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# A Borophagine canid (Carnivora: Canidae: Borophaginae) from the middle Miocene Chesapeake Group of eastern North America

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**Abstract.**—A tooth recovered from the middle Miocene Choptank Formation (Chesapeake Group) of Maryland is identified as a new cynarctin borophagine (Canidae: Borophaginae: Cynarctina), here called *Cynarctus wangi* n. sp. The tooth, identified as a right upper second molar, represents the first carnivoran material reported from the Choptank Formation and part of a limited record of borophagine canids from eastern North America. As *?Cynarctus marylandica* (Berry, 1938), another cynarctin borophagine from the older Calvert Formation, is known only from lower dentition, its generic affinities are uncertain. However, features of this new material are compared to features of *?C. marylandica* through occlusal relationships, allowing for referral to a distinct species. Even so, the Choptank Formation material still offers two possible scenarios regarding its identification. In one, its geographic and stratigraphic provenance could imply that it belongs to *?C. marylandica*. If this were correct, then the generic placement of *?C. marylandica* would be correct and the taxon would be more derived than some other *Cynarctus* species in regard to hypocarnivory, and less derived than others. The second possibility, and the one believed to be most probable, is that a distinct cynarctin borophagine is present in the Chesapeake Group in strata younger than the type specimen of *?C. marylandica*. This new borophagine canid expands the sparse fossil record of this group in northeastern North America and furthers our knowledge of the fossil record of terrestrial taxa in this region.

## Introduction

The first terrestrial mammal fossils known from the Chesapeake Group on the mid-Atlantic coast of the United States were proboscidean remains identified by Harlan (1842). In the over 170 years of collecting since then, hundreds of specimens of terrestrial mammals have been recovered from the marine deposits of the Chesapeake Group (e.g., Harlan, 1842; Cope, 1867; Hayden, 1873; Shattuck, 1904; Berry, 1938; Gazin and Collins, 1950; Blackwelder and Ward, 1976; Tedford and Hunter, 1984; Wright and Eshelman, 1987). The early Barstovian Calvert Formation has had a wide array of both marine and terrestrial mammals collected from its strata (e.g., Gazin and Collins, 1950; Wright and Eshelman, 1987), including carnivorans (Berry, 1938; Tedford and Hunter, 1984). However, only a few terrestrial mammals have been identified from the younger late Barstovian Choptank Formation, including the tayassuids Desmathyus sp. and "Prosthenops" niobrarensis ("Hesperhys" of Gazin and Collins, 1950), the proboscidean cf. Gomphotherium calvertensis (Gazin and Collins, 1950), and the protoceratid artiodactyls Prosynthetoceras sp. and ?Synthetoceras sp. (e.g., Gazin and Collins, 1950; Tedford and Hunter, 1984; Wright and Eshelman, 1987). No carnivoran material has been previously reported from the Choptank Formation.

In the older strata of the underlying Calvert Formation, a partial lower jaw (USNM 15561) of a borophagine dog was

found and named Tomarctus marylandica by Berry (1938). Tedford and Hunter (1984) reviewed various aspects of the Miocene in eastern North America and suggested that Tomarctus marylandica may be referable to Cynarctus. They did, however, also feel that the species would represent a primitive member of Cynarctus and was comparable to other early Barstovian species. In their thorough review of the phylogenetic systematics of the Borophaginae, Wang et al. (1999) found that the only distinct feature of ?C. marylandica (Berry, 1938) that is indicative of Cynarctus is a protostylid (or eoconulid) on the m1. However, the distinct crest on the posterior (or distal) face of the m1 trigonid has not been seen in other borophagines, making it distinct (Wang et al., 1999). Even so, Wang et al. (1999) felt that the identity of ?C. marylandica as a medium-sized borophagine was likely and maintained the questionable referral of ?Cynarctus marylandica to Cynarctus as was proposed by Tedford and Hunter (1984). Regardless of its generic affinity, ?C. marylandica represents one of only three known borophagine dogs from the northeastern United States, with the other two being Metatomarctus canavus (Simpson, 1932) from the late early Hemingfordian of Delaware (and Florida) and Paracynarctus kelloggi (Merriam, 1911) from the late early Hemingfordian of Delaware (Wang et al., 1999).

Due to the location of the Chesapeake Group in the Calvert Cliffs, much of the more recent collecting has been done by amateurs. Stratigraphically, the Chesapeake Group is made up of the older Calvert Formation, the middle Choptank Formation, and the younger St. Mary's Formation (Fig. 1). Fossils collected in situ come from the cliffs themselves. However, fossils frequently fall from the cliffs and are found as float below the cliffs. In addition, fossils can be moved around by wave action. Often, when fossils fall from the cliffs, they are found on the beach below the formation they originated from. While there is not always a certainty of a fossil originating in the closest formation, is does provide a probable geologic formation for fossils found as float, and not in situ, from Calvert Cliffs.

## Locality and repository information

Specimens examined for this study and abbreviated in the text are as follows: AMNH, American Museum of Natural History, New York, New York; UCMP, Museum of Paleontology, University of California at Berkeley; USNM, United States National Museum, Washington, DC. The material discussed within (USNM 534040) comes from the Chesapeake Group of Maryland. Because of where it was collected in the Calvert Cliffs area, it is believed to be from the middle Miocene Choptank Formation.

## Systematic paleontology

Dental terminology used herein follows Hershkovitz (1971) and Dahlberg (1971). Systematic paleontology follows McKenna and Bell (1997) and Wang et al. (1999).

Class Mammalia Linnaeus, 1758 Order Carnivora Bowdich, 1821 Suborder Caniformia Kretzoi, 1943 Infraorder Cynoidea Flower, 1869 Family Canidae Fischer de Waldheim, 1817 Subfamily Borophaginae Simpson, 1945 Tribe Borophagini Wang, Tedford, and Taylor, 1999 Subtribe Cynarctina McGrew, 1937 Genus *Cynarctus* Matthew, 1902

Type species.—Cynarctus saxatilis Matthew, 1902.

Included species.—Cynarctus crucidens Barbour and Cook, 1914; Cynarctus galushai Wang et al., 1999; ?Cynarctus marylandica (Berry, 1938); Cynarctus saxatilis Matthew, 1902; Cynarctus voorhiesi Wang et al., 1999; Cynarctus wangi, n. sp.

*Distribution.*—Early Barstovian of California and Maryland; late Barstovian of California, Colorado, Maryland, and Nebraska; early Clarendonian of Nebraska, South Dakota, and Texas; late Clarendonian of Nebraska; and Clarendonian of Texas.



**Figure 1.** Stratigraphy of the Chesapeake Group formations (modified from Vogt and Eshelman, 1987; Petuch and Drolshagen, 2010; Weems and George, 2013). *?Cynarctus marylandica* was collected from Zone 10 in the Calvert Formation and is marked by ?Cm. *Cynarctus wangi* n. sp. (USNM 534040) is believed to be from the Choptank Formation, which means somewhere between Zones 17 and 19, and is marked by Cw. Note that Petuch and Drolshagen (2010) mentioned a small unit that is found along part of the St. Mary's River called the Chancellor Point Member of the St. Mary's Formation, which is not shown in the figure. BCM = Boston Cliffs Member; CM = Conoy Member; DrM = Drumcliff Member; Fm. = formation; Mbr. = member; SLM = St. Leonard Member; WPM = Windmill Point Member.

*Diagnosis.*—Derived characters that distinguish *Cynarctus* from *Paracynarctus* are an auditory meatus of small diameter with a small lip, M1 transversely narrow and subquadrate, c1 strongly recurved, and p4 posterolingual shelf with weak 'metastylid' occasionally present. In addition, *Cynarctus* and *Paracynarctus* share several derived dental features distinguishable from those of *Metatomarctus* and other, more primitive taxa: a weak subangular lobe, a high mandibular condyle, short P4 relative to M1, enlarged M2, presence of an m1 protostylid, widened m1 talonid, and elongated m2 and m3. Diagnosis after Wang et al. (1999).

*Remarks.*—Wang et al. (1999) thoroughly reviewed *Cynarctus*. For further information, see their discussion of the genus and included species.

Cynarctus wangi new species Figure 2

Holotype.—USNM 534040, right M2.

*Diagnosis.*—Member of *Cynarctus* based on having enlarged M2s with posterior (distal) expansions (Wang et al., 1999), in turn making it a member of the Borophaginae and the Canidae. Further diagnosed from other species of *Cynarctus* by the prominent degree of posterior expansion of the M2 concentrated with the posterior cingulum; reduction of the labial cingulum lateral to the metacone; lack of expansion labially and/or posteriorly in the metacone; less pronounced posterior expansion near the hypocone; less developed metastyle; relatively weak posterior cingulum; and slightly pronounced labial cingulum near the anterior of the tooth.

*Type locality and horizon.*—Chesapeake Group, believed to be from the Choptank Formation (late Barstovian), Calvert County, Maryland.

*Etymology.*—Named in honor of Xiaoming Wang for his work with borophagines, other fossil canids, and carnivorans in general.

Description and remarks.—The right M2 (USNM 534040) of Cynarctus wangi n. sp. is subquadrate in shape and anteroposteriorly (or mesiodistally) elongate, particularly near the lingual portion. Maximum length is 13.44 mm (anteroposteriorly or mesiodistally) and maximum width is 11.77 mm (labiolingually). Paracone is pronounced, with the metacone being slightly reduced in comparison to the former. A distinct valley is present between the paracone and metacone (and between the postparacrista and premetacrista), completely separating them. Metastyle is reduced and less distinct, while only slightly inflated posteriorly (or distally). A labial cingulum is distinct around the paracone and is believed to be reduced around the metacone according to the morphology that is preserved; however, a portion of the cingulum is missing from the specimen lateral to the metacone. Parastyle is relatively indistinct mesial (or anterior) to the paracone. Protocone is pronounced and exhibits a gentle curve. Anteriorly (or mesially), the curved ridge of the protocone reaches the parastyle via the protocrista (or protoloph). Lingual to the protocrista lies another portion of the cingulum, although the protocone creates a disjunct in the elevations between the labial and lingual portions of the cingulum on the anterior (mesial) edge of the tooth. A metaconule is present posterior to the protocone, with a valley separating the two. Metaconule is pronounced, with a distinct curvature posteriorly (distally) toward the metastyle (= transcrista), which is also distinct.





Figure 2. Holotype right M2 of *Cynarctus wangi* n. sp. (USNM 534040). (A) Occlusal view. (B) Illustration of occlusal view. c = cleft; hyp = hypocone; labc = labial (external) cingulum; linc = lingual (internal) cingulum; met = metacone; mts = metastyle; mtl = metaconule; par = paracone; posc = posterior (distal) cingulum; prs = parastyle; pro = protocone. Scale bar = 1 cm.

In addition, the hypocone is pronounced, with its anteroposterior (or mesiodistal) ridge curving toward the lingual ridge of the metaconule, forming the distocrista. However, the distocrista is separated from the metaconule by a valley posterior (distal) to the post-talon basin. A posterior (distal) cingulum lies distal to the metaconule and hypocone as well. Lingual (or internal) cingulum is pronounced, especially as it nears the hypocone, with a cleft present that separates a nearly cusp-like development of the anterolingual (or mesiolingual) cingulum (= entostyle or pericone) from the hypocone. A strong posterior (distal) expansion of the M2 is most pronounced near the hypocone.

*Cynarctus* is characterized by having enlarged M2s with posterior (distal) expansions (Wang et al., 1999). According to AMNH 27543 (holotype) and AMNH 27550, *Cynarctus galushai* has a strongly curved M2, with a more distinct posterior (distal) expansion of the lingual portion than that in *C. wangi* (USNM 534040). The M2 in AMNH 27550 is more complete than that of the holotype (AMNH 27543), allowing for a more thorough comparison. A strong labial cingulum is present on the M2 in AMNH 27543. The protocone in *C. galushai* is relatively gently curved, similar to that in *C. wangi*. However, the metaconule and hypocone are less pronounced in *C. galushai*. As mentioned by Wang et al. (1999, p. 118), the lingual cingulum of the "M2 in *C. galushai* is thickened to suggest an initiation of a conate hypocone," a condition also present in *C. wangi*.

*Cynarctus marylandica* is only known from lower jaw material from USNM 15561 (holotype) and USNM 299471, and so cannot be compared directly to *C. wangi* (USNM 534040).

*Cynarctus saxatilis* is known from multiple M2s from several referred specimens (see Wang et al., 1999). Similar to USNM 534040, the labial cingulum is absent or weak lateral to the metacone in *C. saxatilis*. In addition, the metacone in *C. saxatilis* is relatively small and not expanded posteriorly (distally). In focusing on a referred specimen (UCMP 29891), the M2 is quadrate, with the anteroposterior (mesiodistal) length roughly equal to the labiolingual width. The metacone is more pronounced than that of USNM 534040, being almost equal in size to the paracone. In addition, the protocone is more constricted and more sharply curved, and the metaconule is less pronounced than in USNM 534040.

*Cynarctus voorhiesi* has an isolated left M2 known from a referred specimen (AMNH 49143). The tooth is heavily worn, but as was mentioned by Wang et al. (1999), the M2 is greatly expanded posteriorly (distally), although the hypocone is less posteriorly (distally) expanded than in *C. crucidens* (discussed in the following).

*Cynarctus crucidens* is known from multiple M2s from several referred specimens (see Wang et al., 1999). The M2 is anteroposteriorly (mesiodistally) elongate (and may even exceed the length of the M1). The hypocone is large, aiding in the anteroposterior (mesiodistal) elongation, and posteriorly (distally) situated. The metastyle is well developed. A strong posterior (distal) cingulum is also present. Compared to *C. wangi* (USNM 534040), the protocone is more constricted and strongly curved in *C. crucidens* (particularly AMNH

49312). A slightly smaller and less pronounced metacone and hypocone also differentiate *C. crucidens* from *C. wangi*.

Similar to the enlarged M2s present in *Cynarctus*, several other borophagine genera have M2s that are at least somewhat enlarged and/or quadrate to subquadrate in shape, including *Cormocyon*, *Metatomarctus*, *Oxetocyon*, *Paracynarctus*, *Phlaocyon*, *Psalidocyon*, and *Tomarctus*.

Most of the borophagine genera with enlarged M2s tend to exhibit that expansion in the labiolingual, rather than the anteroposterior (mesiodistal), direction. (e.g., Cormocyon, Metatomarctus, Oxetocyon, Paracynarctus, Phlaocyon, Psalidocyon, Tomarctus). Paracynarctus, however, is more expanded anteroposteriorly (mesiodistally), making it more quadrate in shape and more similar to both Cynarctus and USNM 534040 (with both former genera members of the Cynarctina). When posterior (distal) expansion of the M2 does occur within borophagines, it is frequently focused near the lingual portion of the tooth, giving the tooth a general concave curvature on the posterior (distal) surface (e.g., Cormocyon, Metatomarctus, Oxetocyon, Phlaocyon, Psalidocvon. Tomarctus). This tends to make the teeth less quadrate in shape and often more ovular. Again, Paracynarctus exhibits more expansion posteriorly (distally) with less posterior (distal) curvature, similar to Cynarctus and USNM 534040. The protocone is often strongly curved and connects to the metaconule, which is sometimes offset from the plagiocrista (or metaloph) of the protocone. In many borophagines the metacone is differentiated and expanded in the labial and/or posterior (distal) directions (e.g., Cormocyon, Paracynarctus, Oxetocyon, Phlaocyon, Psalidocyon, Tomarctus). Metatomarctus has a slight expansion of the metacone, less than many other borophagines, but still more prominent than in C. wangi (USNM 534040). In addition, protocones are often at least somewhat reduced and strongly bent or curved (e.g., Cormocyon, Oxetocyon, Paracynarctus, Phlaocyon, Psalidocyon, Tomarctus). The metaconule is commonly less prominent and offset from the protocone (e.g., Cormocyon, Metatomarctus, Oxetocyon, Psalidocyon, Tomarctus). Sometimes the hypocone, particularly the apex, is situated more lingually (e.g., Metatomarctus, Paracynarctus, Psalidocyon, Tomarctus). *Cormocyon*, the In internal (lingual) cingulum is symmetrically more distributed. In *Phlaocyon*, the metaconule and hypocone tend to be situated more closely, while the hypocone is more restricted and not nearly as wide. Similar to USNM 534040, a cleft or valley is present in Paracynarctus that separates the entostyle (or pericone) from the hypocone.

#### Discussion

The enlarged M2, with a majority of the expansion in the anteroposterior (or mesiodistal) direction, shows that USNM 534040 compares most closely with M2s known from Cynarctina (includes *Cynarctus* and *Paracynarctus*). However, USNM 534040 can be distinguished from *Paracynarctus* by several features in the latter, including an expansion of the metacone; a somewhat reduced and strongly bent or curved protocone; and a hypocone, particularly the apex, that is situated more lingually. Overall morphology suggests that the tooth most closely resembles teeth attributed to *Cynarctus* and is why it is here referred to a distinct species within said genus.

Cynarctus is thought to be more hypocarnivorous, or consuming less meat and more nonmeat foods, than Paracynarctus and other borophagines (Wang et al., 1999). In addition, the hypocarnivorous features of Paracynarctus and Cynarctus are believed to be derived features with respect to similar conditions present in Metatomarctus and Desmocyon. Similarly, various parts of the dentition of Cynarctus are rather ursid-like, just as the name implies. Originally, Matthew (1902) believed Cynarctus belonged to the Amphicyonidae, and in later studies maintained that it was not a canid (Matthew, 1924, 1930). However, McGrew (1937, 1938) believed Cynarctus belonged to the Procyonidae because of its hypocarnivorous dentition. Finally, Wang et al. (1999) found Cynarctus to be a canid according to features of the middle ear and a member of the Borophaginae according to various cranial and dental features.

*Cynarctus galushai*, the oldest species of the genus, is known from the early to late Barstovian of California. *?Cynarctus marylandica* is known from the early Barstovian of Maryland. *Cynarctus saxatilis* is known from the late Barstovian of Colorado and Nebraska. *Cynarctus wangi* is now known from the late Barstovian of Maryland. *Cynarctus voorhiesi* is known from the late Barstovian of Nebraska. *Cynarctus crucidens*, the youngest species, is known from the early Clarendonian of South Dakota and the early to late Clarendonian of Nebraska and Texas.

Cynarctus galushai exhibits the most primitive, non-hypocarnivorous, features of the genus (Wang et al., 1999). These are especially evident when compared to C. saxatilis, C. voorhiesi, and C. crucidens. Species of Cynarctus exhibit a general decrease in size, coupled with a general reduction of the premolars and an increase in the size, particularly the posterior (or distal) expansion, of the M2. While other features are discussed by Wang et al. (1999), it is the features of the M2 that are vital to the taxonomic identification of USNM 534040 (C. wangi). While these comparisons were discussed previously, it is evident that several features of C. wangi n. sp. are considered derived features by Wang et al. (1999). The posterior (distal) enlargement of C. wangi is prominent, more so than C. galushai and C. saxatilis, although this is exhibited more with the posterior (distal) cingulum than the hypocone. The labial cingulum appears to be reduced lateral to the metacone in C. wangi, along with a lack of expansion labially and/or posteriorly (distally) in the metacone, conditions similar to those in C. saxatilis, C. voorhiesi, and C. crucidens. The metaconule is also enlarged, more similar to C. voorhiesi and C. crucidens. In addition, the lingual cingulum and hypocone are both enlarged, similar to C. saxatilis, C. voorhiesi, and C. crucidens. Wang et al. (1999) mentioned that C. saxatilis lacks a posterior (distal) expansion near the hypocone on the M2, a feature that implies it is more primitive than C. voorhiesi and C. crucidens, which both exhibit this feature. Cynarctus wangi lies somewhat between these two groups, with general posterior (distal) expansion more than C. saxatilis but less prominent than the expansion exhibited by C. voorhiesi and C. crucidens. General

shape of the tooth is more anteroposteriorly (mesiodistally) elongate than *C. saxatilis* and more similar to *C. voorhiesi* and *C. crucidens*. Conversely, the primitive characters of *C. wangi* include a less pronounced posterior (distal) expansion near the hypocone, less developed metastyle, and a relatively weak posterior (distal) cingulum (in comparison to *C. crucidens*). *Cynarctus wangi* also possesses a slightly pronounced labial cingulum toward the anterior (mesial) of the tooth; this is not as pronounced as in *C. galushai*, but more so than in *C. saxatilis*, *C. voorhiesi*, and *C. crucidens*. *Cynarctus wangi* seems to be more derived than *C. galushai* and less derived than *C. voorhiesi* and *C. crucidens* in terms of *Cynarctus* M2 features. In general, it shows more features in common with *C. voorhiesi* and *C. crucidens* than with *C. saxatilis*, implying *C. wangi* is slightly more derived than the latter taxon.

Comparison with the geographically similar ?C. marylandica is important to consider, although this is difficult as the upper dentition of this taxon is not known. Although only an upper M2 is known from C. wangi (USNM 534040), there is a close relationship between the occlusal surfaces of upper M2s and lower m2s that can give insights into what the hypothetical morphology of a lower m2 from C. wangi could look like. As such, occlusal relationships between upper M2s and lower m2s can be used to aid in comparing C. wangi and ?C. marylandica. In members of Cynarctus that exhibit anteroposterior (mesiodistal) expansion of the upper M2, commonly with a pronounced lingual cingulum near the protocone, the corresponding lower m2 often has an expanded talonid basin permitted by a relatively anteriorly situated (or mesially situated) metaconid. The enlarged grinding surface occludes with the upper M2 protocone and/or lingual cingulum. While this morphology in C. wangi (USNM 534040) seems to be distinct from what would be expected in ?C. marylandica and is distinct from C. galushai, it is more similar to C. saxatilis and C. crucidens. Indeed, a hypothetical lower m2 of C. wangi would have an enlarged hypoconid that would occlude with the large trigon basin in USNM 534040. Given the morphological similarities present of the upper M2 morphology of C. wangi (USNM 534040) with C. saxatilis and C. crucidens (particularly the latter taxon), one would expect the corresponding lower m2 morphology to also show similarities. If this is the case, than the lower m2 of C. wangi would be expected to possess more accessory cusps (namely around and including the protostylid [or eoconulid] and metastylid [or postmetaconulid]) than are present in the ?C. marylandica holotype. Indeed, based on occlusal relationships between upper M2s and lower m2s, the morphological differences between the M2 of C. wangi and the m2 of ?C. marylandica are as different as those observed across different Cynarctus species. This agrees with the argument that USNM 534040 represents a distinct cynarctin taxon.

Phylogenetic constraints on canid tooth morphology may lead to the addition and/or complication of cusp morphology of molars, particularly of the M2 in the upper dentition. Rather than re-evolving an upper M3, it may be easier to add complexity to the M2 that is already present, leading to improved and complicated grinding surfaces. This would be especially important for hypocarnivorous animals and in the more hypocarnivorous members of *Cynarctus* and borophagine canids in general. If *C. wangi* is from the Choptank Formation, as it is believed to be, than it would be roughly late Barstovian in age (see Fig. 1). Regardless, it appears to be younger than the holotype of *?C. marylandica* (early Barstovian, Calvert Formation). Therefore, there are two possible scenarios with respect to USNM 534040. Due to geographic and stratigraphic provenance, there is a possibility that USNM 534040 may be referable to *?C. marylandica*. On the other hand, USNM 534040 could be a younger and more derived species of *Cynarctus* or cynarctin borophagine.

If the first scenario were correct, then the generic placement of ?Cynarctus marylandica would also be correct. It would also suggest that ?C. marylandica has M2s that are more derived than C. galushai and C. saxatilis but less derived than C. voorhiesi and C. crucidens. If the second scenario is correct, then the generic placement of ?C. marylandica cannot be commented on. However, here we argue for the second scenario where a closely related species of cynarctin borophagine is present in slightly younger strata in the same geographic region as ?C. marylandica. In addition, it could be that ?C. marylandica may have given rise to C. wangi, which exhibits M2 features more derived than C. saxatilis but less derived than C. voorhiesi and C. crucidens, potentially providing an example of anagenesis. While it is speculative, such a situation could possibly be showing parallel evolution (more hypocarnivorous behavior) between closely related species, one set in western North America and another set in the east. It is noted that multiple borophagine taxa seem to be present in the late early Hemingfordian of Delaware at the Pollack Farm Site (Wang et al., 1999), so multiple borophagine taxa potentially living together is known from another site in the northeastern United States.

#### Summary

USNM 534040 represents a right M2 of a cynarctin borophagine (Canidae: Borophaginae: Cynarctina), here identified as Cynarctus wangi, and is the first carnivoran reported from the middle Miocene Choptank Formation (Chesapeake Group). However, the presence of another cynarctin borophagine from the Chesapeake Group, ?Cynarctus marylandica from the older Calvert Formation, has potential implications. As ?C. marylandica is known only from lower dentition, its generic affinities are uncertain. Indeed, USNM 534040 advocates two possible scenarios regarding its identification. In one, its geographic and stratigraphic provenance imply that the specimen belongs to ?C. marylandica. If this were correct, then the generic placement of ?C. marylandica would also be correct and the taxon would be more derived toward hypocarnivory than C. galushai and C. saxatilis yet less derived than C. voorhiesi and C. crucidens. However, the second possibility is that the specimen represents a distinct cynarctin borophagine that is also present in the Chesapeake Group, but in strata younger than the type specimen of ?C. marylandica. This latter possibility is argued here and may imply that C. wangi represents the next evolutionary stage of ?C. marlyandica and that anagenesis was occurring in *Cynarctus* during this time. Regardless, the presence of C. wangi expands the sparse fossil record of borophagine canids in northeastern North America and furthers our knowledge of the fossil record of terrestrial taxa in this region.

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#### References

- Barbour, E.H., and Cook, H. J., 1914, Two new fossil dogs of the genus *Cynarctus* from Nebraska: Nebraska Geological Survey, v. 4, p. 225–227.
- Berry, C.T., 1938, A Miocene dog from Maryland: Proceedings of the United States National Museum, v. 85, p. 159–161.
- Blackwelder, B.W., and Ward, L.W., 1976, Stratigraphy of the Chesapeake Group of Maryland and Virginia Guidebook 7b (Northeast-Southeast Sections Joint Meeting 1976): Arlington, Geological Society of America, 52 p.
- Bowdich, T.E., 1821, An Analysis of the Natural Classifications of Mammalia, Paris, J. Smith, 115 p.
- Cope, E.D., 1867, An addition to the vertebrate fauna of the Miocene period, with a synopsis of the extinct Cetacea of the United States: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 19, p. 138–156.
- Dahlberg, A.A., (ed.)., 1971, Dental Morphology and Evolution, Chicago, The University of Chicago Press, 350 p.
- Fischer de Waldheim, G., 1817, Adversaria zoologica. Fasciculus primus: Quaedam ad Mammalium systema et genera illustranda: Mémoires de la Société impériale des naturalistes de Moscou, v. 5, p. 357–446.
- Flower, W.H., 1869, On the value of the characters of the base of the cranium in the classification of the order Carnivora, and on the systematic position of *Bassaris* and other disputed forms: Proceedings of the Zoological Society of London, v. 37, p. 4–37.
- Gazin, C.L., and Collins, R.L., 1950, Remains of land mammals from the Miocene of the Chesapeake Bay region: Smithsonian Miscellaneous Collections, v. 116, p. 1–21.
- Harlan, R., 1842, Notice of two fossil mammals from Brunswick Canal, Georgia; with observations on some of the fossil quadrupeds of the United States: American Journal of Science, v. 42, p. 141–144.
- Hayden, F.V., 1873, Report of the United States Geological Survey of the Territories, Washington, DC, US Government Printing Office, p. 259–260.
- Hershkovitz, P., 1971, Basic crown patterns and cusp homologies of mammalian teeth, *in* Dahlberg, A.A., ed., Dental Morphology and Evolution, Chicago, Illinois, The University of Chicago Press, p. 95–150.
- Kretzoi, M., 1943, Kochitis centenii n. g. n. sp., ein altertümlicher Creodonte aus dem Oberoligozän Siebenbürgens: Földtany Közlöny, v. 73, p. 10–17. 190–195.
- Linnaeus, C., 1758, Systema Naturae, 10th ed., v. 1: Stockholm, Laurentii Sylvii, 824 p.
- Matthew, W.D., 1902, New Canidae from the Miocene of Colorado: Bulletin of the American Museum of Natural History, v. 16, p. 281–290.
- Matthew, W.D., 1924, Third contribution to the Snake Creek fauna: Bulletin of the American Museum of Natural History, v. 50, p. 59–210.
- Matthew, W.D., 1930, The phylogeny of dogs: Journal of Mammalogy, v. 11, p. 117–138.
- McGrew, P.O., 1937, The genus *Cynarctus*: Journal of Paleontology, v. 11, p. 444–449.
- McGrew, P.O., 1938, Dental morphology of the Procyonidae with a description of *Cynarctoides*, gen. nov: Geological Series of Field Museum of Natural History, v. 6, p. 323–339.
- McKenna, M.C., and Bell, S.K., 1997, Classification of Mammals: Above the Species Level, New York, Columbia University Press, 631 p.
- Merriam, J.C., 1911, Tertiary mammal beds of Virgin Valley and Thousand Creek in northwestern Nevada: University of California Publications, Bulletin of the Department of Geology, Berkeley, v. 6, p. 199–306.
- Petuch, E.J., and Drolshagen, M., 2010, Molluscan Paleontology of the Chesapeake Miocene, Boca Raton, CRC Press, 180 p.

- Shattuck, G.B., 1904, Geologic and paleontological relations, with a review of earlier investigations, in Clark, W.B., Shattuck, G.B., and Dan, W.H., eds., The Miocene Deposits of Maryland, Baltimore, Maryland Geological Survey, p. 33-94.
- Simpson, G.G., 1932, Miocene land mammals from Florida: Bulletin of the
- Florida State Geological Survey, v. 10, p. 1–41. Simpson, G.G., 1945, The principles of classification and a classification of mammals: Bulletin of the American Museum of Natural History, v. 8, p. 1-350.
- Tedford, R.H., and Hunter, M.E., 1984, Miocene marine-nonmarine correlations, Atlantic and Gulf Coastal Plains, North America: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 47, p. 129–151. Vogt, P.R., and Eshelman, R.E., 1987, Maryland's Cliffs of Calvert: A fossiliferous
- record of mid-Miocene inner shelf and coastal environments, in Roy, D.C., ed.,

Geological Society of America Centennial Field Guide No. 5, Northeastern Section, Boulder, Colorado, Geological Society of America, p. 9-14. Wang, X., Tedford, R.H., and Taylor, B.E., 1999, Phylogenetic systematics of

- the Borophaginae (Carnivora, Canidae): Bulletin of the American Museum of Natural History, v. 243, p. 1-391.
- Weems, R.E., and George, R.E., 2013, Amphibians and nonmarine turtles from the Miocene Calvert Formation of Delaware, Maryland, and Virginia (USA): Journal of Paleontology, v. 87, p. 570–588.
- Wright, D.B., and Eshelman, R.E., 1987, Miocene Tayassuidae (Mammalia) from the Chesapeake Group of the mid-Atlantic coast and their bearing on marine-nonmarine correlation: Journal of Paleontology, v. 61, p. 604-618.

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