

# On the Socio-Sexual Behaviour of the Extinct Ursid *Indarctos arctoides*: An Approach Based on Its Baculum Size and Morphology

Juan Abella<sup>1,2\*</sup>, Alberto Valenciano<sup>3,4</sup>, Alejandro Pérez-Ramos<sup>5</sup>, Plinio Montoya<sup>6</sup>, Jorge Morales<sup>2</sup>

**1** Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona. Edifici ICP, Campus de la UAB s/n, Barcelona, Spain, **2** Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain, **3** Departamento de Geología Sedimentaria y Cambio Medioambiental. Instituto de Geociencias (CSIC, UCM), Madrid, Spain, **4** Departamento de Paleontología, Facultad de Ciencias Geológicas UCM, Madrid, Spain, **5** Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, Paterna, Spain, **6** Departament de Geologia, Àrea de Paleontologia, Universitat de València, Burjassot, Spain

## Abstract

The fossil bacula, or *os penis*, constitutes a rare subject of study due to its scarcity in the fossil record. In the present paper we describe five bacula attributed to the bear *Indarctos arctoides* Depéret, 1895 from the Batallones-3 site (Madrid Basin, Spain). Both the length and morphology of this fossil bacula enabled us to make interpretative approaches to a series of ecological and ethological characters of this bear. Thus, we suggest that *I. arctoides* could have had prolonged periods of intromission and/or maintenance of intromission during the post-ejaculatory intervals, a multi-male mating system and large home range sizes and/or lower population density. Its size might also have helped females to choose from among the available males.

**Citation:** Abella J, Valenciano A, Pérez-Ramos A, Montoya P, Morales J (2013) On the Socio-Sexual Behaviour of the Extinct Ursid *Indarctos arctoides*: An Approach Based on Its Baculum Size and Morphology. PLoS ONE 8(9): e73711. doi:10.1371/journal.pone.0073711

**Editor:** David Carrier, University of Utah, United States of America

**Received:** March 13, 2013; **Accepted:** July 27, 2013; **Published:** September 18, 2013

**Copyright:** © 2013 Abella et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Funding:** This study was supported by the Spanish Ministerio de Economía y Competitividad (research project CGL2011-25754 and CGL2011-28681) and the research group BSCH-UCM910607. AV was supported by a JAE-Predoc 2011 (CSIC program "Junta para la ampliación de estudios"), co-funded by the European Social Fund. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

\* E-mail: juan.abella@icp.cat

## Introduction

Batallones-3 is one of the nine Late Miocene (Late Vallesian) fossil vertebrate localities of the fossiliferous area of Cerro de los Batallones (Madrid Basin, Spain) [1,2,3,4,5]. Together with the lower levels of Batallones-1 and 2, it is considered to have acted as a natural trap, where carnivorans entered these pseudokarstic cavities and were trapped there [3,6,7,8,9]. In the sample recovered, almost 98% of the fossil mammal remains identified from Batallones-3 belong to carnivorans. Among the fossil species we found remains of the primitive bear *Indarctos arctoides* Déperet, 1895 with a total of 1690 bone elements, belonging to a minimum number of 16 individuals [6]. With several complete or nearly complete skeletons, including skulls, mandibles, vertebrae, scapulae, pelvis, limb bones and even the bacula, this sample is by far the most complete one of this species and probably of the genus.

The baculum or *os penis* is a non-appendicular bone found in the glans tissue, dorsal to the urethra, with its proximal end abutting the distal end of the *corpus cavernosum* [10,11,12] of members of five orders of mammals (specifically, some carnivorans, insectivorans, rodents, bats, and primates) [13,14,15]. The baculum has three developmentally distinct parts: a proximal portion derived from cartilage, a central portion derived from membranous bone, and a distal portion made up of non-lamellar bone. The proximal and central portions fuse and begin to ossify within five days of birth, but the distal portion does not ossify until puberty [16,17,18,19].

Few papers have described the baculum of fossil species, and they have all been merely descriptive and have only compared it with the baculum of extant species [20,21,22].

## Description of the Baculum of *Indarctos arctoides* Déperet, 1895

The studied sample from Batallones-3 consists of five bacula or *os penis*, four of which belong to grown adults and the other one to a sub-adult or young adult, matching quite well with the previous sex determination of the sample from the site, 4–6 of which were males [6].

The baculum of *Indarctos arctoides* (Figure 1H and Supplementary Videos: Video S1–S5) is a slightly sigmoidal elongated bone. Its base (proximal part) is curved dorsally while the apex (distal part) is curved ventrally. It has a triangular section along its length, except at both ends, where the base is oval and the apex is sub-rectangular. It does not have a marked urethral groove, the ventral area therefore being flat except at the apex, where it has a small groove, and the distal zone, which appears somewhat concave. However, it has two longitudinal grooves on its dorsal part, which run along most of the surface from the rough area of the base to close to the apex. The proximal region has a very rough surface, which occupies most of the lateral side of the bone, while in the ventral area a small ridge-shaped structure is developed ventrally. On the dorsal side, the roughened area is not as obvious and is limited to the lateral areas, while the central surface is smooth along the dorsal part of the bone. The apex is completely



**Figure 1. Modified from Didier 1950 and Davis 1964.** Baculum in lateral view of: A *Helarctos malayanus*; B *Ursus thibetanus*; C *Tremarctos ornatus*; D *Ursus americanus*; E *Melursus ursinus*; F *Ursus arctos*; G *Ursus maritimus*; H *Indarctos arctoides*; I Ventral view of the Baculum of *Ailuropoda melanoleuca*; J Dorsal view of the baculum of *Ailuropoda melanoleuca*. doi:10.1371/journal.pone.0073711.g001

preserved in three of the five bacula and its morphology is virtually identical in all three. It consists of a ventrally curved structure with a triangular-shaped longitudinal notch, which occupies the ventral part corresponding to the distal-most part of the urethral groove. Its lateral surface is quite flat, somewhat concave, especially in the specimen BAT-3'10.1062. Its dorsal area is rather oval and with a porous texture. Its central part is slightly sunken forming a slight concavity in BAT-3'10.1062, whereas in BAT-3'08.869 it is fairly flat. In the apical-most zone of the baculum, all these surfaces converge in a sub-rectangular tip that is projected ventrally.

The mean length of the bone is 225.26 mm, the shortest one measuring 191.9 mm and the longest 237.7 mm. However, the shortest baculum was associated *in situ* with a sub-adult skeleton, and we therefore consider it to be an undeveloped baculum, which would have been larger with age [15]. The ontogeny of the baculum has been studied in bears and mustelids [15,23,24]. The length of the baculum in polar bears, for example, almost reaches

its full length before the bear is 10 years of age, and its growth is most rapid between the first and second years of its life [15].

Adult mean length can therefore be established at 233.6 mm. (without taking into account the length of the shorter baculum).

### Comparison

The bacula of most extant species of Ursidae species are relatively long for their body size. However, the baculum of the giant panda (*Ailuropoda melanoleuca*), is the only reduced *os penis* of the family [25,26,27].

The bacula of *Indarctos* from Batallones-3 has been compared to the homologues of all of the extant bear species (Figure 1A–J). Its morphology matches perfectly with that of this family, with an almost straight overall lateral outline, a longitudinal groove on each side of its dorsal region and a distal end slightly curved ventrally. It is easily distinguished from the canid and amphicyonid bacula by the absence of a well-developed urethral groove [21]

**Table 1.** Measurements of the baculum length (in mm) and approximate worldwide average male body size (in Kg) for the eight extant species of Ursidae and the estimated average size calculated for the males of *Indarctos arctoides* from Batallone-3.

Species	Baculum length	Male body size	BL/BS index
<i>Helarctos malayanus</i>	52	60	0,87
<i>Melursus ursinus</i>	151	110	1,37
<i>Ailuropoda melanoleuca</i>	20	120	0,17
<i>Tremarctos Ornatus</i>	104,7	127,5	0,82
<i>Ursus americanus</i>	137	140	0,98
<i>Ursus thibetanus</i>	118,25	150	0,79
<i>Ursus arctos</i>	133,8	253	0,53
<b><i>Indarctos arctoides</i></b>	<b>233,6</b>	<b>265,74</b>	<b>0,88</b>
<i>Ursus maritimus</i>	186,5	500	0,37

The index "baculum length divided by body size" has also been calculated to compare relative sizes. The body size values have been obtained from references [26,53–64].

doi:10.1371/journal.pone.0073711.t001

and from the mustelid bacula by the shape of the lateral outline [22].

When compared to the bacula of the extant bears at a more detailed scale, the os penis of *Indarctos arctoides* is relatively more elongated than that of the other species. Its shape is slightly more sigmoidal and its distal tip is relatively better developed; only the baculum of *Helarctos malayanus* has developed an ossified tip at its distal end (Figure 1A). Furthermore, the apical anatomy has been observed to be intra-specifically diverse in the polar bears, and its apical growth continues into late life in at least some species [15,28,29,30,31,32,33]. In other groups, such as canidae, the tip is cartilaginous and not completely ossified throughout its life cycle [34].

Although *Indarctos* is now considered to be a member of the subfamily Ailuropodinae [35] its baculum is one of the longest os penis, relative to its body size, to be found in the bear family. *Indarctos arctoides* must have been a large bear similar in size to the European brown bear; it had a mean estimated body mass of 202.16 kg; it presented evident sexual dimorphism with a body mass estimated at 265.74 kg for males and 137.30 kg for females [6]. Their bacula could also be expected to be large.

Thus, only taking into account the lengths of the adult bacula from Batallones-3, mean sample length exceeds the largest size of the homologues of both polar and grizzly bears, the largest extant species of Ursidae [15,25,36]. Bacular length in adult polar bears, for example, was reported as 168 mm, 168–194 mm and 151–222 mm by Didier ([25];  $n = 1$ ), Lønø ([36];  $n = 15$ ), and Dyck *et al.* ([15];  $n = 871$ ) respectively.

## Discussion

The relatively long baculum of *Indarctos arctoides* might have been related to several socio-sexual behaviour patterns of this species, such as a prolonged, single-intromission copulatory pattern and/or maintenance of intromission during the post-ejaculatory interval [37,38,39,40].

It has been suggested that larger bacula, together with a more complex genital morphology are observed in species with multi-male mating systems [37,38,41,42], while smaller ones are more

usual in polygynous species, suggesting that multi-male mating may be the female's strategy to evaluate mate choice when mate availability is limited or sequential [43]. There is empirical evidence of post-copulatory selection occurs in species that adopt multi-male matings and in which multiple paternity is observed (e.g. *Ursus americanus* [44]). Furthermore, the baculum may also play a more significant role in monogamous (such as in Canidae) and multi-male mating systems (such as in Mustelidae; [45]) as an indicator of genetic quality in males [46], and is used by females as a way of assessing male quality when mate encounters are disjunct temporally and spatially [47].

Another factor likely to vary among mammalian groups is the degree to which the site of ejaculate deposition in the female tract is critical to fertilization success [48,49], longer bacula could ensure that sperm and/or copulatory plugs are optimally positioned in the female reproductive tract (the position of the latter being critical with regard to maximizing sperm transport) [50] or could facilitate the removal of previously deposited plugs [51,52]. Several studies have also led some researchers to link longer bacula with delayed implantation/embryonic diapause and multi-male mating systems, as a response to environments with acute unfavourable seasons [42].

When comparing baculum length to body size in the Ursidae, it can be observed that larger species such as *Ursus maritimus* and *U. arctos* have relatively shorter bacula than smaller species such as *U. americanus*, *Helarctos malayanus* or *U. thibetanus* (Table 1). It seems that the os penis is relatively shorter in the more sexually dimorphic species, which have a more polygynous mating system and whose competition for the females is intense [65,66,67]. However, in *Indarctos arctoides*, despite being a large-sized and highly dimorphic species [6] the length of the baculum is relatively long compared to other bear species of similar size, probably due to the fact that this feature is likely sexually selected.

The information on the carnivoran association of Batallones-3 is yet to be fully completed, since only several species have been studied [3,6,7,8,9]. However, there are many papers on the association of Batallones-1, which can be used to make comparisons among the carnivorans that these two sites have in common [68,69,70,71,72,73,74,75,76,77,78]. According to the abovementioned papers, some kind of ecological segregations may have enabled all these carnivorans to reduce the frequency of encounters. Furthermore, in Batallones-3, these ecological segregations must have been more acute, reducing the frequency of encounters among many large-sized predators, since there are at least four large species weighing over 100 kg, two more than in Batallones-1 [6,7].

## Inferences Regarding the Socio-sexual Behaviour of *Indarctos arctoides*

The length of the baculum could be related to several sexual, social and ecological behaviour patterns. However, these are either ecological and/or ethological characteristics of this fossil species and are therefore not possible to verify.

Therefore, and based on the features of the baculum of *Indarctos*, we suggest that this species may have had:

1. A prolonged period of intromission and/or maintenance of intromission during the post-ejaculatory interval. The baculum may have acted as a physical support during the penetration and served to maintain vaginal opening during the ejaculatory interval. In extant species a positive relation between the length of the bacula and the time and maintenance of intromission has been described.

- Multi-male mating system. Possibly, the home range of several males overlapped with those of one or more females, enabling fecundation to be more successful in these infrequent sexual encounters.
- The evident sexual dimorphism present in the body size of *Indarctos arctoides* may also have been a characteristic to be considered. Contrary to the relatively shorter baculum found in bear species presenting strong sexual dimorphism, the baculum of *I. arctoides* was comparatively long. This feature, could have caused the females to exhibit preferential mating among the available males, as seen in extant species.
- Indarctos arctoides* could have had large home range sizes and/or a lower population density. In this specific case, the presence of patched forests separated by more open environments may have caused the populations of this bear to be less, thus giving rise to fewer encounters among the individuals.

## Supporting Information

**Video S1 Video of the baculum BAT-3'08.869.**  
(AVI)

**Video S2 Video of the baculum BAT-3'10.428.**

## References

- Morales J, Capitán J, Calvo JP, Sesé C (1992) Nuevo yacimiento de vertebrados del Mioceno Superior al Sur de Madrid (Cerro Batallones, Torrejón de Velasco). *Geogaceta* 12: 77–80.
- Morales J, Alcalá L, Álvarez-Sierra MA, Antón M, Azanza B, et al. (2004) Paleontología del sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid. *Geogaceta* 35: 139–142.
- Morales J, Pozo M, Silva PG, Domingo MS, López-Antoñanzas R, et al. (2008) El sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid: estado actual y perspectivas. In: Esteve J, Meléndez G, editors. *Palaeontologica Nova*, (SEPAZ 8). 41–117.
- Pozo M, Calvo JP, Silva P, Morales J, Peláez-Campomanes P, et al. (2004) Geología del sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid. *Geogaceta* 35: 143–146.
- Calvo JP, Pozo M, Silva P, Morales J (2013) Pattern of sedimentary infilling of fossil mammal traps formed in pseudokarst at Cerro de los Batallones, Madrid Basin, Central Spain. *Sedimentology*, doi: 10.1111/sed.12048.
- Abella J (2011) *Indarctos arctoides* Depéret, 1895 (Carnivora, Mammalia) del yacimiento vallesiano de Batallones 3 (Cuenca de Madrid). Ph.D. Thesis. Universidad Autónoma de Madrid. Madrid, Spain.
- Abella J, Domingo MS, Valenciano A, Montoya P, Morales J (2011) La asociación de Carnívoros de Batallones 3, Mioceno Superior del Cerro de los Batallones, Cuenca de Madrid. In: Marigó J, Pérez de los Ríos M, Minwer-Barakat R, De Miguel D, Bolet, A, editors. *Paleontología i Evolució, Memòria especial 5*, (Institut Català de Paleontologia Miquel Crusafont, Sabadell). 21–24.
- Salesa MJ, Antón M, Morales J, Peigné S (2012) Systematics and phylogeny of the small felines (Carnivora, Felidae) from the Late Miocene of Europe: a new species of Felinae from the Vallesian of Batallones (MN10, Madrid, Spain). *J Syst Palaeontol* 10: 87–102.
- Valenciano A, Abella J, Sanisidro O, Álvarez-Sierra MA, Morales J (2012) A complete skull and mandible of *Eomellivora piveteaui* Ozansoy, 1965 (Carnivora, Mammalia) from Batallones-3 (MN10), Upper Miocene (Madrid, Spain). In: Royo-Torres R, Gascó F, Alcalá L, editors. *Fundamental! 20*. 10th Meeting of the European Association of Vertebrate Paleontologists, (Teruel, Spain). 267–270.
- Vilmann H, Vilmann A (1979) Os penis of the rat. II. Morphology of the mature bone. *Anat Anz* 146: 483–493.
- Williams-Ashman HG (1990) Enigmatic features of penile development and functions. *Persp Biol Med* 33: 335–374.
- Kelly DA (2000) Anatomy of the Baculum–Corpus Cavemosum Interface in the Norway rat (*Rattus norvegicus*), and Implications for Force Transfer During Copulation. *J Morphol* 244: 69–77.
- Burt WH (1960) Bacula of North American mammals. *Misc Publs Mus Zool Univ Mich* No.113: 1–75.
- Romer AS (1970) The vertebrate body. W.B. Saunders, Philadelphia. 601 p.
- Dyck MG, Bourgeois JM, Miller EH (2004) Growth and variation in the bacula of polar bears (*Ursus maritimus*) in the Canadian Arctic. *J Zool* 264: 105–110.
- Ruth EB (1934) The os priapi: a study in bone development. *Anat Rec* 60: 231–249.
- Murakami R, Mizuno T (1984) Histogenesis of the os penis and os clitoridis in rats. *Dev Growth Differ* 26: 419–426.
- Murakami R, Mizuno T (1986) Proximal-distal sequence of development of the skeletal tissues in the penis of rat and the inductive effect of epithelium. *J Embryol Exp Morphol* 92: 133–143.
- Williams-Ashman HG, Reddi AH (1991) Differentiation of mesenchymal tissues during phallic morphogenesis with emphasis on the os penis: roles of androgens and other regulatory agents. *J Steroid Biochem Molec Biol* 39: 873–881.
- Matthew WD (1907) A Lower Miocene Fauna from South Dakota. *Bull Am Mus Nat Hist* 23: 169–219.
- Olsen SJ (1959) The baculum of the Miocene carnivore *Amphicyon*. *J Paleontol* 33: 449–450.
- Harrison JA (1982) The baculum of *Plesioyulo* (Carnivora: Mustelidae). *J Paleontology* 56: 1266–1273.
- Albayrak I, Ozen AS, Kitchener AC (2008) A Contribution to the Age-Class Determination of *Martes foina* Erxleben, 1777 from Turkey (Mammalia: Carnivora). *Turk J Zool* 32: 147–153.
- Schwery O, Köhnemann BA, Michler FU, Brinkmann W (2011) Morphometrical characterisation of a raccoon population from Müritz National Park (Germany) by means of the Os baculum. *Beiträge zur Jagd- und Wildforschung* 36: 605–617.
- Didier R (1950) Étude systématique de l'os pénien des mammifères. *Mammalia* 14: 78–94.
- Davis DD (1964) The Giant Panda. A morphological Study of Evolutionary Mechanism. *Fieldiana Zoology Memoirs* 3: 1–339.
- Ewer RF (1973) The carnivores. Cornell University Press, Ithaca, New York. 494 p.
- Mohr E (1963) Os penis und Os clitoridis der Pinnipedia. *Z Säugetierk* 28: 19–37.
- Scheffer VB, Kenyon KW (1963) Baculum size in pinnipeds. *Z Säugetierk* 28: 38–41.
- Morejohn GV (1975) A phylogeny of otariid seals based on morphology of the baculum. *Rapp P v Réun Cons perm Int Explor Mer* 169: 49–56.
- Miller EH, Pitcher KW, Loughlin TR (2000) Bacula size, growth, and allometry in the largest extant Otariid, the Stellar sea lion (*Eumetopias jubatus*). *J Mammal* 81: 134–144.
- Oosthuizen WH, Miller EH (2000) Bacula and testicular growth and allometry in the Cape fur seal *Arctocephalus p. pusillus* (Ostariidae). *Mar Mamm Sci* 16: 124–140.
- Miller EH (2002) Baculum. In: Perrin WF, Thewissen, HGM, editors. *Encyclopedia of marine mammals*. Academic Press, San Diego. 55–58.
- Evans HE, Delahunta A (2010) Miller's Guide to the Dissection of the Dog. WB Saunders Company, Philadelphia. 303 p.
- Abella J, Alba DM, Robles JM, Valenciano A, Rotgers C, et al. (2012) *Kretzoiarctos* gen. nov., the oldest member of the giant panda clade. *PLoS ONE* 7(11): e48985.
- Lono O (1970) The polar bear (*Ursus maritimus* Phipps) in the Svalbard area. *Nor Polarinst Skr* 149: 1–103.
- Dixon AF (1987) Baculum length and copulatory behavior in Primates. *Am J Primatol* 13: 51–60.
- Dixon AF (1995) Baculum length and copulatory behaviour in carnivores and pinnipeds (Grand Order Ferae). *J Zool* 235: 67–76.

(AVI)

**Video S3 Video of the baculum BAT-3'10.1062.**

(AVI)

**Video S4 Video of the baculum BAT-3'12.815.**

(AVI)

**Video S5 Video of the baculum BAT-3'12.2298.**

(AVI)

## Acknowledgments

We would like to thank Stéphane Peigné and Céline Bens for kindly send us the photographs of the baculum of *Ursus thibetanus* from the collections of the Muséum national d'Histoire naturelle. We also thank the two anonymous reviewers for providing helpful comments and suggestions on previous versions of this article. A.V. was supported by a JAE-Predoc 2011 (CSIC program “Junta para la ampliación de estudios”).

## Author Contributions

Conceived and designed the experiments: JA PM JM. Performed the experiments: JA AV APR. Analyzed the data: JA AV. Contributed reagents/materials/analysis tools: JA AV APR. Wrote the paper: JA JM.

39. Hosken DJ, Jones KE, Chipperfield K, Dixon AF (2001) Is the bat os penis sexually selected? *Behav Ecol Sociobiol* 50: 450–460.
40. Dixon AF, Nyholt J, Anderson M (2004) A positive relationship between baculum length and prolonged intromission patterns in mammals. *Acta Zool Sin* 50: 490–503.
41. Verrell PA (1992) Primate penile morphologies and social systems: further evidence for an association. *Folia Primatol* 59: 114–120.
42. Ferguson SH, Larivière S (2004) Are long penis bones an adaptation to high latitude snowy environments? *Oikos* 105: 255–267.
43. Perez-Barberia FJ, Gordon IJ, Pagel M (2002) The origins of sexual dimorphism in body size in ungulates. *Evol* 56: 1276–1285.
44. Schenk A, Kovacs KM (1995) Multiple mating between black bears revealed by DNA fingerprinting. *Anim Behav* 50: 1483–1490.
45. Baryshnikov GF, Bininda-Emonds RP, Abramov AV (2003) Morphological variability and evolution of the baculum (os penis) in mustelidae (Carnivora). *J Mammal* 84: 673–690.
46. Larivière S, Ferguson SH (2002) On the evolution of the mammalian baculum: vaginal friction, prolonged intromission or induced ovulation? *Mammal Rev* 32: 283–294.
47. Larivière S, Ferguson SH (2003) Evolution of induced ovulation in North American carnivores. *J Mammal* 84: 937–947.
48. Baumgardner DJ, Hartung TG, Sawrey DK, Webster DG, Dewsbury DA (1982) Muroid copulatory plugs and female reproductive tracts: a comparative investigation. *J Mammal* 63: 110–117.
49. Patterson B, Thaler C (1982) The mammalian baculum: hypotheses on the nature of bacular variability. *J Mammal* 63: 1–15.
50. Toner JP, Attas AI, Adler NT (1987) Transcervical sperm transport in the rat: the roles of pre-ejaculatory behavior and copulatory plug fit. *Physiology & Behav* 39: 371–375.
51. O'Hanlon JK, Sachs BD (1986) Fertility of mating in rats (*Rattus norvegicus*): contributions of androgen-dependent morphology and actions of the penis. *J Comp Psychol* 100: 178–187.
52. Raam SA (2007) Sexual Selection and Genital Evolution in Mammals: A Phylogenetic Analysis of Baculum Length. *Am Nat* 169: 360–369.
53. Prater SH (1965) The book of Indian animals. Bombay Natural History Society, Bombay, 324 p.
54. Mondolfi E (1971) El oso frontino. *Defensa de la Naturaleza* 1: 31–35.
55. Dathe H (1975) Malayan sun bears. In: Grzimek B, editors. Grzimek's animal life encyclopedia, Van Nostrand Reinhold Company, New York. 141–142.
56. Peyton B (1980) Ecology, distribution, and food habits of spectacled bears (*Tremarctos ornatus*) in Perú. *J Mammal* 61: 639–652.
57. DeMaster DP, Stirling I (1981) *Ursus maritimus*. Polar bear. *Mammalian Species* 145: 1–7.
58. LeFranc MN, Moss MB, Patnode KA, Sugg WC (1987) Grizzly bear compendium. US Fish and Wildlife Service, Missoula, Montana.
59. Blanchard BM (1987) Size and growth patterns of the Yellowstone grizzly bear. *Int. Conf Bear Res and Manage* 7: 99–107.
60. Kingsley MCS, Nagy JA, Reynolds HV (1988) Growth in length and weight of northern brown bears: differences between sexes and populations. *Can J Zool* 66: 981–986.
61. Stirling I (1993) The living bears. In: Sterling I, editor. Bears: Majestic Creatures of the Wild, Rodale Press, Emmaus. 36–49.
62. Laycock G (1997) Wilderness Legend Grizzly. Northword wildlife series. NorthWord Press, Minocqua, Wisconsin. 143 p.
63. Servheen C, Herrero S, Peyton B (1999) Status Survey of the bears of the World and Global Conservation Action Plan. IUCN, Gland, Switzerland. 309 p.
64. Amstrup SC (2003) Polar bear, *Ursus maritimus*. In: Feldhamer GA, Thompson BC, Chapman JA, editors. Wild Mammals of North America: biology, management, and conservation. John Hopkins University Press, Baltimore. 587–610.
65. Mitani JC, Gros-Louis J, Richards A (1996) Sexual dimorphism, the operational sex ratio, and the intensity of male competition among polygynous primates. *American Naturalist* 147: 966–980.
66. Lindenfors P (2002) Sexually antagonistic selection on primate size. *J of Evol Biol* 15: 595–607.
67. Lindenfors P, Tullberg B, Biuw M (2002) Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behav Ecol and Sociobiol* 52: 188–193.
68. Antón M, Salesa MJ, Pastor JF, Sánchez IM, Fraile S, et al. (2004) Implications of the mastoid anatomy of larger extant felids for the evolution and predatory behaviour of sabretoothed cats (Mammalia, Carnivora, Felidae). *Zool J Linn Soc* 140: 207–221.
69. Antón M, Salesa MJ, Morales J, Turner A (2004) First known complete skulls of the scimitar-toothed cat *Machairodus aphanistus* (felidae, carnivora) from the spanish late miocene site of Batallones-1. *J Vertebr Paleontol* 24: 957–969.
70. Salesa MJ, Antón M, Turner A, Morales J (2005) Aspects of the functional morphology in the cranial and cervical skeleton of the sabre-toothed cat *Paramachairodus ogygia* (Kaup, 1832) (Felidae, Machairodontinae) from the Late Miocene of Spain: implications for the origins of the machairodont killing bite. *Zool J Linn Soc* 144: 363–377.
71. Antón M, Salesa MJ, Pastor JF, Peigné S, Morales J (2006) Implications of the functional anatomy of the hand and forearm of *Ailurus fulgens* (Carnivora, Ailuridae) for the evolution of the 'false-thumb' in pandas. *J Anat* 209: 757–764.
72. Salesa MJ, Antón M, Turner A, Morales J (2006) Inferred behaviour and ecology of the primitive sabre-toothed cat *Paramachairodus ogygia* (Felidae, Machairodontinae) from the Late Miocene of Spain. *J Zool* 268: 243–254.
73. Salesa MJ, Antón M, Peigné S, Morales J (2006) Evidence of a false thumb in a fossil carnivore clarifies the evolution of pandas. *Proc Natl Acad Sci USA* 103: 379–382.
74. Peigné S, Salesa MJ, Antón M, Morales J (2008) A new Amphicyonine (Carnivora: Amphicyonidae) from the Upper Miocene of Batallones-1, Madrid, Spain. *Palaentology* 51: 943–965.
75. Salesa MJ, Antón M, Peigné S, Morales J (2008) Functional anatomy and biomechanics of the postcranial skeleton of *Simocyon batalleri* (Viret, 1929) (Carnivora, Ailuridae) from the Late Miocene of Spain. *Zool J Linn Soc* 152: 593–621.
76. Salesa MJ, Antón M, Turner A, Morales J (2010) Functional anatomy of the forelimb in Promegantereon\* ogygia (Felidae, Machairodontinae, Smilodontini) from the late miocene of Spain and the origins of the sabre-toothed felid model. *J Anat* 216: 381–396.
77. Silicco G, Salesa MJ, Antón M, Pastor JF, Morales J (2011) Comparative anatomy of the frontal sinuses in the primitive sabre-toothed felid Promegantereon ogygia (Felidae, Machairodontinae) and similarly sized extant felines. *Estudios geológicos* 67: 277–290.
78. Domingo MS, Domingo L, Badgley C, Sanisidro O, Morales J (2013) Resource partitioning among top predators in a Miocene food web. *Proc R Soc B*: 280 20122138.