Ailurid carnivoran mammal *Simocyon* from the late Miocene of Spain and the systematics of the genus

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Peigné, S., Salesa, M.J., Antón, M., and Morales, J. 2005. Ailurid carnivoran mammal *Simocyon* from the late Miocene of Spain and the systematics of the genus. *Acta Palaeontologica Polonica* 50 (2): 219–238.

We describe the most complete and best-preserved materials assigned to *Simocyon* from Spain. Specimens come from the late Miocene (Vallesian) locality of Batallones-1, Province of Madrid and are assigned to *Simocyon batalleri*. Cranial, mandibular and dental anatomy of *S. batalleri* from Batallones-1 is described and compared with those of known species of *Simocyon*. We review the systematic status and the definition of the species of *Simocyon* and we analyse the morphological variation within *Simocyon*. Three species are recognized as valid. *S. batalleri* is known from several Vallesian localities (mainly MN 10) of Spain. *S. diaphorus*, from the early Vallesian of Germany (Mammal Zone MN 9), is the geologically oldest European species. The type species *S. primigenius* is Turolian in age and known from several localities of Europe, North America, and China. The species includes the junior synonyms *S. zdanskyi* and *S. marshi*. The status of *Simocyon hungaricus* is not resolved. *Simocyon simpsoni* is excluded here from *Simocyon* and reassigned to its original generic name *Protursus*. On the basis of the material described here, we propose a differential diagnosis for *Simocyon batalleri*. This species is morphologically intermediate between the more primitive *S. diaphorus*, which has a less reduced p3; and the more derived *S. primigenius*, characterized by a modified mandible (e.g., more vertical and more expanded coronoid process, longer angular process). The evolution of the genus *Simocyon* is characterized by a trend toward a more crushing adaptation involving at least a modification of the posterior part of the mandible. A reconstruction of the skull and life appearance of *Simocyon* is proposed.

Key words: Systematics, Mammalia, Carnivora, Ailuridae, *Simocyon*, Miocene, Madrid Basin, Europe.

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Introduction

The red panda *Ailurus fulgens* Cuvier in Geoffroy Saint-Hilaire and Cuvier, 1825 is a small-sized arctoid carnivoran found throughout the Himalayan mountains (between 2200 and 4800 metres in elevation), in northern Myanmar (formerly called Burma) and in southwestern China (Roberts and Gittleman 1984: fig. 4). This species is the only extant representative of its lineage. Recent studies (Bininda-Emonds et al. 1999; Flynn et al. 2000) support the distinction of the red panda lineage from other families of Mustelida (i.e., Procyonidae, Mustelidae, and, in some studies, families of Pinnipedia; see Berta and Adams 2001). The divergence time of the red panda lineage from the Mustelida stem may be 30 Ma (Bininda-Emonds et al. 1999), to 31–37 Ma (Flynn et al. 2000). However, the relatively poor fossil record of the red panda clade (compared to other Mustelida clades) prevents the recognition of late Oligocene–early Miocene ancestors, although *Amphictis* could represent a basal ailurid (see Baskin 1998). One of the earliest members of the *Ailurus fulgens* clade, *Magerictis imperialensis* from the middle Miocene of Spain (Ginsburg et al. 1997), is represented only by a single m2. The Pliocene genus *Parailurus* Schlosser, 1899, known from North America and Eurasia, appears to be the latest and closest extinct relative of *Ailurus* Cuvier in Geoffroy Saint-Hilaire and Cuvier, 1825. Another well-known extinct relative of *Ailurus fulgens* is the genus *Simocyon* Wagner, 1858. The present study focuses on the latter, the systematic position of which has been disputed for years (see Wang 1997). *Simocyon* has been placed within Caniformia, successively considered by previous authors as a canid, an amphicyonid, a mustelid or a procyonid (see Wang 1997). Since Beaumont (1964), this genus has been placed within the Mustelida (e.g., Wolsan 1993). In the most recent classifications (McKenna and Bell 1997; Wang 1997; Baskin 1998; Ginsburg 1999), *Simocyon* is placed in its own subfamily, the Simocyoninae Dawkins, 1868. In these studies, there is no consensus regarding the familial assignment of the Simocyoninae. According to the recent palaeontological and molecular data, we consider here this subfamily to fall within the Ailuridae. Recent investigations on the basicranium (Wang 1997), the dentition (Wang 1997; Baskin 1998; Morlo and Kundrát 2001) and the morphology of the astragalus, which is, according to Tedrow et al. (1999: 492) "nearly identical with [that of] *Ailurus fulgens*", support a sister group relationship of the Simocyoninae to the Ailurinae. In addition, although these latter authors and some others include both subfamilies within the Procyonidae, several recent results of molecular biologists reject the hypothesis that *Ailurus fulgens* is included within, or is the closest sister group of, either the Ursidae or Procyonidae (see Flynn et al. 2000).

As pointed out by Wang (1997: 184), the enigmatic nature of *Simocyon* partly results from its "sudden appearance [in the fossil record] without an immediate predecessor". The genus is only known from North America (late early Hemphillian, i.e., latest late Miocene; Baskin 1998; Tedrow et al. 1999), Europe (Neogene European Land Mammal Zones MN 9-MN 13, i.e., late Miocene; Kretzoi 1952: 28; Morlo 1997; Ginsburg 1999, but the mention of *S. hungaricus* from Polgardi is incorrect) and China (late middle Miocene–early Pliocene; Wang 1997; Wang et al. 1998). Previous studies clearly demonstrate a strong similarity among the species of *Simocyon*. Nevertheless, as previously pointed out (e.g., Wang 1997; Roussiakis 2002), a review of the species of *Simocyon* is still necessary.

The primary goal of our contribution is to present new discoveries of *Simocyon* from Batallones-1, Spain. We describe the most complete Spanish material ever found for the genus *Simocyon*, previously documented by two poorly known species. We discuss the systematic status of the species of *Simocyon* and also propose some functional interpretations of the morphological differences between the material from Batallones-1 and the type species of the genus, *S. primigenius*, which is also well documented.

Locality and geological setting

Cerro de los Batallones is a fossiliferous area of several hectares situated near the village of Torrejón de Velasco, 25 km south of Madrid, Spain (Morales et al. 1992, 2004; Pozo et al. 2003, 2004). As indicated by its name, the area is a low hill, approximately 720 m above sea level. The sediment, composed mainly of sepiolite, green clay, micaceous sand, carbonates and flint, was deposited during the late Vallesian (9 Ma) (Morales et al. 2000; Pozo et al. 2003, 2004). Since 1991, sepiolite mining has allowed the discovery of seven different fossil localities, numbered Batallones-1 to Batallones-7. The taxonomic association found in the Batallones localities is typical of the MN 10 Zone (Morales et al. 2000, 2004). To date, only Batallones-1 has been deeply excavated, yielding an exceptionally rich fauna mostly composed of Carnivora, approximately 60% of the total number of individuals (Antón and Morales 2000: fig. 2.99). The locality of Batallones-1 is the largest site, up to 7 m wide and 12 m long. Bones are found in more or less laminated deposits that are distinctive and display abrupt lateral contacts with the host rocks (Pozo et al. 2003, 2004). As with other localities from Cerro de los Batallones, Batallones-1 is interpreted to have been formed by an underground drainage (piping or tunnel erosion, combined with chambering) followed by *in situ* gypsum dissolution resulting ultimately in the formation of a single hole. The accumulation of bones then took place in small and short-lived lakes which filled the holes and acted as traps for numerous animals, mainly carnivorans (Pozo et al. 2003, 2004). The great percentage of carnivorans, the almost complete absence of bone displacement and the overall structure of the hole suggest a natural trap (Antón and Morales 2000; Pozo et al. 2003, 2004). The carnivoran palaeoguild of Batallones-1 is diverse, with 11 species assigned to five families: Felidae, Amphicyonidae, Mustelidae, Hyaenidae, and Ailuridae. A few remains of other vertebrates are also represented, including large herbivores (Bovidae, Suidae, Cervidae, Rhinocerotidae, Gomphotheriidae, and Equidae), rodents, birds, turtles, lizards, snakes and amphibians (Morales et al. 2000, 2004). As a result of the large number of carnivoran remains, the study of the predator palaeoguild of Batallones-1 has been our primary focus in recent years (e.g., Antón and Morales 2000; Antón et al. 2003, 2004).

Institutional abbreviations.—AFI, Geological Institute, Budapest; DGUV, Departamento de Geología de la Universitat de València; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MNCN, Museo Nacional de Ciencias Naturales-CSIC, Madrid; MNHN, Muséum national d'Histoire naturelle, Paris; MSB, Museo del Seminario, Barcelona; BMNH M, mammal collections at the Natural History Museum, London.

Throughout the text, a lower case letter is used for lower teeth, upper case for upper teeth.

Systematic palaeontology

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Infraorder Arctoidea Flower, 1869

Family Ailuridae Gray, 1843

Subfamily Simocyoninae Dawkins, 1868

Genus *Simocyon* Wagner, 1858

Simocyon batalleri (Viret, 1929)

Figs. 1–11; Tables 1–8.

Cephalogale batalleri; Viret 1929: 565, pl. 8: 1, 2.
pars Simocyon sp.; Fraile et al. 1997: table 1.
Simocyon sp.; Morales et al. 2000: 186.
Simocyon sp.; Antón and Morales 2000: 190–193.
Simocyon sp.; Salesa and Fraile 2000: 253, fig. 2.140.

Holotype: MSB 24933, fragment of right maxilla with P4–M2 (Viret 1929: pl. 8: 1, 2).

Type locality: Sabadell, Barcelona Province, Spain.

Referred material from Batallones-1.—MNCN B-3620, nearly complete skull with left P2, P4–M1 and right P1–P2, P4–M1; MNCN B-3392 and MNCN Bat-1-D7-7-2001 left

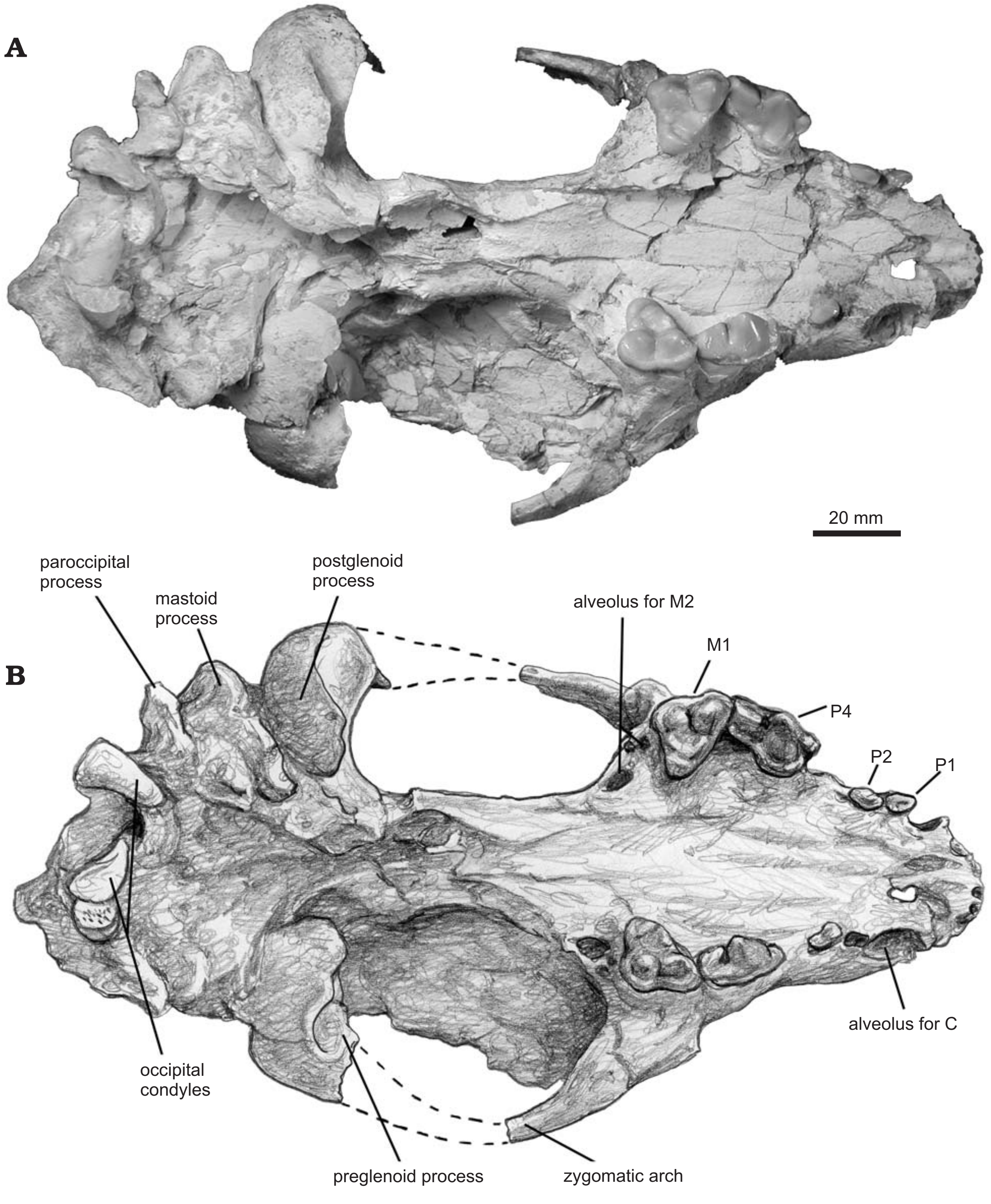

Fig. 1. *Simocyon batalleri* (Viret, 1929), MNCN B-3620, Batallones-1, Madrid Province, Spain, cranium in ventral view. **A**. Photograph. **B**. Schematic drawing showing the main anatomical features of this view (artwork by M. Antón).

and right hemimandibles from the same individual with p1–m1; MNCN B-386, right C1; MNCN B-3235, left M2; MNCN B-4337, right c1; MNCN B-4733, left m2; MNCN B-3238, right m2. MNCN B-3458, nearly complete skull with left P2–M1 and right P1–P2, P4–M1; MNCN B-5430, fragmentary right hemimandible with worn dentition: p2, p4–m2; MNCN B-1890, left C1; MNCN B-5431, right C1; MNCN B-1721, left c1. All specimens are from Batallones-1 and housed in the palaeontological collection of the MNCN.

Our study suggests that the material from Batallones-1 represents two individuals, which, from the dental wear, clearly differ in individual age. The older specimen shows marked dental wear and is slightly smaller than the other one; it is composed of the specimens MNCN B-3458, MNCN B-5430, MNCN B-1890, MNCN B-5431, and MNCN B-1721. The second specimen, a young adult, consists of all remaining specimens: MNCN B-3620, MNCN B-3392, MNCN Bat-1-D7-7-2001, MNCN B-386, MNCN B-3235, MNCN B-4337, MNCN B-4733, and MNCN B-3238. Postcranial remains are associated with the craniodental materials from Batallones-1. Because we here mainly focus on the systematics rather than on the functional morphology and locomotor adaptations of *Simocyon*, the postcranial material will be treated in another paper.

Distribution and age.—Spain only: Sabadell, Vallesian, late Miocene; Batallones-1, Mammal Zone MN 10, late Vallesian, late Miocene.

Differential diagnosis.— *Simocyon batalleri* differs from *S. diaphorus* (Kaup, 1832) in having a more reduced p3; from *S. primigenius* (Roth and Wagner, 1854) in having a less reduced p3 and a mandible with coronoid process less developed anteroposteriorly, more posteriorly oriented, postmolar space longer, angular process longer and ventrodorsally flattened, mandibular condyle lower relative to the occlusal plane.

Description

Skull (Figs. 1–3, Table 1).—The two specimens are nearly complete but mostly compressed and fragmented. They are too damaged, however, to provide an accurate measurement of their basal cranial length. The nasomaxillary, palatinomaxillary, and frontomaxillary sutures are not distinct on the two skulls and may have been fused as in other cranial specimens previously described (Wang 1997). As far as we can see, there are no major differences in the overall shape and morphology between these skulls and the single complete skull assigned to the genus described by Wang (1997: fig. 2B, IVPP V12162, basicranial length is ca. 175 mm). As in the latter specimen, the material from Batallones-1 has a short rostrum and a palate which strongly widens posteriorly to P3, a small postorbital process on the frontal and a more reduced one on the jugal, a high and thin-bladed sagittal and posteriorly projected nuchal crests, a strongly arched zygomatic, a posteriorly extended palatine border, a well-developed postglenoid process, and a basicranial morphology with a similar disposition of foramina, similarly developed and oriented processes, and a little-inflated auditory bulla with a long external auditory meatus. In details, however, the skulls from Batallones display some differences or provide additional information. Thus, the infraorbital foramina are smaller and more transversely compressed than in the Chinese skull from Fugu. Only the right major palatine foramina is distinct in MNCN B-3620; it is small and at the level of M1. On the skull MNCN B-3458, the palatine sulcus is visible on the right side from the level of the distal border of the canine to that of the mesial border of M1. In addition to a strong postglenoid process, there is also a significant, laterally located, preglenoid process which contributes to secure the articulation with the mandible like in, although slightly less developed than, e.g., *Gulo* and *Meles*.

Table 1. Measurements of the cranium and mandible of *Simocyon batalleri* from Batallones-1 (in millimeters). The young individual consists of the specimens MNCN B-3620, 3392, 386, 3235, 4337, 4733, 3238, MNCN Bat-1-D7-7-2001; the old individual consists of MNCN B-3458, 1890, 1721, 5430, 5431. Abbreviations: –, measurement not applicable; *, estimate; BL, distance from anterior tip of premaxillary to the anteriormost margin of the foramen magnum; D, depth of mandibular ramus; Dia, length of diastema; HCP, shortest distance from the tip of the coronoid process to the ventral margin of the mandible below the masseteric fossa; Lcond–m1, distance between the condyle and the carnassial notch; Linc–magnum, distance between the posterior margin of incisive foramen to the anteriormost margin of the foramen magnum; Lpalate, distance from the anteriormost margin of premaxillary to the posteriormost margin of the palate; Lp1–m2, distance between the mesial alveolar margin of p1 and distal alveolar margin of m2 (other distances are similarly defined); Lt md, total length of the mandible, from anterior tip of the ramus to the posteriormost margin of the condyle; nmes, dimension non measurable (e.g., tooth partly and/or poorly preserved); np, tooth not preserved; Tp3, maximum thickness of the mandible below the main cusp of p3 (measured below the m1 protoconid for Tm1).

	Young individuals		Old individual	
Mandible	right	left	right	left
Tp3	10.5	10.2	11.8	–
Tm1	12.5	12.7	13.1	–
Lp1–m2	71.0	71.0	72.7	–
Dp2–p3	22.6	22.6	22.2	–
Dp3–p4	22.0	21.8	24.0	–
Dp4–m1	23.9	23.5	27.0	–
Dm1–m2	25.3	25.9	29.0	–
Ddistm2	29.2	29.2	31.0	–
HCP	65.2	65.8	np	–
Lcond–m1	82.5	83.0	np	–
Lt md	135.0–140.0*		nmes	–
Skull				
Dia P1–P2	–	–	–	2.3
Dia P2–P4	12.7*	9.6	–	8.4
LP1–M2	nmes	63.5	58.2	–
LP4–M2	43.6	42.3	41.1	42.0
Linc–magnum	nmes		154.5	
Lpalate	111.1		90.0	
BL	180.6		nmes	

Upper dentition (Figs. 1, 3, 4A, 5; Table 2).—No incisors are preserved on the two skulls. From alveoli, I1 and I2 were similar in size while I3 was markedly larger than the others. A 2 mm-long diastema separates I3 from C1. This latter has an inflated root having mesially, and slightly lingually on some specimens (e.g., MNCN B-1890), a groove which

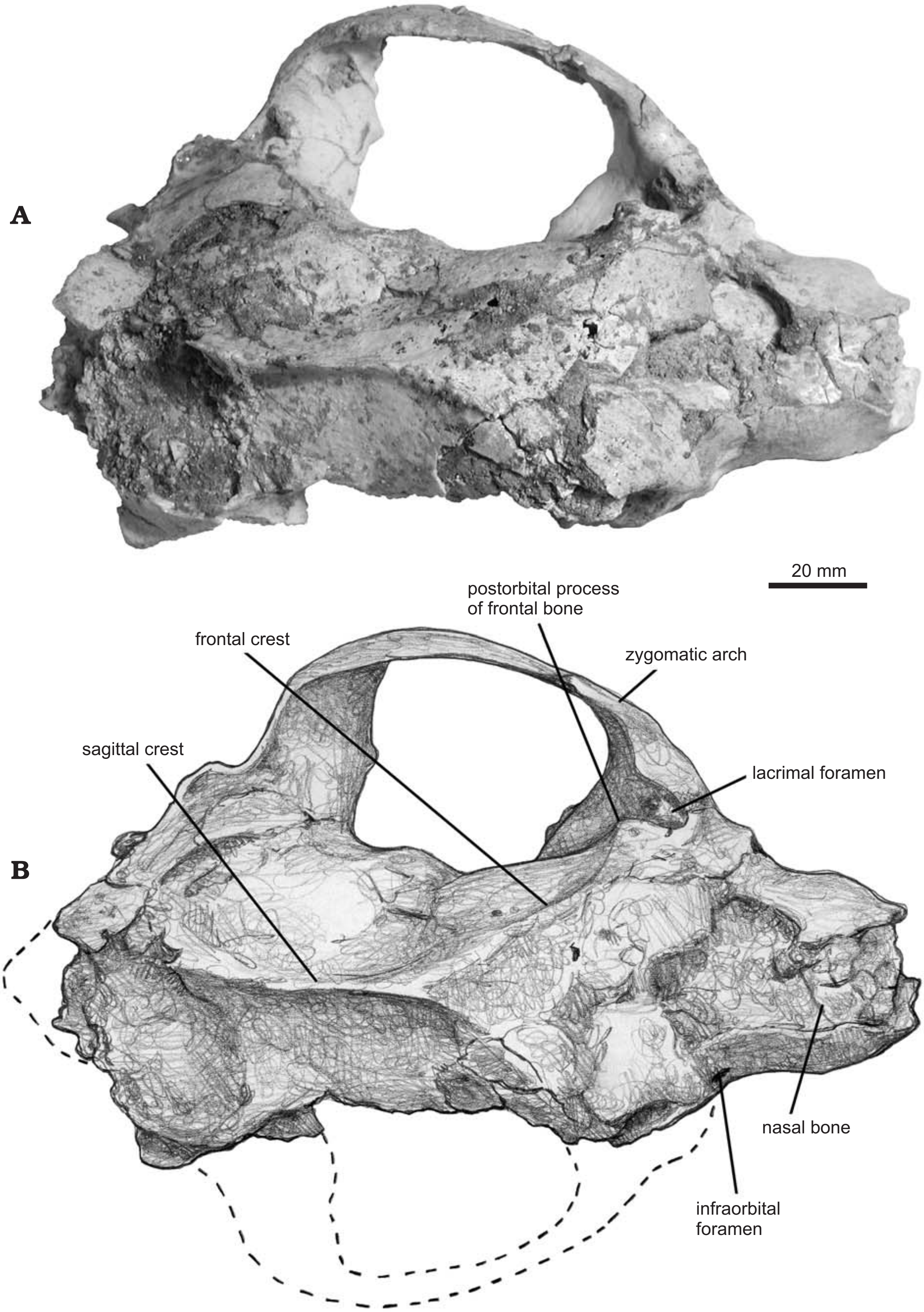

Fig. 2. *Simocyon batalleri*, MNCN B-3458, Batallones-1, Madrid Province, Spain, cranium in dorsal view. **A**. Photo. **B**. Schematic drawing showing the main anatomical features of this view (artwork by M. Antón).

Table 2. Dental measurements of *Simocyon batalleri* from Batallones-1 (in millimeters). The young individual consists of the specimens MNCN B-3620, 3392, 386, 3235, 4337, 4733, 3238, MNCN Bat-1-D7-7-2001; the old individual consists of MNCN B-3458, 1890, 1721, 5430, 5431. Abbreviations: –, measurement not applicable; H, height of the crown of cuspid, i.e., shortest distance from the tip to the dentine-enamel junction; Hpam1, greatest distance from the tip to the dentine-enamel junction on the mesiobuccal face of m1 paraconid; HpaP4, shortest distance from the tip of the paracone to the dentine-enamel junction on the buccal face of P4; Hprdm1, shortest distance from the tip to the dentine-enamel junction on the buccal face of m1 protoconid; L, mesiodistal length; nmes, dimension non measurable (e.g., tooth partly and/or poorly preserved); np, tooth not preserved; abs, tooth absent; LlingP4, length from the mesial border of the protocone to the distal border of the metastyle of P4; W, buccolingual width; Ltrd, maximum length of the trigonid; WdistM1, greatest distance between the buccal border of the metacone and the lingual margin of M1.

	Young individual		Old individual	
	right	left	right	left
Lc1	11.0	np	np	11.0
Wc1	8.3	np	np	7.7
Hc1 ling	14.3	np	np	nmes
Hc1 lab	20.1	np	np	nmes
Lp1	5.7	4.6	np	–
Wp1	3.5	3.7	np	–
Lp2	7.4	7.8	6.9	–
Wp2	4.3	4.4	3.5	–
Hp2	4.1	4.0	3.5	–
Lp3	8.4	8.1	np	–
Wp3	4.4	4.3	np	–
Hp3	3.3	3.9	–	–
Lp4	13.5	13.7	11.9	–
Wp4	7.9	7.9	7.4	–
Hp4	8.7	8.6	nmes	–
Lm1	24.3	24.4	24.0	–
Wm1	10.5	10.4	8.9	–
Hprdm1	12.4	12.4	nmes	–
Hpadm1	9.9	9.7	nmes	–
Ltrdm1	19.1	18.8	nmes	–
Lm2	16.0	16.0	15.9	–
Wm2	8.4	8.4	7.6	–
Ltrdm2	8.0	7.9	nmes	–
LC1	11.6	np	11.2	11.6
WC1	9.0	np	8.3	8.4
HC ling	18.2	np	nmes	nmes
HC lab	22.8	np	nmes	nmes
LP1	np	np	4.6	abs
WP1	np	np	3.2	abs
LP2	nmes	6.60	6.5	6.5
WP2	nmes	3.90	3.3	3.3
HP2	3.7	3.90	nmes	3.3
LP3	abs	abs	abs	7.3
WP3	abs	abs	abs	3.6
HP3	–	–	–	3.7
LP4	20.9	20.4	19.5	19.4
WP4	12.3	12.2	11.4	11.6
LlingP4	19.2	19.3	19.0	19.0
HpaP4	12.2	12.4	nmes	nmes
LM1	17.0	16.7	15.7	16.2
WM1	20.0	19.7	18.6	18.7
WdistM1	16.6	16.6	15.4	15.6
LM2	np	7.5	np	np
WM2	np	13.2	np	np

reaches the root tip. The crown is short, with a marked lingual and, on MNCN B-386 (Fig. 4), buccal cingulum. Two prominent ridges are present distally and mesiolingually. A groove is present on the distal half of the buccal face. The P1 is absent on the left tooth row in MNCN B-3458. When preserved, it is very reduced and single-rooted, with a simple and moderately elongated crown. A short diastema separates the P1 from P2. This latter is two-rooted, larger, and more elongated than P1. Its main cusp is also more prominent and mesially located. The P3 is present only on the left side of the skull MNCN B-3458 (Fig. 3); otherwise, a significant diastema separates P2 from P4 (Table 1). That tooth is very similar to, but slightly larger and with a main cusp taller than, P2; a short diastema separates P3 and P4. The P4 is robust and trenchant. Its paracone is high and followed by a short metastyle. A well-developed parastyle is present and separates from the paracone by a distinct yet small notch. The protocone is absent as a discrete cusp and replaced by a strong cingulum marked by a small depression; it is located across the level of the notch separating the paracone and parastyle. The cingulum is visible all around the tooth, but well developed only lingually. The M1 is very large and roughly triangular in shape. The paracone is markedly larger and more buccally located than the metacone; the two cusps are separate by a deep notch. The protocone and trigon crests are low; a small but distinct metaconule is present, located at the distal border. The central basin is shallow. The lingual cingulum is developed and restricted to the distolingual corner. The distal border of the tooth is very concave and lacks any cingulum. In contrast, the buccal and mesial cingula are marked, the former the most developed. The M2 is three-rooted, with the two buccal roots closely disposed. The crown is low and transversely elongated. In occlusal view, the lingual half curved backward resulting in a strongly concave distal border. The paracone is much larger than the metacone. The trigon crest is very low and consists of a curve running from the mesial basis of the paracone to the distolingual angle. Except on the distal border, the cingulum is visible but remains reduced (Fig. 5).

Mandible (Fig. 6, Table 1).—It is more slender in the youngest individual (MNCN B-3392 and MNCN Bat-1-D7-7-2001) than in the oldest one (MNCN B-5430). Its anteriormost part is not preserved on the material. The ramus and, in particular, the cheek tooth row, display a marked outward curvature, with p4 being the most buccally located tooth. The ramus is shallow throughout its anteroposterior length. The ventral rim is gently curved over most of its length, being con-

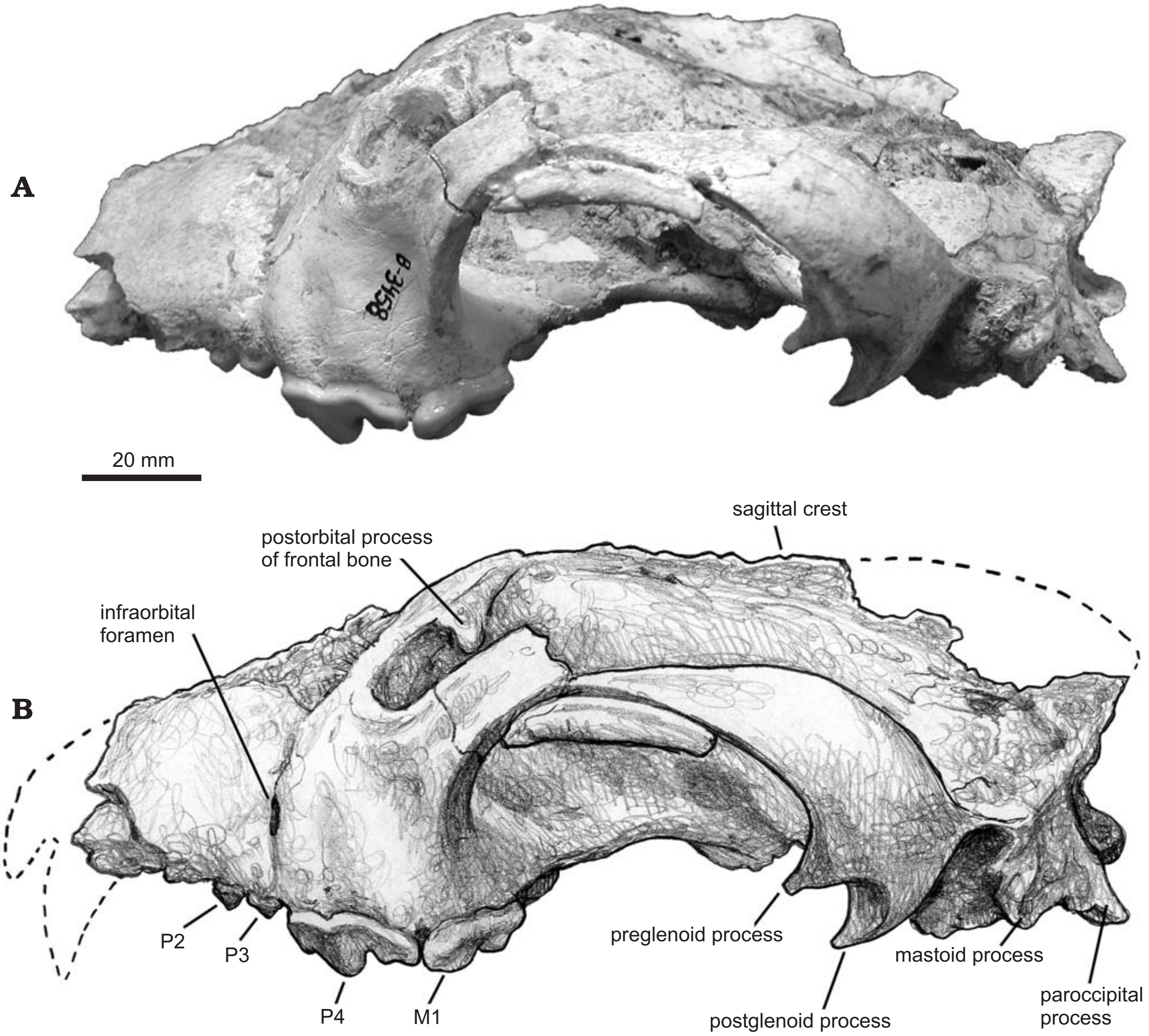

Fig.. 3. *Simocyon batalleri*, MNCN B-3458, Batallones-1, Madrid Province, Spain, cranium in left lateral view. **A**. Photograph. **B**. Schematic drawing showing the main anatomical features of this view (artwork by M. Antón).

cave beneath the masseteric fossa. A large mental foramen is present below the distal root of p2, and a smaller one lies beneath the mesial root of p4. The posterior part of the mandible is particularly well preserved and allows a valuable comparison with *Simocyon primigenius*, the only species of the genus that also preserves this part. The coronoid process is tall and, in contrast to *Simocyon primigenius* from Pikermi and China, markedly more backwardly oriented and less anteroposteriorly developed at its top. The postmolar space in the Spanish material is longer than in *S. primigenius*. The masseteric fossa is very deep in comparison with, e.g., *Ailurus*, *Gulo* or *Meles*, which may indicate a greater development of the pars profunda of the masseter muscle. A horizontal ridge delimits the dorsal border of the fossa; its ventral border expands laterally as a strong ridge, which corresponds to the diagonal ridge described by Gaspard (1964: fig. 1) in extant canids. This ridge continues posteriorly to the angular process, which is markedly longer than in *Simocyon primigenius* (Fig. 9; see also Wang 1997: fig. 1), projecting backward below the condyle. In comparison with that of canids, the angular region of *Simocyon* is more simply structured. Laterally, except for a strong diagonal ridge and a small mesial tubercle, no additional facets and crests can be distinguished. The facet for the muscle pterygoideus lateralis is a shallow, anteroposteriorly expanded depression. The internal crest is very thin and separates this depression from the small, narrow, and elongated attachment area for the muscle pterygoideus medialis. Ventrally, a low ridge separates this latter surface from the attachment area for the muscle masseter superficialis. The condyle is transversely developed and is most similar to that of *Gulo gulo*, except that the dorsal part of the articular surface is more developed forward in the latter.

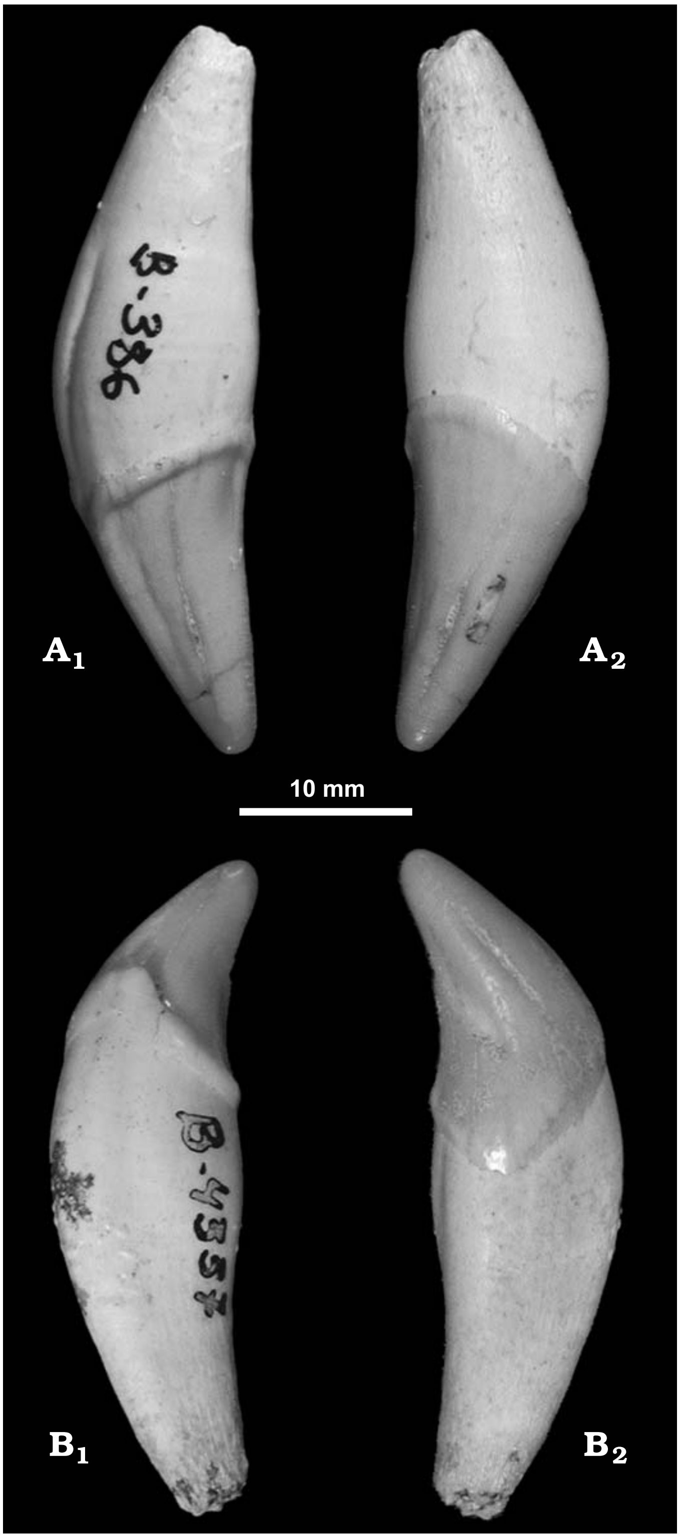

Fig. 4. *Simocyon batalleri*, Batallones-1, Madrid Province, Spain. **A**. MNCN B-386, right upper canine in , lingual (A_1) and buccal (A_2) views. **B**. MNCN B-4337, right lower canine in lingual (B_1) and buccal (B_2) views.

Lower dentition (Figs. 4B, 6, Table 2).—No incisors are preserved. The lower canine is about the size of the upper one, except that it has a shorter crown. The latter is strongly recumbent and has a slight distal ridge and a much stronger mesiolingual one. The cingulum is nearly as developed as in upper canines. A small basal prominent cusp (cusp-like structure) is present at the intersection between the cingulum and the mesiolingual ridge. A groove is present on the buccal face, similarly developed and placed as in upper canines. In occlusal view, the cheek tooth row appears markedly curved labiad as in other species of *Simocyon*. Teeth are closely set together and there is no diastema. All premolars are present and very reduced. The p1 is a single-rooted and tiny tooth with a very simple and oval-shaped crown. The p2 is larger and two-rooted; it is more elongated and has a main cusp located mesially, a tiny but distinct mesial accessory cusp, and a small heel. The p3 is very similar in shape and morphology to p2, and it is only slightly more elongated. In comparison to these teeth, p4 is much larger and more laterally inflated. The crown has its widest part at the level of the main cusp, which is clearly lower than the m1 paraconid. There is no mesial accessory cusp, but a prominent ridge that curves lingually. A well-developed distal accessory cusp is present. The cingulid is absent buccally, little-marked lingually, and well-developed distally. The m1 is distinguished by a reduced, crest-like metaconid, which is located distolingually on the protoconid. The metaconid distal face is very oblique in lingual view. The talonid is about the width of the trigonid and one third of the total length of m1. The hypoconid crest is low, slightly trenchant, and located buccally. A shallow notch separates the hypoconid crest from the protoconid. The lingual border is lower than the buccal one, and displays a slightly prominent entoconid distally. There is no trigonid basin but a shallow, longitudinal groove located distal to the metaconid. The m2 is elongated and has a low crown. The paraconid is reduced to a small crest located on the mesialmost border of the tooth and transversely oriented. The protoconid and metaconid are blunt cuspids. The protoconid is pyramidal and the metaconid, which is lower, is clearly distal to it. The talonid is very long, about the half of the total m2 length (see Table 2). It is clearly narrower than the trigonid and tapers posteriorly. It has a shallow depression lingually. The only distinct feature is the presence of a buccal ridge, which consists of two low crests separated by a shallow notch. These may correspond to the vestigial hypoconid and, distally, the hypoconulid. The lingual border displays no ridge. The cingulum is not distinct, except mesiobuccally where it remains little developed, however.

Comparisons and discussion

As many as seven species have been assigned to *Simocyon*. Some of them are poorly documented and their taxonomic status, diagnosis, and/or geographic distribution have not been well defined in previous studies. To promote clarity and facilitate morphological comparisons, we first review these details for the species previously assigned to *Simocyon*. Tables 3 and 4 present the measurements of the species of *Simocyon*.

Table 3. Measurement of the lower teeth of *Simocyon* species. Abbreviations: –, measurement not applicable; *, estimate; abs, tooth absent; H, height of the crown of cuspid, i.e., shortest distance from the tip to the dentine-enamel junction; Hpam1, greatest distance from the tip to the dentine-enamel junction on the mesiobuccal face of m1 paraconid; Hprdm1, shortest distance from the tip to the dentine-enamel junction on the buccal face of m1 protoconid; L, mesiodistal length; Ltrd, maximum length of the trigonid; m, mean; nmes, dimension non measurable (e.g., tooth partly and/or poorly preserved); np, tooth not preserved; W, buccolingual width. If applicable, sample size is indicated between brackets following the mean. Except for ratios, all measurements are in millimeters. [1] From personal data and Roussiakis (2002); [2] from Wang (1997); [3] from Tedrow et al. (1999).

	S. batalleri from Bat-1		*S. primigenius*[1] from Europe		*S. primigenius*[2] from China		*S. hungaricus*	*S. diaphorus*	*Simocyon marshi*[3]	
	m	range	m	range	m	range	type	type	m	range
Lc1	11.00 (2)	11.00–11.00	12.20 (3)	12.00–12.60	10.85 (2)	10.60–11.10	–	np	np	–
Wc1	8.00 (2)	7.70–8.30	9.38 (2)	8.85–9.90	8.55 (2)	8.50–8.60	–	np	np	–
Lc1/Wc1	1.38 (2)	1.32–1.42	1.31 (2)	1.27–1.36	1.27 (2)	1.23–1.31	–	–	–	–
Lp1	5.15	–	np or abs	–	5.25 (2)	5.20–5.30	–	np	abs	–
Wp1	3.60	–	np or abs	–	4.00 (2)	3.60–4.40	–	np	abs	–
Lp2	7.25 (2)	6.90–7.60	abs	–	6.30	–	abs	np	abs	–
Wp2	3.93 (2)	3.50–4.35	abs	–	3.90	–	abs	np	abs	–
Hp2	3.78 (2)	3.50–4.05	–	–	nmes	–	–	–	–	–
Lp3	8.25	–	abs	–	6.90	–	7.20	9.70	abs	–
Wp3	4.35	–	abs	–	3.70	–	3.50	5.40	abs	–
Hp3	3.85	–	–	–	nmes	–	3.20	nmes	–	–
Lp4	12.75 (2)	11.90–13.60	14.24 (7)	13.50–15.10	13.45 (2)	13.20–13.70	12.20	14.40	15.10 (2)	13.80–16.40
Wp4	7.65 (2)	7.40–7.90	9.03 (5)	8.75–9.20	8.20 (2)	7.90–8.50	7.30	7.60	8.60 (2)	8.00–9.20
Hp4	8.65	–	10.15 (2)	9.90–10.40	nmes	–	8.50	np	–	–
Lp4/Wp4	1.66 (2)	1.61–1.72	1.56 (5)	1.50–1.67	1.64 (2)	1.55–1.73	1.67	1.89	1.75 (2)	1.73–1.78
Hp4/Lp4	0.64	–	0.72 (2)	0.70–0.75	–	–	0.70	–	–	–
Lm1	24.18 (2)	24.00–24.35	23.38 (8)	22.50–25.00	21.90 (3)	21.00–23.00	22.80	26.40	23.45 (2)	22.50–24.40
Wm1	9.68 (2)	8.90–10.45	10.13 (8)	9.70–11.00	9.77 (3)	9.50–9.90	9.80	10.90	10.55 (2)	10.00–11.10
Hprdm1	12.40	–	12.18 (3)	12.05–12.30	nmes	–	nmes	13.20*	nmes	–
Hpadm1	9.80	–	9.50 (2)	9.30–9.70	nmes	–	nmes	nmes	nmes	–
Ltrdm1	18.95	–	17.43 (4)	16.80–17.90	nmes	–	16.70	20.00	nmes	–
Ltrdm1/Lm1	0.78	–	0.76 (4)	0.75–0.77	–	–	0.73	0.75	–	–
Lm1/Wm1	2.51 (2)	2.33–2.70	2.31 (8)	2.26–2.40	2.24 (3)	2.19–2.32	2.33	2.42	2.22 (2)	2.20–2.25
Lm2	15.95 (7)	15.90–16.00	16.49 (7)	15.50–17.40	15.07 (3)	14.00–15.90	np	16.80	17.20	–
Wm2	8.00 (2)	7.60–8.40	8.68 (6)	8.40–9.10	8.50 (3)	8.10–8.80	np	9.50	9.70	–
Ltrdm2	7.95	–	8.54 (5)	7.90–9.20	nmes	–	–	nmes	nmes	–
Lm2/Wm2	2.00 (2)	1.90–2.09	1.91 (6)	1.72–2.02	1.77 (3)	1.73–1.81	–	1.77	1.77	–
Lp3/Lp4	0.61	–	–	–	0.52	–	0.59	0.67	–	–
Lp4/Lm1	0.53 (2)	0.50–0.56	0.61 (7)	0.59–0.64	0.60 (2)	0.57–0.63	0.54	0.55	0.64 (2)	0.61–0.67
Lm2/Lm1	0.66 (2)	0.66–0.66	0.71 (7)	0.64–0.75	0.69 (3)	0.67–0.73	–	0.64	0.70	–

***Simocyon diaphorus* (Kaup, 1832)**.—This is the earliest known European species of the genus. It comes from the early Vallesian locality of Eppelsheim (Mammal Zone MN 9; Fig. 8) and was described by Kaup (1832) on the basis of a fragment of left mandible with p2–m2, which is the only known specimen for the species. Although the original specimen has been lost since 1861 (*fide* Morlo 1997: 13), a plaster cast, which is housed in the Natural History Museum, London, has been here studied (BMNH M 412; see also Lydekker 1885: 145). Unfortunately, the cast does not perfectly preserve every detail. In addition, it displays marked differences from Kaup's illustrations, including p3 longer, no evidence for the presence of a mesial cuspid on p4, m1 metaconid less posteriorly located and in a similar position to that in other *Simocyon* spp.

***Simocyon primigenius* (Roth and Wagner, 1854)**.—This is the type species of the genus. In Spain, it is known only by an isolated right M2 (CG-S/S in the collection of MNCN; see Alcalá 1994: pl. 4: a) from the middle Turolian locality of Cerro de la Garita (Mammal Zone MN 12), also named Concud, after a small village very near the locality (Alcalá 1994; Fraile et al. 1997). The species is better known from Pikermi (MN 12, Greece), the type locality of this species (Fig. 8) and from China, where it has been described under different names. Two species are distinguished there: *S. zdanskyi* Kretzoi in Kadic and Kretzoi, 1927 and *S. primigenius* from the Baode and Yushe Basins. Both species are known by cranial material described by Zdansky (1924: 4–9, pl. 1: 2, 3, pl. 2: 1, 2) and Wang (1997) respectively. Kretzoi

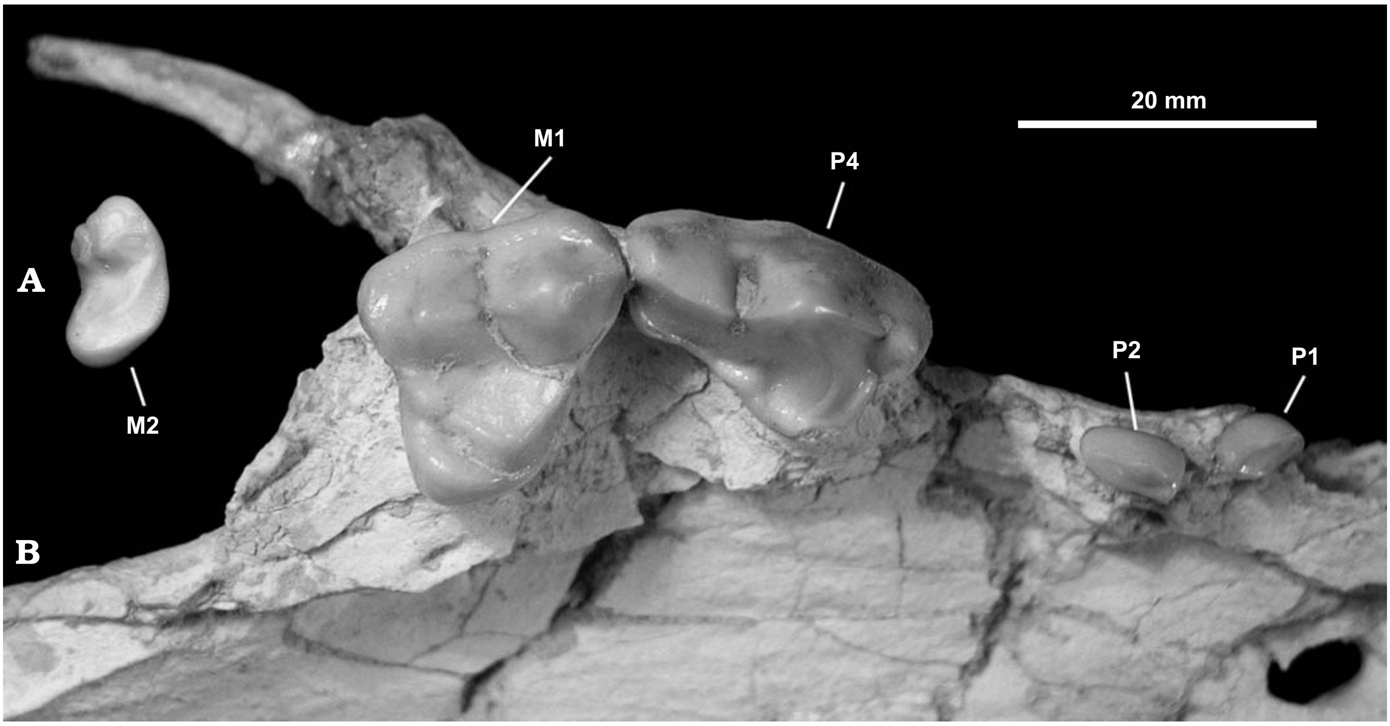

Fig. 5. *Simocyon batalleri*, Batallones-1, Madrid Province, Spain. **A**. MNCN B-3235, left M2 in occlusal view (showed inverted). **B**. MNCN B-3620, upper right toothrow in occlusal view.

(in Kadic and Kretzoi 1927) and Zdansky (1924), in the description of the holotype of *S. zdanskyi*, did not provide diagnostic characters to distinguish this species from *S. primigenius*. These species are very similar indeed, which is also indicated by the loss of P2–P3 and p2–p3 and a coronoid process vertically oriented (nearly at a right angle with the ramus) with a well-rounded tip. Following Pilgrim (1931) and Wang (1997), we consider the differences between these two species insufficient to support a specific distinction. *Simocyon zdanskyi* is therefore a junior synonym of *S. primigenius*. Wang (1997) considers all Chinese *Simocyon* conspecific with *S. primigenius*, stating that the morphological differences distinguishing the Chinese specimens from the Pikermi sample result from individual variation. The Fugu skull described by Wang (1997) differs from *S. primigenius* from Pikermi and Baode by the presence of P2 and p2–p3 but it otherwise has similar dental and mandibular morphology (e.g., sub-vertical coronoid process). The only North American species, *S. marshi* (Thorpe, 1921), is known from fragmentary lower dentitions from the Rattlesnake Fauna (John Day Basin) of eastern Oregon, from south-eastern Idaho and from Nevada (Baskin 1998; Tedrow et al. 1999). The morphology of *S. marshi* is very similar to that of *S. primigenius* (e.g., absence of p2–p3), which indicates a close relationship according to Wang (1997) and Tedrow et al. (1999). We agree with Wang (1997) that the North American species is, at best, a geographic subspecies of *S. primigenius*.

The material assigned to *Simocyon primigenius*, *S. marshi*, and *S. zdanskyi* is used as a single sample in subsequent analyses.

***Simocyon hungaricus* Kretzoi in Kadic and Kretzoi (1927)**.—This species was first mentioned in Kadic and Kretzoi (1927: 9) on the basis of three specimens discovered at Csákvár (Mammal Zone MN 11, Hungary; Fig. 8), but no type specimen was selected in this publication. Kretzoi (1951) briefly described and selected the most complete syntype specimen, a fragment of right hemimandible with p3–m1 (AFI-OB 3791) as the lectotype specimen (not a holotype as indicated by Kretzoi 1951). The species has never been illustrated. On the cast of the lectotype that we studied, the single alveolus of p1 is closely applied against that of the canine. There is no evidence of a p2, which is confirmed by the observation of the original material (Michael Morlo personal communication to SP 11.07.2003). A 7 mm-space separates p1 from p3, which is as reduced as in *S. primigenius*.

***Simocyon batalleri* (Viret, 1929)**.—This species, which is known only from the Vallesian of Spain, was originally assigned to *Cephalogale* (Viret 1929) and, subsequently, to *Metarctos* (Pilgrim 1931; Viret 1933a; Crusafont and Casanovas 1973), which is a junior synonym of *Simocyon* (Lydekker 1885; Thenius 1949; see also Wang 1997). *S. batalleri* has been considered either as valid (e.g., Wang 1997; Roussiakis 2002), or synonymized with *S. primigenius* (e.g., Morlo 1997), or even not mentioned (e.g., Werdelin 1996). We here confirm the generic assignment of this Spanish species. *Simocyon batalleri* was described by Viret (1929: pl. 8: 1, 2) on the basis of a right maxilla fragment with P4–M1 (MSB 24933; Fig. 7A) found by Dr. Bataller in sediments exposed by the excavation of an underground rail-

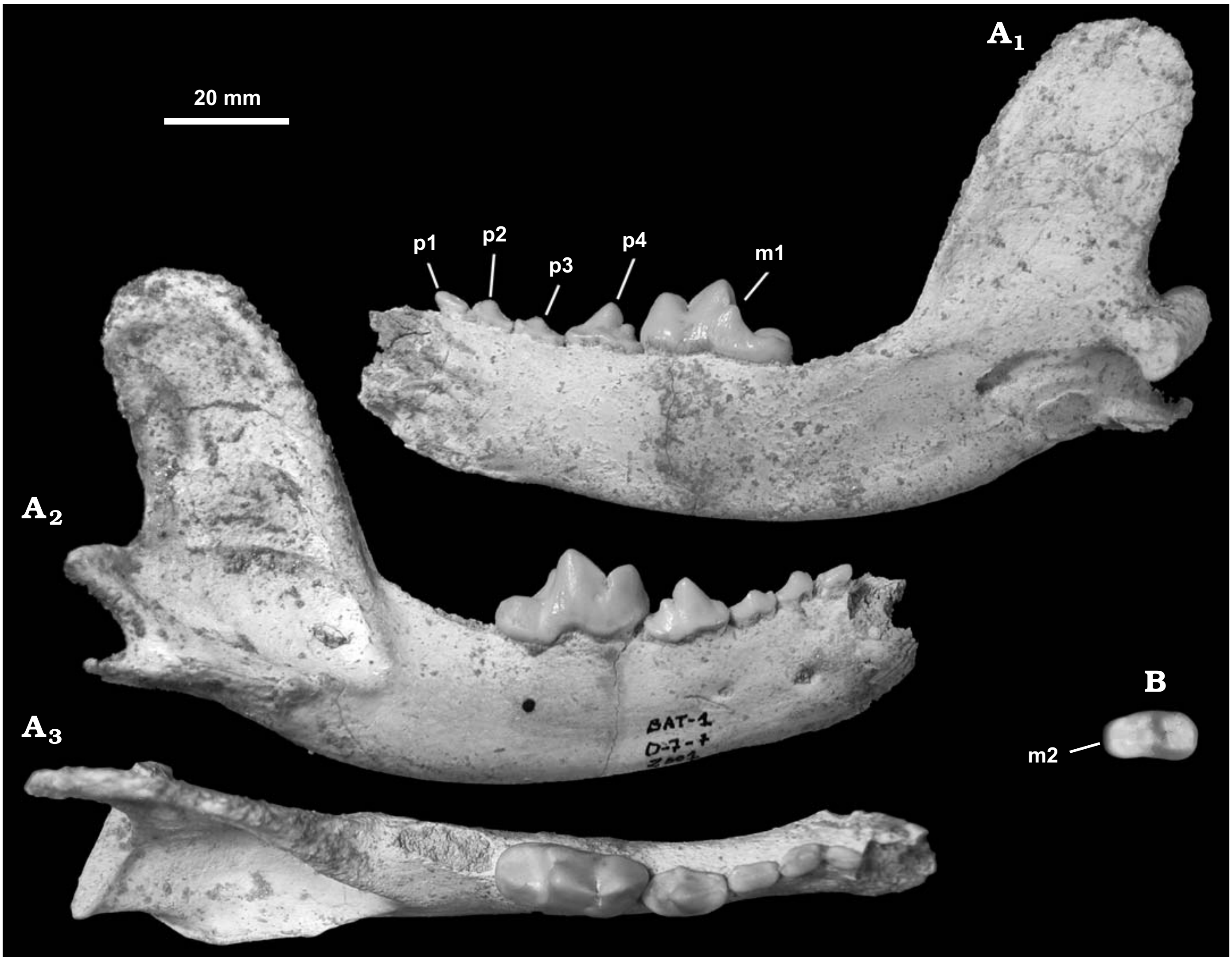

Fig. 6. *Simocyon batalleri*, Batallones-1, Madrid Province, Spain. **A**. MNCN BAT-1-D7-7-2001, right hemimandible with p1–m1 in lingual (A_1), lateral (A_2), and dorsal (A_3) views. **B**. MNCN B-3238, right m2 in occlusal view.

way below the city of Sabadell (Villalta and Crusafont 1943). The stratigraphic provenance of the specimen is not precise but localities in the Sabadell area are mainly Vallesian in age (Fig. 8; Agustí et al. 1983–1984). *Simocyon batalleri* is also known from a left M1 described by Villalta and Crusafont (1948: fig. 1, pl. 1: 1) from "Bóvila Sagués", a site which belongs to a complex of late Vallesian (Mammal Zone MN 10) localities located between the villages of Tarrasa and Viladecavalls (Crusafont 1952); Sant Miguel de Taudell is a name also used by later authors (e.g., Fraile et al. 1997: *Simocyon* sp. therein) in reference to this specimen. The M1 from "Bóvila Sagués" is morphologically similar to that of the holotype.

Simocyon simpsoni **(Crusafont and Kurtén, 1976)**.—Crusafont and Kurtén (1976: figs. 16, 17) described *Protursus simpsoni* on the basis of a left m2 from Can Llobateres (Vallesian, Spain). According to these authors, this species was an ursid closely related to *Ursavus*. Thenius (1977), however, demonstrated that *Protursus* was not an ursid and synonymized it with *Simocyon*. We agree that *Protursus simpsoni* is more closely related to *Simocyon* than to bears; the synonymy between *Protursus* and *Simocyon*, however, is not well supported. The m2s of *P. simpsoni* and *Simocyon* spp. display an overall similarity regarding the elongation of the tooth and the relative proportion of the talonid and trigonid. In details, however, the m2 of *Simocyon* differ from that of *Protursus* in being much larger overall, more elongated and in having no paraconid, a smaller and more posteriorly located metaconid, and a talonid less structured: two low crests occupy the buccal rim in *Simocyon*, whereas two crest-like "hypoconids" in addition to one "hypoconulid" in the distalmost part are present in *Protursus* (using the dental nomenclature of Crusafont and Kurtén 1976). Moreover, the lingual rim does not have any cusp in *Simocyon* from e.g., Batallones-1, whereas there are "two distinct, faintly defined cusps" in *P. simpsoni* (Crusafont and Kurtén 1976: 23). We therefore disagree with the assignment of the species *simp-*

Table 4. Measurements of the upper teeth of *Simocyon* species. Abbreviations: –, measurement not applicable; abs, tooth absent; H, height of the crown of cuspid, i.e., shortest distance from the tip to the dentine-enamel junction; HpaP4, shortest distance from the tip of the paracone to the dentine-enamel junction on the buccal face of P4; L, mesiodistal length; m, mean; nmes, dimension non measurable (e.g., tooth partly and/or poorly preserved); LlingP4, length from the mesial border of the protocone to the distal border of the metastyle of P4; np, tooth not preserved; W, buccolingual width; WdistM1, greatest distance between the buccal border of the metacone and the lingual margin of M1. Sample size is indicated between brackets following the mean. Except for ratios, all measurements are in millimeters. [1] From personal data and Roussiakis (2002); [2] from Wang (1997).

	S. batalleri from Bat-1		*S. primigenius* from Europe[1]		*Simocyon* from China[2]		*S. batalleri* from Catalonia	
	m	range	m	range	m	range	m	range
LC1	11.50 (2)	11.40–11.60	14.00	–	10.85 (2)	10.70–11.00	–	–
WC1	8.68 (2)	8.35–9.00	10.05	–	8.25 (2)	7.70–8.80	–	–
LC1/WC1	1.33 (2)	1.29–1.37	1.39	–	1.32 (2)	1.25–1.39	–	–
LP1	4.60	–	6.00	–	5.55 (2)	5.10–6.00	–	–
WP1	3.20	–	4.00	–	3.90 (2)	3.90–3.90	–	–
LP2	6.55 (2)	6.50–6.60	abs	–	5.90	–	–	–
WP2	3.60 (2)	3.30–3.90	abs	–	3.70	–	–	–
HP2	3.55 (2)	3.30–3.80	abs	–	nmes	–	–	–
LP3	7.30	–	abs	–	abs	–	–	–
WP3	3.60	–	abs	–	abs	–	np	–
HP3	3.70	–	abs	–	abs	–	np	–
LP4	20.05 (2)	19.45–20.65	21.05 (2)	20.50–21.60	19.40 (3)	19.10–19.80	20.20	–
WP4	11.88 (2)	11.50–12.25	12.55 (2)	12.00–13.10	11.63 (3)	10.80–13.10	12.70	–
LlingP4	19.13 (2)	19.00–19.25	nmes	–	nmes	–	18.90	–
HpaP4	12.30	–	nmes	–	nmes	–	nmes	–
LP4/WP4	1.69 (2)	1.69–1.69	1.68 (2)	1.65–1.71	1.68 (3)	1.51–1.79	1.59	–
LM1	16.40 (2)	15.95–16.85	15.85 (2)	15.50–16.20	15.20 (2)	14.90–15.50	15.50 (2)	15.00–16.00
WM1	19.25 (2)	18.65–19.85	19.88 (2)	19.00–20.75	18.20 (2)	17.00–19.40	18.50 (2)	17.00–20.00
WdistM1	16.05 (2)	15.50–16.60	18.50	–	nmes	–	17.20	–
WM1/LM1	1.17 (2)	1.17–1.18	1.25 (2)	1.23–1.28	1.20 (2)	1.10–1.30	1.19 (2)	1.13–1.25
LM2	7.50	–	8.87 (3)	8.50–9.10	8.15 (2)	7.90–8.40	8.50	–
WM2	13.20	–	14.50 (3)	14.00–14.90	13.80 (2)	13.00–14.60	13.90	–
WM2/LM2	1.76	–	1.64 (3)	1.60–1.66	1.69 (2)	1.65–1.74	1.63	–

soni to the genus *Simocyon* and propose to retain the generic name *Protursus* proposed by Crusafont and Kurtén (1976). The talonid elongation and structure of m2 of *P. simpsoni* place this species within the Ailuridae along with other taxa previously placed in this family, the genera *Ailurus*, *Parailurus*, *Simocyon*, *Magerictis* Ginsburg, Morales, Soria, and Herraez, 1997, and *Alopecocyon* Camp and Vanderhoof, 1940 (= *Alopecodon* Viret, 1933b); for the assignment of these genera, see Ginsburg et al. (1997) and Baskin (1998). According to Baskin (1998), the North American genus *Actiocyon* Stock, 1947 and at least some species of *Amphictis* Pomel, 1853 are closely related to this clade.

***Simocyon* sp.**—Besides Batallones-1, several additional occurrences of *Simocyon* sp. are recorded from the late Miocene of Spain: a proximal fragment of right Mc IV (MNCN 14663) from the area of Concud (Montoya and Alberdi 1995: fig. 7.2) and a fragment of right Mc IV (DGUV-CR16-22) from Crevillente-16 (MN 10; Montoya and Alberdi 1995: fig. 7.1). Both specimens are very similar to the Mc IV of *Simocyon* from Batallones-1 (MNCN B-3780, MNCN B/S-218; see Montoya and Alberdi 1995: fig. 7.3), though MNCN 14663 is more gracile and belongs to a smaller individual. The generic assignment is confirmed here for these fragmentary specimens of Mc IV. This material is not diagnostic at a specific level, though the stratigraphic origin suggests that the specimen from Concud (Mammal Zone MN 12) belongs to *S. primigenius* and that from Crevillente-16 (MN 10) belongs to *S. batalleri*. The mention by Fraile et al. (1997) of the presence of *Simocyon* sp. from the Turolian locality of Venta del Moro (MN 13) is not confirmed here by a re-examination of the material discovered since the review of Morales (1984).

Other remains that have been assigned to *Simocyon* sp. include an individual from Montredon, France (MN 10, late Miocene; Fig. 8), represented by a fragmentary mandible with p4–m2 on both sides. The description and illustrations provided by Beaumont (1988) indicate a great similarity between this individual and our material. According to Beaumont, if p3 is present, it should be well separated from p4. The space in front of p4 may result from the absence of p3 in this individual, however. There is no evidence that the premolar reduction in *Simocyon* sp. from Montredon reached that occurring in specimens from Pikermi (loss of p2–p3 and

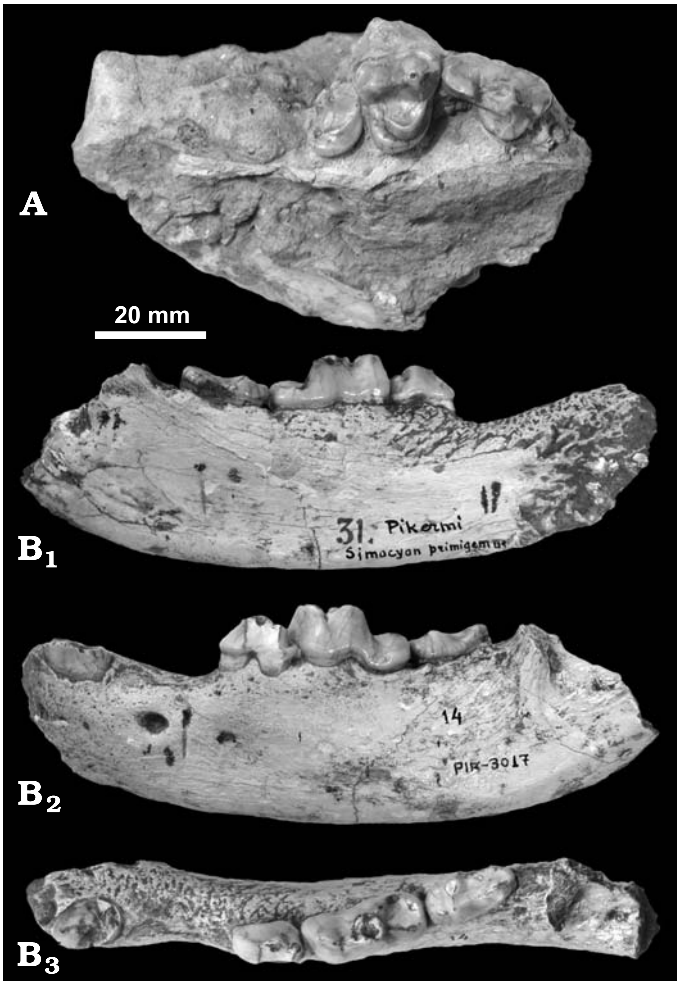

Fig. 7. **A**. *Simocyon batalleri*, MSB 24933, Sabadell, Barcelona province, Spain, right maxilla with P4–M2 in occlusal view. **B**. *Simocyon primigenius*, MNHN-PIK 3017, Pikermi, Greece, fragmentary left mandible with p4–m1 in lingual (B_1), lateral (B_2), and dorsal (B_3) views.

presence of diastema between p1 and p4). Some specimens from the German locality of Dorn-Dürkheim-1 (Mammal Zone MN 11, Turolian; Fig. 8) have been described by Morlo (1997). The material is very fragmentary and does not display marked differences with the material from Batallones-1. The main differences regard p4, which is less elongate than in our material and has a surprisingly strong mesial accessory cusp, much larger than the tiny cusp observed in Pikermi or Chinese specimens. The lingual fragment of M1 illustrated by Morlo (1997: pl. 1: 2) presents no marked differences in comparison with our materials. Recently, a small *Simocyon* sp. has also been described from the late middle Miocene of Junggar Basin, China (Wang et al. 1998), hence documenting the earliest appearance of the genus.

Morphological variation within *Simocyon*.—A central issue concerning the systematics of the genus *Simocyon* is whether *S. diaphorus*, *S. batalleri*, and *S. hungaricus* are distinct from each other and from the type species *S. primigenius*. We investigated morphological variation within *Simocyon* on the basis

Table 5. Summary statistics of the lower teeth and mandible for the studied sample of *Simocyon* specimens. Abbreviations: CV, coefficient of variation; D, depth of mandibular ramus; Dia, length of diastema; H, height of the crown of cuspid, i.e., shortest distance from the tip to the dentine-enamel junction; Hpam1, greatest distance from the tip to the dentine-enamel junction on the mesiobuccal face of m1 paraconid; Hprdm1, shortest distance from the tip to the dentine-enamel junction on the buccal face of m1 protoconid; L, mesiodistal length; Lt md, total length of the mandible, from anterior tip of the ramus to the posteriormost margin of the condyle; Ltrd, maximum length of the trigonid; N, sample size; m, mean; SD, one standard deviation; Tp3, maximum thickness of the mandible below the main cusp of p3 (measured below the m1 protoconid for Tm1); W, buccolingual width.

	N	m	range	SD	CV
Lc1	7	11.44	10.40–12.60	0.77	6.97
Wc1	6	8.64	7.70–9.90	0.73	8.78
L/Wc1	6	1.32	1.21–1.43	0.07	5.89
Lp3	4	8.01	6.90–9.70	1.27	16.78
Wp3	4	4.24	3.50–5.40	0.86	21.46
L/wp3	4	1.90	1.80–2.06	0.11	6.17
Lp3/Lp4	4	0.60	0.52–0.67	0.06	11.00
Lp4	15	13.93	11.90–16.40	1.10	8.03
Wp4	14	8.38	7.30–9.20	0.69	8.44
L/Wp4	14	1.67	1.50–1.89	0.12	7.29
Hp4	4	9.36	8.50–10.40	0.93	10.60
H/Lp4	4	0.69	0.64–0.75	0.05	7.02
Lp4/Lm1	15	0.59	0.50–0.67	0.05	7.78
Lm1	17	23.36	21.00–26.40	1.27	5.53
Wm1	17	10.02	8.75–11.10	0.65	6.55
Ltrdm1	6	17.94	16.70–20.00	1.30	7.58
Hprdm1	5	12.43	12.05–13.20	0.45	3.80
Hpadm1	3	9.60	9.30–9.80	0.26	2.99
Hprd/Lm1	5	0.52	0.50–0.54	0.02	3.08
Hpad/Lm1	3	0.41	0.40–0.42	0.01	2.36
Ltrd/Lm1	6	0.76	0.73–0.78	0.02	2.36
L/Wm1	17	2.34	2.19–2.70	0.14	5.97
Lm2	14	16.18	14.00–17.40	0.92	5.78
Wm2	14	8.91	7.60–12.00	1.04	11.88
L/Wm2	14	1.83	1.33–2.09	0.19	10.31
Ltrdm2	3	8.42	7.95–9.20	0.68	8.78
Ltrd/Lm2	3	0.50	0.49–0.53	0.02	4.60
L/Wm2	14	1.83	1.33–2.09	0.19	10.31
Lm2/Lm1	14	0.69	0.64–0.75	0.04	6.25
Wm2/Wm1	14	0.89	0.80–1.09	0.07	7.72
Tp3	4	11.67	10.35–12.95	1.06	9.69
Tm1	5	13.46	12.60–14.00	0.61	4.73
Diac–p4	5	17.53	14.50–21.15	2.52	15.11
Dp3–p4	5	23.33	20.00–26.00	2.38	10.73
Dp4–m1	6	26.83	22.00–29.50	3.27	12.70
Dm1–m2	6	27.98	23.00–31.50	3.11	11.56
Ddistm2	5	30.96	29.20–32.60	1.20	4.08
Lt md	2	129.57	119.00–140.15	14.96	12.98

Table 6. Summary statistics of the lower teeth and mandible for the sample of *Simocyon primigenius*. Abbreviations: –, measurement not applicable; CV, coefficient of variation; D, depth of mandibular ramus; Dia, length of diastema; H, height of the crown of cuspid, i.e., shortest distance from the tip to the dentine-enamel junction; Hpam1, greatest distance from the tip to the dentine-enamel junction on the mesiobuccal face of m1 paraconid; Hprdm1, shortest distance from the tip to the dentine-enamel junction on the buccal face of m1 protoconid; L, mesiodistal length; Lt md, total length of the mandible, from anterior tip of the ramus to the posteriormost margin of the condyle; Ltrd, maximum length of the trigonid; N, sample size; m, mean; SD, one standard deviation; Tp3, maximum thickness of the mandible below the main cusp of p3 (measured below the m1 protoconid for Tm1); W, buccolingual width.

	N	m	range	SD	CV
Lc1	5	11.62	10.40–12.60	0.87	7.84
Wc1	4	8.96	8.50–9.90	0.64	7.61
L/Wc1	4	1.29	1.21–1.36	0.06	5.08
Lp3	1	6.90	–	–	–
Wp3	1	3.70	–	–	–
L/wp3	1	1.86	–	–	–
Lp3/Lp4	1	0.52	–	–	–
Lp4	11	14.25	13.20–16.40	0.91	6.55
Wp4	10	8.71	7.90–9.20	0.49	5.80
L/Wp4	10	1.64	1.50–1.80	0.12	7.21
Hp4	2	10.15	9.90–10.40	0.35	3.92
H/Lp4	2	0.72	0.70–0.75	0.04	5.62
Lp4/Lm1	11	0.62	0.57–0.67	0.03	4.39
Lm1	13	23.05	21.00–25.00	1.07	4.72
Wm1	13	10.02	8.75–11.10	0.61	6.18
Ltrdm1	3	17.33	16.80–17.90	0.55	3.44
Hprdm1	3	12.18	12.05–12.30	0.13	1.12
Hpadm1	2	9.50	9.30–9.70	0.28	3.35
Hprd/Lm1	3	0.53	0.53–0.54	0.00	0.93
Hpad/Lm1	2	0.41	0.41–0.42	0.01	2.31
Ltrd/Lm1	3	0.76	0.75–0.77	0.01	2.02
L/Wm1	13	2.30	2.19–2.62	0.11	4.97
Lm2	11	16.17	14.00–17.40	1.02	6.47
Wm2	11	9.02	8.10–12.00	1.08	12.20
L/Wm2	11	1.81	1.33–2.02	0.19	10.81
Ltrdm2	2	8.65	8.10–9.20	0.78	10.12
Ltrd/Lm2	2	0.51	0.49–0.53	0.03	6.38
L/Wm2	11	1.81	1.33–2.02	0.19	10.81
Lm2/Lm1	11	0.70	0.64–0.75	0.04	6.09
Wm2/Wm1	11	0.90	0.84–1.09	0.07	7.96
Tp3	1	12.95	–	–	–
Tm1	2	14.00	14.00–14.00	–	–
Diac-p4	4	17.84	14.50–21.15	2.80	16.69
Dp3-p4	2	25.38	24.75–26.00	0.88	3.92
Dp4-m1	3	29.43	29.30–29.50	0.12	0.43
Dm1-m2	3	30.10	29.00–31.50	1.28	4.60
Ddistm2	3	31.53	31.00–32.60	0.92	3.17
Lt md	2	129.57	119.00–140.15	14.96	12.98

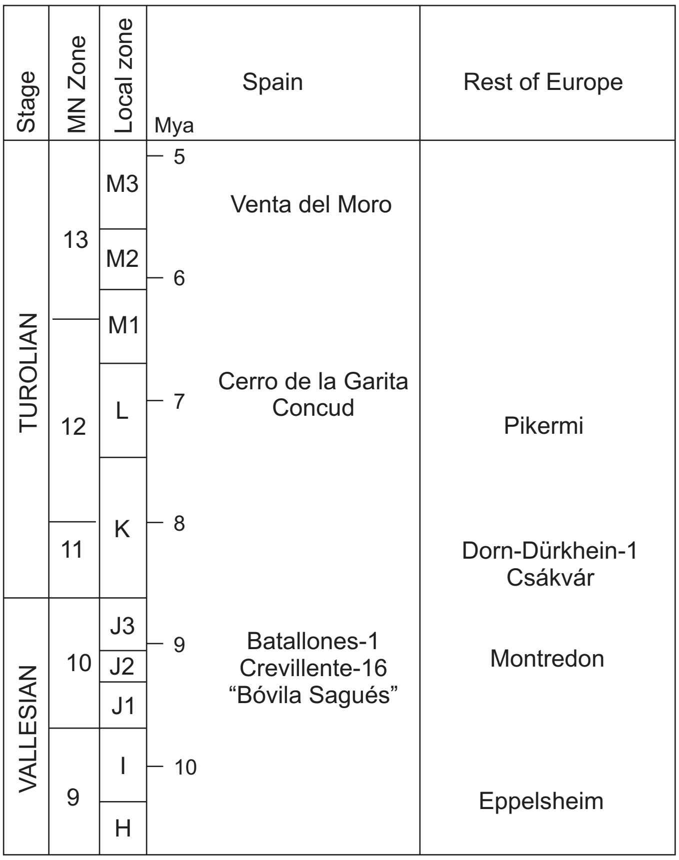

Fig. 8. Stratigraphic distribution of the European localities discussed in the text. Stratigraphic data are from Bruijn et al. (1992) except that for Batallones-1 (Morales et al. 1992, 2000, 2004), Crevillente-16 (Montoya and Alberdi 1995) and “Bóvila Sagués” (see Crusafont 1952) which is in the area of Tarrasa (or Terrassa).

of dental measurements and proportions between the species of the genus. For comparison, we used statistics for lower tooth row measurements and ratios for the entire studied sample of *Simocyon* spp. (Table 5) and *S. primigenius* (Table 6). The coefficient of variation (CV) of each measurement has been calculated, as corrected by Scherrer (1984) for the samples: N = (1+1/(4×N))×(100×SD/m), with N = sample size; SD = standard deviation; m = mean. In the entire sample of *Simocyon* spp., most of the CVs are similar to those found for dental measurements of extant species, e.g., *Vulpes vulpes* (see Szuma 2000) and *Martes* spp. (Wolsan et al. 1985). CVs of the lower tooth measurements range from 2.99 to 21.46; the least variable tooth is m1 and the most variable one is p3. Thirteen variables show a CV approaching or greater than 10 but for six of these (especially those regarding m2), this is only or mainly due to the great individual variation observed in *Simocyon primigenius* (see Table 6). The seven other variables showing a high CV may provide a basis for distinguishing more than one species in the entire sample of *Simocyon* specimens (see also Gingerich 1974 for the use of CVs to distinguish closely related sympatric species). These variables regard especially p3 and the depth of the mandibular corpus. A

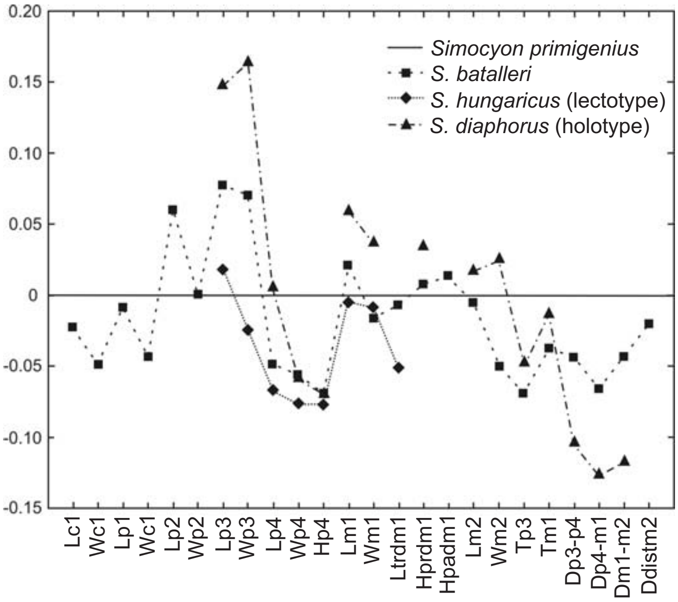

Fig. 9. Ratio diagram showing the species of *Simocyon*. The standard is a mean of the entire sample of *Simocyon primigenius*, including the material assigned to *S. zdanskyi* and *S. marshi*.

log ratio diagram incorporating the measurements of the lower teeth and mandible also support distinct values for these variables at a specific level (Fig. 9). Statistics for the upper tooth row are presented in Table 7 (entire sample of *Simocyon*) and Table 8 (*S. primigenius*). CVs of the upper teeth measurements range from 4.05 to 11.72; the least variable tooth is P4 and the most variable one is C1. The dimensions of the upper canine show a great variation in the entire sample (Table 7) but this is because of the marked intraspecific variation of this tooth in *S. primigenius* (Table 8). There is hence no basis in measurements or proportions of upper teeth for distinguishing more than one species in the studied sample of *Simocyon* specimens.

Comparisons.—We describe in this paper the new material of *Simocyon* from the locality Batallones-1 from Spain, which we assign to *Simocyon batalleri* (Viret, 1929). The new material from Batallones-1 differs insignificantly from the holotype of *S. batalleri* from Sabadell, Barcelona province (Fig. 7A) in having a more transversely elongated M2. Other differences concern the structure of P4, which in specimens from Batallones-1 shows a slightly less developed parastyle and a more distally expanded protocone cingulum. We regard these differences as ranging within the individual variation, and we see no reason to erect a new species of *Simocyon* for the new material described herein.

As the material from Batallones-1 is more rich and better preserved than that previously known of *S. batalleri* from Sabadell, we base the comparisons of *S. batalleri* with other species of *Simocyon* mostly on the material from Batallones-1.

Table 7. Summary statistics of the upper teeth for the studied sample of *Simocyon* specimens. Abbreviations: CV, coefficient of variation; distM1, greatest distance between the buccal border of the metacone and the lingual margin of M1; H, height of the crown of cuspid, i.e. shortest distance from the tip to the dentine-enamel junction; L, mesiodistal length; N, sample size; m, mean; SD, one standard deviation; W, buccolingual width.

	N	m	range	SD	CV
LC1	5	11.74	10.70–14.00	1.31	11.72
WC1	5	8.78	7.70–10.05	0.87	10.38
L/WC1	5	1.34	1.25–1.39	0.06	5.06
LP4	8	20.08	19.10–21.60	0.83	4.28
WP4	8	12.06	10.80–13.10	0.90	7.68
L/WP4	8	1.67	1.51–1.79	0.09	5.33
LP4/WM1	7	1.05	0.99–1.16	0.06	5.50
LM1	7	15.84	14.90–16.85	0.62	4.05
WM1	7	19.24	17.00–20.75	1.20	6.48
WdistM1	4	16.93	15.50–18.50	1.24	7.81
L/WM1	7	0.83	0.77–0.91	0.05	6.25
LM2	5	8.38	7.50–9.00	0.54	6.83
WM2	5	14.14	13.20–15.00	0.69	5.13
L/WM2	5	0.59	0.57–0.61	0.02	3.45

Table 8. Summary statistics of the upper teeth for the sample of *Simocyon primigenius*. See Table 7 for abbreviations.

	N	m	range	SD	CV
LC1	3	11.90	10.70–14.00	1.82	16.61
WC1	3	8.85	7.70–10.05	1.18	14.39
L/WC1	3	1.34	1.25–1.39	0.08	6.58
LP4	5	20.06	19.10–21.60	1.02	5.32
WP4	5	12.00	10.80–13.10	1.10	9.64
L/WP4	5	1.68	1.51–1.79	0.11	6.62
LP4/WM1	4	1.07	0.99–1.16	0.07	7.15
LM1	4	15.53	14.90–16.20	0.53	3.64
WM1	4	19.04	17.00–20.75	1.55	8.66
WdistM1	1	18.50	18.50–18.50	–	–
L/WM1	4	0.82	0.77–0.91	0.07	8.43
LM2	3	8.63	8.40–9.00	0.32	4.03
WM2	3	14.53	14.00–15.00	0.50	3.75
L/WM2	3	0.59	0.58–0.61	0.02	3.04

Simocyon batalleri differs from *S. diaphorus* in having a deeper mandible and a more reduced p3 (Fig. 9). The depth of the mandible is not diagnostic and may be related to the individual age. This character is strongly variable among Batallones-1 specimens, with the old individual from Batallones-1 having a markedly deeper mandible than the young one (Table 1).

The dentition of *Simocyon batalleri* from Batallones-1 is very similar to that of *S. primigenius*. The lack of P2–P3 and p2–p3, which is relatively constant in *S. primigenius* from Pikermi, is not diagnostic. Thus, the premolar number is variable in *S. batalleri* from Batallones-1 (MNCN B-3458 lacks

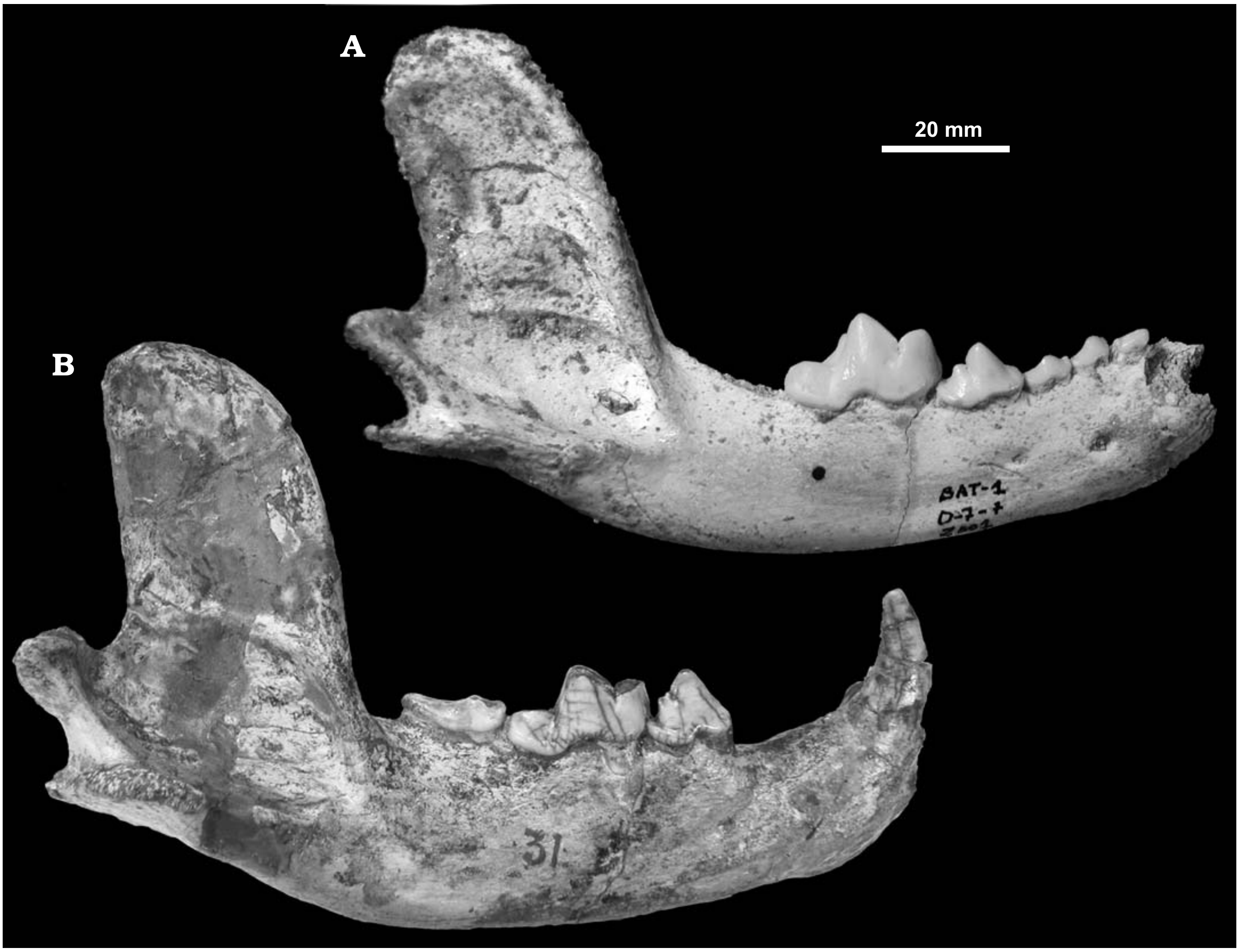

Fig. 10. **A**. *Simocyon batalleri*, MNCN BAT-1-D7-7-2001, Batallones-1, Madrid Province, Spain, right hemimandible with p1–m1 in lateral view. **B**. *Simocyon primigenius*, MNHN-PIK 3020, Pikermi, Greece, right hemimandible with c, p4, m1 and m2 in lateral view.

the left P1 and the right P3 while MNCN B-3620 lacks both P3) and, especially, in *S. primigenius* from China. We did not find a clear difference in the dental morphology or proportions of *S. batalleri* from Batallones-1 and *S. primigenius*, except a more reduced p3 in our material compared to that in *S. primigenius*. In contrast, the mandible displays distinct morphological changes. A fundamental difference between *S. batalleri* and *S. primigenius* concerns the morphology of the posterior part of the mandible. The specimens of *S. batalleri* differ from *S. primigenius* in having a coronoid process distinctly more posteriorly oriented, a lesser anteroposterior development of the top of the process, a shorter postmolar space and a longer angular process (Fig. 10). Such differences have biomechanical implications that we discuss in the next section dealing with the functional and adaptive aspects of the masticatory apparatus.

Compared to the lectotype of *S. hungaricus*, the specimens of *S. batalleri* from Batallones-1 do not show morphological differences. The lack of p2 in *S. hungaricus* is not diagnostic at a specific level. The status of *S. hungaricus* remains unresolved.

Summing up, we recognize three valid species of *Simocyon*, the most primitive of which is *S. diaphorus*, known from early Vallesian of Germany, the most derived *S. primigenius* from the Turolian of Europe and China; *S. batalleri* described herein in detail on the basis of the new Vallesian material from Spain (locality Batallones-1) is in some respects morphologically intermediate between *S. diaphorus* and *S. primigenius*.

Functional and adaptative aspects of the masticatory apparatus

The trend in the dentition of *Simocyon* indicates an emphasis on the crushing function of the posterior premolars, at the expense of the anterior premolars and of the grinding posterior

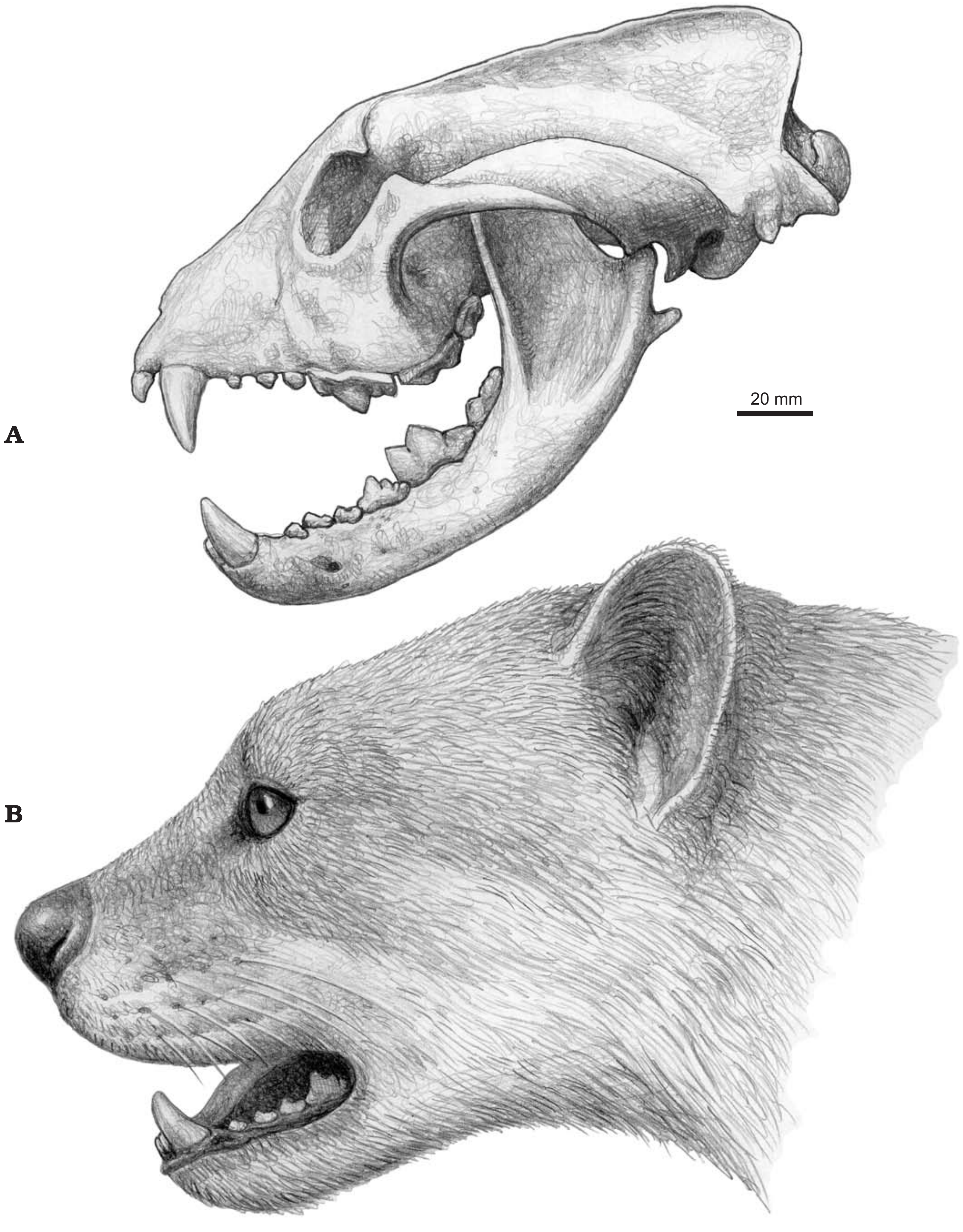

Fig. 11. Skull (**A**) and life appearance (**B**) of *Simocyon batalleri* (artwork by M. Antón).

molars, while the cranio-mandibular features allow the masticatory muscles to provide the necessary power for a strong crushing bite at the level of P4/p4. Along with these trends, *Simocyon* also displays an emphasis on the shearing action of the carnassials, indicating a more carnivorous diet than that of any other ailurid or procyonid. These two trends involve cranial, mandibular, and dental features. Thus, the shortening of the rostrum is greater in more advanced species such as *S. primigenius* in relation to the loss of some premolars. Although the number of premolars may vary in the different species, it remains clear that earlier species (*S. diaphorus*, *S. batalleri*) did not have reduced premolars (in particular p3) that are as they are in *S. primigenius*. Another feature accompanying theses trends is the displacement of the mandibular condyle above the level of the occlusal plane of the dentition, which is particularly clear from *S. batalleri* to *S. primigenius*. We also note in *S. primigenius* from Pikermi the reduction of the angular process and a deeper masseteric fossa relative to *S. batalleri*, in which the angular process is relatively long (Fig. 10). The insertion areas for the pterygoid muscles are very well preserved in the Spanish individuals, and that for the pterygoideus lateralis much more expanded than that for the pterygoideus medialis. Whether these differences are only of specific value or related to masticatory biomechanics has to be confirmed. The relative verticalization of the coronoid process is a distinct feature differentiating *S. primigenius* compared to *S. batalleri*, in which the process remains posteriorly oriented (Fig. 10). The meaning of this difference is not clear, but the presence of a more vertical ramus implies some modifications in the muscles masseter and temporalis, which insert in this part of the mandible; in *S. primigenius* the fibres of the temporalis muscle would be disposed more vertically than in *S. batalleri*, suggesting a more powerful and efficient crushing bite. Together with the reduction and/or loss of premolars, one possible trend to be confirmed with additional specimens is the enlargement of the p4 (especially the height of the main cusp) in *S. primigenius* compared to other species. The p4 thus becomes the main bone-cracking tooth as in specialized borophagine canids (e.g., *Borophagus*; see Werdelin 1989). Finally, the vaulting of the skull is a common trend in species of *Simocyon*.

The development of the above listed features in *Simocyon* reveals a marked convergence with the later members of the canid subfamily Borophaginae, especially *Borophagus* (senior subjective synonym of *Osteoborus*, see Werdelin 1989; see also Wang et al. 1999). These derived borophagines were hunters and scavengers with a considerable ability for bone crushing, as evidenced not only by their cranio-dental morphology, but also by the heavy apical wear in their dentition. The resemblance between *Simocyon* (as reconstructed here in Fig. 11) and these canids undoubtedly indicates some similarity of feeding and/or diet. However, in contrast to *Simocyon*, the crushing function of the dentition in *Borophagus* is more developed, as supported by heavy apical wear of P4/p4, and extended to an m1 that also displays a heavy wear and therefore loses its cutting edge (Werdelin 1989). It appears that bone cracking in *Simocyon* was not so important as in borophagines. A less extreme development of crushing premolars and smaller body size in *Simocyon* also argue against a borophagine-like, bone-crushing niche. One possible interpretation is that the adaptations for crushing in *Simocyon* were related to a full utilization of prey items, possibly small-sized mammals, which were eaten complete with bones and all. At any rate, it has been suggested that the niche overlap between *Simocyon* and the borophagines was important enough to seriously limit the expansion of the former in the Miocene of North America, where the latter were evolving a successful radiation, especially the *Borophagus* lineage (Tedrow et al. 1999). A similar niche overlap may result in the absence of large hyaenids in Batallones-1, although these were well diversified in other late Miocene localities. The Batallones-1 assemblage includes another carnivoran with bone-crushing abilities, *Amphicyon*, very similar in some dental traits to *Simocyon*, such as the reduction of the anterior premolars. Nevertheless, *Amphicyon* also reduced the p4, focusing the crushing function on the posterior molars. Thus, these two models of crushing carnivorans probably reflect different diets, which, besides the body size, much larger in *Amphicyon* than in *Simocyon*, would have given place to a complete ecological separation between them.

Acknowledgements

We thank all people who participated in the excavations at Batallones-1, and the Comunidad Autónoma de Madrid (Dirección General de Patrimonio Histórico) for the continuous funding support and the research permissions. Particular thanks are due to Dr. Sebastián Calzada (MSB) for loaning the holotype of *Simocyon batalleri*, to Dr. Jerry Hooker (Natural History Museum, London) for access to the only cast of the holotype of *Simocyon diaphorus*, to Prof. Louis de Bonis (University of Poitiers) for access to a cast of the lectotype of *S. hungaricus*, to Prof. Pascal Tassy and Dr. Claire Sagne (MNHN) for access to materials from Pikermi, to Dr. Jordi Agustí (Institut Miguel Crusafont, Sabadell) for providing information about the material from the Vallès-Penedès area, and to Prof. Alan Turner (Liverpool John Moores University) for reviewing the English of the manuscript. We are grateful to the reviewers of this work, Prof. Jon A. Baskin and Prof. Mieczysław Wolsan, for their constructive comments that greatly improved the manuscript. Part of this study was financially supported by the project MCYT-DGI BTE2002-00410 (Dirección General de Investigación-MCYT), EX2003-0243 (Secretaría de Estado de Educación y Universidades and European Social Funding), Grant 6964-01 (National Geographic Society), and by the Fondation Singer-Polignac, Paris to the senior author.

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