

# THE MORPHOLOGY OF THE UPPER FOURTH PREMOLAR IN *TROCHARION ALBANENSE* MAJOR, 1903 (MUSTELIDAE: LEPTARCTINAE) AND THE INDEPENDENT LOSS OF THE CARNASSIAL NOTCH IN LEPTARCTINES AND OTHER MUSTELIDS

La morfología del cuarto premolar superior en *Trocharion albanense* Major, 1903 (Mustelidae: Leptarctinae) y la pérdida independiente de la incisión de la carnífera en los leptarctinos y otros mustélidos

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## ABSTRACT

The discovery of new craniodental remains of the leptarctine mustelid *Trocharion albanense* from several Late Aragonian (Middle Miocene) localities of Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, Spain) enables the description of several features previously unknown for this taxon. This, in its turn, permits to further evaluate the phylogenetic position of this taxon with regard to other Leptarctinae. Here we show that the phylogenetic position of *Trocharion* is highly dependent on whether the character presence/absence of carnassial notch in the upper fourth premolar is considered as a valid feature. Unlike the most derived leptarctines and crown mustelids (or neomustelids), *Trocharion* still retains a notch in the upper carnassial, thus resembling the condition displayed by the Oligocene paleomustelid *Plesictis*. This might be interpreted in two different ways: (1) *Trocharion* occupies a much more basal phylogenetic position than previously suspected, i.e. preceding the leptarctine-neomustelid split; or (2) *Trocharion* is the basalmost member of the Leptarctinae and the carnassial notch was lost twice. The presence of a variously developed carnassial notch in other, more derived and undoubted leptarctines strongly supports the latter hypothesis, i.e. that the carnassial notch was lost independently in leptarctines and in the lineage leading to neomustelids. It is concluded that, on the basis of currently available evidence, *Trocharion* is most likely a

basal leptarctine, although further fossil evidence showing middle-ear features would be required in order to settle this issue more definitively.

**Keywords.** Carnivora, Evolution, Neogene, Paleobiology.

## RESUMEN

El descubrimiento de nuevos restos cráneo-dentales del mustélido leptarctino *Trocharion albanense*, a partir de varias localidades del Aragoniense Superior (Mioceno Medio) del Abocador de Can Mata (Cuenca del Vallès-Penedès, Cataluña, España), permite la descripción de varios caracteres previamente desconocidos para este taxón. Ello, a su vez, permite volver a evaluar la posición filogenética de este taxón con respecto a otros Leptarctinae. Mostramos aquí que la posición filogenética de *Trocharion* depende en gran medida de si se considera válido el carácter presencia/ausencia de incisión de la carnífera en el cuarto premolar superior. A diferencia de los leptarctinos más derivados y los mustélidos corona (o neomustélidos), *Trocharion* aun retiene una incisión en la carnífera superior, recordando así la condición del paleomustélido oligoceno *Plesictis*. Esto puede interpretarse de dos formas distintas: (1) *Trocharion* ocupa una posición filogenética más basal de lo que se sospechaba previamente, i.e. anterior a la divergencia entre leptarctinos y neomustélidos; o (2) *Trocharion* es el miembro más basal de los Leptarctinae y la incisión de la carnífera en otros leptarctinos indudables y más derivados favorece esta segunda hipótesis, según la cual la incisión de la carnífera se perdió independientemente en los leptarctinos y en el linaje que conduce a los neomustélidos. Se concluye que, en base a la evidencia actualmente disponible, *Trocharion* es con mayor probabilidad un leptarctino basal, aunque serían necesarias más evidencias que mostrasen los caracteres del oído medio para poder llegar a conclusiones más definitivas sobre esta cuestión.

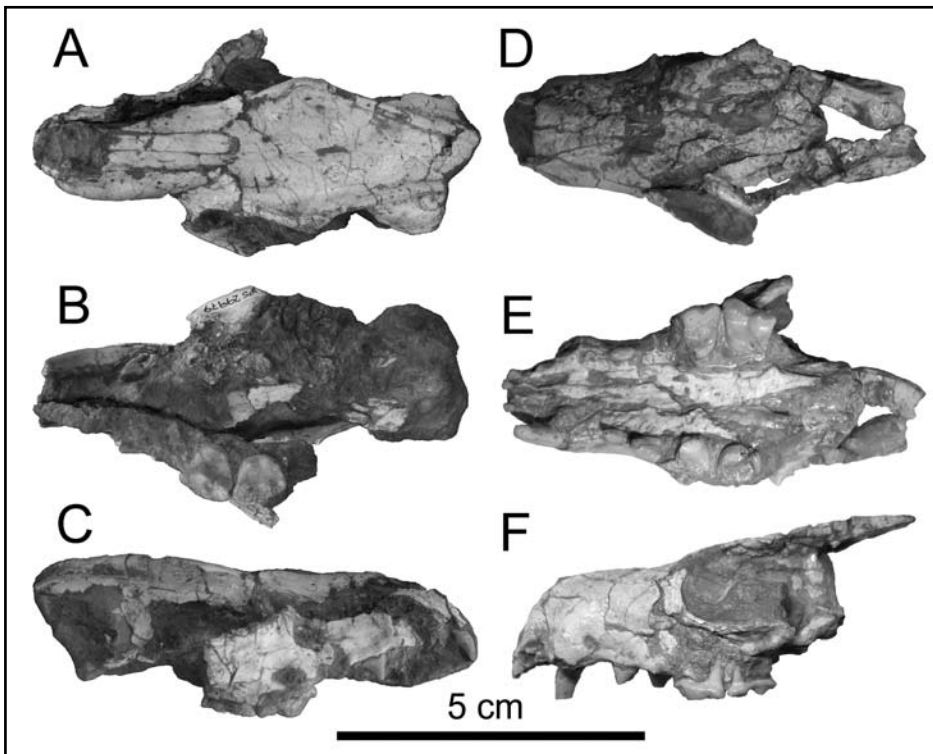
**Palabras clave:** Carnivora, Evolución, Neógeno, Paleobiología.

## INTRODUCTION

Mustelids are currently the most diverse carnivoran family, further displaying a large amount of ecomorphological diversity and a wide distribution. As a result, deciphering the phylogenetic relationships of this family is hampered due to evolutionary convergence and the existence of several periods of rapid cladogenesis (Koepfli *et al.*, 2008). Recent advances in molecular phylogenetics have significantly contributed to deciphering the relationships between extant members of this family (e.g., Koepfli *et al.*, 2008). However, reconstructing its evolutionary history further requires considering the extinct representatives of the family. Members of the stem lineage of the Mustelidae are informally referred to as 'paleomustelids', while crown-group mustelids are referred to as 'neomustelids' (Baskin, 1998; Wang *et al.*, 2004; Koepfli *et al.*, 2008). The affinities of several paleomustelid genera with neomustelids, however, is far from clear. This includes the extinct subfamily Leptarctinae, distributed throughout Eurasia and North America, and which is of particular interest for deciphering the origin of neomustelids.

The recent discovery of new craniodental remains of the leptarctine mustelid *Trocharion albanense* Major, 1903 from Abocador de Can Mata (ACM; Middle Miocene, Vallès-Penedès Basin, Catalonia, Spain; see Alba *et al.*, 2006) will enable the reevaluation of the phylogenetic position of this taxon, which in its turn bears significant implications for the origin of the whole subfamily. *Trocharion albanense* was originally described on the basis of material from La Grive (Major, 1903), being later reported from other European localities (see review in Ginsburg, 1999). Its occurrence in the Iberian Peninsula is restricted to the Vallès-Penedès Basin, where it has been reported from Sant Quirze (Villalta Comella & Crusafont Pairó, 1944), Can Llobateres (Petter, 1967), Castell de Barberà (Petter, 1976) and several ACM localities (C4-A1, C5-D1, C6-A2 and C6-Cb).

The new material of *Trocharion* from ACM includes two partial crania (Figure 1) that reveal features thus far unknown for this taxon, such as the presence of a double temporal crest and deep zygomatic arches, which strengthen its leptarctine status. The retention of several primitive features in



**Figure 1.** Two partial crania of *Trocharion albanense* Major, 1903: (A-C) IPS29979 from ACM/BDA and (D-F) IPS44028 from ACM/C6-Cb, in (A, D) dorsal, (B, E) palatal and (C, F) lateral views.

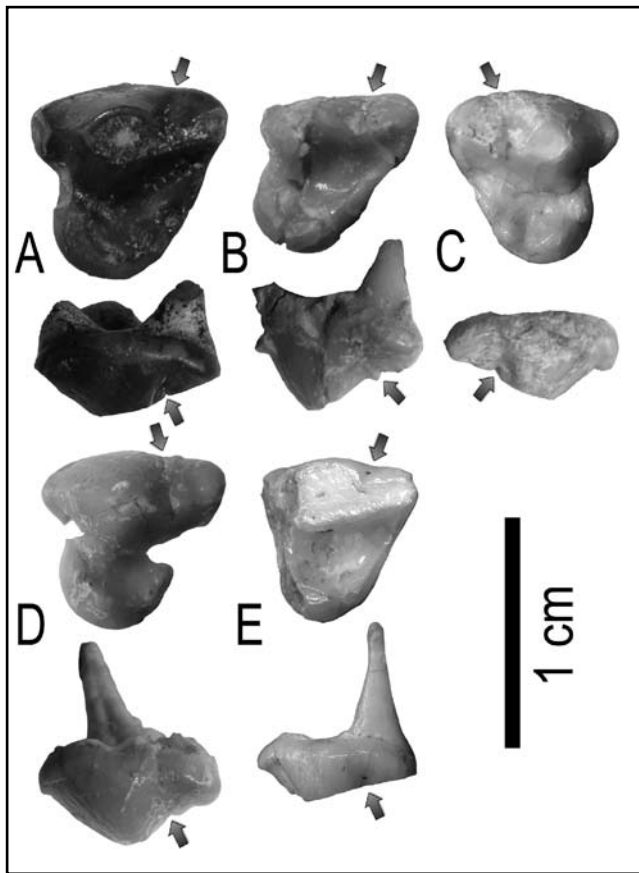
*Trocharion*, such as the presence of a carnassial notch on the upper fourth premolar, suggest that this genus is the basalmost member of the Leptarctinae. It has been previously suggested, however, that the loss of the carnassial notch is a synapomorphy of the Leptarctinae (Wang *et al.*, 2004), leading to the alternative phylogenetic hypothesis that *Trocharion* could be a basal mustelid preceding the divergence between leptarctines and mustelids of modern aspect (or 'neomustelids'). In this communication, we explore the evolutionary implications of both alternatives, with particular emphasis on the loss of the carnassial notch in the Mustelidae.

## MATERIALS AND METHODS

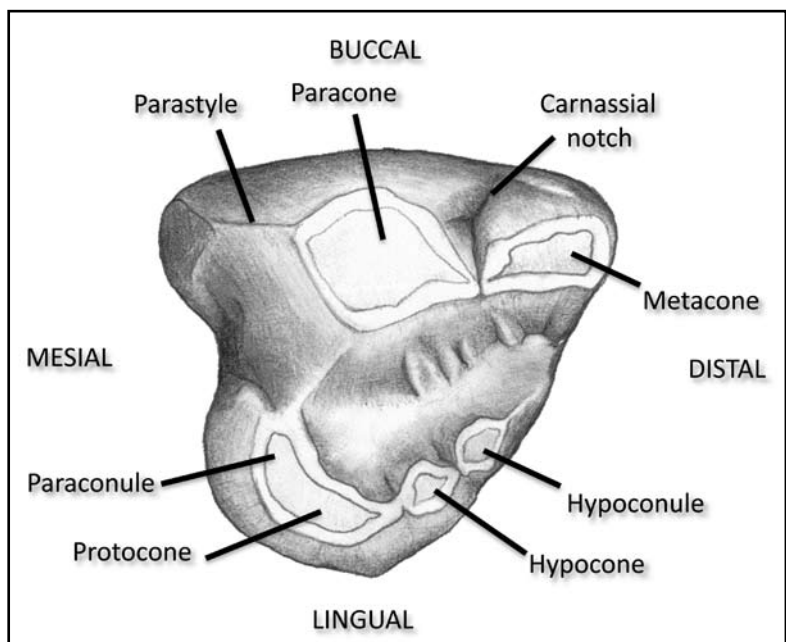
Five  $P^4$  of *Trocharion albanense* are described in this paper (Figure 2): IPS33217h and IPS33221, from Castell de Barberà; IPS29979 from ACM/BDA; IPS44028 from ACM/C6-Cb; and IPS46276 from ACM/C5-D1. The latter specimen and those from Castell de Barberà are isolated dental remains, whereas the remaining  $P^4$  from ACM do belong to the two partial crania (Figure 1).

## RESULTS

The upper carnassial ( $P^4$ ) of *Trocharion albanense* (Figures 2 and 3) displays a triangular occlusal outline, being much longer buccally than lingually. This premolar is larger and displays a more developed occlusal relief than the remaining ones. On the buccal moiety of the crown, the prominent and conical paracone is separated from the more elongated and less prominent metacone by a moderately-developed groove that corresponds to the so-called carnassial notch; on the buccal wall of the crown, it does not extend until the crown base, but it is not merely a shallow depression, since in occlusal view it interrupts the contact between the paracone and metacone. There is also a small parastyle. On the lingual moiety of the crown, there is a crest that bears an elongated but distinct protocone and a much smaller hypocone. A small and conical paraconule is mesially situated with respect to the protocone, whereas an additional secondary cuspule (hypoconule) is situated on the distolingual corner of the crown, separated from the hypocone by a deep groove.



**Figure 2.** Upper fourth premolar (upper carnassial) of *Trocharion albanense* Major, 1903, in both occlusal and buccal views: (A) IPS33217h from Castell de Barberà; (B) IPS33221 from Castell de Barberà; (C) IPS29979 from ACM/BDA; (D) IPS46276 from ACM/C5-D1; and (E) IPS44028 from ACM/C6-Cb. Arrows indicate the position of the carnassial notch, which is present in all specimens, although in (E) it is less evident due to the advanced degree of wear. Note that, although the notch does not reach the crown base, it is not merely a shallow depression on the buccal wall of the crown, but rather a deep groove that, in occlusal view, interrupts the contact between the paracone and the metacone.



**Figure 3.** Schematic drawing of a P<sup>4</sup> in occlusal view, indicating the main morphological features. Original art by Marta Palmero.

## DISCUSSION

The new cranial material of *Trocharion* recently recovered from ACM reveals several features that strengthen its leptarctine status, such as the presence of a double temporal crest and deep zygomatic arches. At the same time, however, the new material has shown several primitive features that were previously unsuspected for a leptarctine, such as the long muzzle and the retention of upper first premolars. Among these primitive features, the possession of a true carnassial notch stands out for its evolutionary implications. The new craniodental evidence from ACM indicates that *Trocharion* occupies a more basal phylogenetic position than previously hypothesized. Qiu & Schmidt-Kittler (1982), for example, suggested that *Trocharion* was a basal leptarctine, but hypothesized that *Craterogale* had diverged first. The present analysis, on the contrary, indicates that *Trocharion* occupies a more basal position than *Craterogale*, and the question arises as to whether the former taxon should be considered a leptarctine after all.

The cladistic analysis performed by Wang et al. (2004), which unfortunately could not include *Trocharion* due to the lack of cranial material, supported the existence of a Mustelidae clade, which was placed as the sister-group of the clade constituted by neomustelids and *Paragale*+*Plesiogale*, with *Plesictis* preceding the divergence of both clades. According to this analysis, the monophyly of the Mustelidae would be supported by several synapomorphies, including among others the loss of the carnassial notch. Accordingly, Wang et al. (2004) inferred that *Trocharion* should have a craniodental morphology as advanced as other leptarctines. This is however contradicted by the new craniodental remains from ACM, which indicate that *Trocharion* must occupy a more basal position. In fact, the most likely phylogenetic position for *Trocharion* depends to a large extent on whether the presence/absence of carnassial notch is taken into account.

There is not doubt that the lack of a carnassial notch and the loss of the P<sup>1</sup> are derived features for the mustelids (e.g., Wolsan, 1993; Baskin, 1998), but the possibility remains that these features were independently lost in several lineages. *Trocharion* shares several features with *Plesictis*, which is the earliest primitive musteloid

to display a double temporal crest (Wang et al., 2004). These features include an unshortened muzzle, the retention of upper premolars and a carnassial notch (Wang et al., 2004). This shared features are nevertheless symplesiomorphic, so that their presence in *Trocharion* must not necessarily indicate a close relationship with *Plesictis* and can be neither interpreted as necessarily excluding a closer relationship between *Trocharion* and other leptarctines.

According to Baskin (1998, p. 155), the primitive retention of a carnassial notch on the P<sup>4</sup> characterizes the paraphyletic group termed 'paleomustelids', although on the basis of the most parsimonious cladogram derived by Wang et al. (2004), the loss of the carnassial notch would not be a synapomorphy only of neomustelids (or 'mustelids of modern aspect': Baskin, 1998), but rather of the clade including leptarctines, neomustelids, *Paragale* and *Plesiogale*. According to this, the retention of the carnassial notch in *Trocharion* should be either interpreted as indicating an early branching of this taxon (i.e., preceding the leptarctine-neomustelid split) or alternatively as indicating that this character was independently lost in both leptarctines and neomustelids.

The latter hypothesis was already favored by Qiu & Schmidt-Kittler (1982), but has been recently challenged by Wang et al. (2004), according to whom *Trocharion* would merely display a «remnant carnassial notch» (Wang et al., 2004: p. 414). It is unclear why the notch of *Trocharion*, albeit admittedly not particularly well-developed, should be qualified as a «remnant». In fact, besides *Trocharion*, the leptarctine *Hypsoparia* (sometimes synonymized with *Leptarctus*) also retains a true carnassial notch (Qiu & Schmidt-Kittler, 1982; Lim & Martin, 2002). A vestigial condition is indeed found in *Leptarctus*, in which the paracone and metacone are separated by a long depression that stretches to the crown base (Qiu & Schmidt-Kittler, 1982). Only the leptarctines *Craterogale* and *Kinometaxia* do not display a carnassial notch, while in *Schultzogale* the available P<sup>4</sup> is too damaged to be able to ascertain this trait (Wang et al., 2004).

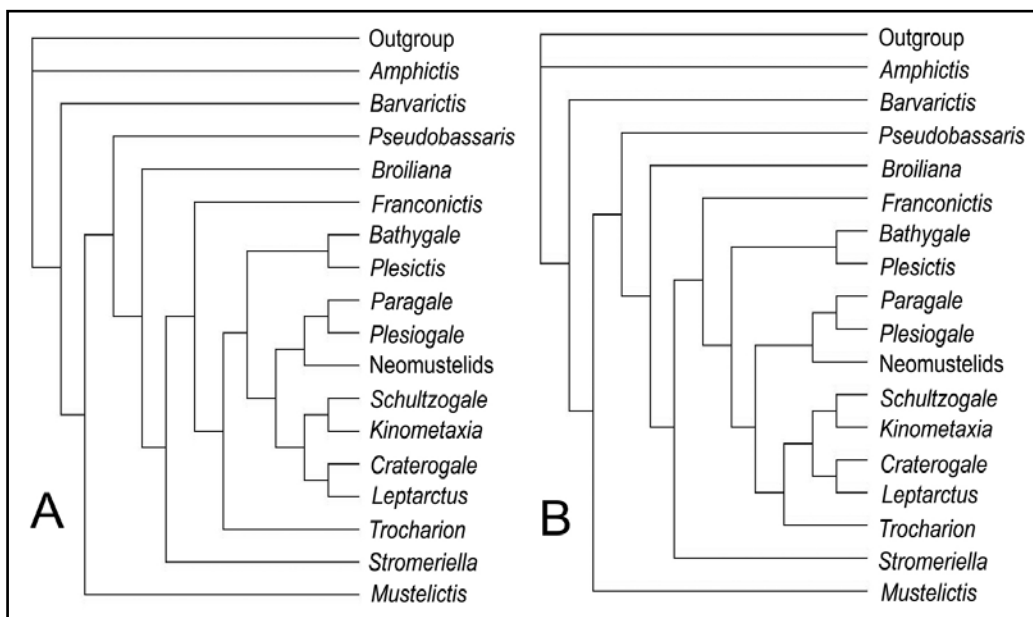
Interestingly, when the presence/absence of carnassial notch is not taken into account, *Trocharion* is best interpreted as the basalmost member of

the leptarctines, while the phylogenetic position of the other taxa included by Wang *et al.* (2004) in their cladistic analysis remains unchanged. Thus, *Plesictis* (which retains a carnassial notch) stands as a primitive taxon preceding the leptarctine-neomustelid divergence, while *Paragale*+*Plesiogale* (which already lack the notch) stand as the sister-clade of neomustelids. In the case of *Paragale* and *Plesiogale*, from the Early Miocene of Europe, this is attributable to several advanced features that ally them more closely with neomustelids, while the middle ear morphology of *Plesictis*, from the Late Oligocene of Europe, clearly show its primitive status. All this evidence taken together strongly suggests that, as previously suggested by Qiu & Schmidt-Kittler (1982), the carnassial notch was independently lost in leptarctines and the lineage leading to neomustelids.

suggests that this feature was independently lost more than once. We therefore favor the hypothesis that *Trocharion* is the basalmost member of the Leptarctinae. Unfortunately, available remains do not show middle-ear features, which would be required in order to more definitively settle the issue of whether *Trocharion* is closely related to undisputable leptarctines as a basal member of this clade.

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**Table 4.** A, Single shortest tree (75 steps) recovered by PAUP\* by means of the Branch and Bound option on a 18x31 data matrix (Table 1). B, Single shortest tree (71 steps) obtained with the same methodology but removing character 13 (development of the carnassial notch).

## CONCLUSIONS

If the presence/absence of carnassial notch is considered a valid (homologous) feature, *Trocharion* might be interpreted as a very primitive musteloid, more comparable to the Late Oligocene *Plesictis* and thus preceding the leptarctine-neomustelid splitting. The presence of a variously-developed carnassial notch in some other leptarctines, however, already

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