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Robert M. HUNT & Daniel A. YATKOLA†

Memorial Stéphane Peigné – Carnivores of the Cenozoic –

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A new species of the amphicyonid carnivore *Cynelos* Jourdan, 1862 from the early Miocene of North America

Robert M. HUNT Jr
Department of Earth and Atmospheric Sciences,
University of Nebraska, Lincoln, NE 68588 (United States)
rhunt2@unl.edu

Daniel A. YATKOLA†
Division of Vertebrate Paleontology,
University of Nebraska, Lincoln, NE 68588 (United States)

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ABSTRACT
The Neogene sediments of the North American midcontinent, undisturbed by tectonism, have long been the source of abundant well-preserved mammalian faunas critical to the definition of the North American Land Mammal ages (NALMA). In western Nebraska the early Miocene interval (*c.* 23 to 16 Ma) is exceptional for its succession of Arikareean and Hemingfordian mammals that establish a biostratigraphic standard for the region. Fluvial sands, silts, and gravels of the paleovalleys and floodplains of the Runningwater Formation (*c.* 18 Ma) have yielded a rich carnivore assemblage of more than 24 species, many of these representing Old World lineages that migrated into North America via the Bering corridor. Amphicyonid carnivores, among the largest of the Runningwater predators, often surpass their Old World equivalents in completeness and condition, and include species of the immigrant genus *Cynelos* Jourdan, 1862. Here is described the only intact skull and jaws of *Cynelos* known from the New World. It is assigned to a new species, *Cynelos stenos* n. sp., that in its size, the association of a cranium with articulated mandibles, and in its dentition (occlusal detail of P4-M3, m1-3) differs from all others of this genus previously reported from both North America and Europe.

KEY WORDS
Nebraska,
Miocene,
Carnivora,
Amphicyonidae,
new species.

RÉSUMÉ
Une espèce nouvelle du carnivore amphicyonidé Cynelos *du Miocène inférieur d'Amérique du Nord.*
Les sédiments néogènes situés au centre de l'Amérique du Nord, n'ont pas été perturbés par des phénomènes tectoniques et, depuis longtemps, ils ont fourni d'abondants fossiles de mammifères bien préservés, essentiels pour la définition des âges des mammifères terrestres d'Amérique du Nord (NALMA). Dans l'ouest du Nebraska, le Miocène inférieur (environ 23 à 16 Ma) est exceptionnel pour sa succession de mammifères arikaréens et hémingfordiens, qui établissent un standard biostratigraphique pour la région. Les sables fluviatiles, les limons et les graviers des paléovallées et des plaines inondables de la formation Runningwater (*c.* 18 Ma) ont donné un riche assemblage de carnivores avec plus de 24 espèces, dont beaucoup représentent des lignées de l'Ancien Monde ayant migré en Amérique du Nord par le corridor de Bering. Les carnivores amphicyonidés, parmi les plus grands des prédateurs de Runningwater, dépassent souvent leurs équivalents du Vieux Monde en termes de complétude et de préservation ; ils incluent des espèces du genre immigrant *Cynelos* Jourdan, 1862. Ici sont décrits le seul crâne intact et les mâchoires d'un *Cynelos* du Nouveau Monde. Il est attribué à une nouvelle espèce, *Cynelos stenos* n. sp. Connue par l'association d'un crâne et d'une mandibule articulée, cette espèce diffère par sa taille et sa dention (détail occlusal de P4-M3, m1-3) de toutes les autres espèces de ce genre précédemment décrites d'Amérique et d'Europe.

MOTS CLÉS
Nebraska,
Miocène,
Carnivora,
Amphicyonidae,
espèce nouvelle.

INTRODUCTION

At the advent of the Miocene, amphicyonine beardogs (Carnivora, Amphicyonidae) began to arrive in the North American midcontinent, representing lineages previously known only in the Old World. During the early Miocene (*c.* 23 to 16 Ma) these species successfully occupied the niche for large predatory carnivores, reaching a climax in the earlier mid-Miocene and then are not seen after *c.* 14 Ma. *Cynelos* Jourdan, 1862 and *Ysengrinia* Ginsburg, 1965 first recognized during the *c.* 22-23 Ma interval in the late and latest Arikareean (Ar3-Ar4) are followed by *Amphicyon*, Lartet, 1836 appearing at *c.* 18 Ma in the early Hemingfordian (He1). In Europe, these genera are represented primarily by dental material due to the prevalence at sites of isolated teeth, partial dentitions in jaws, and unassociated postcranials. Intact crania are exceptional. However, Miocene sediments of the Great Plains on occasion yield well-preserved skulls of these beardogs: here we report the first associated cranium and mandibles of *Cynelos* from North America. It was found with an early Hemingfordian (He1) mammalian fauna in fluvial channel sands of the early Miocene Runningwater Formation in northwest Nebraska. This paper is dedicated to Stéphane Peigné, Muséum national d'Histoire naturelle, Département Histoire de la Terre, Paris, an exceptional colleague and friend long familiar with study of amphicyonid carnivores.

MATERIAL AND METHODS

A detailed description of the unique cranium and associated mandibles of this Hemingfordian *Cynelos* is given here. Its excellent preservation and articulation of jaws with the skull when it was discovered has not been reported previously for *Cynelos* either in the North American Miocene or in the Old World. Species of the genus are primarily based on European dental material defined by size, shape, and occlusal detail of the teeth: here definition of the new species relied on dental comparison with the most similar previously-described western European material of the genus: *Cynelos helbingi* (Dehm, 1950) and *C. lemanensis* (Pomel, 1846). The comparative sample included casts of *Cynelos* assembled in the collections of the University of Nebraska State Museum and the American Museum of Natural History, New York. Estimation of dental variation was obtained from measurements of teeth compiled from the rare *Cynelos* populations from Wintershof-West (Bavaria) and Ulm-Westtangente (Baden-Württemberg), southern Germany, and from the Bridgeport Quarries, Nebraska, U.S.A. Additional analysis of the paleogeographic distribution and dentitions of species of *Cynelos* can be found in Hunt & Stepleton (2015).

Measurements were made with digital calipers to the nearest 0.1 mm; location of dental measurements are shown in Figure 1 and 2. Comparative craniodental data are provided in Tables 1 to 3. The measurements for Table 2 were obtained by enlargement of figures 46 and 47 from Dehm (1950) with the data points then projected to the ordinate and abscissa of each of his graphs and the resulting measurement recorded in Table 2.

Abbreviations

AMNH	American Museum of Natural History, New York;
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich;
F:AM	Frick Collection, American Museum of Natural History, New York;
MNHN	Muséum national d'Histoire naturelle, Paris;
MHNL	Muséum d'Histoire naturelle de Lyon, Lyon;
OCPC	Orange County Paleontological Collection, The Cooper Center, Dept. of Geological Sciences, California State University, Fullerton;
SMNS	Staatliches Museum für Naturkunde, Stuttgart;
UNSM	Vertebrate Paleontology, University of Nebraska State Museum, Lincoln.

SYSTEMATICS

Order CARNIVORA Bowdich, 1821
Infraorder ARCTOIDEA Flower, 1869
Family AMPHICYONIDAE Haeckel, 1866
Subfamily AMPHICYONINAE Trouessart, 1885

Genus *Cynelos* Jourdan, 1862

Cynelos stenos n. sp.
(Figs 3-6; Table 1)

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"*Cynelos* n. sp. II" – Hunt 1998: 211.

Cynelos sp. B – Hunt 2002: 35.

HOLOTYPE. — UNSM 44723, a cranium and associated mandibles, with both left and right upper and lower dentition (P1-M3: p1-m3); the left P1-p1 each represented by a single alveolus; the left upper and right lower canines; left I2 and left i3. A partial femur and fragments are attributed to the cranial material. Collected by D. A. Yatkola and William Rovnak, University of Nebraska State Museum. Daniel Yatkola discovered UNSM 44723 during his doctoral study of the Miocene stratigraphy and mammalian fauna of northwest Nebraska (Yatkola 1978).

ETYMOLOGY. — From the Greek "stenos" (στενός) (= narrow). The species nomen emphasizes the narrowness of the skull in dorsal view relative to the broader-skulled large contemporary early Miocene amphicyonids *Amphicyon galushai* Hunt, 2003 and *Daphoenodon* (*Borocyon*) *robustum* (Peterson, 1910).

TYPE LOCALITY. — UNSM 44723 was found in a basal arkosic sand and gravel channel at the stratotype locality of the Runningwater Formation (Cook, 1965), Box Butte Co., northwest Nebraska. The site was designated Runningwater Quarry by its discoverer M. F. Skinner of the American Museum's Frick Laboratory, and was later reopened by UNSM under the direction of Daniel Yatkola. The fauna is conserved in the F:AM and UNSM collections.

GEOLOGICAL AGE. — Early Miocene *c.* 18 Ma.

DESCRIPTION

Cynelos stenos n. sp. (UNSM 44723) represents the first occurrence in the North American Miocene of a complete skull of the genus with mandibles in articulation. Only two other skulls of *Cynelos* are known in the early Miocene of North America: the skull of *Cynelos idoneus* (AMNH 20495) from the late Hemingfordian (He2) of western Nebraska and the skull of *Cynelos malasi* (OCPC 21791) from the latest Arikareean (Ar4) of southern California. No skulls were found with the *Cynelos* population sampled from the early Hemingfordian Bridgeport Quarries, western Nebraska, where the genus was represented by over 60 isolated cheek teeth, two maxillae, three mandibles, and numerous postcranials. The skulls attributed to the genus in North America from the early middle Miocene (*c.* 14.8 to 16 Ma) are those of the large early Barstovian *C. sinapius* from the Olcott Formation, Sioux County, Nebraska, including one (AMNH 18257: Matthew 1924: figs 22-23) very similar in form to the skull of *C. stenos* n. sp. except for its much larger size. Such narrow skulls probably characterize

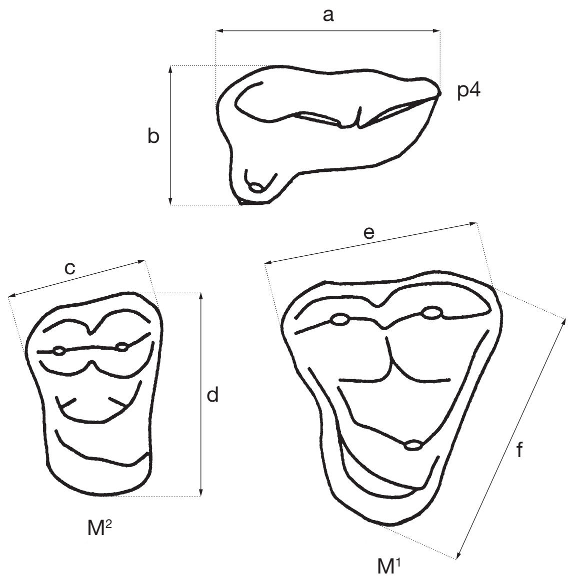

FIG. 1. — Dental measurements for species of the amphicyonid *Cynelos* Jourdan, 1862. Abbreviations: **a**, greatest length of P4 from mesial base of paracone to distal limit of metastylar blade; **b**, greatest width of P4 from lingual border of protocone to labial base of paracone; **c**, greatest labial length of M2; **d**, greatest M2 width from paracone to lingual cingulum; **e**, greatest labial length of M1; **f**, greatest M1 width from paracone to lingual cingulum.

the Miocene species of *Cynelos* in North America, including the terminal species, *C. sinapius*.

Cranium (Figs 3; 4)

The skull is essentially uncrushed preserving its cranial proportions and a nearly intact dentition except for damaged canines and the loss of incisors. It is exceptional in retaining the basicranial region. The sutures of the cranium remain open in the rostral area but due to age have closed elsewhere or are obscured by breakage.

Viewed from above, the cranium is quite narrow compared to the larger contemporary amphicyonid species (*Amphicyon galushai*, *Daphoenodon* [*B.*] *robustum*) that possess much broader skulls. Relative to skull length, the rostrum is short and rather constricted at the level of the P2. Behind this constriction the palate broadens to include the crushing dentition comprising the prominent molars and carnassials. At the posterior palatal border, the nasal cavity opens at the nasal choanal aperture into a ventrally open narrow nasopharyngeal fossa (9 cm in length, 2 cm in width) that continues to the basicranial region. The considerable breadth of both the basicranium and palate contrast with the intervening narrow interorbital area. Within the broad basicranium the auditory regions have been preserved with minimal damage. Despite loss of the ventral floor, the auditory bulla retains a capsular flask-like form with short bony external auditory meatus that differs from the more plesiomorphic condition of the bulla in the skull of *Cynelos lemanensis* from St.-Gérand, France (Hunt & Stepleton 2015: fig. 8). The *C. stenos* n. sp. bulla was not large, 2 cm in width, and only slightly inflated.

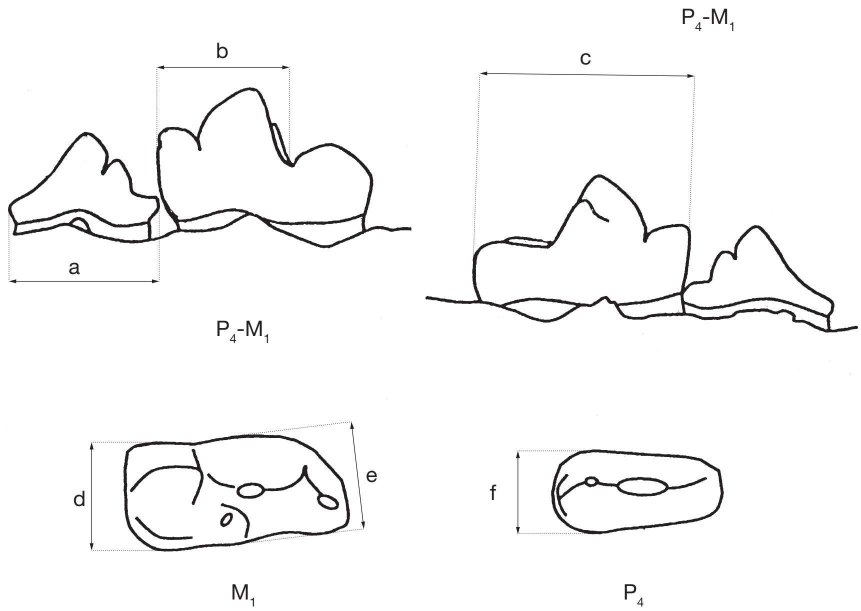

FIG. 2. — Dental measurements for species of the amphicyonid *Cynelos* Jourdan, 1862. Abbreviations: **a**, greatest length of p4; **b**, m1 trigonid length from mesial edge of paraconid to central distal base of protoconid; **c**, greatest length of m1; **d**, greatest width of the m1 talonid (also for m2); **e**, greatest width of the m1 trigonid (also for m2); **f**, distal width of p4 (and for p2-p3).

TABLE 1. — Measurements (in mm) of length and width of the lower teeth of *Cynelos stenos* n. sp. (UNSM 44723, holotype): upper row, right dentition; lower row, left dentition. Distal width is measured for premolars; trigonid width for m1-3.

p1	p2	p3	p4	m1	m2	m3	p1-4	m1-3	p2-m2
6.3 × 3.7	10.3 × 4.8	11.9 × 5.5	16.4 × 9.1	25.3 × 12.4	16.5 × 12.1	12.8 × 9.7	60.4	53.8	90.0
–	10.3 × 4.9	12.1 × 5.5	16.0 × 8.9	25.2 × 12.4	16.4 × 12.2	12.8 × 9.7	–	54.6	92.3

Measurements of length and width of the left upper teeth (in mm) of *Cynelos stenos* n. sp. (UNSM 44723, holotype).

P1	P2	P3	P4	M1	M2	M3	P1-M3	P2-M3	P2-M2
7.3 × 5.5	11.1 × 4.5	12.8 × 6.2	22.4 × 14.2	19.2 × 24.6	15.0 × 22.2	9.2 × 14.9	109.6	96.5	91.6

Measurements of the cranium (in mm) of *Cynelos stenos* n. sp. (UNSM 44723, holotype).

Skull length	324 mm (premaxillary border to tip of inion)
Postorbital length	18 cm (postorbital process to tip of inion)
Basilar length of skull	29 cm
Palatal width at P4-M1 embrasure	*c.* 54 mm (*c.* 59 mm, 5 mm added due to crushing)
Rostral constriction at P2	*c.* 38 mm (*c.* 43 mm, 5 mm added due to crushing)
Rostral expansion at canines	*c.* 50 mm (*c.* 55 mm, 5 mm added due to crushing)
Palatal length	14 cm (premaxillary border to posterior limit of palatine)
Palatal width	*c.* 72 mm (transverse width including M1s)
Basioccipital, greatest width	37 mm
Occipital condylar width	50 mm
Frontal width	70 mm (measured between the postorbital processes)
Sagittal crest	33 mm (height above braincase)
Nasal length	80 mm
Maxilla height above P4	*c.* 73 mm
Preorbital skull length	120 mm (orbital margin to tip of premaxilla
Postorbital skull length	208 mm (orbital margin to inion)
Orbital margin to occipital condyle	181 mm (measured from lacrimal border)

In profile the skull has a short, deep rostrum expanded at the canines that slopes gradually upward to the forehead to form a broad frontal region housing inflated frontal sinuses at the level of the postorbital processes. From the frontals the skull roof narrows posteriorly, forming a tall thin sagittal crest 12 cm in length and 5 mm in width that reaches its maximum height (4 cm) above the braincase. The crest then tapers to its termination at the inion. The braincase

Fig. 3. — *Cynelos stenos* n. sp., UNSM 44723, Runningwater Formation, Runningwater Quarry (early Hemingfordian), Box Butte Co., Nebraska. Cranium in right lateral view (**A**) and in ventral view (**B**). Scale bars: 5 cm.

volume is not large and suggests the less developed brain described by Radinsky (1980). The greater part of the skull (⅔rds) lies behind orbits that are set low below the frontal region: here what seems an exceptionally narrow and deep interorbital area intervenes between the orbits and the braincase – much of this interval was occupied by the large temporal and pterygoid musculature essential to the feeding mechanics of this species.

Mandibles (Fig. 5)

The conjoined mandibles preserve nearly the complete lower dentition; the dentaries are firmly interdigitated at the mandibular symphysis to form an incipient ankylosis in this mature individual. The jaws are elongate (length, *c.* 23 cm: articular condyle to canine) in keeping with the length of the skull and are not especially deep below the teeth (4.3 cm below m2). Behind the rather shallow masseteric fossae are wide articular condyles, set low at the back of the mandible nearly at the level of the toothrow, indicating nearly simultaneous occlusion of carnassials and molars (P4-M3, p4-m3) at jaw closure.

Upper Dentition (Fig. 6; Table 1)

The dentition is fully erupted indicating from its moderate wear a mature adult; the canines and slender rostrum suggest a female. The right canine alveolus (L × W, 21.1 × 13.9 mm) retained the root. The damaged left canine (L × W, 18.2 × 12.5 mm, measured at the base of the enamel) is broken off at the tip but has mesial and distal thin enamel ridges. All

Fig. 4. — *Cynelos stenos* n. sp., UNSM 44723, Runningwater Formation, Runningwater Quarry (early Hemingfordian), Box Butte Co., Nebraska. Cranium in dorsal view. Note the narrow cranium, constricted rostrum, broad frontal region, and tall thin sagittal crest above the small braincase. Scale bar: 5 cm.

Table 2. — Measurements (in mm) of the m1 and m2 from *Cynelos helbingi* (Dehm, 1950), Wintershof-West, Bavaria (from Dehm 1950). Due to a tapered talonid, Dehm (1950) measured m2 width across the trigonid.

	m1 L	m1W	m2L	m2W
	27.1	13.2	17.7	11.3
	25.8	12.5	16.9	10.9
	25.8	12.2	16.8	10.6
	25.4	12.0	16.7	10.7
	25.3	11.9	15.9	10.9
	25.3	11.8	15.1	10.2
	25.2	11.3	15.0	10.2
	25.2	11.2	14.8	9.7
	25.0	11.4	14.7	9.9
	24.8	11.5	14.7	10.3
	24.4	10.9	14.3	9.5
	24.3	10.7	13.9	9.3
	23.8	11.3	13.8	8.8
	23.6	10.3	13.4	8.3
	23.5	9.9	13.3	8.3
	23.4	9.7	13.2	9.7
	23.2	10.1	13.2	8.6
	23.2	10.3	13.0	9.2
	23.0	10.2	12.9	8.4
	22.9	10.8	12.8	8.8
	22.7	10.5	12.7	8.2
	22.5	10.1	–	–
	22.2	10.1	–	–
	21.5	9.9	–	–
	21.5	9.7	–	–
	20.8	9.8	–	–
	19.8	9.2	–	–
N	27	27	21	21
mean	23.75	10.83	14.51	9.61
standard deviation	1.71	0.99	1.53	0.98
CV	7.2	9.2	10.5	10.2

incisors were lost except the left I1 (L × W, 6.3 × 4.1 mm); however, the I3 alveoli are large relative to those for I1-I2 showing that I3 was much larger than the small I1-I2.

The P1-P3 are reduced and separated by diastemata. The left P1 is represented by a small circular alveolus and is separated from P2 by 5 mm. The low P2 (L × W, 11.1 × 4.5 mm) has two roots, a single apical cusp with a mesial and more extended distal slope and short distal shelf; the P2-P3 diastema is 9.2 mm. P3 has the same form as P2 but is larger (L × W, 12.8 × 6.2 mm) with a wider distal shelf and a sloping mesial face; the P3-P4 diastema is 3.2 mm. The P4 is short relative to the molars; feeding on hard material has blunted the once-sharper paracone and metastylar blade. The small low protocone does not protrude far lingually and is slightly retracted. A thin enamel ridge runs from the P4 paracone to a weak parastyle and there is a weak labial cingulum. The M1-M2 are moderately worn teeth forming a formidable crushing platform together with the small M3. The M1 paracone is larger and although worn was slightly taller than the metacone. A cingulum occupies the labial margin and extends a short distance to the mesial base of the paracone and distal base of the metacone. The cingulum is weak to absent on the mesial and distal sides of the tooth but expands to form a prominent lingual cingulum. The M1 protocone was closer to the mesial border of the tooth and is situated at the lingual apex of the protocone basin. A thin straight mesial enamel ridge extends from the protocone to a weak paraconule at the base of the paracone. A thin slightly curved distal ridge extends from the protocone to the base of the metacone but without a metaconule: the mesial and distal ridges enclose the protocone basin. The M2 is somewhat smaller than M1 – its protocone forms the apex of an arcuate crest but, where the protocone of M1 is nearer the mesial margin of the tooth, the M2 protocone is more centrally situated. The M2 metacone is slightly reduced relative to the paracone. On M2 the straight mesial and curved distal ridges are weaker without evident conules. The M2 protocone is worn as in M1 but where in M1 the mesial ridge ended at the base of the paracone, in M2 the mesial ridge reached the mesial border of the tooth to join the cingulum; there is a weak swelling along the ridge. In occlusal view M1 and M2 both extend lingually to form an enamel platform, each tooth surrounded by a prominent lingual cingulum. The small M3 contacted the distal margin of M2; a small low paracone and much reduced metacone are aligned along its labial side. A shallow basin bordered mesially by a weak ridge lies between protocone and paracone; the distal ridge is absent. The small lingual extension of M3 is surrounded by a marked cingulum.

Fig. 5. — *Cynelos stenos* n. sp., UNSM 44723, Runningwater Formation, Runningwater Quarry (early Hemingfordian), Box Butte Co., Nebraska. Right and left associated mandibles. Scale bar: 5 cm.

Fig. 6. — *Cynelos stenos* n. sp., UNSM 44723, Runningwater Formation, Runningwater Quarry (early Hemingfordian), Box Butte Co., Nebraska. Palatal view of the cranium with right P2-M3 (broken P1) and left P3-M3, partial P2, and P1 alveolus. Plant roots have eroded the enamel on the right M1-M2. Scale bar: 3 cm.

Lower Dentition (Fig. 5; Table 1)

The incisors in this individual are damaged; however, only i2 and i3 were present in life – the i1s failed to erupt due to marked narrowing of the symphyseal region. The heavily worn left i3 (L × W, 6.8 × 5.4 mm) is the only surviving incisor; only the broken root of the left i2 remains. The right i2-i3 alveoli are present and show that the root of i3 extended beneath the root of i2 due to crowding of the incisors in the symphysis – Dehm (1950: 24) also observed this in *C. helbingi*. The well-worn right canine is 16.4 mm in length, 11.5 mm in width measured at the base of the enamel. Relative to their evident length, the mandibles are rather gracile and not deep even below the molars. The p1-p3 are much reduced compared to p4 and are separated by diastemata: 14.6 mm between canine and p1; 3.4 mm between p1-p2; 9.2 mm between p2-p3; 3.5 mm between p3-p4. The p4 is much larger than p3, and wide distally where it abuts the mesial face of m1. The p2-p3 do not show wear and only the

Table 3. — Measurements (in mm) of length and width of m1 and m2 of *Cynelos lemanensis* (Pomel, 1846) compared to *Cynelos stenos* n. sp. Abbreviations: **Wtri**, trigonid width; **Wtal**, talonid width. Ulm data from Peigné & Heizmann (2003).

Mus. No.	m1 L	m1 Wtri	m1 Wtal	m2 L	m2 Wtri	m2 Wtal	m1-m2 L
Cynelos lemanensis							
AMNH 11005	21.8	9.9	10.1	15.3	9.7	10.3	37.1
MHNL-La85 type	20.5	9.2	9.6	–	–	–	–
AMNH 97778	20.0	8.8	8.3	14.3	9.6	9.2	34.5
AMNH 11004	18.6	8.1	8.4	12.2	7.8	8.2	30.7
Ulm-Westtangente maximum	22.4	10.3	11.0	15.0	10.3	–	37.4
Ulm-Westtangente minimum	18.6	8.4	8.4	12.75	8.5	–	31.35
Cynelos stenos n. sp.							
UNSM 44723	25.3	12.4	12.0	16.5	12.1	10.8	40.6

tip of the principal cusp of p4 is slightly worn in contrast to the worn m1-m2 where processing of hard gristle and bone is evident in this mature individual.

In youth the paraconid and protoconid of the m1 may have 'sheared' for a time against the paracone/metastylar blade of P4 but in this individual the m1 protoconid and paraconid have become blunted from wear, as has the tip of the metaconid. The tall M1 paracone deeply grooved the distolabial corner of the m1 protoconid while the prominent m1 hypoconid occluded between the M1 paracone and metacone when entering the protocone basin. This latter action akin to a mortar-in-pestle created the mesial part of the m1-m3 crushing platform.

The m2 trigonid occluded between M1 and M2 where its robust protoconid-metaconid and small mesial basin abraded the distolabial corner of M1, and the mesial face of the M2 paracone. The low m2 hypoconid occluded against the M2 paracone, then as the bite closed, the broad m2 talonid contacted the M2 lingual platform. The slightly elevated mesial face of m3 with weak protoconid occluded with the distal face of the M2 metacone; the distal m3 with low hypoconid abraded the low platform comprising the entire M3. The occlusion of m2-m3 with the distal margin of M1 and with M2-M3 created the distal half of the crushing surface. The pronounced wear on P4-M1-M2 and m1-m2 of *C. stenos* n. sp. indicates that food processing was concentrated on these teeth. In this individual the orientation of wear surfaces on cusps of P4-M2 and m1-m2 when occluded suggests that this type of wear results primarily from crushing hard items such as bone rather than by direct tooth-on-tooth contact.

Food Processing

With increasing age, molars and also carnassials of this amphicyonine beardog seem to function more in crushing than in shearing or slicing. Crushing occurred as carnassials as well as molars came into near simultaneous occlusion with jaw closure because of the placement of the articular condyles at the level of the toothrow. Often in living larger carnivores with slicing carnassials, rotation of the mandible about its long axis makes possible a close registration of P4 with m1 for cutting meat during jaw closure. However, ankylosis at the mandibular symphysis in *C. stenos* n. sp. prevented this axial rotation and precise carnassial registration so that shear has been subordinated to a crushing role. The crushing function becomes obvious when the skull and mandibles are articulated: both left and right upper and lower cheek teeth occlude without requiring ipsilateral-contralateral shifting of the lower jaws during mastication. Whether grinding by the molars (as opposed to crushing) occurred during food processing is doubtful due to a limited capability of the mandibular articular condyles to shift from side-to-side within the glenoid fossae of the skull.

Comparison

Cynelos stenos n. sp. (Table 1) is distinguished from the smaller European species of the genus, *C. crassidens* (Filhol, 1874), *C. rugosidens* (Schlosser, 1899), and *C. schlosseri* (Dehm, 1950), and the North American *C. malasi* Hunt and Stepleton, 2015 by its much larger overall size of skull, mandibles, and dentition. *Cynelos stenos* n. sp. is more similar in size to the European *C. lemanensis* and *C. helbingi* but differs from the former by much larger cheek teeth (P4, M1, M2, see Hunt & Stepleton 2015: figs 9-11; m1, m2, Table 3) including cheek teeth of the *C. lemanensis* population from Ulm-Westtangente (Peigné & Heizmann 2003). P4, M1, M2 of *C. stenos* n. sp. exceed in size all but the largest individuals of the Bavarian *C. helbingi* (Hunt & Stepleton 2015: figs 9-11) as do m1 and m2 (Tables 1, 2; Figs 9, 10). Consequently, *C. stenos* n. sp. has evolved a broader molar platform (comprising occlusion of M1, M2, M3 with m2, m3, and the m1 talonid) for crushing hard foods than is seen in *C. helbingi* and in *C. lemanensis*. All younger North American species of *Cynelos* from the late Hemingfordian (*C. idoneus* Matthew, 1924, basilar length of skull, 33-34 cm) and early Barstovian (*C. sinapius* Matthew, 1902, basilar length, 39-44 cm) are larger carnivores than *C. stenos* n. sp. (basilar length, 29 cm) and both species continue the further expansion of the molar platform.

ANALYSIS AND DISCUSSION

When the dentition of *C. stenos* n. sp. is compared among the European species of the genus, there is an evident similarity to teeth of the large sample of *C. helbingi* from Wintershof-

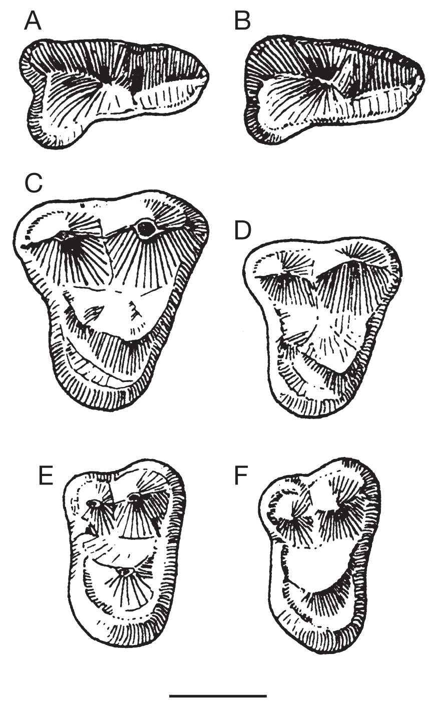

Fig. 7. — Variation in size and occlusal form of P4, M1, and M2 of *Cynelos helbingi* (Dehm, 1950), Wintershof-West, southern Germany (from Dehm 1950: figs 29, 30; 35-37, 39): **A**, P4 mesial border indented, protocone prominent (12395); **B**, P4 mesial border not indented, protocone recessed (12387); **C**, large M1, labial border long (12347); **D**, small M1(12361); **E**, M2, mesial border straight, metacone reduced (12376); **F**, M2, mesial border irregular, metacone not as reduced (12379). Catalog numbers from Sammlung München 1937 II. Scale bar: 1 cm.

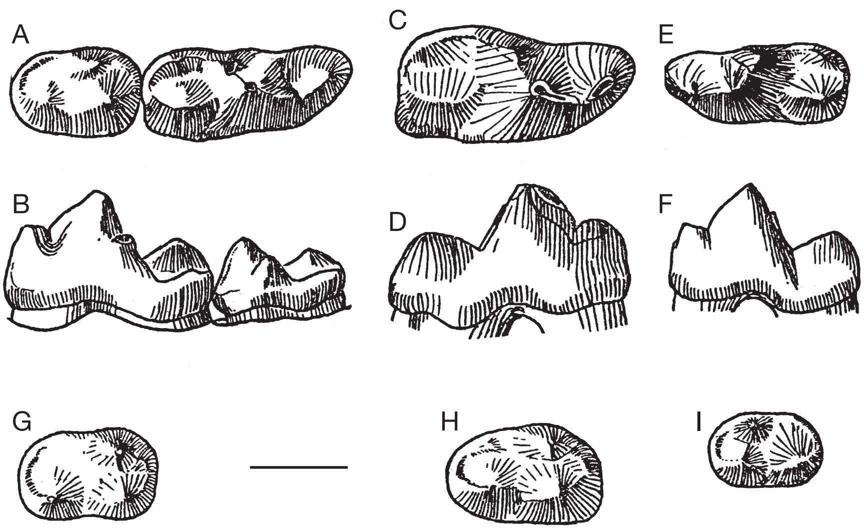

Fig. 8. — Variation in size and occlusal form of m1, m2, and m3 of *Cynelos helbingi* (Dehm, 1950), Wintershof-West, southern Germany (from Dehm 1950: figs 18, 21-25): **A**, **B**, holotype m1-m2 of the species, occlusal and lingual views (12293); **C**, **D**, large m1 in occlusal and labial views (12315); **E**, **F**, small m1, occlusal and labial views (12338); **G**, right m2, intermediate size (12842); **H**, right m2, large (12836); **I**, left m2, small (12834), all m2s in occlusal view. Catalog numbers from Sammlung München 1937 II. Scale bar: 1 cm.

West (Dehm 1950). Although dentitions in jaws were rare at the Bavarian locality, Dehm's analysis of the numerous upper and lower teeth provided a detailed description of the dental characteristics of the species and showed that the teeth from this locality varied substantially (Figs 7; 8). Here the size, form, and occlusal cusp patterns of the teeth of *C. stenos* n. sp., are compared with those dental features in the Wintershof-West sample. Of particular interest is that slight differences in tooth shape and in the form of cusps, cuspules, thin crests, incisures, and cingula can be interpreted as enamel variants specific to local populations of the genus as observed for *C. helbingi* by Dehm (1950) and more recently for *C. lemanensis* by Peigné & Heizmann (2003) and apparently lack a significant role in occlusal mechanics.

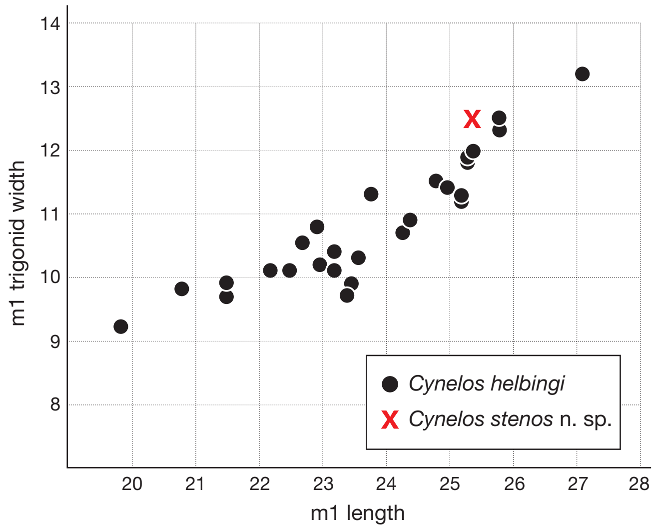

Fig. 9. — Bivariate graph of m1 dimensions (in mm) of *Cynelos helbingi* (Dehm, 1950) (Wintershof-West, southern Germany) relative to m1 of *Cynelos stenos* n. sp. (UNSM 44723, western Nebraska). *Cynelos helbingi* measurements from Dehm (1950).

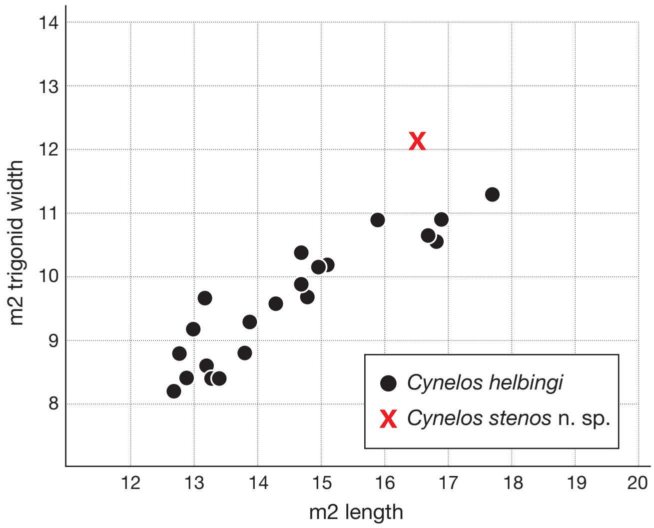

Fig. 10. — Bivariate graph of m2 dimensions (in mm) in *Cynelos helbingi* (Dehm, 1950) (Wintershof-West, southern Germany) relative to m2 of *Cynelos stenos* n. sp. (UNSM 44723, western Nebraska). *Cynelos helbingi* data from Dehm (1950). Note the larger broad m2 in *C. stenos* n. sp.

Lower teeth: analysis

The dimensions of m1-m2 of *C. stenos* n. sp. (Table 1) and dimensions of the diagnostic m1-m2 of *C. helbingi*, Table 2) are compared graphically (Figs 9; 10).

Both lengths and widths of m1 and the length of m2 of *C. stenos* n. sp. fall in the uppermost part of the range for these measurements in *C. helbingi*; significantly, the width of the crushing m2 trigonid exceeds those of the entire sample at Wintershof-West. However, lengths (16.0, 16.4 mm), distal widths (8.9, 9.1 mm), and heights (10.3, 10.3 mm) of p4 of *C. stenos* n. sp. exceed these measurements for all 10 p4s of the Wintershof sample and the larger m3 of *C. stenos* n. sp. exceeds in length and width all individuals of *C. helbingi*.

Upper teeth: analysis

A bivariate graph of P4 length and width places *C. stenos* n. sp. beyond the largest individuals of *C. helbingi* including the large teeth assigned to *C. cf. C. helbingi* by Ginsburg (2000) from Selles-sur-Cher (France). Moreover, similar bivariate graphs for both M1and M2 show *C. stenos* n. sp. exceeds the entire sample of *C. helbingi* except for the single largest individual. Graphs of these dimensions of P4, M1, and M2 for *C. helbingi*, *C. lemanensis*, and other species of *Cynelos* appear in Hunt & Stepleton (2015).

CONCLUSION

Variation in size, shape, and occlusal cusp pattern in teeth is common among species of *Cynelos*. Peigné & Heizmann (2003: 103, SMNS collection) described evident occlusal variation in *C. lemanensis* from the Ulm-Westtangente population: for example, in 8 individuals the only constant features of M1 were the presence of the transversal enamel crest and a crest at the base of the paracone. The existence of an M1 paraconule or metaconule, and occurrence of crests at the bases of the metacone and metaconule seen in some *C. lemanensis*, all proved to be variable traits.

Dehm (1950: 24-27) was aware of similar marked variation among the teeth of *C. helbingi* at Wintershof-West, describing and emphasizing the differences that existed in the diagnostic cheek teeth (p4, m1, m2; P4, M1, M2) [at that time Dehm placed both *helbingi* and *lemanensis* in the genus *Amphicyon*]. Dehm (1950: 28) also considered the amount of variation that he observed in the Aquitanian *Amphicyon lemanensis* Pomel, 1846 from St.-Gérand-le-Puy and from Ulm to be comparable to the amount of variation he had identified in *Amphicyon helbingi* at Wintershof-West (Figs 7; 8). The size and form of the teeth in both species varied in such a similar manner that he restricted his analysis to a limited number of distinguishing features: teeth of *C. helbingi* relative to *C. lemanensis* showed more prominent cusps and occlusal relief on M1 and m1 and in proportional relations of the molars.

Having considered the variation recognized for the diagnostic cheek teeth of *Cynelos*, we conclude that the teeth of *C. stenos* n. sp., while comparing most closely with *C. helbingi*, exceed the limits of dental variation in the Bavarian beardog. Some occlusal features of cheek teeth in *C. helbingi* can be recognized in the molars and carnassials of *C. stenos* n. sp. The form and cusp pattern of m1 of *C. stenos* n. sp. compares well with the *C. helbingi* holotype m1(BSP-1937-II-12293) and the striking mesial position of the m2 trigonid confined to the front of the tooth occurs in both species. Most obvious is the tall M1 paracone that incises the distal protoconid of m1, cutting a distinct groove; the mesial placement of the M1 protocone and centrally situated M2 protocone; and the form of the mesial and distal crests enclosing the central basin of M1-M2. Yet M1 shape differs in the two species: the mesial border of M1 in *C. stenos* n. sp. is concave but is straight in *C. helbingi*; and the more developed lingual cingulum in the former species entirely surrounds the protocone whereas in *C. helbingi* it is restricted to the distolingual corner. M2 in *C. stenos* n. sp. is more quadrate in form and a wider and larger molar than all but a single individual of *C. helbingi.* Although P4 in *C. stenos* n. sp. matches one figured by Dehm (1950: 26) in form and cusp placement, it is larger than all P4s of *C. helbingi*, while the size of M1-M2 of *C. stenos* n. sp. falls at the upper limit for these molars in *C. helbingi*. Notably in *C. stenos* n. sp., the quadrate M2 occludes with a massive m2 broader than the entire m2 sample of *C. helbingi* (Fig. 10), identifying a distinguishing trait — the greater distal expansion of the molar platform in the Nebraska carnivore relative to *C. helbingi*. If intact maxillary and mandibular dentitions of *C. helbingi* had survived, we probably would find the largest individuals similar to *C. stenos* n. sp. in many dental characteristics and occlusal mechanics but would find lacking the nascent distal expansion of the molar row evidenced by M2-3/m2-3 in *C. stenos* n. sp. These differences reflect the evolving trend in early and mid-Miocene *Cynelos* species to develop a larger molar platform for crushing yet with more limited precision in shearing by the carnassials.

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REFERENCES

Cook H. J. 1965. — Runningwater Formation, Middle Miocene of Nebraska. *American Museum Novitates* 2227: 1-7. http://hdl.handle.net/2246/4666

Dehm R. 1950. — Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. *Abhandlungen der Bayerischen Akademie der Wissenschaften (Mathematisch-natur-wissenschaftliche Klasse)* 58: 1-141.

Ginsburg L. 2000. — Chronologie des dépôt miocènes du Blésois à la Bretagne. *Symbioses, n. sér.* 2: 3-16.

Hunt R. M. Jr 1998. — Amphicyonidae, *in* Janis C., Scott K. & Jacobs L. (eds), *Tertiary Mammals of North America*. Cambridge University Press, Cambridge and New York: 196-227.

Hunt R. M. Jr 2002. — New amphicyonid carnivorans (Mammalia, Daphoeninae) from the early Miocene of southeastern Wyoming. *American Museum Novitates* 3385: 1-41. https://doi.org/10.1206/0003-0082(2002)385<0001:NACMDF>2.0.CO;2

Hunt R. M. Jr 2003. — Intercontinental migration of large mammalian carnivores: earliest occurrence of the Old World beardog *Amphicyon* (Carnivora, Amphicyonidae) in North America. *Bulletin of the American Museum of Natural History* 13 (279): 77-115. https://doi.org/10.1206/0003-0090(2003)279<0077:C>2.0.CO;2

Hunt R. M. Jr & Stepleton E. 2015. — A skull of the immigrant Eurasian beardog *Cynelos* (Carnivora, Amphicyonidae) from the early Miocene of southern California. *Journal of Vertebrate Paleontology* 35 (1): e891229(1-19). https://doi.org/10.1080/02724634.2014.891229

Matthew W. D. 1924. — Third contribution to the Snake Creek fauna. *Bulletin of the American Museum of Natural History* 50 (2): 59-210. http://hdl.handle.net/2246/1312

Peigné S. & Heizmann E. P. J. 2003. — The Amphicyonidae (Mammalia: Carnivora) from Ulm-Westtangente (MN2, Early Miocene), Baden-Württemberg, Germany – Systematics and ecomorphology. *Stuttgarter Beiträge zur Naturkunde, Ser. B (Geologie und Paläontologie)* 343: 1-133.

Peterson O. A. 1910. — Description of new carnivores from the Miocene of western Nebraska. *Memoir of the Carnegie Museum* 4 (5): 205-278. http://www.biodiversitylibrary.org/page/34978348

Radinsky L. 1980. — Endocasts of amphicyonid carnivorans. *American Museum Novitates* 2694: 1-11. http://hdl.handle.net/2246/3529

Yatkola D. A. 1978. — *Tertiary Stratigraphy of the Niobrara River valley, Marsland Quadrangle, Western Nebraska. Nebraska Geological Survey Paper*. Vol. 19: Conservation & Survey Division, University of Nebraska, Lincoln: 1-66.

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