Inferred behaviour and ecology of the primitive sabre-toothed cat *Paramachairodus ogygia* (Felidae, Machairodontinae) from the Late Miocene of Spain

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**Keywords**

behaviour; ecology; Felidae; Miocene; *Paramachairodus*.

**Abstract**

The Late Miocene (Late Vallesian, MN 10, about 9 Mya) carnivore trap of Batallones-1 (Madrid, Spain) has yielded a large sample of two species of sabre-toothed cats: the puma-sized *Paramachairodus ogygia* and the tiger-sized *Machairodus aphanistus*. This has allowed, for the first time, complete studies of the biomechanics and comparative anatomy of these animals. Focusing our study on the small species, *Par. ogygia*, the most richly represented and best known carnivore from Batallones-1, we attempt to infer some aspects of the behaviour and ecology of this early sabre-toothed cat, such as breeding behaviour, the degree of social interaction between individuals, sexual dimorphism, preferred habitat and prey size. Our results suggest that *Par. ogygia* was a solitary felid with a low sexual dimorphism index, which in turn indicates low competition between males for access to females, and some degree of tolerance between adults, so that young adults were allowed to share the territory of their mothers for some time after maturity. The machairodont adaptations of *Par. ogygia* indicate that this species was able to subdue and kill prey in less time than pantherines do, thus minimizing the risk of injury and the energetic costs of this action. In a wider context, the carnivore guild of Batallones-1 and the overall mammal community indicate that the landscape around the trap was a wooded habitat. Batallones-1 is thus establishing itself as one of the most important European Late Miocene fossil localities, not only for the study of the anatomy and biomechanics of the early sabre-toothed cats but also for our understanding of the intra- and inter-specific ecological relationships of the first members of this specialized subfamily of felids.

**Introduction**

Inferences about the palaeobiology of fossil carnivores can be made based on field studies of extant species. However, because this group of mammals is not usually well represented in fossil sites, it is rare that these studies can include inferences about population structure, sexual dimorphism or age group representation. The Late Miocene (Late Vallesian, MN 10) carnivore trap of Batallones-1 (Madrid, Spain) has yielded a large sample of several species of carnivorans, and is now one of the most important European localities for investigation of the mammalian communities of that epoch. The site was formed as an irregular cavity in sepiolite levels, later filled with greenish clay. It acted as a natural trap for many animals, attracting mainly Carnivora (98% of the total macromammal sample in number of bones) that were probably trapped while attempting to scavenge (Fig. 1). Among them, abundant remains of two species of sabre-toothed cats have been found: *Paramachairodus ogygia* (Kaup, 1832) and *Machairodus aphanistus* (Kaup, 1832). We focus our study on the former, which is the most richly represented carnivorans of the Batallones-1 sample. This species was previously one of the most poorly known Late Miocene machairodontines, but thanks to the large amount of available skeletal elements, it is now possible to infer many aspects of its biomechanics (Salesa, 2002; Salesa et al., 2005) and palaeoecology.

The walls of sepiolite of the trap made escape very difficult, because when this mineral is wet its surface becomes slippery, and under these conditions, even big cats were not able to climb out. Because the cavity was being filled with clay, the bottom of the trap would have been covered with wet mud, which would have hindered the movement of animals and probably induced hypothermia, contributing to their more or less rapid death (Morales et al., 2000, 2004; Salesa, 2002; Antón et al., 2003). At least seven additional and contemporaneous cavities have been
identified in the Batallones area, and although only Batallones-1 has been thoroughly excavated all of them fit with a general geological process of piping, which in this case consisted of the erosion of sepiolite levels by water along fractures, causing collapses and the development of karst-like (‘pseudokarst’) topography, already described in other areas by Halliday (1960). This is the major project responsible for the formation of the Batallones fossil site complex (Antón et al., 2003; Morales et al., 2004; Pozo et al., 2004), providing one of the most complete samples of Late Miocene sabre-toothed cats.

Materials and methods

All the skeletal remains of the mammals of Batallones-1, including the sample of *Par. ogygia* analysed in this study, are held in the collections of the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain). Measurements were taken using a digital calliper. Data on the minimum number of individuals (MNI) of each species of carnivoran were taken from Antón & Morales (2000). The sexual dimorphism index of *Par. ogygia* was calculated following the ‘average method’ of Van Valkenburgh & Sacco (2002), which is based on four measurements of skull and dentition; this method, which divides the sample into two sub-samples, ‘males’ and ‘females’, offers a good indication of the size divergence between the sexes.

The body weight of *Par. ogygia* was estimated by Salesa (2002) as 28-65 kg, which is within the range of an extant puma. There were no previous estimates of the body weight of *M. aphanistus*, so we used the regression formula of Van Valkenburgh (1990) for Felidae to estimate it on the base of the skull basal length of six individuals from Batallones-1 (Table 1). The results, between 100 and 240 kg, placed *M. aphanistus* within the range of extant tigers and lions.

### Table 1 Estimated body weight of *Machairodus aphanistus* from Batallones-1: BL (skull), basal length of the skull, measured from the anterior border of incisors to the anterior margin of foramen magnum

<table>
<thead>
<tr>
<th>Number</th>
<th>BL (Skull)</th>
<th>Body weight (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B-4272</td>
<td>257.0</td>
<td>130.28</td>
</tr>
<tr>
<td>B-1523</td>
<td>237.0</td>
<td>101.27</td>
</tr>
<tr>
<td>B-4711</td>
<td>310.0</td>
<td>233.42</td>
</tr>
<tr>
<td>B-5445</td>
<td>313.0</td>
<td>240.52</td>
</tr>
<tr>
<td>B-4151(1)</td>
<td>264.0</td>
<td>141.64</td>
</tr>
<tr>
<td>B-6046</td>
<td>246.0</td>
<td>113.71</td>
</tr>
</tbody>
</table>

The faunal association of Batallones-1 is one of the richest of the Late Miocene of Eurasia, and includes fishes, amphibians, reptiles, birds and mammals (Morales et al., 2000, 2004). Nevertheless, the majority of the sample (98% of the total bone sample) is of Carnivora. This is unusual in fossil localities, because with carnivorans totalling about 11% of the total mammal biomass in extant ecosystems (White et al., 1984), the presence of this group in the fossil samples usually totals around 7% of individuals (White et al., 1984; Antón & Morales, 2000). The existence of such a large proportion of carnivorans in Batallones-1 is explained as a consequence of the presence of carcasses of animals that had died within the trap (Antón & Morales, 2000; Morales et al., 2000; Salesa, 2002). The absence of significant water flow...
after the accumulation of the sample prevented the total disarticulation of the skeletons, allowing excellent preservation of the fossils and the presence of practically complete skeletons (Morales et al., 2000, 2004).

The most abundant components of the mammal fauna of Batallones-1, around 29% of the total (Fig. 2), are the sabre-toothed cats, with two species represented: the puma-sized *Paramachairodus ogygia*, with at least 18 individuals recorded (16% of the mammal palaeocommunity) (Figs 2 and 3), and the tiger-sized *Machairodus aphanistus*, with 14 individuals (13% of the mammal palaeocommunity) (Figs 2 and 3; Table 2) (Antón & Morales, 2000). There are two species of primitive felines, one of *Felis*-size and other of *Lynx*-size; they represent only 4% of the sample (Figs 2 and 4). The bear-dog *Amphicyon sp. aff. A. castellanus* Ginsburg, Morales & Soria (1981) is relatively abundant, with at least 12 individuals (11% of the mammal sample) (Figs 2 and 5). The primitive hyaenid

**Figure 2** Relative abundance of the different groups of mammals present in the Batallones-1 sample.

**Table 2** Minimum number of individuals (MNI) for the main mammal groups represented in the Batallones-1 palaeocommunity

<table>
<thead>
<tr>
<th>Species</th>
<th>MNI (A)</th>
<th>MNI (J)</th>
<th>MNI (T)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insectivora</td>
<td>8</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>Rodentia indet.</td>
<td>7</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Castoridae</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Prolagus crusafonti</em></td>
<td>16</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td><em>Simocyon batalleri</em></td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td><em>Martes</em> sp.</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td><em>Propotorius</em> sp.</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Sabadelictis</em> sp.</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Mustelidae indet.</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Amphicyon sp. aff. A. castellanus</em></td>
<td>6</td>
<td>6</td>
<td>12</td>
</tr>
<tr>
<td><em>Protictitherium crassum</em></td>
<td>9</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td><em>Felinae</em> indet. sp. 1</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Felinae</em> indet. sp. 2</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td><em>Paramachairodus ogygia</em></td>
<td>17</td>
<td>1</td>
<td>18</td>
</tr>
<tr>
<td><em>Machairodus aphanistus</em></td>
<td>12</td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td><em>Tetralophodon longirostris</em></td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Hipparion</em> sp.</td>
<td>4</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td><em>Aceratherium incisivum</em></td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td><em>Microstonyx</em> sp.</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Cervidae</em> indet.</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Hiantanomeryx</em> sp.</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>

MNI (A), minimal number of adult individuals; MNI (J), minimal number of juvenile individuals; MNI (T), minimal number of total individuals.

**Figure 3** Fossil Carnivora from Batallones-1: (a) B-4778, skull and mandible of *Paramachairodus ogygia* in lateral view; (b) B-5445, skull and mandible of *Machairodus aphanistus* in lateral view.
Protictitherium crassum (Depéret, 1892), with nine individuals (8%), is the fourth most abundant Carnivora (Figs 2 and 3), whereas the ailurid Simocyon batalleri (Viret, 1929) (Fig. 5) is one of the less represented, with only two individuals (2%) (Peigné et al., 2005). Mustelids total 6% of the sample, being represented by four species, the marten Martes sp., two skunks (Sabadelictis sp. and Proputorius sp.) and one undetermined species. It is noticeable that the fossil pika (Lagomorpha) Prolagus crusafonti (López Martínez, 1975) (in López Martínez & Thaler, 1975) is almost as abundant as Par. ogygia, with 16 individuals and 15% of the total mammal community. The micro-mammal fauna of Batallones-1 also includes insectivores (8% of the sample), such as the moonrat Galerix sp. and two other undetermined species, and rodents (7%), such as the squirrel Spermophilinus sp., the beaver Steneofiber sp., the mouse Progonomys hispanicus Michaux, 1971 and two species of undetermined cricetid (hamsters) and zapodid (jumping mice). The presence of the mouse Prog. hispanicus dates this locality to the early part of the Late Miocene, Neogene European Land Mammal Zone 10 (MN 10) of Mein (1975), about 9 million years ago (Morales et al., 2000, 2004).

The mammal association also includes a small number of ungulate taxa; these are the mastodont Tetralophodon longirostris Kaup, 1832 (representing only 1% of the total sample), the hornless rhinoceros Aceratherium incisivum Kaup, 1832 (3%), the tridactyl equid Hipparion sp. (4%), the hornless ruminant Hispanomeryx sp. (2%), the giant pig Microstonyx sp. (only 1%) and two species of undetermined cervids and bovids (1%) (Morales et al., 2000).

**Discussion**

**Habitat preference in big cats**

The three-dimensional structure of the habitat, which can be highly variable, clearly determines several aspects of mammalian behaviour (Eisenberg & Lockhart, 1972; Geist, 1974). Among large cats, some species such as jaguar Panthera onca, clouded leopard Neofelis nebulosa and tiger Panthera tigris are mainly found in highly structured habitats, typically dense forest (Mazák, 1981; Seymour, 1989; Turner & Antón, 1997; Alderton, 1998). However, the tiger can also be found in the ecotone between forest and grassland, or even in mountain valleys of pine woods in Manchuria and near the Amur river (Mazák, 1981), and jaguars have been reported in low-structured habitats such as deserts and prairies (Seymour, 1989), while leopards Panthera pardus and pumas Puma concolor can occupy a range of very different habitats, from arid savannas to dense tropical forests (Currier, 1983; Nowak & Paradiso, 1983; Johnson et al., 1993; Alderton, 1998; Bothma & Walker, 1999). Lions Panthera leo and cheetahs Acinonyx jubatus are found in low-structured habitats, such as savannas or grasslands with some shrub coverage (Nowak & Paradiso, 1983; Alderton, 1998; Bothma & Walker, 1999). The snow leopard Uncia uncia also occupies low-structured habitats, such as rocky areas in Asia between 1400 and 3200 m of altitude, occasionally reaching 4300 m (Hemmer, 1972; Gonyea, 1976a; Nowak & Paradiso, 1983; Alderton, 1998).
Although the habitat preference of some species of felids may be variable, they can probably be considered to derive from closed habitat dwellers (Turner & Antón, 1997). In general, felids have not derived too much from the primitive body plan of the Early Miocene forms (Helbing, 1928; Beaumont, 1961; Turner & Antón, 1997), such as Proailurus lemanensis (Filhol, 1879) and although there are some cursorial forms, such as Acinonyx jubatus or to a lesser extent, U. uncia (Turner & Antón, 1997), felids lack the adaptations to sustained terrestrial locomotion in open environments seen in some other Carnivora, such as canids or hyaenids.

Inferences on the habitat of Batallones-1

The fact that sabre-toothed felids are the most abundant Carnivora of the Batallones-1 sample (Table 2) has ecological implications, because classical studies of vertebrate ecology have shown that intra- and inter-specific competition for resources produce different patterns of habitat use (Lack, 1945; MacArthur, 1958; Lanciani, 1970; Laerm, 1974; Gonyea & Ashworth, 1975; Rabinowitz & Nottingham, 1986; Bothma & Walker, 1999; Palomares & Caro, 1999). According to this, when different species of extant felids live in sympathy a marked segregation exists between them, with the small-sized species constantly avoiding encounters with the large ones, which can be very violent. It is known that lions and leopards kill adults and cubs of other felids, and that leopards are killed by lions and tigers (Turner & Antón, 1997), felids lack the adaptations to sustained terrestrial locomotion in open environments, sympatry is possible because cheetahs constantly avoid encounters with lions, hunting during the hours of maximum heat when lions and hyaenas tend to be inactive and resting in the shade (Hanby & Bygott, 1979; Durant, 2000). There is also sympathy among felids of similar size, such as pumas and jaguars in most of the American continent (Nuñez, Miller & Lindzey, 2000), but this is only possible when resources are rich enough to allow the maintenance of both species, which develop a marked ecological segregation between them mainly based on the avoidance of adult encounters (Rabinowitz & Nottingham, 1986; Nuñez et al., 2000).

In summary, the sympathy of two large cat species seems to be determined not only by the presence of enough tree cover, but also by high prey biomass (Seidensticker, 1976). In the case of lions and leopards, this sympathy is facilitated by the fact that leopards preferably occupy wooded sections of the habitat, less favourable for lions (Bailey, 1993). The body proportions of *Par. ogygia* and *M. aphanistus* are very similar to those of the extant pantherine cats (Salesa, 2002; Antón et al., 2003), probably reflecting similar habitat preferences, that is, wooded environments. The predominance of *Par. ogygia* in Batallones-1 could imply that the trap was in a wooded area with at least enough cover to allow this species to coexist with the larger *M. aphanistus* (Antón & Morales, 2000). Preliminary observations of the post-cranial remains of the two species of small feline cats from Batallones-1 show them to be relatively gracile and thus comparable with extant species such as *Felis sylvestris*, *Felis lybica* and *Lynx pardinus*. These extant species occupy a wide range of habitats (Kitchener, 1991; Antón & Morales, 2000), so the presence of these felines in Batallones-1 does not allow precise ecological interpretations. Nevertheless, the high diversity of felids in this locality implies a segregation of niches between the different species, much more probable in a wooded environment.

Among the Mustelidae, the extant species of the genus Martes are associated with forested habitats (Nowak & Paradiso, 1983) and, although some species can occupy rocky areas, prairies and riversides, they always avoid treeless environments (Powell, 1981; Clark et al., 1987). Thus, the presence of marten in Batallones-1 supports the notion of a wooded habitat for this locality. Extant skunks occupy a wide range of habitats (Nowak & Paradiso, 1983; Antón & Morales, 2000), so that the presence of Sabadellic-tis and Propoturio in Batallones-1 gives little information about the palaeohabitat of the trap surroundings.

The only extant Ailuridae is the red panda, *Ailurus fulgens*, which inhabits the forests of China, Nepal and Burma (Nowak & Paradiso, 1983; Roberts & Gittleman, 1984). Its diet consists mainly of bamboo, but it also includes insects, small mammals, eggs, fruits and leaves (Nowak & Paradiso, 1983; Roberts & Gittleman, 1984). Nevertheless, although *S. batalleri* is thought to be related to *A. fulgens* (Wang, 1997), it has a very different dentition that seems to be adapted to a diet based on flesh and carrion (Baskin, 1998; Antón & Morales, 2000; Salesa & Fraile, 2000) and probably included small vertebrates (Peigné et al., 2005). This animal does not show any cursorial adaptations in its appendicular skeleton, so it is probable that it inhabited at least moderately wooded areas.

The population of Amphicyon sp. aff. *A. castellanus* from Batallones-1 is one of the richest samples of bear-dogs known in the European fossil record (Morales et al., 2000). Amphicyonoids were powerfully built carnivorans, from the size of a wolf to that of a brown bear, which inhabited North America and Eurasia during the Oligocene and Miocene. Their dentitions show adaptations to a carnivorous diet, but also have strong post-carnassial teeth, probably reflecting their abilities as both scavengers and hunters. Nevertheless, the dentition of the Batallones-1 *Amphicyon* is more hypercarnivorous than that of previous species of this genus, probably reflecting a late adaptation of this species to more active hunting (Morales et al., 2000; Salesa & Fraile, 2000).

*Protictitherium crassum* is an early and primitive member of the family Hyaeinidae (Werdelin & Solounias, 1991), with the approximate size and proportions of the extant African
civet, *Civettictis civetta* (Antón & Morales, 2000). The latter inhabits both forested and more or less open environments, but always with enough vegetational cover to find refuge (Nowak & Paradiso, 1983; Ray, 1995). The dentition of *Prot. crassum* does not show the adaptations to bone cracking seen in the later hyaenids, and it probably would have been an opportunistic carnivora, with a diet and behaviour more similar to that of a jackal than to that of an extinct hyaenid.

The herbivore sample of Batallones-1 is scarce (12% of the total sample), although the presence of some taxa with low cheek teeth, such as cervids, mastodonts, *Hispanomeryx*, and *Aceratherium*, suggest the presence of a wooded habitat. It is also noticeable that the most probable grazers or at least mixed-feeders, *Hipparion* and the bovids, are really rare in the sample.

In summary, the faunal association of Batallones-1 suggests a wooded habitat for this locality, probably a more or less dense woodland, with enough cover to allow the sympatry of two species of large felids, the presence of several species of small carnivorans (which need some cover to protect them from the attack of the large predators) and the feeding of large browsers such as mastodonts or rhinos.

Other factors, such as the presence of bovids and hippo- ionine horses, indicate the presence of more open, grassy patches in the vicinity of the site.

**Sociability and sexual dimorphism in Felidae**

**Social behaviour in felids**

Most of the extant felines lead solitary lives, and only in the breeding season do they form pairs that last only a few weeks (Nowak & Paradiso, 1983; Alderton, 1998; Bothma & Walker, 1999). Only lions have the kind of behaviour that can be considered as social (Leyhausen, 1979; Caro, 1989, 1994), although it has been observed that tigers inhabiting open environments can form groups, and male cheetahs often form coalitions (Alderton, 1998; Bothma & Walker, 1999). Nevertheless, none of the species live in complete isolation, because they use several types of marks to keep in contact with other individuals. These may be scent (territorial marking with urine), visual (scratching on trees) or vocal, used singly or in combination (Nowak & Paradiso, 1983; Bailey, 1993; Daniel, 1996; Alderton, 1998).

Felids are highly territorial animals, that is, they occupy very well-delimited areas (home ranges or territories) that are defended against other adults of the same species. Each individual marks the limits of its range in order to show that the area is occupied (Bailey, 1993; Turner & Antón, 1997; Alderton, 1998). In most of the species, male territories include several, smaller female territories (Rabinowitz & Nottingham, 1986; Bailey, 1993). There are some exceptions, such as lions, in which groups of two to five related males defend a huge range occupied by a pride of related females (Nowak & Paradiso, 1983; Alderton, 1998; Bothma & Walker, 1999). Cheetah male coalitions may include non-related individuals (Nowell & Jackson, 1996), and can occupy territories of between 12 and 150 km² that include the smaller female territories. There are also solitary cheetah individuals that do not defend territories, moving through huge areas (Nowak & Paradiso, 1983; Nowell & Jackson, 1996), but in other cases groups of 14 individuals have been reported in areas in which lions and hyaenas have been exterminated (Nowell & Jackson, 1996).

Territory size in large cats is variable, because it depends on the sex and age of the owner, and available prey biomass (Currier, 1983; Bailey, 1993). Thus, the territory of a male leopard can vary between 16.4 and 96.1 km², and that of a female between 5.6 and 29.9 km² (Bailey, 1993). A pride of lions can occupy a territory as large as 470 km² (Bothma & Walker, 1999), whereas the territories of male tigers vary between 380 km² in the case of Indian individuals and the 1000 km² of those from central Asia (Mazák, 1981). Male jaguars have territories of between 28 and 40 km², whereas those of females tend to be around 10 km² (Rabinowitz & Nottingham, 1986; Seymour, 1989). Male pumas tend to have larger territories than females, but in both cases they are highly variable, between 96 and 243 km² (Currier, 1983).

**Sexual dimorphism in felids**

Sexual dimorphism in mammals has been associated with a high level of competition between males for access to females (Short & Balaban, 1994; Weckerly, 1998). Among the Carnivora, sexual dimorphism is more marked in canine size than in other dental features or skull size, and these differences can be related to thebreeding system. Species in which a male defends a group of females tend to be more dimorphic than those with monogamous pairs or groups of males and females (Gittleman & Van Valkenburgh, 1997; Weckerly, 1998; Van Valkenburgh & Sacco, 2002). Felids are dimorphic animals, but mainly in reference to body size, with the mane of male lions being a unique example of morphological variation between sexes among the family.

Table 3 shows the sexual dimorphism index for several species of extant Felinae and the sabre-toothed cats *Smilodon fatalis*, *Par. ogygia* and *M. aphanistus*. The most dimorphic species are *Pan. pardinus* and *Pan. leo*, which is very interesting in view of the different breeding system of these two felids. Lions have a very competitive system, with males defending a large group of females (Alderton, 1998; Bothma & Walker, 1999), which would explain the high sexual dimorphism index (Bertram, 1979; Van Valkenburgh & Sacco, 2002). On the other hand, leopards are basically solitary animals, probably more so than any other pantherine (Bailey, 1993), which suggests that there is no clear relationship between the sexual dimorphism index and the presence of social systems in Felidae.

The development of sociability in felids has been seen as associated with the habitat and prey biomass rather than the breeding system (Turner & Antón, 1997; Alderton, 1998; Funston et al., 1998). Thus, the social behaviour of lions has been explained as a consequence of their special habitat, much more low-structured than that of other felids; for a
Cheetahs exhibit a higher degree of sociability, with males usually forming groups of three that can include non-related individuals (Nowell & Jackson, 1996). There is no competition between males for access to females, and males simply breed with those females that enter their area (Nowell & Jackson, 1996). There is no active defence of territory, and, although they mark the limits by urine and scratching, each group of males tries not to come into contact with others (Nowak & Paradiso, 1983). Finally, the least dimorphic felids of the modern sample studied, *Caracal caracal* and *Leptailurus serval*, are both supposed to be solitary, with male ranges including those of the females (Nowell & Jackson, 1996). Nevertheless, groups of caracals composed of juveniles and adults have been reported (Nowak & Paradiso, 1983; Nowell & Jackson, 1996; Alderton, 1998).

Among the fossil Felidae, the Pleistocene tiger-sized sabre-toothed cat *Smilodon fatalis* has a low sexual dimorphism index, identical to that of the jaguar. For this species a social model has been inferred that would be completely different from any other seen in extant felids; monogamous couples within larger groups, similar to that of wolves (Van Valkenburgh & Sacco, 2002). The latter authors suggest that the huge sample of *Smilodon fatalis* from the carnivore-trap locality of Rancho La Brea, at least 2400 individuals (Miller, 1968), and the presence of individuals with severe but healed pathologies makes it improbable that this felid was solitary. In this locality, the ratio between *Smilodon fatalis* and the other sympatric large cat, the American lion *Panthera atrox* is 30:1 (Merriam & Stock, 1932), which could be reflecting the predictable difference between social and solitary felids. But if that is the case then the American lion would be solitary, just the opposite of its extant close relative, *Panthera leo*. In our view, this proportion could also mean some kind of ecological segregation between *Smilodon fatalis* and *Panthera atrox* in the use of resources, which would produce a marked difference in the pattern of trapping, and thus in the representation of each species. In any event, inferences about the presence or lack of social grouping in fossil felids probably need to take more account of the relationship between body size, prey size and density, and the defence of cubs and territory in relatively open environments, which are thought to be the major factors involved in the origin of grouping in modern lions (Packer, 1986; Turner & Antón, 1997; Bothma & Walker, 1999; Yamaguchi et al., 2004). Across other families of Carnivora, it is these factors also that influence the presence of social groupings, rather than the type of breeding system (Van Valkenburgh, Sacco & Wang, 2003). From this point of view, the forest affinities of the Batallones-1 mammalian fauna do not especially favour the notion of social groupings in its larger carnivores.

Table 3 also shows that the sexual dimorphism index of *Panthera ogygia* is similar to that of cheetahs and jaguars. This would reflect a low level of competition between males, just as in some extant large cats. In the Batallones-1 sample, there is only one pathologic individual, with the four left metatarsals broken and healed when the animal was alive (Fig. 6). Nevertheless, they fused incorrectly and the animal was probably unable to run or hunt by itself for some time.

### Table 3 Sexual dimorphism index for several species of extant and fossil Felidae

<table>
<thead>
<tr>
<th>Species</th>
<th>BL (Skull)</th>
<th>MIL (upper C)</th>
<th>BB (upper C)</th>
<th>M1 (lower C)</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Caracal caracal</em></td>
<td>1.08</td>
<td>1.09</td>
<td>1.12</td>
<td>1.08</td>
<td>1.07</td>
</tr>
<tr>
<td><em>Leptailurus serval</em></td>
<td>1.08</td>
<td>1.10</td>
<td>1.14</td>
<td>0.97</td>
<td>1.07</td>
</tr>
<tr>
<td><em>Smilodon fatalis</em></td>
<td>1.06</td>
<td>1.09</td>
<td>1.12</td>
<td>1.07</td>
<td>1.09</td>
</tr>
<tr>
<td><em>Panthera onca</em></td>
<td>1.06</td>
<td>1.12</td>
<td>1.11</td>
<td>1.06</td>
<td>1.09</td>
</tr>
<tr>
<td><em>Puma concolor</em></td>
<td>1.08</td>
<td>1.14</td>
<td>1.09</td>
<td>1.04</td>
<td>1.09</td>
</tr>
<tr>
<td><em>Acinonyx jubatus</em></td>
<td>1.10</td>
<td>1.15</td>
<td>1.11</td>
<td>1.09</td>
<td>1.10</td>
</tr>
<tr>
<td><em>Paramachairodus ogygia</em></td>
<td>1.09</td>
<td>1.11</td>
<td>1.11</td>
<td>1.09</td>
<td>1.10</td>
</tr>
<tr>
<td><em>Lynx rufus</em></td>
<td>1.10</td>
<td>1.16</td>
<td>1.11</td>
<td>1.06</td>
<td>1.11</td>
</tr>
<tr>
<td><em>Felis silvestris</em></td>
<td>1.10</td>
<td>1.15</td>
<td>1.13</td>
<td>1.08</td>
<td>1.12</td>
</tr>
<tr>
<td><em>Felis chaus</em></td>
<td>1.07</td>
<td>1.16</td>
<td>1.15</td>
<td>1.10</td>
<td>1.12</td>
</tr>
<tr>
<td><em>Panthera tigris</em></td>
<td>1.16</td>
<td>1.16</td>
<td>1.08</td>
<td>1.12</td>
<td>1.13</td>
</tr>
<tr>
<td><em>Machairodus aphanistus</em></td>
<td>1.24</td>
<td>1.22</td>
<td>1.16</td>
<td>1.10</td>
<td>1.18</td>
</tr>
<tr>
<td><em>Panthera leo</em></td>
<td>1.12</td>
<td>1.25</td>
<td>1.23</td>
<td>1.13</td>
<td>1.18</td>
</tr>
<tr>
<td><em>Panthera pardus</em></td>
<td>1.13</td>
<td>1.24</td>
<td>1.26</td>
<td>1.12</td>
<td>1.19</td>
</tr>
</tbody>
</table>

Four measurements are used to calculate this index: BL (Skull), basal length of the skull, measured from the anterior border of incisors to the anterior margin of foramen magnum; MIL (upper C), mesiodistal length of upper canines; BB (upper C), buccolingual breadth of upper canines; ML (upper C), mesiodistal length of M1. An average index between these four measurements is also provided. Data were taken from Salesa (2002) (for *Par. ogygia*, Antón et al. (2004) (for *M. aphanistus*) and Van Valkenburgh & Sacco (2002) (for the remaining species).
considerable time after the injury. The presence of this individual in the sample poses some interesting questions about the territoriality of *Par. ogygia*. It is clear that this individual fed after its accident, so it survived until it was trapped in Batallones-1. It is known that temporarily ill leopards feed on carrion, and even healthy individuals do so (Houston, 1979; Bailey, 1993; Daniel, 1996; Bothma & Walker, 1999) but chronically ill individuals die before healing, whereas lions in similar circumstances often survive thanks to their social system (Bailey, 1993). It is highly probable that *Par. ogygia* included carrion in its diet, and its presence in the Batallones-1 trap strongly supports this, but it is also hard to believe that an injured individual could survive only with carrion. This resource is not so abundant and constant as prey, and the amphicyonids alone would have been a serious competitor for a crippled individual of *Par. ogygia*. We suggest that *Par. ogygia* developed some degree of tolerance between adults, as jaguars do, and that an injured individual could therefore feed on the carcasses left by the territory owner. Based on the antero-posterior length of the proximal epiphysis of metatarsal III, this individual is included in the sub-sample of ‘females’. So if this individual was a young female it could have been tolerated by its mother, remaining in her territory and thus feeding on the remains left by her, as occurs with leopards (Bailey, 1993).

In summary, we suggest that the probable territorial behaviour for *Par. ogygia* would be very similar to that of jaguars, in which males defend large, overlapping territories that include smaller territories of several females (Rawn-Schatzinger & Nottingham, 1986; Seymour, 1989). This model is similar to that of the leopard, but in this species male territories never overlap (Bailey, 1993), which could explain the different sexual dimorphism index of this species with respect to *Par. ogygia* and jaguar.

**Demographic structure of the population of Par. ogygia from Batallones-1**

If *Par. ogygia* were a social felid, as lions are, it would be expected that the sample from Batallones-1 had juveniles, which would have followed the adults and been trapped as well. Nevertheless, although the sample of *Par. ogygia* from Batallones-1 is composed of at least 18 individuals, all are young adults (with permanent but unworn dentition) with the exception of only one sub-adult (Salesa, 2002). This virtual absence of young supports the idea of a solitary lifestyle for *Par. ogygia*, like most of the big cats, in which females leave the cubs hidden when hunting (Antón & Morales, 2000). It is interesting that in the fieldwork of Bailey (1993), which consisted of the use of traps to capture and place transmitters on leopards, he observed that individuals less than one year old and females with cubs were never caught. The most frequently trapped individuals were adult males, and the best trapping period was the dry season (Bailey, 1993). So, if *Par. ogygia* behaved more like jaguars and leopards than lions, the presence of juveniles in the trap would be highly improbable, as is the case. But in addition to the scarcity of juveniles, the sample from Batallones-1 has another interesting feature: it is mostly composed of young adults, that is, individuals with the complete permanent dentition, but without any trace of wear. These animals, which would have recently become independent of their mothers, would not as yet have had any territory, moving instead through the ranges of other adults and being more easily attracted by an easy meal, such as carrion. This age distribution therefore suggests that the sample of *Par. ogygia* trapped in Batallones-1 corresponds to that fraction of non-resident young individuals, both males and females, which were in a phase of dispersion. In the case of leopards, such individuals are more daring – or less cautious – than adults, and they have been seen crossing rivers in spate, whereas resident adults only cross at times of lower water (Bailey, 1993). It has also been noticed that among these individuals, males are even more inclined to make these incursions than females, which remain longer with the mother, especially if there is good availability of food (Bailey, 1993). If this pattern of dispersion behaviour applied to the young adults of *Par. ogygia*, it is likely that they were trapped in Batallones-1 more often than the resident adults.

**Prey size of Par. ogygia**

The extremely strong forelimbs of some derived sabre-toothed cats, such as *Smilodon* have been interpreted as an adaptation to cope with larger prey than pantherines (Gonyea, 1976b; Emerson & Radiinsky, 1980; Akersten, 1985; Rawn-Schatzinger, 1992; Türner & Antón, 1997). However, these strong forelimbs are already present in *Par. ogygia*, which also shows some primitive morphology in other
characters and a moderate body size (Salesa, 2002; Salesa et al., 2005). We recently proposed an alternative hypothesis to explain the appearance of these early miacirodont adaptations (Salesa et al., 2005), suggesting that they were developed to subdue prey quickly, thus minimizing the risk of canine breakage and decreasing the energy used in the hunt. Thus, the earlier species of miacirodonts would have been able to kill prey faster than sympatric Carnivora of comparable size and prey preference, and this advantage would have helped the sabre-toothed cats become the dominant predators in the faunas of Late Miocene.

Extant felines of size similar to Par. ogygia (up to 68 kg) prey upon animals of very different sizes: leopards hunt animals from 20 to 100 kg (Seidensticker, 1976; Johnson et al., 1993) whereas pumas and jaguars usually hunt smaller animals, between 1 and 30 kg (Rabinowitz & Nottingham, 1986; Nuñez et al., 2000). Jaguars in rain forests take mammal prey species in proportion to their occurrence (Rabinowitz & Nottingham, 1986; Emmons, 1987), so the relative abundance of small prey in their diet may reflect a lack of available large prey rather than real preference. The herbivorous fauna from Batallones-1 included the mastodont Tetranchodon longirostris, the three-toed equid Hipparion sp., the hornless rhinoceros Aceratherium incisivum, the large pig Microstonyx sp., the primitive small ruminant Hispanomeryx sp., and several species of undetermined bovid and cervid (Morales et al., 2000). In view of the size of Par. ogygia, it is probable that the most likely prey were juvenile individuals of Hipparion and Microstonyx, and perhaps the adults of cervids and bovids. Mastodonts, rhinos and the adult individuals of equids and pigs would be too large to be a target for this sabre-toothed cat, whereas Hispanomeryx would be too small. The equid from Batallones-1 is close to the size of extant zebra, so probably only juveniles and sub-adults would be within the prey range of Par. ogygia. These equids are considered to have been open country dwellers (Alberdi & Bonadonna, 1990; Bernor et al., 1990; Forsten, 1991), and with Batallones-1 being probably a wooded area the relative abundance of Hipparion in the vicinity would have been low and encounters with Par. ogygia rare. The weight of the large pig Microstonyx has been estimated at 300 kg (Alcalá, 1994). Like the extant Suinae, it would probably live in small groups that moved through the woodlands, with the young being actively defended against any predator (Nowak & Paradiso, 1983). Thus, in view of the size of an adult Microstonyx, the risk of trying to snatch a piglet would usually be too high for Par. ogygia.

The weigh of Cervidae and Bovidae from Batallones-1 cannot be estimated, because there is not enough material for determination even to the genus level. The weight range of extant cervids is between 7 (genus Pudu) and 825 kg (Alces alces) (Nowak & Paradiso, 1983), but the more common cervids present in the Vallesian faunas of the Iberian Peninsula were Amphiprion anocerus and Euproct dircranocerus (Azanza, 1989; Azanza et al., 1997), about the size of an extant fallow deer Dama dama or between 40 and 100 kg (Nowak & Paradiso, 1983). For the bovids, four species are known from that period in the Iberian Peninsula: Protrago-
cerus chantrei, Austroportax latifrons, Miostragocerus pannonicus and Tragoportax gaudryi (Alcalá, Morales & Soria, 1990). All these species fall in about the same size range, with weight estimates varying between 46 and 72 kg (Alcalá, 1994). At these sizes, the cervids and bovids of Batallones-1 would be natural prey for Par. ogygia.

The body size of Hispanomeryx would be within the lower part of the range of the extant hornless ruminant Moschus, which weighs between 7 and 17 kg (Nowak & Paradiso, 1983), although given the special adaptations of Par. ogygia for the canine shear-bite (Salesa et al., 2005), it is probable that Par. ogygia ignored such small prey. Extant felids kill small animals by biting on the nape or directly on the skull, using their rounded-section canines (Gonyea, 1976b; Akersten, 1985; Turner & Antón, 1997), but if any sabre-toothed cat tried to do this they would have risked breaking the laterally flattened upper canines. For this reason, it is more probable that they developed some behavioural mechanism to minimize that risk, such as ignoring prey below a given size. It is likely that miacirodontines developed this ethological trait early in their evolution, and so narrowed their prey size range in comparison with that of felines, which hunt both large and small animals. This high specialization has been pointed out as one of the possible reasons for the gradual decline and final extinction of the sabre-toothed cats in the Pleistocene (Turner & Antón, 1997, 1999; Turner, 1999). For this reason, Par. ogygia probably hunted animals within the upper part of the prey range of a similar-sized pantherine, but the kill is likely to have been achieved in a faster and safer way than in the latter, making the hunt more efficient. The development of this strategy was probably the key reason for the sabre-toothed cats becoming the dominant predators in the land mammal faunas from the Late Miocene to Late Pleistocene.

**Conclusions**

The coexistence of two species of large cats in the fossil sample of Batallones-1, Par. ogygia and M. aphanistus, is used to infer a wooded habitat for this Late Vallesian fossil locality from Spain. There are other factors that support this interpretation, such as the high diversity of felids, with four species, or the presence in the fauna of the genus Martes, whose extant species are associated with forested environments, and a large community of browsing herbivores.

The structure of the population of Par. ogygia found in Batallones-1, and the inferred sexual dimorphism of this species, suggest a solitary pattern of behaviour with a high level of tolerance between the resident adult males, resembling extant pantherines such as jaguars or pumas and differing from leopards, which exhibit a lower level of tolerance between males. The sample of Par. ogygia trapped in Batallones-1 clearly corresponds to that fraction of young adults that are looking for a territory, a stage when they would be more easily attracted to carrion than would resident adults. The absence of cubs indicates that the hunting behaviour of Par. ogygia was very similar to extant solitary pantherines such as jaguars or leopards, in which cubs and young remain
hidden while the mother hunts. If Par. ogygia had developed any kind of social system, cubs and adults would have remained together most of the time, and thus there would be a greater number of cubs trapped in Batallones-1.

This primitive sabre-toothed cat developed strong forelimbs and a huge pollex, which would have led to reducing the time of prey subduing and the risk of injury during the hunt rather than enabling it to kill significantly larger prey than extant pantherines of similar body size (Salesa et al., 2005). Thus, the habitual prey of Par. ogygia would have been within the size range of that taken by an extant pantherine, such as cervids and bovids, present also in the Batallones-1 sample. Nevertheless, the elongated and laterally flattened upper canines of Par. ogygia were probably associated with a behavioural avoidance of smaller prey, hunting of which would have enhanced the risk of bone contact and the consequent breakage of the upper canines. This specialization, absent in felines, would have led to a narrower prey range and could have been one of the main causes of the eventual extinctions of the sabre-toothed cats.

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References


