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Affinity of *Arctomeles dimolodontus* and other Old-World Badgers (Melinae: Mustelidae: Carnivora)

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Abstract

Mustelids, members of the weasel family, are the most species rich and ecologically diverse family within the order Carnivora. However, fossil mustelids are poorly understood due to their rarity in the fossil record. Fossils of “Eurasian” badgers in particular, subfamily Melinae, only include three stem and two crown genera: *Arctomeles*, *Arctonyx*, *Ferinstrix*, *Meles*, and *Melodon*. Today, melines are restricted to the Old World, but fossils of stem taxa have also been discovered in North America. Here, we discuss the occurrence of the fossil meline *Arctomeles dimolodontus* currently known only from the Gray Fossil Site of East Tennessee, USA, and its phylogenetic position within stem Melinae. A total of 34 dental characters across 8 taxa were selected because some taxa, such as “*Arctomeles*” *sotnikovae* and *Ferinstrix vorax*, are known only from teeth (or cranial fragments). A search of all possible trees using PAUP (set for maximum parsimony) yielded a single most parsimonious tree. Topology of that tree suggests that *Ferinstrix* is nested within crown group Melinae, rather than the stem group, and is the sister to extant *Arctonyx*, the hog badger. Results also suggest that “*Arctomeles*” *sotnikovae* does not group within the monophyletic clade formed by *A. dimolodontus* and *A. pliocaenicus*, but instead nests “*A.*” *sotnikovae* as a closely related, but separate, lineage to *Melodon*. Based on these findings, we propose that the ancestral stock of crown Melinae is more closely related to *Arctomeles* than *Meles* as previous research has suggested. Furthermore, the dental morphology within stem Melinae is relatively conservative for a generalized diet, although exceptions exist in some derived forms, such as *Arctonyx* and *Ferinstrix*, which may explain why PAUP nested the two as sister taxa. *Arctonyx* is an exclusively Old-World lineage, so it is likely that the *Arctonyx-Ferinstrix* clade had an Old-World origin, after which *Ferinstrix* migrated into North America and *Arctonyx* remained in the Old World. This begs the question: why do some melines migrate into North America while other contemporary forms do not? All stem meline genera have occurrences from Eurasia, yet only *Arctomeles* and *Ferinstrix* are known to have migrated into North America. This is likely because of the environmental constraints on where these different genera can live, but much remains unknown about the ecology of fossil melines to know for certain. Further study of this disparity can lead to a greater understanding of how the earth’s climate has changed since the Neogene and how this change impacts flora and fauna.

Introduction

The extinct badger genus, *Arctomeles*, was first described from Europe, and subsequently included four species from the Old-World, *A. pliocaenicus*, *A. ferus*, *A. genevauxi*, and *A. suillus*, until the discoveries of two species from North America, “*A.*” *sotnikovae* from Ellesmere Island, Canada and *A. dimolodontus* from East Tennessee, USA (Viret, 1939; Teilhard de Chardin, 1945; Roshchin, 1949; Stach, 1951; Tedford and Harrington, 2003; Wallace and Wang, 2004). This genus, according to Wallace and Wang (2004), is a basal member of the Eurasian subfamily Melinae, which today is restricted to the Old World, but rare fossil taxa attributed to this subfamily have been discovered across three widespread localities in North America, including those mentioned above and *Ferinstrix vorax* from Hagerman Fossil Beds in Idaho, USA (Bjork, 1970; Wolsan and Sotnikova, 2013).

Though *Taxidea taxus*, the American badger, was traditionally grouped within Melinae, genetic analyses now show a separate evolutionary history from the primarily Old-World meline badgers (Koeplli et al., 2008; Sato, 2016; Law, et al. 2018); and in fact, distinct from all other members of the family. As a result, it seems that the taxa mentioned thus far are among several musteloids that have converged upon a “badger” ecomorph; in addition to the stink badgers (Mephitidae) of Southeast Asia and the honey badgers (Mellivorinae) of Africa/Asia (Owen, 2006; Sato, 2016).

According to Koeplli et al. (2008), the extant melines *Meles*, the Eurasian badger, and *Arctonyx*, the hog badger, are sister taxa that diverged around 4.4 Ma to 3.6 Ma. Additionally, Madurell-Malapeira et al. (2009) propose that *Arctomeles*, *Arctonyx*, and *Meles* diverged in the early Pliocene of Asia from a “*Meles*” stock. *Melodon* and *Ferinstrix* are two extinct meline genera known alongside *Arctomeles*, although little is known about these taxa (Wolsan and Sotnikova, 2013). *Melodon* is believed to be a basal meline, and is known only from Asia, which supports a Eurasian origin for stem Melinae (Zdanksy, 1924; Wolsan and Sotnikova, 2013). *Ferinstrix* is known from both Asia and North America; *F. rapax* from Asia and *F. vorax* from North America (Bjork, 1970; Wolsan and Sotnikova, 2013). *Ferinstrix* is a relatively large stem meline, with uniquely hypercarnivorous dentition; in contrast to the mostly generalized dentition possessed by the rest of stem Melinae (Wolsan and Sotnikova, 2013; Sato, 2016).

Fossils of *Arctomeles dimolodontus* were first reported from the Gray Fossil Site (GFS) of East Tennessee, USA (Wallace and Wang, 2004); an early Pliocene-aged sinkhole deposit that records a hot, humid woodlands environment which was home to a wide variety of flora and fauna (Schubert and Mead, 2011; Samuels and Schap, 2021). *A. dimolodontus* is one of the most abundant fossil carnivorans found at the GFS, possessing an MN of 5 individuals based on right P4 and M1. Original description from Wallace and Wang (2004) included a simple description and cladistic analysis based solely on upper dentition, but new cranial material warrants a more detailed description and analysis including more meline taxa. However, fossil remains of other North American melines (“*A.*” *sotnikovae* and *F. vorax*) are scarce and fragmentary, with descriptions consisting only of craniodental material. Furthermore, according to Wallace and Wang (2004), “*A.*” *sotnikovae* most likely belongs in the genus *Melodon* instead, based on a reexamination of its P4 morphology in comparison to the P4 of other *Melodon* and *Arctomeles* species. Thus, there would be a total of three stem meline genera known from North America.

Methods

Specimens were observed for character selection using digital images as well as physical specimens. Physical specimens include ETMNH-Z 252 *Meles meles*, ETMNH 8270 *Arctomeles dimolodontus*, USNM 256678 *Arctonyx collaris*, and USNM 152622 *Meles meles*. Digital images include Figures 3-8 of UMMP 53343 *Ferinstrix vorax* and GIN-BF 987 *F. rapax* from Wolsan and Sotnikova (2013), figures of *Arctomeles pliocaenicus* from Stach (1951), and PMU M3814 *Melodon incertum*. *Arctonyx collaris*, *Meles meles*, and *Melodon incertum* are used as representatives of their genera in this cladistic analysis. Some basal melines, such as *Arctomeles ferus*, *A. genevauxi*, and *A. suillus*, were not included because of limited access.

A character matrix was created with a total of 34 characters across 8 taxa (Table 1). Characters were selected on the dentition of stem Melinae specimens because some of these taxa, such as “*Arctomeles*” *sotnikovae* and *Ferinstrix vorax*, are known only from fragmentary dental material, (Bjork, 1970; Tedford and Harrington, 2003). Characters were analyzed with PAUP set to maximum parsimony to run the cladistic analysis. Additionally, where missing character states exist for the outgroup, *Melodon incertum*, the basal character state 0 is hypothesized based on the most likely ancestral condition.



Figure 1. Extant meline badgers: *Meles meles*, the Eurasian badger (Left), and *Arctonyx collaris*, the hog badger (Right).

Note: Extant badger images by Byrdyak, Kallerna, and Limpারণpathanakij posted on Wikimedia Commons

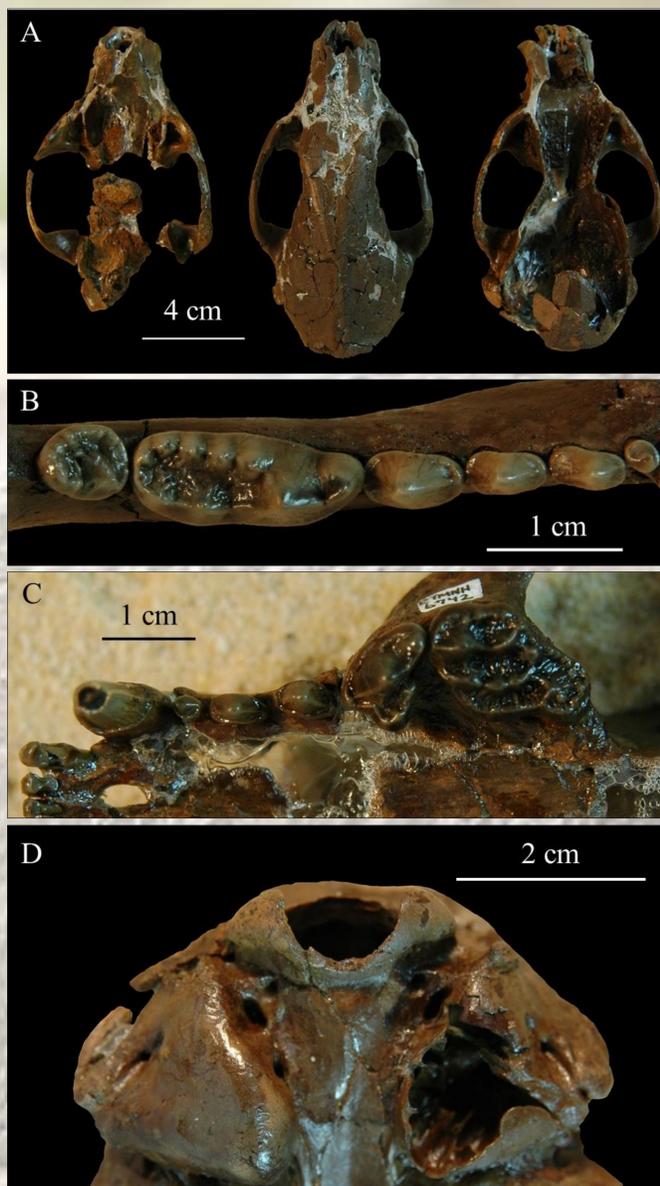


Figure 2. Dorsal view of three partial skulls (ETMNH 10880, 8270, 6742 from left to right) of *Arctomeles dimolodontus* (A). Occlusal view of right dentary (ETMNH 8270) of *A. dimolodontus* (B). Occlusal view of left maxillary (ETMNH 6742) of *A. dimolodontus* (C). Ventral view of basicranium (ETMNH 6742) of *A. dimolodontus* (D).

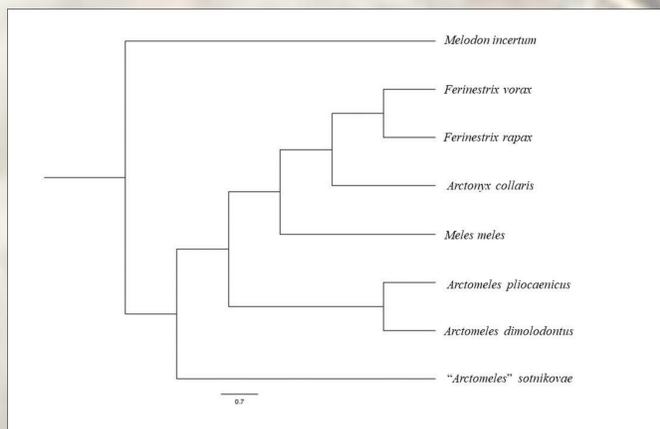


Figure 3. Most parsimonious tree based on 34 craniodental characters across 8 Melinae taxa (see Table 1).

Results

PAUP retained a single most parsimonious tree (Figure 3), after analyzing over 10,395 possible phylogenies, with a tree length of 59, consistency index (CI) of 0.7288 (0.6923 excluding uninformative characters), homoplasy index (HI) of 0.2712 (0.3077 excluding uninformative characters), retention index (RI) of 0.6444, and the rescaled consistency index of 0.4697. Five characters, based on the presence of a styler shelf on the premolars, proved to be parsimony uninformative: all taxa examined retain the basal state. The Bootstrap analyses on 1000 replicates resulted in a 50% majority consensus tree (Figure 3). The consensus tree yielded a polytomy among *M. meles*, the *Arctomeles* clade, and the *Arctonyx-Ferinstrix* clade with a bootstrap value of 57. The *Arctomeles* clade yielded a bootstrap value of 61. The *Arctonyx-Ferinstrix* clade yielded a bootstrap value of 69, and the *Ferinstrix* clade yielded a bootstrap value of 88.

Table 1. Character Matrix

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34		
<i>Meles meles</i>	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	1	0	1	0	0	1	0	0	0	1	1	1	1		
<i>Arctonyx collaris</i>	2	1	2	1	0	2	2	0	0	0	0	1	0	0	1	0	0	2	1	1	0	1	1	0	1	0	1	2	1	1	1	2	0	0	1	
<i>Arctomeles dimolodontus</i>	0	0	1	0	1	0	0	1	0	1	0	0	0	0	2	1	0	0	1	1	1	0	1	1	0	1	1	0	0	0	1	1	1	1	1	
<i>Arctomeles sotnikovae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
<i>Arctomeles pliocaenicus</i>	?	?	?	?	?	?	?	0	0	0	0	0	0	0	?	0	0	0	1	1	1	0	1	1	0	1	1	0	0	0	1	?	?	?	?	1
<i>Ferinstrix rapax</i>	1	0	1	2	1	2	2	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	0	1	0	3	2	2	2	3	1	0	0	0	0	
<i>Ferinstrix vorax</i>	?	?	?	2	1	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Melodon incertum</i>	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Note: “?” designates characters that cannot be scored

Discussion

Character states do not follow a linear trend in derived characters. For instance, tooth crowding appears to go in two different evolutionary directions among the observed stem melines relative to the basal condition: more crowded and less crowded. Future cladistic analyses will include additional and refined characters of the basicranium (Figure 2). Cladistic results presented here suggest that *Ferinstrix* is nested within the crown group Melinae, rather than the stem group as previously suggested by Wolsan and Sotnikova (2013). Moreover, our analysis (Figure 3) presents the sister taxon of *Ferinstrix* as *Arctonyx*. According to Koeplli et al. (2008), molecular evidence suggests the divergence of *Arctonyx* and *Meles* around 4.4 Ma to 3.6 Ma. Fossils show that *Ferinstrix* existed from at least 3.6 Ma to 3.1 Ma (Bjork 1970; Wolsan and Sotnikova, 2013), supporting the divergence of *Ferinstrix* after *Meles* and *Arctonyx* as proposed by Koeplli et al. (2008). Results here also suggests that “*Arctomeles*” *sotnikovae* does not group within the monophyletic clade formed by *A. dimolodontus* and *A. pliocaenicus*. Wallace and Wang (2004) also suggest that “*A.*” *sotnikovae* does not belong within the genus *Arctomeles*, but instead appears closer to the genus *Melodon*. Conversely, our phylogeny suggests that “*A.*” *sotnikovae* is a closely related, but separate, lineage from *Melodon*. If true, the taxon may represent a new genus.

Madurell-Malapeira et al. (2009) proposed that *Arctomeles*, *Arctonyx*, and *Meles* evolved from a “*Meles*” stock, yet our results suggest an earlier divergence of *Arctomeles* than *Meles*. Therefore, we propose that the ancestral stock of crown Melinae is more closely related to *Arctomeles* than *Meles*. Furthermore, the dental morphology within stem Melinae is relatively conservative with a generalized diet, although exceptions exist in the derived forms with specialized diets such as *Arctonyx* and *Ferinstrix*. This conservative dental morphology reflects the broad ecology of non-specialist melines. *Arctonyx* is an exclusively Old-World lineage, so it is likely that the *Arctonyx-Ferinstrix* clade had an Old-World origin, after which *Ferinstrix* migrated into North America and *Arctonyx* remained in the Old World.

Conclusions

- *Ferinstrix* is nested within crown Melinae, rather than as a basal member.
- *Arctonyx* and *Ferinstrix* are sister taxa; likely because of their highly specialized dentition.
- Based on these findings, the ancestral stock of crown Melinae is more closely related to *Arctomeles*, than *Meles*.
- Generic reassignment of “*Arctomeles*” *sotnikovae*, proposed by Wallace and Wang (2004), is supported. Moreover, “*A.*” *sotnikovae* falls outside the higher clades suggesting a unique classification.

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