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A NEW AMPHICYON FROM THE DEEP RIVER MIOCENE

BY PAUL O. McGREW
ASSISTANT, PALEONTOLOGY

In 1898 Mr. Elmer S. Riggs and Dr. Oliver C. Farrington obtained a small collection of mammals from the Deep River beds of Montana. *Mesogaulus ballensis* has been described from this collection (Riggs, 1899) and a new species of *Amphicyon* is described here.

The specimen of *Amphicyon*, consisting of the anterior portion of skull, jaws, axis, and proximal end of an ulna, was collected by Mr. Riggs on Rabbit Creek, about ten miles northwest of White Sulphur Springs, Montana, and hence almost in the center of the fossiliferous area indicated by Scott (1898). *Merychippus*, *Dromomeryx*, and an undetermined merycochoerid were obtained from the same locality and apparently from the same horizon. This association indicates upper Miocene or true Deep River age (Douglass, 1903).

Amphicyon riggsi[1] sp. nov.

Holotype.—F.M. No. P12029. Anterior portion of skull with complete dentition (except for $M^{\underline{3}}$), jaw, proximal portion of ulna, and axis. $C^{\underline{1}}$ and $M_{\overline{3}}$ not fully erupted.

Locality and horizon.—Deep River beds, about three miles above mouth of Rabbit Creek, ten miles northwest of White Sulphur Springs, Montana.

Diagnosis.—Small (see Measurements, p. 346); premolars unreduced; upper premolars not widely spaced (relatively); lower premolars closely spaced; protocone of $P^{\underline{4}}$ prominent, situated internal to and but little anterior to the paracone, directed lingually and but slightly anteriorly; $P_{\overline{4}}$ with small posterior accessory cusp.

Discussion.—Upper dentition: The incisors are simple, relatively large, and widely spaced. $I^{\underline{1}-\underline{2}}$ each bears a posterior basal shelf

[1] For Mr. Elmer S. Riggs, who collected the specimen.

but no accessory cuspules. $I^{\underline{3}}$ is large, robust, and caniniform, with a low, external, vertical ridge, and a greatly expanded posterior base.

The canine is large, long, and but slightly recurved. It bears a rather sharp posterior ridge and a low anterior one.

The first premolar, lying 2 mm. behind the canine, is rather small, and single-rooted. It is composed of a single median cusp which is connected with the anterior and posterior borders of the tooth by sharp antero-posterior crests. The transverse width is about two-thirds of the antero-posterior length. $P^{\underline{2}}$ is double-rooted and is separated from $P^{\underline{1}}$ by a short diastema 5 mm. in length. It has a rather high, simple, median cusp with a crest running anteriorly and posteriorly from it. There is a broad swelling along the postero-internal base, making the tooth more than half as broad as it is long. $P^{\underline{3}}$ is one-third longer, antero-posteriorly, than $P^{\underline{2}}$ and is separated from it by a diastema of 3 mm. The posterior half is transversely expanded.

The carnassial is large and rather massive. The paracone is the highest cusp and lies about halfway between the anterior and posterior borders of the tooth. A low ridge runs forward from the paracone to the greatly reduced parastyle. The metacone forms a trenchant crest about 7 mm. in length. The protocone is prominent and extends inward and slightly anterior to a point about 7 mm. from the lingual base of the paracone. It is situated well behind the anterior edge of the tooth.

The first molar is quite *Canis*-like. It is roughly triangular in general outline with a relatively narrow inner half which is directed slightly posteriorly. The paracone is large and higher than the metacone. A low shelf, rather than a distinct cingulum, constitutes the outer border of the tooth. The protocone forms the apex of a V-shaped shelf extending inward from the bases of the paracone and metacone. The protoconule and metaconule are barely discernible. Lingual and posterior to the protocone is a very broad cingular shelf which bears no distinct hypocone. $M^{\underline{2}}$ is but little smaller than $M^{\underline{1}}$. It is roughly oval in outline and its inner part is nearly as broad as the outer. The paracone is but slightly larger and higher than the metacone, and both cusps are much lower than the corresponding ones on $M^{\underline{1}}$. The protocone and the ridges running antero-externally and postero-externally from it are exceedingly low. The small metaconule lies close to the base of the metacone. The protoconule is essentially absent. The inner cingular shelf is much broader than that of $M^{\underline{1}}$ and forms a complete half-circle, lingual to the protocone.

$M^{\underline{3}}$ is wanting in this specimen and the maxillary is broken in such a way that it is impossible to determine whether or not it was ever

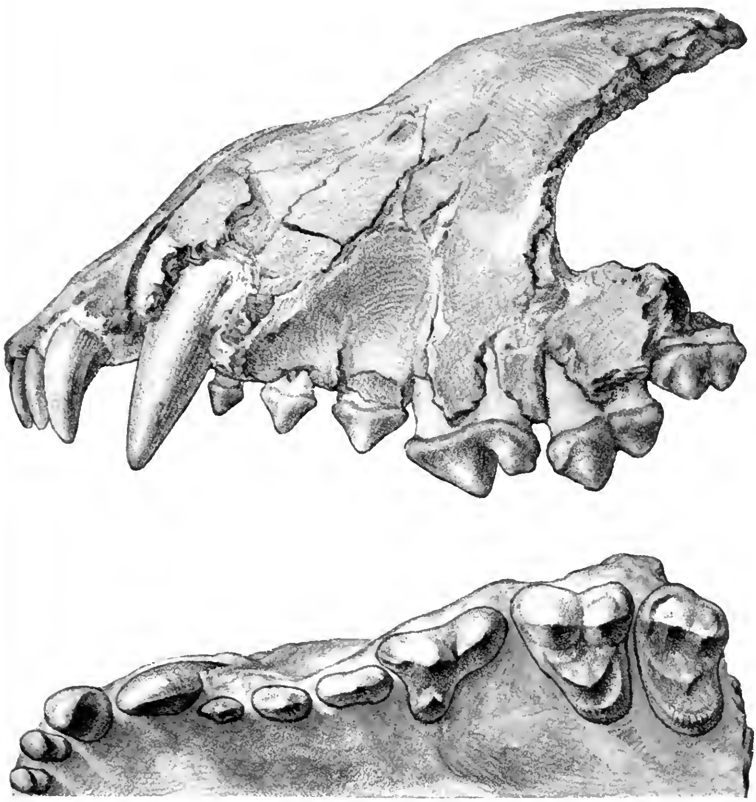

FIG. 95. *Amphicyon riggsi* sp. nov. F.M. No. P12029, holotype. Lateral and ventral views of facial region of skull, with upper dentition. × ⅔.

present. I assume that $M^{\underline{3}}$ was present in this species, however, since $M_{\overline{3}}$ is very strongly developed.

Lower dentition: The lower incisors, canines, and $P_{\overline{1}}$ are lost. $P_{\overline{2}-\overline{4}}$ are similar in most respects to $P^{\underline{1}-\underline{3}}$, but are less reduced. $P_{\overline{2}}$ is about one-half as broad as it is long and has rather strong crests running anteriorly and posteriorly from the median cusp. $P_{\overline{3}}$ and $P_{\overline{4}}$ are successively larger and on both the inner basal swellings are limited to the posterior half of the tooth. Posterior cingula are absent on $P_{\overline{2}}$ and $P_{\overline{3}}$, but a prominent cingulum is present on $P_{\overline{4}}$. A

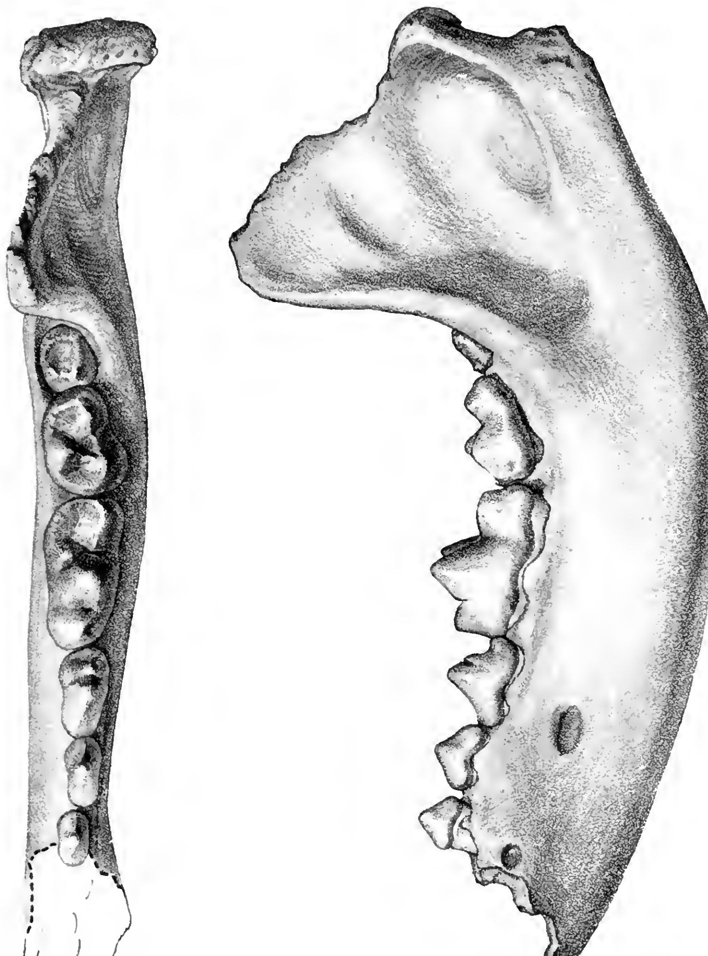

FIG. 96. *Amphicyon riggsi* sp. nov. F.M. No. P12029, holotype. Lateral and dorsal views of left ramus with lower dentition. × ⅔.

low accessory cuspule is present on the posterior slope of the median cusp of $P_{\overline{4}}$. $P_{\overline{3}}$ is separated very slightly from $P_{\overline{2}}$ (by 1.5 mm.) and is in contact with $P_{\overline{4}}$. The latter, in turn, is in contact with $M_{\overline{1}}$.

The first molar is rather massive and its cusps are high. The paraconid part of the blade is little more than half as high as the protoconid and is 5 mm. long, measured from the anterior base of the protoconid. The protoconid is high and is situated immediately posterior to the paraconid. The metaconid arises from the postero-internal slope of the protoconid; it is higher than the paraconid but lower than the protoconid. The posterior slope of the protoconid-metaconid forms an angle of about 35° with the transverse axis of the tooth. The relatively high talonid comprises about one-third of the length of the tooth. The hypoconid lies directly behind the protoconid; it is nearly as high as the paraconid and much stronger and higher than the entoconid. The inner slope of the hypoconid and the external slope of the entoconid unite to form an antero-posterior valley. This lies near the inner border of the tooth and is enclosed posteriorly by a low ridge connecting the posterior slopes of the hypoconid and entoconid. $M_{\overline{2}}$ is large and massive, its width at the trigonid being about two-thirds of the length of the tooth. The protoconid and metaconid are equal in size and height, the latter cusp being postero-lingual to the former. Anteriorly the tooth is bounded by a low crescentic ridge which is connected externally to the protoconid and internally to the metaconid. The paraconid is absent. The antero-posterior length of the talonid is less than one-half that of the trigonid. The hypoconid is more medial in position than that of $M_{\overline{1}}$, is trenchant, and relatively very strong. The entoconid is low and forms the lingual border of the talonid. The hypoconal and entoconal ridges meet posteriorly to form a crescentic posterior border. $M_{\overline{3}}$ is only partially erupted but the crown is visible. It is more than half as long as $M_{\overline{2}}$. The protoconid and metaconid are subequal. A ridge runs posteriorly from the protoconid to unite with the hypoconid. A serrate ridge extends transversely across the posterior border of the tooth.

Skull: The skull is large and massive, with high maxillaries. Only the facial region is preserved and it is so crushed that a detailed description might be misleading; hence it will not be described.

Ramus: The ramus of *A. riggsi* is relatively slender, distinctly more so than most species of the genus. In keeping with the unreduced premolars the horizontal ramus is as deep under $P_{\overline{2}}$ as it is under $M_{\overline{2}}$. The symphysis terminates posteriorly beneath $P_{\overline{2}}$. A small mental foramen is present under the anterior portion of $P_{\overline{2}}$ and a larger one under the anterior portion of $P_{\overline{4}}$. Beneath $M_{\overline{2}}$ and $M_{\overline{3}}$ the ventral border of the ramus bends rather sharply upward. The ascending ramus is relatively low and heavy. The masseteric

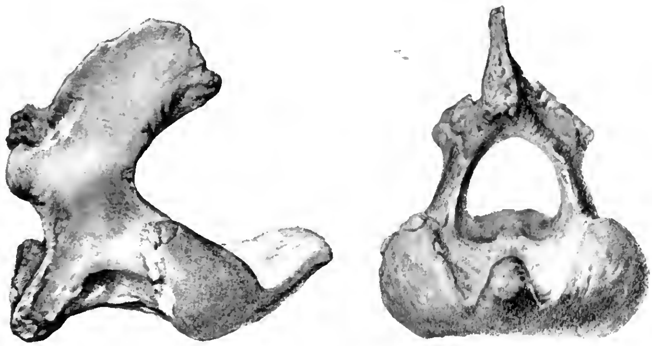

FIG. 97. *Amphicyon riggsi* sp. nov. F.M. No. P12029, holotype. Lateral and anterior views of axis. × ⅔.

fossa is deep, contains but few rugosities and extends forward to a point below $M_{\overline{3}}$.

MEASUREMENTS

(*In millimeters*)*

	I^1	I^2	I^3	C	P^1	P^2	P^3	P^4	M^1	M^2
A-p.	7.0	9.0	13	15	7	12	15.5	26.5	22.0	19
Tr.	4.8	5.9	10	9	5	7	7.8	17.8	30.2	29

	$P_{\overline{2}}$	$P_{\overline{3}}$	$P_{\overline{4}}$	$M_{\overline{1}}$	$M_{\overline{2}}$	$M_{\overline{3}}$
A-p.	10.9	13.8	18.8	31.0	21.6	14.0
Tr.	6.0	6.5	9.0	14.3	16.0	5.5

Depth of ramus under $P_{\overline{2}}$ 37
Depth of ramus under $M_{\overline{2}}$ 38
Distance from inferior base of angular process to top of coronoid process 83

*All measurements maximum diameters.

Axis: A nearly complete axis associated with the skull and jaw and unquestionably from the same individual offers some interesting comparisons with *Daphaenodon* and *Canis*. The axis of *Daphaenodon* is modified in much the same manner as that of *A. riggsi*, but in the latter, divergence from the *Canis* type is carried further (cf. fig. 98).

The axis of *A. riggsi* as a whole is short antero-posteriorly, and high. The hypophysial keel agrees with that of *Daphaenodon* and *Daphaenus* in being low, inconspicuous, and grading posteriorly into the convex body of the centrum.[1]

[1] Peterson (1910, pp. 216, 217) indicated that there is a strong hypophysial keel on the axis of *Daphaenodon*. Actually this is not the case, as the keel is low

The anterior ventral face of the centrum is nearly horizontal antero-posteriorly, and posteriorly it is rather deeply concave, agreeing in this character with *Daphaenodon.* The anterior articular surfaces are more expanded dorsally than those of *Canis,* again approaching those of *Daphaenodon.* The odontoid process agrees with that of *Daphaenodon* and *Daphaenus* and differs greatly from

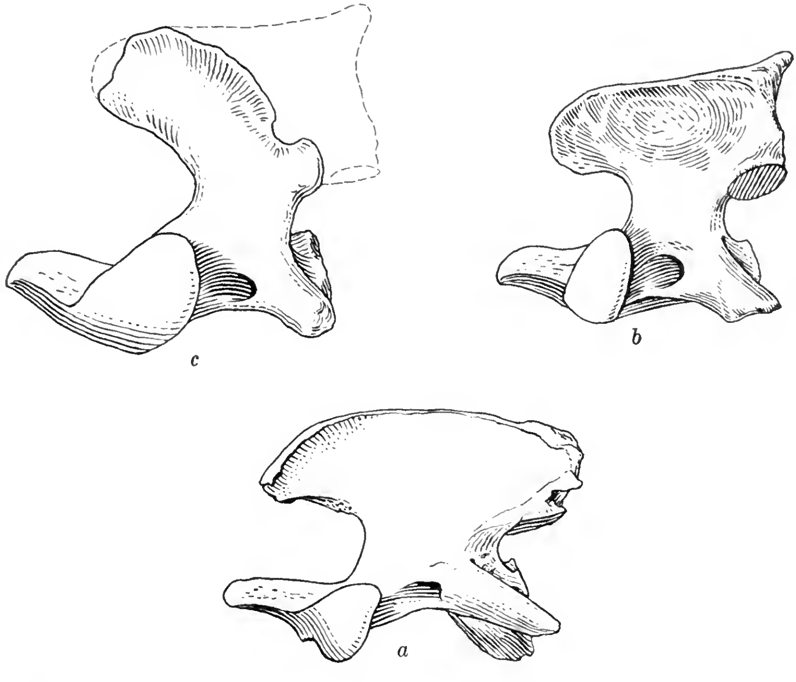

FIG. 98. Axis vertebrae. a, *Canis;* b, *Daphaenodon* (from Peterson); c, *Amphicyon riggsi.* × ⅔.

that of *Canis.* It is short, broad, heavy, and directed upward. The transverse processes are like those of *Daphaenodon* in being short, heavy, and directed more ventrally than in *Canis.* There are no inferior branches on the transverse processes as described by Peterson for *Daphaenodon.* The anterior opening of the vertebrarterial canal is much more ventral in position than in *Canis* and a little more so than in *Daphaenodon.* The neural canal and laminae

and inconspicuous as it is on *Daphaenus* and *A. riggsi.* The posterior "broader area" on the axis of *Daphaenodon*, as described by Peterson, is formed by two diverging, low ridges extending posteriorly from the keel. Mr. John Burke kindly sent the axis from the splendid skeleton of *Daphaenodon* in the Carnegie Museum to me for comparison.

are short antero-posteriorly, as in *Daphaenodon*. The small portion of the neural spine preserved is insufficient for detailed comparison.

Ulna: The ulna, at least in its proximal end, differs greatly from that of *Canis* and closely approaches that of the bears; many of its modifications are foreshadowed in *Daphaenodon*. The ulna of *A. riggsi* is much more massive than that of *Canis*. The sigmoid notch is proportionately larger and more twisted than in *Canis* and its articular surface is greatly expanded dorso-medially, as in the bears. The ventral portion of the sigmoid notch extends more anteriorly than in *Canis* or *Daphaenodon*, reaching a point about 15 mm. anterior to the proximal part of the notch. The posterior part of the articular surface for the radius is expanded, as in the ursids, terminating posteriorly on a rather large process. Similarly, the anterior part of the articular surface for the radius is expanded and projects much farther forward than in *Canis*. There is a wide, medial groove posterior to the sigmoid notch extending from below the radial articulation surface to well upon the olecranon. Most of the olecranon is lacking from the present specimen, but it was probably short. The shaft is expanded antero-posteriorly and compressed laterally.

COMPARISONS

Most species of *Amphicyon* are based upon such fragmentary specimens that it is difficult to make adequate comparisons of them with *A. riggsi*. The new form differs from most American and Old World species by its smaller size and larger and less spaced premolars.

A. ingens Matthew (1924), *A. sinapius*[1] Matthew (1902), and *A. reinheimeri* Cook (1926) are much larger than *A. riggsi* and have more reduced and widely spaced premolars.

A. frendens Matthew (1924) is again much larger and further differs from *A. riggsi* in having lost the entoconid of $M_{\overline{2}}$.

Some species are about equal in size to *A. riggsi* and although for the most part they are based on fragmental specimens, there seem to be sufficient differences in tooth structure between them and the new species to establish its claim to distinction.

A. idoneus Matthew (1924) is about the same size as *A. riggsi* but the protocone of $P^{\underline{4}}$ in the former species is much less prominent, the parastyle is much more external and the metacone of $M^{\underline{1}}$ is less strongly developed.

[1] *A. amnicola* Cook (1909) is a synonym of this species, according to Matthew (1924).

A. pontoni Simpson (1930) differs from *A. riggsi* in having a non-trenchant talonid on $M_{\overline{2}}$ and in having a strong cuspate entoconid.

Certainly the nearest known American ally of *A. riggsi* is *A. americanus* Wortman (1901).[1] Although the two species are of almost the same size, *A. riggsi* may be distinguished by the following characters: (1) premolars less reduced and less widely spaced; (2)

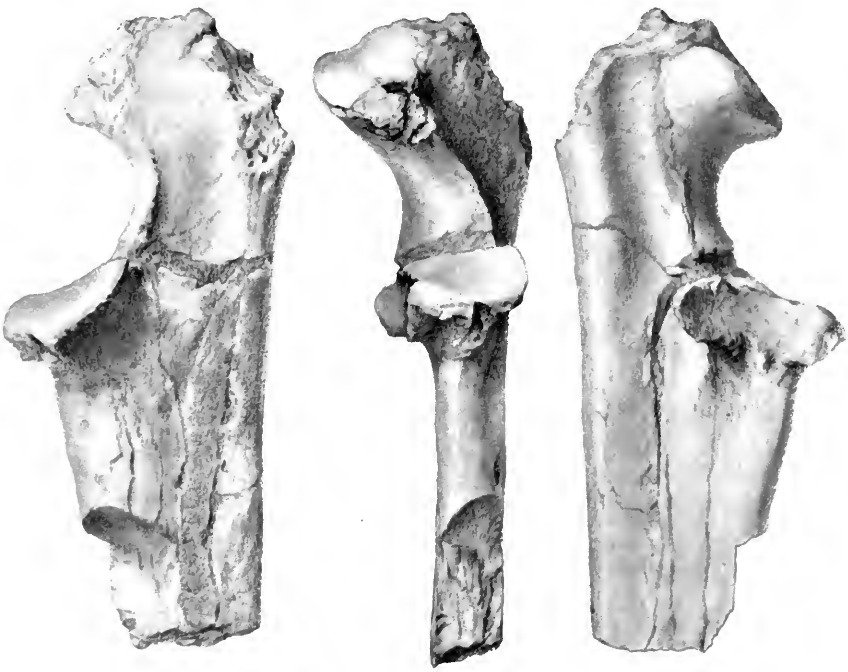

FIG. 99. *Amphicyon riggsi* sp. nov. F.M. No. P12029, holotype. Lateral, anterior, and medial views of proximal portion of left ulna. × ⅔.

protocone of $P^{\underline{4}}$ more posterior and directed more nearly at a right angle to the antero-posterior axis; (3) inner cingulum of $M^{\underline{1}}$ extending more anteriorly; (4) inner portion of $M^{\underline{2}}$ relatively much broader antero-posteriorly and inner cingulum more expanded.

There are several Old World species of *Amphicyon* (e.g. *A. shahbazi, A. palaeindicus, A. aurelianensis*) which appear on the basis of fragmentary specimens to be close to *A. riggsi*. The geographic separation seems to warrant specific differentiation and when more

[1] Wortman's figure is somewhat inaccurate, and not natural size as indicated, each dimension being smaller than that of the specimen. A better figure of this specimen may be found in Scott (1937, p. 579). Dr. G. Edward Lewis kindly supplied information regarding the holotype of this species.

complete material of the Old World species is available this taxonomic division will probably be supported by structural characters.

Knowledge of this new species of *Amphicyon* does not call for further speculation on the relationships and phylogeny of the amphicyonine dogs. It is sufficient to say that the small size, unreduced premolars, and essential lack of diastemata of *A. riggsi* indicate that the species is primitive among the amphicyons, and that in these primitive characters it approaches *Daphaenodon.* This lends support to the opinion of Matthew (1924), Peterson (1910), and others that *Amphicyon* is a direct descendant of *Daphaenodon.* This conclusion is further supported by the close approach of the axis and ulna of *A. riggsi* to those of *Daphaenodon.*

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