (1986); bottom, life appearance of the head of *Chasmaporthetes lunensis* (Art by M. Antón).

the more generalized carnivoran condition observed in canids and in primitive hyaenids, advanced hyaenids such as *C. lunensis* and modern hyaenas display an enlargement of the area for insertion of the *obliquus capitis anterior*, thanks to the development

of a bony surface that bridges the gap between mastoid and paroccipital. The ventral projection of both processes also contributes to enlarge the area for muscular insertion, and consequently a large portion of the fibres attach below the level of the occipital condyles, thus contributing to head depression. At the same time, the ventral projection of the paroccipital tip contributes to a change in the function of the *digastricus*, which has relatively shorter fibres than in a canid or in a primitive hyaenid where the process points backwards, and whose contraction may contribute not only to opening the mandible but also to stabilize the mandible joint during strong biting.

It is interesting to notice that the percrocitids, a group of bone-crushing carnivores which converged remarkably with true hyaenas in the morphology of their masticatory apparatus, also developed enlarged, ventrally projecting mastoids, reaching spectacular proportions in the terminal taxon *Dinocrocota gigantea* (Qiu *et al.*, 1988). In that species, the paroccipital is relatively small, but the mastoid projects antero-ventrally to the point of completely enclosing the auditory meatus, pointing, as in *C. lunensis* and modern hyaenas to an emphasis on the head depressing action of the atlanto-mastoid musculature.

Muzzle shape

The high, broad muzzle of *C. lunensis* is distinctive (figs. 3A and 5A), and its difference with modern hyaenas is comparable to the difference between hypercarnivore dogs such as the African wild dog (*Lycaon*) and the dhole (*Cuon*), and the more generalist dogs of the genus *Canis*. These differences may stem in part from the greater emphasis on canine bite during the killing of large prey, but it is also possible that the enlarged anterior nasal opening is related to increased air intake during and just after high-speed chase.

Evolution

The mosaic nature of the masticatory apparatus in *C. lunensis*, with a mixture of primitive features with derived adaptations for hypercarnivory and others that seem typical of bone-cracking hyaenas, makes it complex to interpret its evolutionary process. In the phylogenetic scheme proposed by Werdelin & Solounias (1991), *Chasmaporthetes* and the related genera *Hyaenictis* and *Lycyaena*

occupy an intermediate position between modern-grade Hyaeninae and the more primitive “dog-like hyaenas” of the genera *Hyaenictitherium*, *Hyaenotherium* and *Thalassictis*. The cranial features revealed by the skull from Puebla de Valverde generally fit well with this model, with the majority of derived features (especially the narrow, trenchant premolars) being best explained as adaptations for hypercarnivory, superimposed on a primitive skull design not unlike that of *H. wongii*. On the other hand, some features that *C. lunensis* shares with bone-cracking hyaenines, including the modified mastoid region and the caudal extension of the frontal sinus, would seem to point to convergence with the latter, or at least to the presence of a common ancestor of *Chasmaporthetes* and the Hyaeninae which had developed these features beyond the point observed in *H. wongii*. One such taxon could be *Hyaenictitherium hyaenoides*, which according to Werdelin & Solunias (1991: 87) displays more hyaenine characters than *H. wongii*, although, as far as can be judged from published figures, the mastoid region in this taxon remains relatively primitive, and the degree of caudal extension of the frontal sinus is unknown.

Paleobiology

The morphological features discussed above seem to fit well with the traditional view of *Chasmaporthetes* as a more active predator than either its extant relatives or the sympatric hyaenid *Pliocrocota perrieri*. *Chasmaporthetes* has been described on occasion as a “cat-like” hyaena (Kurtén, 1968), because its trenchant dentition and the cursorial adaptations evident in its appendicular skeleton bring to mind the modern cheetah. Furthermore, if *Chasmaporthetes* were a solitary hunter like the cheetah, then its relative scarcity in the fossil record would simply reflect its solitary lifestyle, while the more abundantly represented *Pliocrocota* could be interpreted as a group-denning scavenger, like the extant spotted and brown hyaenas. But the supposed similarities with the cats may be misleading in terms of reconstructing the ecological niche of the “hunting hyaenas”.

In fact, the overall resemblance of the skull of *C. lunensis* to that of the modern *Lycaon*, discussed above, suggests a broad functional similarity, while the skulls of both animals differ greatly from the rounded, short cranium of the cheetah, which is perfectly suited for dispatching gazelle-sized prey with

a killing bite to the throat, thanks to the increased strength of the canine bite provided by the short muzzle. The muzzle of *C. lunensis* is not significantly shorter than average for a hyaenid, and was more suited for the typical tearing bite of modern dogs and hyenas. The implication of this difference in the mechanics of the bite is that *Chasmaporthetes*, like modern large canids and hyaenids, would require group action in order to kill medium and large prey. The forelimbs of *C. lunensis* are elongated and gracile, and similar in functional terms to those of other hyaenids (Schaub, 1941). Such limbs were as unsuited as those of any dog or hyaena for grasping or holding prey, a factor that further underlines the need of group action if large prey was to be taken.

It thus seems that *C. lunensis* most probably was a group hunter much like modern spotted hyaenas and larger canids are. But the presence of undeniable adaptations for bone cracking, and the similarity in body size with *P. perrieri*, clearly point toward a degree of competition between the two species for the carcasses of ungulates. Yet the obviously greater bone-cracking abilities in the dentition of the latter suggest that it was the more markedly scavenging animal, while *C. lunensis* may have used its crushing premolars to more fully utilize the carcasses of its own prey, and not so much to consume scavenged carrion. In fact, while animals like *Lycaon* or *Cuon* are called hypercarnivores in contrast to other dogs that have more generalized dentitions, they retain, like other dogs, a rather complete dentition with considerable crushing ability, and thus can utilize the carcasses of their prey down to the bones. But *Lycaon* in particular only rarely scavenges (Creel & Creel, 2002), and it is quite probable that *C. lunensis* was much less adept than *P. perrieri* to scavenging the carcasses of animals it had not hunted. In sites where the presence of hyaenids is related to their proclivity to scavenge on the carcasses of other animals that were accumulating prior to burial, it would make sense that *P. perrieri* was the more abundantly represented species.

ACKNOWLEDGEMENTS

We would like to have a warm memory for Dr. Dolores Soria, whose PhD about fossil hyaenids contained the first description of the *Chasmaporthetes lunensis* skull from La Puebla de Valverde. Thanks to project CGL 2005 - 03900/BTE of the Ministry of Education and Science, Spain. We wish to thank F. Pastor, from the Facultad de Medicina, Universidad de Valladolid (Spain), for carrying the dissection of a striped hyaena (*Hyaena hyaena*), which served as reference for the anatomical reconstruction of *Chasmaporthetes lunensis* pre-

sented here. Thanks also to E. Santos, from the Laboratorio de Evolución Humana of the University of Burgos (Spain) for carrying out the CT scanning of the skull described in this paper and providing technical information about the procedure.

References

- Adrover, R., Aguirre, E., Heintz, E., Moissenet, E. & Morales, J. (1974). Formaciones plio-pleistocenas del Llano de Sarrión. *Coloq. Intern. Bioestratigrafía Continental del Neógeno superior y Cuaternario inferior*, Teruel II, guía 3-10, Montpellier, Libro guía, 69-83.
- Aguirre, E. & Soto, E. (1974). Nuevo fósil de Cercopitécido en el Pleistoceno inferior de La Puebla de Valverde (Teruel). *Estudios Geol.*, 30: 213-217.
- Aguirre, E. & Soto, E. (1978). *Paradolichophitecus* in La Puebla de Valverde, Spain: Cercophitecoidea in European Neogene Stratigraphy. *J. Hum. Evol.*, 7: 559-565.
- Argant, A. (2004). Les Carnivores du gisement Pliocene final de Saint-Vallier (Drôme, France). *Geobios*, 37: 133-182.
- Berta, A. (1981). The Plio-Pleistocene *Hyaena Chasmaporthetes ossifragus* from Florida. *J. Vertebr. Paleontol.*, 1: 341-356.
- Bonifay, M. F. (1971). Carnivores quaternaires du Sud-Est de la France. *Mém. Mus. Nat. Hist. Nat.*, 21: 1-377.
- Bowdich, T. E. (1821). An analysis of the natural classification of mammalia for the use of students and travellers. J. Smith, Paris, 115 pp.
- Creel, S. & Creel N. (2002). *The African Wild Dog: Behavior, Ecology and Conservation*. Princeton University Press, Princeton, 341 pp.
- Crusafont Pairó, M., Hartenberger, J. L. & Heintz, E. (1964). Un nouveau gisement de Mammifères fossiles d'âge villafranchien à La Puebla de Valverde (Province de Teruel, Espagne). *C. R. Hebd. Séanc. Acad. Sci., Paris*, 258: 2869-2871.
- Crusafont, M. & Aguirre, E. (1971). *Euryboas lunensis* et *Hyaena donnezani* associées, en Espagne dans le gisement d'âge Pliocène terminal de Layna (Soria). *C. R. Acad. Sci., Paris, série D*, 273: 2476-2478.
- Davis, D. D. (1964). The giant panda: a morphological study of evolutionary mechanisms. *Fieldiana: Zoology Mem.*, 3: 1-339.
- Del Campana, D. (1914). La *Lycyaena lunensis* n. sp. dell'ossario pliocenico di Olivola (Val di Magra). *Paleontogr. Italica*, 20: 87-104.
- Gaspard, M. (1971). Anatomie comparative et fonctionnelle de la musculature masticatrice chez les Carnivores. *Mém. Mus. Nat. Hist. Nat., nouvelle série, série A Zoologie*, 63: 1-214.
- Gautier, F. & Heintz, E. (1974). Le gisement villafranchien de La Puebla de Valverde (Province de Teruel, Espagne). *Bull. Mus. Hist. Nat., 3^e série, n^o 228, Sciences de la Terre*, 36: 113-133.
- Gray, J. E. (1869). Catalogue of carnivorous, pachydermatous and edentate mammalia in the British Museum. British Museum (Natural History), London, 398 pp.
- Guerin, C. & Heintz, E. (1971). *Dicerorhinus etruscus* (Falconer, 1859), Rhinocerotidae, Mammalia, du Villafranchien de La Puebla de Valverde (Teruel, Espagne). *Bull. Mus. Hist. Nat., 3^e série, n^o 18, Sciences de la Terre*, 2: 13-22.
- Hay, O. P. (1921). Descriptions of species of Pleistocene vertebrata, types or specimens most of which are preserved in the United States National Museum. *Proc. U. S. Nat. Mus.*, 59: 599-642.
- Heintz, E. & Aguirre, E. (1976). Le bois de *Croizetocerus ramosus pueblensis*, Cervidè de la faune villafranchienne de La Puebla de Valverde, Teruel (Espagne). *Estudios Geol.*, 32: 569-572.
- Heintz, E. (1970). Les Cervidés villafranchiens de France et d'Espagne. *Mem. Mus. Nat. Hist. Nat., N. S., série C, Sciences de la Terre*, 22: 1-303.
- Heintz, E. (1978). La faune villafranchienne de La Puebla de Valverde, Teruel, Espagne. Composition qualitative et quantitative. *Géol. Méditerranéenne*, 5: 277-280.
- Heintz, E., Delson, E. & Crusafont Pairó, M. (1971). Descubrimiento del género *Macaca* en el yacimiento de La Puebla de Valverde (Teruel). *Bol. R. Soc. Esp. Hist. Nat. (Geología)*, 69: 299-302.
- Kurtén, B. (1968). *Pleistocene Mammals of Europe*. Weidenfeld and Nicolson, London, 317 pp.
- Kurtén, B. & Crusafont Pairó, M. (1977). Villafranchian Carnivores (Mammalia) from La Puebla de Valverde (Teruel, Spain). *Comm. Biolo.*, 85: 1-39.
- Kurtén, B. & Werdelin, L. (1988). A review of the genus *Chasmaporthetes* Hay, 1921 (Carnivora, Hyaenidae). *J. Vertebr. Paleontol.*, 8: 46-66.
- Qiu, Z., Xie, J. & Yan, D. (1988). Discovery of the skull of *Dinocrocuta gigantea*. *Vertebr. Palasiatica*, 26: 128-138.
- Schaub, S. (1941). Eines neues Hyaenidengenuss von der Montagne de Perrier. *Eclogae Geologicae Helveticae*, 34: 279-286.
- Schaub, S. (1943). Die oberpliocene Säugetierfauna von Senez und ihre verbreitungsgeschichtliche Stellung. *Eclogae Geol. Helvet.*, 36: 270-289.
- Soria, D. (1979). *Hiénidos fósiles de España: revisión de la Familia Hyaenidae del Neógeno Superior y Pleistoceno Inferior*. Tesis doctoral, Universidad Complutense de Madrid, 203 pp.
- Turnbull, W. D. (1970). Mammalian Masticatory Apparatus. *Fieldiana: Geology*, 18: 149-356.
- Villalta, J. F. (1952). Contribución al conocimiento de la fauna de mamíferos fósiles del Plioceno de Villarroya (Logroño). *Bol. Inst. Geol. Min. España*, 64: 1-203.
- Viret, J. (1954). Le loess à bancs durcis de Saint Vallier (Drôme) et sa faune de Mammifères Villafranchiens. *Nouv. Arch. Mus. Hist. Nat., Lyon*, 4: 1-200.
- Werdelin, L. & Solounias, N. (1990). Studies of fossil hyaenids: the genus *Adcrocuta* and the interrelationships of some hyaenid taxa. *Zool. J. Linnean Soc.*, 98: 363-386.
- Werdelin, L. & Solounias, N. (1991). The Hyaenidae: taxonomy, systematics, and evolution. *Fossils and Strata*, 30: 1-104.

Recibido el 19 de octubre de 2006
Aceptado el 16 de noviembre de 2006