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Article in *Journal of Mammalian Evolution* · October 2021

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Megantereon adroveri from the Early Pleistocene of Taurida Cave, Crimea, and the European Lineage of Dirk-toothed Cats

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Accepted: 29 September 2021

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Abstract

Recent field surveys performed in the newly-discovered Taurida Cave (Crimea, Russia, Late Villafranchian, 1.8–1.5 Ma) enabled us to unearth dentognathic remains of the dirk-toothed cat *Megantereon*. Here we describe in detail the recovered remains further comparing it anatomically and biometrically with coeval Eurasian and African sites. The performed analysis suggests the inclusion of the Taurida remains in the hypodigm of the Villafranchian European species *Megantereon adroveri*, a medium-sized saber-toothed cat poorly known in Europe as a consequence of the scarcity and fragmentary nature of the known remains. Our results and the putative transitional characters displayed by the Taurida specimen support the idea put forward by previous authors of a continuous European lineage of dirk-toothed cats.

Keywords *Megantereon* · Machairodontinae · Mandibular corpus · Pleistocene · Late Villafranchian · Crimea · Russia

Abbreviations

CFU	Vernadsky Crimean Federal University
H	height
L	length
PIN	Borissiak Paleontological Institute, Russian Academy of Sciences
W	width
ZIN	Zoological Institute, Russian Academy of Sciences
ZMMU	Zoological Museum of the Lomonosov Moscow State University

Introduction

The genus *Megantereon* includes several species of medium-sized saber-toothed cats scarcely recorded, mainly known only on the basis of fragmented and isolated

dentognathic remains, in the Plio-Pleistocene of the Old World and North America (Antón 2013). *Megantereon* was an ambush predator with massive forelimbs that was the size of a jaguar and has been traditionally classified in the tribe Smilodontini (subfamily Machairodontinae), phylogenetically closely related to the American genus *Smilodon* (Antón 2013).

Megantereon probably originated in North America according to the earliest records in the Bone Valley Formation of Florida (ca. 4.5 Ma; Berta and Galiano 1983; Wallace and Hulbert 2013). The earliest record in the Old World comes from the South Turkwel site in Kenya (ca. 3.5 Ma; Werdelin and Lewis 2000); however, unpublished African remains can be referred to 4.4 Ma (Werdelin and Peigné 2010), coeval with the first American records. In turn, the oldest European records can be related with the Early Villafranchian Perrier – Les Etouaires assemblage (ca. 2.8 Ma; Nomade et al. 2014). In Asia, the best sample of *Megantereon* comes from the Middle Villafranchian Longdan site, China (ca. 2.4–2.2 Ma; Qiu et al. 2004) and can be traced until the Middle Pleistocene of Zhoukoudian-1 (Pei 1934). In the latter case, this represents the last record of this genus in the Old World.

The taxonomy and phylogenetic relationships within the different formerly described species of *Megantereon* have been matters of harsh debate in the last four decades; such a debate is probably the consequence of their scarce

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and fragmentary record (Viret 1954; Ficcarelli 1979). Turner (1987) was the one of the first scholars who tried to organize the taxonomy of Old World *Megantereon* remains. According to this author's opinion, all Eurasian and African remains can be accommodated in the species *Megantereon cultridens* (Cuvier, 1824), which is characterized by a high degree of intraspecific variability and sexual dimorphism. On the contrary, Pons-Moyà (1987) and Sardella (1998) included all the known Eurasian specimens in *M. cultridens*, which putatively display several evolutionary convergences with the African *Megantereon whitei*. Then, Qiu et al. (2004), in a monograph of the Longdan fauna, reviewed the Eurasian record of the *Megantereon* genus and concluded that *Megantereon nihowanensis* Teilhard de Chardin and Piveteau, 1930 is the species recorded in the Middle Villafranchian of China (Longdan and Nihewan Loc. 18) and *Megantereon lantianensis* Hu and Qi, 1978 is the species recorded in the Late Villafranchian. Werdelin and Lewis (2000), in their description of the South Turkwel Kenyan carnivore sample, erected the species *Megantereon ekidoit* Werdelin and Lewis, 2000. This species differs from the youngest *M. whitei* in the absence of p3 and the morphology of the mandibular ramus. Taking into account the last morphological features, Werdelin and Lewis (2000) concluded that *M. ekidoit* is the earliest and the most primitive African species. Werdelin and Lewis (2000) also included all the European samples in a phylogenetic lineage composed of two forms, *M. cultridens* and *M. adroveri* (for further discussion see Lewis and Werdelin 2010; Werdelin and Flink 2018). Finally, in a series of publications, Martínez-Navarro and Palmqvist (1995, 1996) and Palmqvist et al. (2007) supported a new hypothesis on the origin and dispersal of *Megantereon*, including all Eurasian Early–Middle Villafranchian forms in *M. cultridens* and all the African ones in *M. whitei*. According to these authors, around ca. 2.0 Ma, *M. whitei* dispersed from Africa to Eurasia and replaced *M. cultridens*, thus remaining the only recorded species until its disappearance.

In this paper, we favor the opinion of Pons-Moyà (1987), Turner (1987), Sardella (1998), Werdelin and Lewis (2000), and Werdelin and Flink (2018) and consider all European forms as members of a phylogenetic lineage composed of two chronospecies: *M. cultridens* and *M. adroveri*.

We describe a well-preserved hemimandible of *Megantereon* recently unearthed from the Taurida Cave in Crimea (Russia) and compare it morphologically and biometrically to remains from coeval Eurasian sites.

Table 1 Measurements of the lower teeth of *Megantereon adroveri* from Taurida Cave (specimen PIN No. 5644/95).

Teeth	L	W	H
i3	7.3	5.7	11.2
c1	10.9	7.2	15.3
p2	8.1	4.7	6.4
p3	13.0	5.3	-
p4	14.8	7.6	-
m1	20.1	9.8	14.5

Age and Geological Setting

The Taurida Cave and its large cave system were rediscovered in 2018 during the construction of the Taurida Highway from Simferopol to Kerch. The karstic system is located on the northern macroslope of the Crimean Mountains, in the interfluvium of the Beshterek and Fundukla rivers (tributaries of the Zuya river, Salgir river basin). A large number of fossil terrestrial vertebrate bones were found in the southern corridor of the cave and in the small side hall of the Hyena Den (see Lopatin et al. 2019 for a synthesis and a complete faunal list). The preliminary results of the first field surveys revealed a diverse faunal assemblage likely corresponding to the Late Villafranchian European biochron (Rook and Martínez-Navarro 2010; Madurell-Malapeira et al. 2014) and the Psekupsian faunal assemblage of Russia. The bone-bearing layers of the Taurida Cave display a chronological range of 1.8–1.5 Ma according to the last published data (Lavrov et al. 2019; Lopatin et al. 2019; Vislobokova et al. 2019, 2020).

Results

Family Felidae Fischer, 1817

Subfamily Machairodontinae Gill, 1872

Megantereon Croizet and Jobert, 1828

Megantereon adroveri Pons-Moyà, 1987

Referred specimen—A partial right mandibular corpus (specimen PIN No. 5644/95) with preserved i3, c1, p2 and m1 and alveoli of i2 and p3–p4.

Measurements—Table 1.

Description—The mandibular corpus is slender and narrow, the ventral edge has a straight ventral profile



Fig. 1 *Megantereon adroveri* mandibular corpus with i3–c1, p2, and m1 from Taurida Cave (specimen PIN No. 5644/95) in **a**, buccal view; **b**, lingual view; and **c**, occlusal view. **d**, detail of p2 and alveolus of p3. Scale bar equals 2 cm in **a–c** and 1 cm in **d**.

behind the symphysis. The symphysis is oriented practically vertically (Fig. 1a). The anterior surface of the symphysis is separated from the buccal corpus surface by a sharpened bone ridge. The mental flange is well defined and expanded ventrally. Three mental foramina are visible (Fig. 1a). The masseteric fossa is triangular, and its anterior margin is located on the line at the middle length of m1 protostylid.

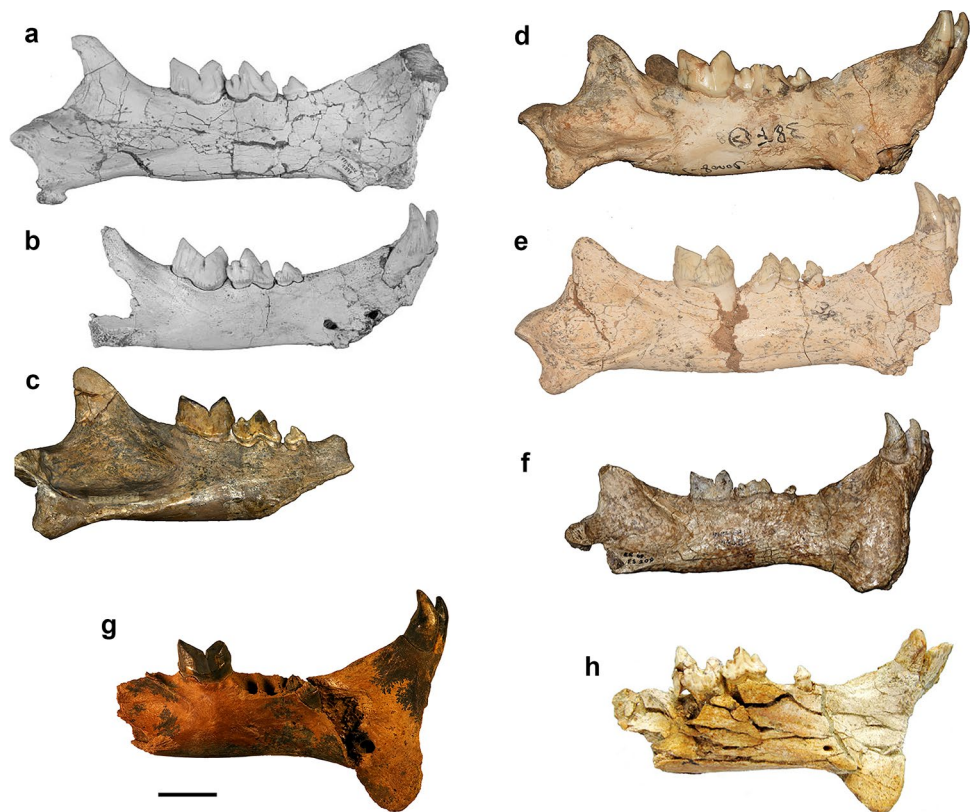
Concerning dentition, the i3 crown is slightly curved distally. There are pronounced lateral and medial ridges and a well-defined lateral basal tubercle. The c1 crown is also curved distally, but in a stronger way as compared to i3. A well-defined medial ridge is visible in c1, with a poorly defined basal tubercle. The c1–p3 diastema is mesiodistally long. In the corpus, an atavistic single-rooted p2 is erupting just buccally to the p3 mesial alveolus (Fig. 1d). The p2 is triangular in occlusal view, displaying a main cusp and two cusplids: a mesial and a distal one. The labial and lingual cingulids are well expressed. The alveoli of a two-rooted p3 and p4 are visible in occlusal view (Fig. 1c). Finally, and concerning the first lower molar, the paraconid is two times mesiodistally longer than the protoconid. The caudal surface of the protoconid forms the cutting ridge (the postprotocristid), at the base of which there is a tiny rudimentary talonid. The parastylid and protostylid form an angle of about 90° in the parasagittal plane (in buccal view). The buccal surface of the tooth is convex, whereas the lingual surface is flat.

Discussion

Comparisons Between the Taurida Specimen and Coeval European *Megantereon* Remains

From our point of view, based only on anatomical characters, we favor the idea that the European records attest to the presence of two different forms that putatively can be included in a single phylogenetic lineage (sensu Lewis and Werdelin 2010). In this scenario, it seems that the earliest European records (e.g., Perrier – Les Etouaires and Saint Vallier; Early and Middle Villafranchian) apparently display more primitive characters, including: a less developed mental flange; two-rooted p3 with strong distal accessory cusplid and distal cingulid; mesiodistally short c1–p3 diastema; few mesially and upright projected c1 and incisors; and a developed and high coronoid process (Fig. 2a–c; Croizet and Jobert 1828; Viret 1954; Ficcarelli 1979; Pons-Moyà 1987; Sardella 1998; Palmqvist et al. 2007; Sardella et al. 2008). Nevertheless, as usually happens, these characters are the most commonly displayed by *M. cultridens*, and several specimens display other features that can be interpreted as derived for the European *Megantereon* lineage or even transitional to the Late Villafranchian forms or simply intraspecific variability. For instance, a few specimens show an incipient diastema between p3 and p4, including specimens from Upper Valdarno, Fonelas P1, Senèze, and

Fig. 2 Pleistocene *Megantereon* mandibular remains from the Old World in right buccal view. European Middle–Late Villafranchian: **a**, mandible of *M. cultridens* from Fonelas P-1 (Spain; FPI-2002-1391); **b**, mandible of *M. cultridens* from Fonelas P-1 (Spain; FPI-2002-5001); **c**, mandible of *M. cultridens* from Upper Valdarno (Italy; IGF-827). Asian Middle–Late Villafranchian: **d** and **e**, mandibles of *M. nihowanensis* from Longdan (China). African late Early Pleistocene: **f**, mandible of *M. whitei* from Koobi Fora Okote Mb. (Kenia; ER793). European Epivillafranchian: **g**, corpus of *M. adroveri* from Taurida (Russia; PIN No. 5644/95); **h**, corpus of *M. adroveri* from Apollonia-1 (Greece; APL-12). Scale bar equals 2 cm



Les Etouaires; others display a small p3 without a distal cingulid and a less developed p3 distal accessory cuspid, such as Fonelas, Upper Valdarno, and Senèze (Fig. 2a–c; Ficarelli 1979; Christiansen and Adolfssen 2007; Palmqvist et al. 2007). The observed variability in the listed characters can be interpreted as a general trend of evolutionary changes, prompted by the effect of mosaic evolution and exacerbated by the scarce paleontological record.

On the other side, Late Villafranchian and Epivillafranchian specimens putatively display more advanced features, such as: a more developed mental flange; mesiodistally long c1–p3 diastema; reduced p3 without accessory cuspid; large p3–p4 diastema; small p4 compared to m1; and c1 and incisors more projected mesially and upright (Fig. 2h). The latter features can be seen in the specimens from Dmanisi (Georgia; ca. 1.8 Ma), Venta Micena (Spain; ca. 1.5 Ma), and Apollonia-1 (Greece; 1.1 Ma) (Fig. 2g–h; Martínez-Navarro and Palmqvist 1995; Vekua 1995; Koufos 2018).

The Taurida specimen shares with the last forms strongly mesially projected c1 and incisors, a more developed and ventrally projected mental flange, a long c1–p3 diastema, and a small p4 alveolus compared with that of m1. However, the Taurida specimen also displays a two-rooted p3 and only an incipient diastema between p3–p4, characters traditionally considered as primitive in the *Megantereon* lineage but that we consider to be variable among samples, as explained by previous authors (Turner 1987; Sardella 1998).

Comparisons of Taurida Specimen with Coeval Asian *Megantereon* Remains

The Asian scenario is more complicated, with several species described that putatively represent a phylogenetic lineage: *M. microta* Zhu et al., 2015 > *M. nihowanensis* > *M. inexpectatus* Teilhard de Chardin, 1939 > *M. lantianensis* (Zhu et al. 2020 and references therein). According to Zhu et al. (2020), an early form of small size included in *M. microta* displays a short diastema, two-rooted p3, poorly developed mental flange, and a moderately developed coronoid process. The later forms, exemplified by Longdan and Saber-tooth Cave specimens, display a single-rooted p3, longer diastema, small coronoid process, and sometimes a tiny diastema between p3–p4 (Fig. 2d–e; Qiu et al. 2004; Zhu et al. 2020). The younger late Early Pleistocene and Middle Pleistocene forms are less common in Asia, only recorded by a single mandible from Lantian and a cranium of *M. inexpectatus* from Zhoukoudian-Loc.1 (Zhu et al. 2020). The Lantian mandible putatively displays more derived character states, with a small and single-rooted p3, a long diastema between c1–p3, and a well-developed p3–p4 diastema (Hu and Qi 1978).

The Taurida specimen apparently displays a more developed and ventrally projected mental flange, more protruding c1 and incisors, and a straighter profile of the corpus than all Chinese specimens (Fig. 2d–e, g).

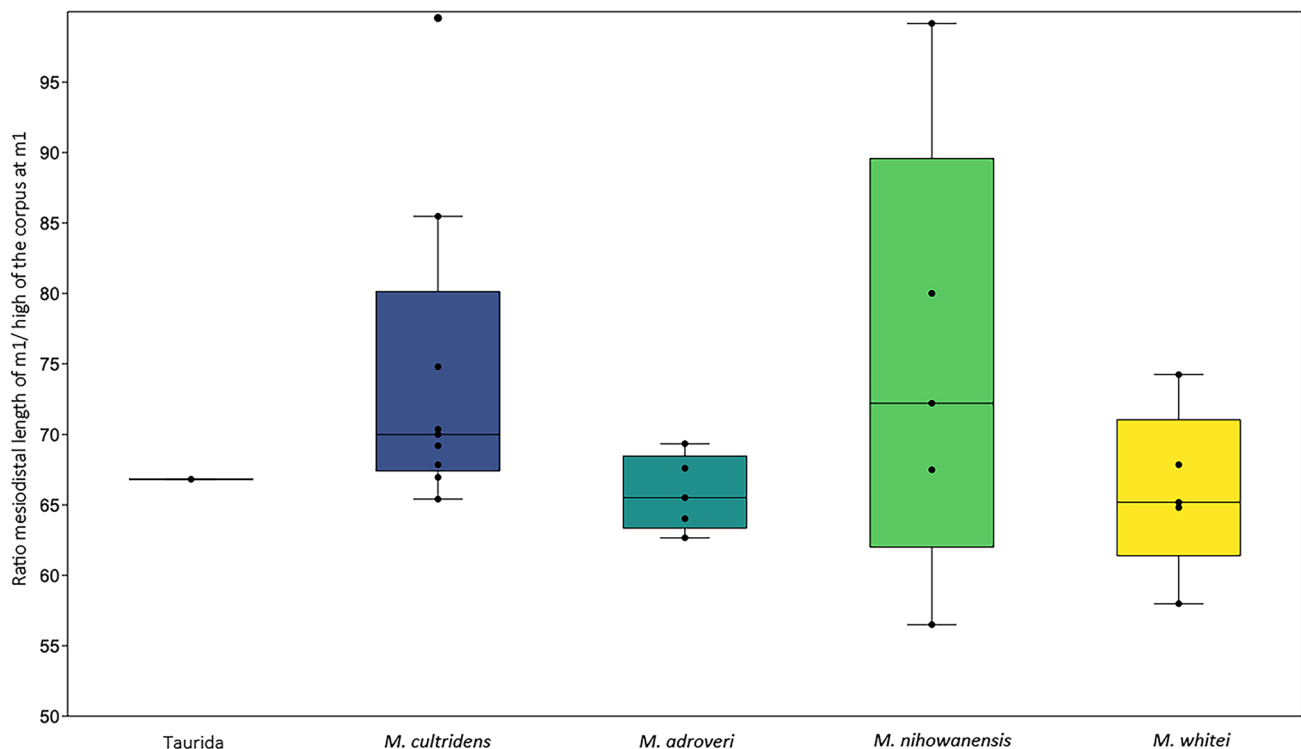


Fig. 3 Boxplots of mesiodistal length of m1 to height of corpus below m1 ratio (%) of Eurasian specimens of the genus *Megantereon*

Comparisons of Taurida Specimen with Coeval African *Megantereon* Remains

As compared with the Taurida specimen, the most complete *Megantereon whitei* specimens (i.e., Koobi Fora Okote Mb and Afar) display a less developed and ventrally projected mental flange and less protruding incisors, which are more primitive features (both ca. 1.8–1.5 Ma; Fig. 2f–h). On the other hand, the Koobi Fora mandible shows a very small p3 (not in the Afar one) and a large p3–p4 diastema compared to the Taurida specimen (Ficcarelli 1979; Lewis and Werdelin 2010). Additionally, *M. whitei* specimens display large lower incisors compared to the Crimean specimen (Fig. 2). This may be related to mosaic (heterochronic) evolution and the specialization of the feeding apparatus (the incisors).

Taxonomic Attribution of Taurida *Megantereon*

The studied specimen displays an atavistic p2, which is not rare in the *Megantereon* fossil record and is also noted in Monte Argentario *Megantereon adroveri* and Sabertooth Cave *Megantereon nihowanensis* (Iurino and Sardella 2014; Zhu et al. 2020). This feature is here interpreted as an atavistic tooth without taxonomic significance, as it is also present in rare occasions in extant *Lynx lynx* and *Panthera pardus* (J. M.-M. pers. observ.).

Taking into account the single and fragmentary nature of the Taurida specimen, a few inferences can be made. The presence of a double-rooted p3 is here interpreted as a putatively primitive character state for the European *Megantereon* lineage, although it is necessary to make such an inference with caution considering the intraspecific variability observed in this lineage (sensu Turner 1987 and Sardella 1998). A well-developed and ventrally projected mental flange, mesiodistal elongated c1–p3 diastema, and the upright and mesially projected canine and incisors are clearly advanced character states in the *Megantereon* lineage that resemble the condition showed by Dmanisi, Argentario, and Apollonia-1 *M. adroveri* (Fig. 2g–h; Vekua 1995; Sardella 1998; Koufos 2018). It is also worth noting the smaller alveolar mesiodistal length of the Taurida p4 compared to m1, a putatively derived character state for European *Megantereon*, as already stated by Martínez-Navarro and Palmqvist (1996; Fig. 2).

Finally, we compared the mandibular robustness (mesiodistal length of m1 / height of the corpus below m1) in all the analyzed specimens (Eurasian and African) with a boxplot (Fig. 3). The results show a quite homogeneous pattern in the *Megantereon* record. Nevertheless, the values of *M. cultridens* are generally higher than *M. adroveri*, with the Taurida specimen in the middle of the variability observed by the two European species. The values for

Asian species appear too wide, from 55 to 98%. In turn, the African fossils have a range similar to but greater than *M. adroveri*, putatively explained by their adaptative convergences (Fig. 3).

Therefore, and according to the reported evidence, we refer the Taurida specimen to *Megantereon adroveri* (sensu Lewis and Werdelin 2010); i.e., it is a European *Megantereon* with advanced character states different from coeval African *M. whitei* (Fig. 2f–h). We regard the maxillary fragment from Taurida previously described by Lavrov et al. (2019, fig. 2) as *Megantereon* sp., as already published.

Conclusions

The taxonomy and phylogenetic relationships of Eurasian and African Pleistocene dirk-toothed cats have been a matter of intense debate in recent decades, probably because of their scanty record. Here we describe a fragment of the mandibular corpus of *Megantereon* from the newly discovered site of Taurida that displays more derived features as compared with chronologically older European and Asian specimens traditionally referred to *M. cultridens* and *M. microta* > *M. nihowanensis*, respectively. The studied specimen shares features in common with European and Asian sites from the latest Early Pleistocene (e.g., Apollonia-1, Monte Argentario, and Lantian) and clearly differs from coeval African specimens (e.g., Koobi Fora Okote Mb). According to the former characters, we refer the Taurida specimen to *M. adroveri*, i.e., a European *Megantereon* with advanced characters. Our results support the idea of other authors (e.g., Werdelin and Lewis 2000) of a continuous European lineage of dirk-toothed cats despite the claims of other recent authors of a putative African dispersion of *M. whitei* into Europe during the Late Villafranchian.

Acknowledgments The authors thank L. Werdelin, B. Martínez-Navarro, Q. Jiangzuo and J. B. Fourvel for useful discussions and suggestions during the last months. We also thank Q. Jiangzuo, L. Werdelin, A. Arribas, L. Rook, S. Bartolini Lucenti and G. Koufos giving us permission for reproduce/figure specimens under their care. The authors express their gratitude to all participants in the excavations in the Taurida Cave and especially to A.M. Berezkin. We also express our special gratitude to the organizers of the excavations, Dean of the Faculty of Geography of CFU B.A. Vakhruhev and G.V. Samokhin, employees of CFU D.B. Startsev and S.V. Tokarev. We sincerely thank the staff of ZMMU S.V. Volkov, S.V. Kruskop, V.S. Lebedev, A.A. Lisovsky, V.E. Lytvyn for advice and assistance in the work. The comments of two anonymous reviewers and the editor D. Croft significantly improved an early version of this work.

Funding The work of J.M.-M. has been funded by the Agencia Estatal de Investigación-European Regional Development Fund of the European Union (CGL2017-82654-P, AEI/FEDER-UE) and the Generalitat de Catalunya (CERCA Program). J.M.-M. is member of the consolidated research group 2017 SGR 116 (AGAUR, Generalitat de Catalunya).

Availability of Data and Material The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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