

On the Original Author and Year of Description of the Extinct Hyaenid *Pachycrocuta brevirostris*

Authors: Alba, David M., Vinuesa, Víctor, and Madurell-Malapeira, Joan

Source: Acta Palaeontologica Polonica, 60(3) : 573-576

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.00017.2013>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



On the original author and year of description of the extinct hyaenid *Pachycrocuta brevirostris*

DAVID M. ALBA, VÍCTOR VINUESA, and JOAN MADURELL-MALAPEIRA

The International Code of Zoological Nomenclature recommends providing the author and year of original description of any taxon, when first mentioned in a publication, which is useful for both taxonomic and nomenclatural reasons. Here we show that the authorship of the extinct hyaenid taxon *Hyaena brevirostris*, type species of the genus *Pachycrocuta*, has been incorrectly attributed to “Aymard, 1846” for more than a century on the basis of a publication that never existed. Our bibliographic research indicates that the first published work in which the name was employed—Gervais’ (1848–1852) *Zoologie et Paléontologie françaises*, the part dealing with carnivorans being issued in 1850—fulfils the criteria of availability. Given that Gervais did not attribute the description to Aymard, but merely employed the latter’s name in reference to a museum label/record (which does not constitute a valid indication), the correct name with authorship for this taxon is *Pachycrocuta brevirostris* (Gervais, 1850).

Introduction

The giant short-faced hyena, *Pachycrocuta brevirostris*—type species of genus *Pachycrocuta* Kretzoi, 1938—is a widespread extinct hyaenid, customarily classified in the bone-cracking ecomorphotype due to the possession of craniodental adaptations for breaking bones (Turner et al. 2008; Palmqvist et al. 2011) and further characterized by shortened distal limb segments—suggesting a body type well suited to dismembering and carrying large portions of ungulate carcasses (Palmqvist et al. 2011). With an estimated body mass of more than 110 kg, *P. brevirostris* is likely to have been the largest hyena that ever existed (Turner and Antón 1996; Palmqvist et al. 2011). It is first recorded in the Pliocene of both East Africa and Asia, ca. 3.0 Ma onwards (Werdelin and Solounias 1991; Werdelin and Lewis 2005; Palmqvist et al. 2011). In Europe its earliest appearance is not documented until later, ca. 2.0 Ma (Napoleone et al. 2003). The record of *P. brevirostris* extends to the Plio-Pleistocene boundary (2.6 Ma) in East Africa and until the middle Pleistocene (ca. 0.4 Ma) in Asia (Palmqvist et al. 2011), whereas in Europe it is a relatively common element among early Pleistocene faunal assemblages until 0.83 Ma (Turner and Antón 1996; Turner et al. 2008; Madurell-Malapeira et al. 2010).

Here we show that, for more than a century, the authorship of *P. brevirostris* has been incorrectly attributed to “Aymard, 1846” on the basis of a publication that never existed. In a strict

sense, the original author and year of description of a taxon do not form part of its name. However, the International Code of Zoological Nomenclature (ICZN 1999) regulates their use (e.g., Article 51.3), further specifying that the citation of the authorship is optional, “although customary and often advisable” (Article 51.1). The Code therefore recommends reporting such data at least once in each work dealing with a taxon (Recommendation 51A), because this is important for distinguishing homonyms and identifying names that are not in their original combinations. Moreover, an accurate report of the year of publication of any taxon is also of utmost significance for applying the Principle of Priority (Article 23), which rules the use of synonyms and homonyms. Most journals dealing with systematic paleontology therefore strictly adhere to the recommendation to report original author and date, and in some cases—such as in the *Acta Palaeontologica Polonica* and the *Journal of Vertebrate Paleontology*—they further recommend or even require the corresponding citation to be included in the list of references. Accessing the original descriptions for taxa described in the 18th or 19th Century has been a problem for many scientists, especially those working in small institutions far from the large libraries of long established museums or universities. Such difficulties have, however, largely been ameliorated during the last decade, thanks to the free access provided by digital repositories to old literature that is nowadays in the public domain. The usefulness of such repositories—as well as the need to always check the original description—is illustrated here by the case of *P. brevirostris*.

Nomenclatural history

The purported original description.—The genus *Pachycrocuta* was erected by Kretzoi (1938: 118), who designated *Pachycrocuta brevirostris* as its type species (“genoholotypus”). Kretzoi (1938) attributed the authorship of the species to Aymard (without specifying the year of description or providing the citation in the list of references), as previously done by other authors (e.g., Gervais 1848–1852; Pictet 1853; Pomel 1853; Gaudry 1862; Weithofer 1889; Boule 1893; Soergel 1936). Subsequent authors similarly attributed the authorship of this binomen to Aymard, either without noting the year of publication (Brongersma 1937; Ficcarelli and Torre 1970; Pons-Moyà 1982; Turner and Antón 1996; Kretzoi and Kretzoi 2000; Palmqvist et al. 2011) or, more commonly, attributing it to 1846 (Kurtén

1956, 1972; Howell and Petter 1980; Julià and Villalta 1984; Kurtén and Garevski 1989; Werdelin and Solounias 1991; Werdelin 1999; Stefen and Rensberger 1999; Turner 2001; Moullé et al. 2006; Arribas and Garrido 2008; Turner et al. 2008; Madurell-Malapeira et al. 2009; Werdelin and Peigné 2010)—just to report a selection of the most representative citations. Some of the above-mentioned authors (Howell and Petter 1980; Julià and Villalta 1984; Werdelin and Solounias 1991; Werdelin 1999; Arribas and Garrido 2008; Turner et al. 2008; Madurell-Malapeira et al. 2009) further reported the complete bibliographic reference that ought presumably to correspond to the original description of *Hyaena brevirostris*.

According to Howell and Petter (1980), *Hyaena brevirostris* was described by Aymard in a paper entitled “Communication sur le gisement de Sainzelles” [Communication on the site of Sainzelles], on pages 153–155 of volume 13 of *Annales de la Société d’Agriculture, Sciences, Arts et Commerce du Puy* in 1846. The remaining above-mentioned authors provided the same reference, or a similar one, with some variants regarding the name of the journal (Werdelin 1999; Arribas and Garrido 2008) and/or volume number (12 instead of 13; Turner et al. 2008; Madurell-Malapeira et al. 2009). When we tried to check this citation, we discovered that it did not exist in either volume 12 (supposedly published in 1846, but see below) or in volume 13 (apparently published in 1849)—or in any previous volume of that journal.

Aymard published a paper on an extinct artiodactyl (*Entelodon magnus*) in volume 12 of the above-mentioned journal, corresponding to the years 1842–1846, and dated to the year 1846. However, throughout the text there are several references to the year 1847, and as noted in Sherborn’s (1924: 2160, 3825) *Index Animalium*—see also the searchable online version of Sherborn’s compendium (<http://www.sil.si.edu/digitalcollections/indexanimalium/>), made available by the Smithsonian Institution Libraries—the accompanying wrapper indicates that it was not published until 1848. Besides *E. magnus* Aymard, 1848, this author further described other taxa (mainly in footnotes), such as the genus *Bothriodon* Aymard, 1848. In one of the footnotes, Aymard (1848: 259) referred to a previous report by him to the society on the fauna from Sainzelle—the type locality of *P. brevirostris*, spelled “Sainzelles” from Boule (1893) onwards—but did not describe or employ the nomen *Hyaena brevirostris*. In volume 13, Aymard did not report on the fauna from this site or name the species. Merely, in the proceedings of the *Société d’Agriculture, Sciences, Arts et Commerce du Puy* for the years 1847–1848, published in that volume, de Brive (1849) referred to a “notice” by Aymard on the circumstances that may have caused the accumulation of fossil bones at Sainzelles, although the binomen *Hyaena brevirostris* was not employed.

To our knowledge, the earliest paper by Aymard in which the name of the taxon was used is Aymard (1854a), published in volume 18 of the same journal—corresponding to the proceedings of year 1853, but with the cover date 1854. The title of this contribution, however, does not match that referred to the year 1846 by recent authors: “Acquisitions d’ossements fossiles trouvés à Sainzelle, commune de Polignac; aperçu descriptif sur ce curieux

gisement et détermination des espèces fossiles qu’il renferme” [Acquisitions of fossil bones found at Sainzelle, town of Polignac; descriptive overview of this curious site and determination of the fossil species that it contains]. Galobart et al. (2003) are the only authors we found to refer the description of the species to 1853, whereas Savage and Russell (1983: 348, 356, 376) referred the authorship to “Aymard, 1854?”—the question mark presumably indicating uncertainties in the year of the description. Although neither of these authors provided the bibliographic reference, they were most likely referring to Aymard (1854a), because Aymard (1854b) did not mention this taxon. However, Aymard (1854a) did not provide any description or indication for the name of the taxon, so that *Hyaena brevirostris* Aymard, 1854a does not fulfill the criteria of nomenclatural availability for names published before 1931 (ICZN, 1999: article 12)—which require the publication of the name “accompanied by a description or a definition ... or by an indication” (Article 12.1).

Finally, according to Gaudry (1862) and Weithofer (1889), the binomen *Hyaena brevirostris* was erected somewhat later by Aymard, in the 22nd session of the *Congrès scientifique de France* of year 1855, published the following year (Anonymous 1856: 271). Aymard certainly mentioned the name of the species in the proceedings of that meeting (Anonymous 1856: 271, our translation from the French original): “a species, erected on the basis of an almost complete cranium (*hyaena* [sic!] *brevirostris*. Aym.) has been confirmed by the concordant observations by Mr. Gervais and Mr. Pictet”. According to the Code, if a name is made available in a report of a meeting, the person responsible for the name (and not the secretary or reporter) is the author of the name (Article 50.2). However, like his previous publication (Aymard 1854a), such a short note does not fulfill the criteria of availability, so that *Hyaena brevirostris* Aymard, 1856 must also be considered a nomen nudum.

The true original description.—The erroneous attribution of the taxon’s authorship to “Aymard, 1846” by most recent authors probably stems from an incorrect interpretation of Boule’s (1893) introductory lines in the first detailed description of the holotype cranium of *Hyaena brevirostris*. According to Boule (1893: 85, our translation from the French original), Aymard discovered the cranium ca. 1845 in the surroundings of Le Puy, being “deposited in the Musée du Puy and registered with the name *Hyaena brevirostris*, Aym.” Boule (1893) noted that Aymard reported on this cranium in several notes, but the only bibliographic citation provided by him was volume 12 (attributed by him to year 1846) of the above-mentioned annals—which, as already explained, were published in 1848 and do not include any mention of this taxon. Boule’s (1893) citation of Aymard was reproduced (also without title) by Kurtén (1972: 120) as the original description of this species, although the latter author was cautious enough as to state that he had not actually seen it (“not seen; fide Boule, 1893”). At some point, however, an erroneous title became associated with the author Aymard and the year 1846, which was subsequently copied from one author to another. To our knowledge, Howell and Petter (1980) were the first authors to publish the incorrect reference for the original description of the species. These

authors might have mixed the year provided by Kurtén (1972) while referring in fact to the contribution by Aymard (1854a). The latter begins without a title—which is however stated in the summary provided two pages before in the same journal—and this might explain why either Howell and Petter (1980), or some other previous authors, eventually provided a different generic title for Aymard's contribution. In any case, the significance of Boule's (1893: 86) comment on the fact that paleontologist Paul Gervais had studied the cranium and “was able to give a short diagnosis in the first edition of his *Paléontologie française*” remained unnoticed by most researchers, probably because of the fact that Gervais (1848–1849), Pictet (1853), and Boule (1893) all attributed the taxon to Aymard.

The attribution of the authorship to Aymard notwithstanding, when referring to the taxon Pictet (1853: 223) only provided a reference to Gervais' book. Although succinct, the description provided by the latter (Gervais 1848–1852: 122, our translation from the French original) is enough to confer availability to the name *Hyaena brevirostris*: “Fossil from Sainzelle, town of Polignac, near of Le Puy. I have studied in the museum of this town two hyena cranial fragments from Sainzelle: they indicate a size at least equal to that of *H. spelaea*; but the upper jaw has a transverse molar very similar to that of *H. fusca* and *vulgaris*. The lower carnassial is 0.030 m long, and the upper one 0.045 m long; the vertical plane of the lower jaw is very elevated.” The fact that Gervais (1848–1852) attributed the authorship to Aymard is irrelevant for nomenclatural purposes, since the author of a name is the person who first published it in a way that satisfies the criteria of availability (Article 50.1). Only “if it is clear from the contents that some person other than an author of the work is alone responsible for both the name [...] and for satisfying the criteria of availability other than actual publication, then that other person is the author of the name or act. If the identity of that other person is not explicit in the work itself, then the author is deemed to be the person who published the work.” (Article 50.1.1). Gervais (1848–1852: 122) first employed the name without referring it to any author, and only in the following line he stated “*H. brev.*, Aymard, *Mus. du Puy.*”—i.e., he referred to a museum label or record, instead of providing the bibliographic citation, as he customarily did for other taxa. This fact indicates that Gervais was providing a description based on his own observations—instead of referring to any previous publication by Aymard—and that he merely referred the authorship to the latter on the basis of a museum label or record. The reference to a geological horizon, or specimen label cannot be considered an indication in the sense of the Code (Article 12.3), and given that there is no explicit statement in Gervais (1848–1852) attributing the description to Aymard, in application of the above-mentioned Article 50.1.1, the authorship of *Hyaena brevirostris* must be attributed to Gervais.

Gervais' (1848–1852) book was issued in several parts during successive years. In those cases, the Code dictates that the date of publication of each part is to be separately determined (Article 21.5). According to Wagner (1851), the part dealing with carnivorans was published in 1850, and hence the nomen *Hyaena brevirostris* must be attributed to “Gervais, 1850.” This is further

confirmed by Sherborn's (1924: 885) *Index Animalium*, in which this author (and not Aymard) is credited for the authorship of the taxon. To our knowledge, Sherborn's (1924) brief statement is the only previous instance in which the authorship of *Hyaena brevirostris* has been correctly attributed to Gervais instead of Aymard.

Conclusions

Although it is not mandatory, the International Code of Zoological Nomenclature (ICZN, 1999) recommends providing the author and year of original description of any taxon, when first mentioned in a publication. This is useful for several reasons, both taxonomic (i.e., information retrieval) and nomenclatural (e.g., determination of priority of synonyms and homonyms). Here we show that the authorship of the extinct hyaenid *Pachycrocuta brevirostris* has been incorrectly attributed to “Aymard, 1846” for more than a century, on the basis of a publication that never existed. Our bibliographic research indicates that the first publication in which the name is employed—*Zoologie et Paléontologie françaises* by Gervais (1848–1852; the part dealing with carnivorans being published in 1850)—fulfils the criteria of availability. Subsequent use of the same binomen by Aymard (1854a) does not fulfill the criteria of availability and, in any case, it would not have priority over Gervais (1848–1852). Given that the latter author did not attribute the description to Aymard, but merely employed the latter's name in reference to a museum label/record (which does not constitute a valid indication), the correct name with authorship for this taxon must be *Pachycrocuta brevirostris* (Gervais, 1850).

Acknowledgements.—This work would not have been possible without the bibliographic resources provided by various digital repositories of old scientific literature—Biodiversity Heritage Library (<http://www.biodiversitylibrary.org/>), Internet Archive (<http://archive.org/>), Gallica—Bibliothèque nationale de France (<http://gallica.bnf.fr/>), and HathiTrust Digital Library (<http://www.hathitrust.org/>)—to which we are most grateful. We also thank Stephanie Maiolino (Stony Brook University, USA) for help with the literature, as well as Lars Werdelin (Swedish Museum of Natural History, Stockholm, Sweden) and an anonymous reviewer for helpful comments on a previous version of this paper. This work has been funded by the Spanish Ministerio de Economía y Competitividad (CGL2011-28681 and RYC-2009-04533 to DMA) as well as the Generalitat de Catalunya (2009 SGR 754 GRC).

References

- Anonymous 1856. La paléontologie de la Haute-Loire offre-t-elle, pour certains époques, des caractères qui la particularisent? In: *Congrès Scientifique de France. Vingt-deuxième Session, Tenue au Puy en Septembre 1955. Tome Premier*, 261–277. Derache, Paris.
- Arribas, A. and Garrido, G. 2008. Hiénidos [*Pachycrocuta brevirostris* (Aymard, 1846) y *Hyaena brunnea* Thunberg, 1820] del yacimiento de Fonelas P-1 (Cuenca de Guadix, Granada). In: A. Arribas (ed.), *Vertebrados del Plioceno Superior Terminal en el Suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas*. Instituto Geológico y Minero de España, Madrid. *Cuadernos del Museo Geominero* 10: 201–230.
- Aymard, A. 1848. Essai monographique sur un nouveau genre de Mammifère fossile trouvé dans la Haute-Loire, et nommé *Entélodon*. *Annales de la Société d'Agriculture Sciences, Arts et Commerce du Puy* 12: 227–268.

- Aymard, M. 1854a. Acquisitions d'ossements fossiles trouvés à Sainzelle, commune de Polignac; aperçu descriptif sur ce curieux gisement et détermination des espèces fossiles qu'il renferme. *Annales de la Société d'Agriculture Sciences, Arts et Commerce du Puy* 18: 51–54.
- Aymard, A. 1854b. Des terrains fossilifères du bassin supérieur de la Loire. *Comptes Rendus des Séances de l'Académie des Sciences Paris* 38: 673–677.
- Boule, M. 1893. Description de l'*Hyaena brevirostris* du Pliocène de Sainzelles près le Puy (Haute-Loire). *Annales des Sciences Naturelles Zoologie et Paléontologie* 15: 85–97.
- Brongersma, L.D. 1937. On fossil remains of a hyaenid from Java. *Zoologische Mededelingen* 20: 186–202.
- Brive, A. de 1849. Compte-rendu des travaux de la Société lu le même jour. *Annales de la Société d'Agriculture Sciences, Arts et Commerce du Puy* 13: 9–36.
- Ficcarelli, G. and Torre, D. 1970. Remarks on the taxonomy of hyaenids. *Palaeontographia Italica* 66: 13–33.
- Galobart, À., Antón, M., and Maroto, J. 2003. Hiénidos y cánidos de los yacimientos de Incarcal (Girona, NE de la Península Ibérica). Una aproximación a la paleobiología del hiénido del Pleistoceno inferior. *Paleontologia i Evolució* 34: 79–98.
- Gaudry, A. 1862. *Animaux Fossiles et Géologie de l'Attique, d'après les Recherches Faites en 1855–56 et 1860*. 474 pp. F. Savy, Paris.
- Gervais, P. 1848–1852. *Zoologie et Paléontologie Françaises. Nouvelles Recherches sur les Animaux Vivants et Fossiles de la France. Tome I. Contenant l'Énumération Méthodique et Descriptive des Espèces ainsi que les Principes de leur Distribution Géographique et Paléontologique*. 271 pp. Arthus Bertrand, Paris.
- Howell, F.C. and Petter, G. 1980. The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae). Their relationships with Miocene icthiheres: *Palhyaena* and *Hyaenicitherium*. *Geobios* 13: 579–623.
- International Commission on Zoological Nomenclature (ICZN) 1999. *International Code of Zoological Nomenclature. Fourth Edition*. 306 pp. The International Trust for Zoological Nomenclature, London.
- Julià, R. and Villalta, J.F. de 1984. El yacimiento de vertebrados del Pleistoceno inferior de Crespià (Girona, NE de la Península Ibérica). *Acta Geològica Hispànica* 19: 129–138.
- Kretzoi, M. 1938. Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfaua. *Annales Musei Nationalis Hungarici* 31: 88–157.
- Kretzoi, M. and Kretzoi, M. 2000. *Index Generum et Subgenerum Mammalium; Pars 137, Section 1*. 433 pp. Backhuys Publishers, Leiden.
- Kurtén, B. 1956. The status and affinities of *Hyaena sinensis* Owen and *Hyaena ultima* Matsumoto. *American Museum Novitates* 1764: 1–48.
- Kurtén, B. 1972. Fossil Hyaenidae from the excavations at Stránská Skála. *Anthropos* 20: 113–120.
- Kurtén, B. and Garevski, R. 1989. Giant hyena, *Hyaena brevirostris* Aymard (Mammalia, Carnivora), from the Middle Pleistocene of Manastirec, Yugoslavia. *Annales Zoologici Fennici* 26: 145–147.
- Madurell-Malapeira, J., Alba, D.M., and Moyà-Solà, S. 2009. Carnivora from the late Early Pleistocene of Cal Guardiola (Terrassa, Vallès-Penedès Basin, Catalonia, Spain). *Journal of Paleontology* 83: 969–974.
- Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., and Berástegui, X. 2010. The Vallparadis section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quaternary Science Reviews* 29: 2972–2982.
- Moullé, P.-E., Lacombat, F., and Echassoux, A. 2006. Apport des grands mammifères de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes, France) à la connaissance du cadre biochronologique de la seconde moitié du Pléistocène inférieur d'Europe. *L'Anthropologie* 110: 837–849.
- Napoleone, G., Albianelli, A., Azzaroli, A., Bertini, A., Magi, M., and Mazzini, M. 2003. Calibration of the Upper Valdarno basin to the Plio-Pleistocene for correlating the Apennine continental sequences. *Il Quaternario* 16: 131–166.
- Palmqvist, P., Martínez-Navarro, B., Pérez-Claros, J.A., Torregrosa, V., Figueirido, B., Jiménez-Arenas, J.M., Espigares, M.P., Ros-Montoya, S., and De Renzi, M. 2011. The giant hyena *Pachycrocuta brevirostris*: Modelling the bone-cracking behavior of an extinct carnivore. *Quaternary International* 243: 61–79.
- Pictet, F.-J. 1853. *Traité de Paléontologie ou Histoire Naturelle des Animaux Fossiles Considérés dans leurs Rapports Zoologiques et Géologiques. Tome Premier. Seconde Édition*. 584 pp. J.-B. Baillièrre, Paris.
- Pomel, A. 1853. *Catalogue Méthodique et Descriptif des Vertébrés Fossiles Découverts dans le Bassin Hydrographique Supérieur de la Loire, et surtout dans la Vallée de son Affluent Principal, l'Allier*. 193 pp. J.-B. Baillièrre, Paris.
- Pons-Moyà, J. 1982. Hyaenidae (Carnivora, Mammalia) del Pleistoceno inferior de Cueva Victoria (Murcia, España). *Endins* 9: 45–48.
- Savage, D.E. and Russell, D.E. 1983. *Mammalian Paleofaunas of the World*. 432 pp. Addison-Wesley Publishing Company, Reading.
- Sherborn, C.D. 1924. Section 2, Pt. 4 (1801–1850), Index Bail.-Byzos. In: *Index Animalium*, 641–943. Trustees of the British Museum, London.
- Soergel, W. 1936. *Hyaena brevirostris* Aymard und *Hyaena* ex aff. *Crocotta* Erxl. aus den Kiesen von Süßenborn. *Zeitschrift der Deutschen Geologischen Gesellschaft* 88: 525–539.
- Stefen, C. and Rensberger, J.M. 1999. The specialized structure of hyaenid enamel: description and development within the lineage—including percrocutids. *Scanning Microscopy* 13: 363–380.
- Turner, A. 2001. Remains of *Pachycrocuta brevirostris* (Mammalia, Hyaenidae) from the Lower Pleistocene site of Untermassfeld near Meiningen. In: H.D. Kahlke and R.D. Kahlke (eds.), *Das Pleistozän von Untermassfeld in Thüringen*, 673–690. Rudolf Harbelt Verlag, Bonn.
- Turner, A. and Antón, M. 1996. The giant hyaena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios* 29: 455–468.
- Turner, A., Antón, M., and Werdelin, L. 2008. Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios* 41: 677–687.
- Wagner, A. 1851. Bericht über die Leistungen in der Naturgeschichte der Säugthiere während des Jahres 1850. *Archiv für Naturgeschichte* 17 (1): 1–32.
- Weithofer, K.A. 1889. Die fossilen Hyänen des Arnthales in Toskana. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 55: 337–357.
- Werdelin, L. 1999. *Pachycrocuta* (hyaenids) from the Pliocene of east Africa. *Paläontologische Zeitschrift* 73: 157–165.
- Werdelin, L. and Lewis, M. 2005. Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. *Zoological Journal of the Linnean Society* 144: 121–144.
- Werdelin, L. and Peigné, S. 2010. Carnivora. In: L. Werdelin and W.J. Sanders (eds.), *Cenozoic Mammals of Africa*, 603–657. University of California Press, Berkeley.
- Werdelin, L. and Solounias, N. 1991. The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata* 30: 1–104.

David M. Alba [david.alba@icp.cat], Institut Català de Paleontologia Miquel Crusafont, ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain; Dipartimento di Scienze della Terra, Università di Torino, Via Valperga Caluso 35, 10125 Torino, Italy.
 Víctor Vinuesa [victor.vinuesa@icp.cat] and Joan Madurell-Malapeira [joan.madurell@icp.cat], Institut Català de Paleontologia Miquel Crusafont, ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

Received 12 August 2013, accepted 6 October 2013, available online 7 November 2013.

Copyright © 2015 D.M. Alba 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.