First evidence of pathology in the forelimb of the Late Miocene saber-toothed felid *Promegantereon ogygia* (Machairodontinae, Smilodontini)

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Running title: Pathological fossil radius of *Promegantereon*

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ABSTRACT

We examine the first evidence of pathology in the forelimb of the primitive saber-toothed felid *Promegantereon ogygia*, observed in a radius from the late Miocene (Vallesian, MN 10) site of La Roma 2 (Teruel, Spain). This fossil is the first evidence of a member of the Machairodontinae in this locality, and the first fossil of this species found in the Miocene basin of Teruel. The radius shows an exostosis shaped as a rough and wide bony crest probably caused by the lesion and posterior ossification of part of the tendon of the muscle abductor pollicis longus, an important extensor and abductor of the thumb. The lesion was probably due to a tearing or to high levels of exertion experienced by this muscle over a relatively long time, a general type of lesion also observed in other vertebrate fossils. With saber-toothed felids using their thumbs to immobilize prey during the hunt, the studied lesion probably affected in a significant manner the predatory abilities of the animal, causing at least a decrease in its hunting success rate.

Key words: Paleopathology; Anatomy; Felidae; Forelimb; Machairodontinae; Miocene
INTRODUCTION

The site of La Roma 2 (Late Miocene, Late Vallesian, MN10) is in the northern area of the Teruel Basin, between the small villages of Peralejos and Alfambra (Teruel, Spain). Its fossil-bearing level of grey clay marls is interpreted within the context of a marginal lacustrine environment that experienced episodic flooding events (Alcalá 1994; Pesquero and Alcalá, 2008; Pesquero et al., 2011). The faunal list includes several species of mammalian herbivores, such as the tridactyl equid Hipparion laromae Pesquero, Alberdi and Alcalá, 2006, the suid Microstonyx major (Gervais, 1848-1852), the bovids Tragoportax gaudryi (Kretzoi, 1941) and Aragoral madejar Alcalá and Morales, 1997, the hornless ruminant Micromeryx soriae Sánchez et al., 2009, the rhinocerotids Alicornops alfambrensis (Cerdeño and Alcalá, 1989), Aceratherium incisivum Kaup, 1832a, and Lartetotherium schleiermacheri (Kaup, 1832a), one species of Proboscidea indet., and two species of Hyaenidae, Hyaenictitherium sp., and Lycyaena chaeretis (Gaudry, 1862); the latter considered to be responsible for the accumulation of hundreds of coprolites (Alcalá et al., 1989-1990; Alcalá, 1994; Cerdeño and Alcalá, 1989; van der Made et al., 1992; Alcalá, 1994; Alcalá and Morales, 1997; Sánchez et al., 2009; Pesquero et al., 2011). The pollen contained in these coprolites suggests a mixture of habitats around the site, with relatively dense woodlands beside less vegetated areas with a high percentage of herbaceous plants, developed under a temperate climate (Pesquero et al., 2010).

The primitive saber-toothed (Machairodontine) felid Promegantereon ogygia is known from a few Late Miocene European localities, such as Eppelsheim (Germany, MN 9) and Crevillente-2 (Spain, MN 11) (Kaup, 1832b; Montoya, 1994; Salesa et al., 2010b). However, it is best known from the Cerro de los Batallones fossil sites, in central Spain, which have yielded almost complete skeletons of several individuals mainly from two
localities, Batallones-1 and Batallones-3, besides a rich community of Vallesian (MN 10) Carnivora (Morales et al., 2000, 2004; Salesa, 2002; Antón et al., 2004a; Abella, 2011; Peigné et al., 2005, 2008; Salesa et al., 2005, 2006, 2008, 2010a, 2010b, 2012; Siliceo et al., 2011; Valenciano et al., 2012). Because some species of saber-toothed felids were strongly built animals, it was suggested that the whole group specialized in taking relatively larger prey than those of extant pantherins (Gonyea, 1976a; Emerson and Radinsky, 1980; Akersten, 1985; Rawn-Schatzinger, 1992; Turner and Antón, 1997), something that can only have been possible in the case of the later, large and highly specialized machairodonts such as *Smilodon* or *Homotherium*. In the case of the puma-sized *P. ogygia*, the strong forelimbs and other machairodont features suggest that the origin of the machairodont adaptations was related to the advantage of reducing the time employed in prey immobilization, rather than to changes in prey size (Salesa et al., 2005, 2006, 2010a). Thus, this primitive species had already developed the machairodont killing technique, which is thought to have involved a well-aimed bite to the throat of an immobilized prey, so as to damage blood vessels and trachea and thus produce a rapid death (Antón and Galobart, 1999; Antón et al., 2004a, 2005). Once the prey was subdued, the saber-toothed cat used its long and laterally flattened upper canines to cut its throat by way of a head-depression movement in which the mandible served as an anchor (Akersten, 1985; Antón et al., 2004b; Turner and Antón, 1997).

The radius from La Roma 2 exhibits a few differences to the homologous pieces of *P. ogygia* from both Batallones-1 and Batallones-3, among them the proportions of the proximal epiphysis, narrower in La Roma 2, and the orientation of this proximal part, which is clearly medially inclined in comparison with the radii from the Batallones sites. Nevertheless, given the exostosis observed in the fossil from Teruel, the described differences are likely to be directly related to this pathology. Several pathologies related to high tensions in the forelimb are known in the huge sample of *Smilodon fatalis* from Rancho La Brea (Merriam and Stock,
1932; Drexler and Zappe, 1956; Shaw, 1992; Mestel, 1993) but none have been described for primitive saber-toothed felids such as *P. ogygia*. The only previously described pathology for this species is an abnormally healed fracture of the four metatarsals in an individual from Batallones-1 (Salesa et al., 2006) Thus, the radius from La Roma 2 constitutes the second pathological observation in this species.

MATERIALS AND METHODS

The fossil of *P. ogygia* analyzed in this study, a right radius catalogued as RO-4635, comes from the Spanish Late Vallesian (Late Miocene, MN 10) site of La Roma 2 (Alfambra, Teruel), and it is housed in the Fundación Conjunto Paleontológico de Teruel-Dinópolis & Museo Aragonés de Paleontología (Teruel, Spain). It was compared with the large sample of radii of this species from the Spanish Late Miocene sites of Batallones-1 (46 specimens) and Batallones-3 (6 specimens), housed at the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain). This huge collection of radii includes specimens belonging to both adult and sub-adult individuals, and although some of them are partially broken, most of the specimens are complete and in a good state of preservation. Thus, it was possible to discern the degree of variability in the anatomical features of the radius in *P. ogygia*, as well as the actual anatomy of a hypothetical non-pathological radius, something essential in order to tackle any biomechanical inference.

The anatomical descriptions follow the terminology used by Barone (2010) and the Nomina Anatomica Veterinaria (2005).

RESULTS

Anatomy of the radius of *Promegantereon ogygia* from La Roma 2
As described by Salesa et al. (2010b), the radius of *P. ogygia* resembles that of a pantherin felid both in general proportions and detailed morphology, suggesting similarity in function. The radius from La Roma 2 is slightly larger that the largest specimens from Batallones-1 and Batallones-3 (Fig. 1). The proximal epiphysis is concave, elliptical, its plane being strongly medially inclined, much more so than in the radii from the Batallones sites; this feature is very evident, but it could be due to the pathology seen in the distal part, its functional implication being uncertain. The medial border of the proximal epiphysis is clearly projected from the diaphysis, whereas the lateral one is just slightly inclined medially. The radial tuberosity for the muscle biceps brachii is large, elliptical, proximo-distally elongated and with a ridged lateral margin; the size of this structure is relatively larger than that of most of the specimens from Batallones. The diaphysis is relatively smooth, cranio-caudally compressed, with the distal part slightly curved caudally. On its medial border, developed along its distal half there is a rough scar, distally projected, for the attachment of the muscle pronator teres; this scar seems to be related to radius size when looking at the Batallones sample, in which the largest specimens have a similarly developed scar. On the proximal half of the lateral border of the diaphysis there is another rough scar for the attachment of the radial head of the muscle flexor digitorum profundus. In the middle of the caudal face of the diaphysis there is a round, slightly projected tuberosity interpreted as the attachment area for the deep antebrachial ligament. This is a highly variable structure within the Batallones sample, where it varies from a series of longitudinal scars to a marked rough tuberosity. Distally to this structure there is a smooth surface for the insertion of the muscle pronator quadratus. On the cranial face of the diaphysis a smooth ridge for the muscle supinator is observed, developed from the proximo-lateral margin to the disto-medial. Just distally to this surface, a large structure, interpreted as the ossification of part of the tendon of the muscle...
abductor pollicis longus, is observed (Fig. 2). A similar structure has been observed, although less developed, in human radii (Galtés and Morera, 2007) and in those of dogs (Hittmair et al., 2012), supporting our interpretation. The structure grows from the lateral border, in a disto-medial direction, and it is strongly projected cranially. Both lateral and medial margins of the pathological structure show a kind of groove that probably accommodated the tendons of the extensor muscles that run distally to attach onto the digits of the manus (Fig. 2). The distal epiphysis of the radius shows a large radial styloid process, and proximally to this, a very rough, medially projected bony sheet for the attachment of the muscle brachioradialis. The lateral facet for articulation with the ulna is broken. On the cranial face of the distal epiphysis there is a large cranial tubercle.

DISCUSSION

Pathological Interpretation

The isolated nature of the described pathology in the radius from La Roma 2 discards its origin as a degenerative or congenital lesion. On the contrary, the described exostosis indicates that a process of bone remodeling was developed after some kind of lesion that affected the muscle abductor pollicis longus or at least its tendon (Fig. 3), producing an inflammation, and possibly causing forelimb lameness. This has been described in dogs under the name of syndrome of stenosing tenosynovitis of the abductor pollicis longus, a lesion typically caused by repetitive motions related to quick turns, stops and jumping over obstacles (Morgan and Volvekamp, 2004; Hittmair et al., 2012). In humans this lesion is known as de Quervain’s disease, reportedly caused by repetitive movements of the wrist or overuse of the thumb (Chatterjee, 1992; Diwaker and Stothard, 1995). In our fossil, the lesion could be
caused by a stress injury or repetitive overexertion of the muscle. Comparable injuries may occasionally result in an avulsion with fracture, as observed in other fossil bones (Shaw, 1992; McCarthy and Fressia, 1998; McWhinney et al., 2001). The periosteal mass and spur observed in the radius from La Roma 2 would then represent the reparative process after the lesion (Shaw, 1992; McWhinney et al., 2001).

**Functional discussion**

The muscle extensor carpi obliquus, although developed as a muscular mass having a single distal tendon, is interpreted by Barone (2010) as the fusion of the muscular masses of the abductor digiti I longus (=abductor pollicis longus) and extensor digiti I brevis (=extensor pollicis brevis), two muscles that have independent distal tendons in primates (Kimura and Takai, 1970; Michilsens et al., 2009; Oishi et al., 2009). Nevertheless, most of the authors recognize a single muscle abductor digiti I longus in Carnivora with the denomination of muscle abductor pollicis longus (Evans, 1993; Fisher et al., 2009; Julik et al., 2012) and for that reason we use the latter name here. This muscle, very developed in felids (Barone, 1967; Julik et al., 2012), originates on a wide area including the cranio-lateral margin of the proximal epiphyses of both radius and ulna (Fig. 3); it runs under the muscles extensor digitorum communis and extensor digitorum lateralis, curving medio-distally over the tendons of the cranial radial muscles; it attaches by a short and wide tendon onto the proximal border of the first metacarpal (Barone, 1967, 2010; Vollmerhaus and Roos, 2001). The muscle abductor pollicis longus is an important extensor and abductor of the thumb (Evans, 1993; Barone, 2010), and thus it plays an important role in the hunting activity of felids, which use their grasping capacities for subduing prey before applying a bite on the throat, muzzle or nape of the victim (Gonyea, 1976b, 1978; Akersten, 1985; Turner and Antón, 1997). This was
even more important in saber-toothed felids, which due to the fragility of their elongated and laterally flattened upper canines had to immobilize their prey completely before biting on its throat, thus avoiding both contact with bone and lateral tensions, which could cause the breakage of the canines (Akersten, 1985; Antón et al., 2004b; Biknevicius and van Valkenburgh, 1996; Salesa et al., 2005, 2006, 2010a; Turner and Antón, 1997). Thus, one of the most remarkable features of the saber-toothed forelimb is the presence of a relatively large metacarpal I and distal phalanx of thumb when compared to similarly sized felines, a character also related to a relatively higher grasping strength (Gonyea, 1978; Salesa et al., 2010a; Turner and Antón, 1997). This character is already present in the most primitive members of Machairodontinae, such as *Pseudaelurus quadridentatus* and *Promegantereon ogygia* (Peigné, 2012; Salesa et al., 2010a) indicating the strong connection between elongated and flattened upper canines and the development of mechanisms avoiding their breakage.

The presence of the described pathology on the radius from La Roma 2 is unusual, as this or similar structures are unknown within the huge sample of radii from Batallones-1 and Batallones-3. In any case, apart from the described exostosis and a slight medial inclination of its proximal epiphysis, the radius has an overall “normal” aspect, which probably indicates that the injury was not serious enough to cause the complete crippling of the animal. As it has been described in *Smilodon fatalis* from Rancho La Brea (Shaw, 1992) when these lesions occur in chronically re-injured areas, the exostosis become quite extensive and massive, which is not the case of the specimen from La Roma 2. At the very least, however, the studied pathology would have hampered the ability of this individual for grasping with the right forepaw, an action involved in both subduing prey and climbing. Thus, the animal was not only affected in its hunting capacities, with a probable critical decrease in its hunting success rate, but also in its avoidance behavior of other, larger carnivorans, such as the sympatric...
tiger-sized *Machairodus aphanistus* (Salesa et al., 2006). It remains unknown whether the individual healed completely or died before the pathology became more extensive, at least until more fossils of this individual are found at La Roma 2.
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FIGURE LEGENDS

Fig. 1. Comparison between selected radii of *Promegantereon ogygia*; **A—C**, RO-4635 right radius from La Roma 2 (Teruel, Spain) in **A**, cranial; **B**, medial; **C**, lateral views; **D**, BAT-1’05 D8-80, right radius from Batallones-1 (Madrid, Spain) in cranial view; **E**, BAT-3’11 2282, left radius from Batallones-3 (Madrid, Spain) in cranial view (showed reversed). The arrow indicates the described exostosis affecting the muscle abductor pollicis longus in the radius from La Roma 2.

Fig. 2. Detailed view of the exostosis of the radius RO-4635 from La Roma 2 (Teruel, Spain); **A**, cranial; **B**, medial; **C**, lateral views.

Fig. 3. Cranial view of the radius RO-4635 from La Roma 2 (Teruel, Spain) with reconstructed muscle abductor pollicis longus (**apl**), its tendon (**tapl**), its attachment on the proximal phalanx of thumb (**ppt**), and the discussed exostosis (**ex**); the unpreserved elements of the forelimb are shown in soft line (Artwork by M. Antón).
Fig. 1. Comparison between selected radii of Promegantereon ogygia; A—C, RO-4635 right radius from La Roma 2 (Teruel, Spain) in A, cranial; B, medial; C, lateral views; D, BAT-1’05 D8-80, right radius from Batallones-1 (Madrid, Spain) in cranial view; E, BAT-3’11 2282, left radius from Batallones-3 (Madrid, Spain) in cranial view (showed reversed). The arrow indicates the described exostosis affecting the muscle abductor pollicis longus in the radius from La Roma 2.

173x165mm (600 x 600 DPI)
Fig. 2. Detailed view of the exostosis of the radius RO-4635 from La Roma 2 (Teruel, Spain); A, cranial; B, medial; C, lateral views.
131x93mm (300 x 300 DPI)
Fig. 3. Cranial view of the radius RO-4635 from La Roma 2 (Teruel, Spain) with reconstructed muscle abductor pollicis longus (apl), its tendon (tapl), its attachment on the proximal phalanx of thumb (ppt), and the discussed exostosis (ex); the unpreserved elements of the forelimb are shown in soft line (Artwork by M. Antón).

221x545mm (600 x 600 DPI)