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Cymaprimadontidae

A New Family of Insectivores

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I. Introduction

During the summer of 1965, Mr. K. Kietzke of the Field Museum staff collected a partial right mandible of an animal which is, even on cursory examination, a new form. The specimen occurred near the top of the Crazy Johnson Member of the Chadron Formation in South Dakota. The matrix is a slightly-cemented bentonitic mudstone with abundant, very fine sand grains. Paleogeographically, the fossil occurred approximately a mile north of the northern edge of the zone of channel-fill sediments designated the Red River Valley (Clark, 1937).

The bone is soft and white, with pale olive enamel on the teeth. Unfortunately, crystalline calcite fills many of the cracks and cavities, and permeates even the most intimate structure of the bone, which greatly increased the difficulties of preparation and X-ray photography.

Subsequent search of the Museum's collection disclosed a left mandible, UC 349, of a form related to but not congeneric with the first. This was in the collection recently acquired from the Walker Museum. Unfortunately this second specimen, collected by Baur in 1894, has as field data: "Oligocene of South Dakota, White River Badlands." The matrix is a fine sand, better cemented and slightly coarser than that of the Chadron specimen. The bone is hard and dark gray with a limonite incrustation, and the single tooth preserved is dark brown. X-ray reveals limonite filling the pulp cavities of the tooth roots. Preservation resembles that of the Lower Nodular Zone, Scenic Member, Brule Formation; as will be devel-

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oped later, the anatomical characters also suggest that this second jaw is younger than the first. However, I have seen bone and preservation of this sort occasionally in the Peanut Peak Member the Chadron. The specimen should be regarded as of Oligocene age, probably Orellan (Brule), but possibly late Chadronian.

In view of the problematical age plus the fact that only the dental ramus and M_3 are preserved, I shall describe this second specimen without giving it a generic and specific name. It will be used to aid in delimiting the new family.

Figures 3-6 were drawn by Dr. T. Perenyi; Figures 1 and 2 are by the author.

II. Description

Order Insectivora

The supra-familial taxonomy of the numerous families, both fossil and recent, previously grouped within this order, is in such a state of flux that only a specialist can form significant judgments.

The Early Tertiary and Recent families which seem most closely related to the new one proposed here have been variously classified, but have not previously been regarded as closely related to each other. It seems most practical, therefore, to describe the new family, indicate its possible relationship to others, and refer it to the Insectivora. This leaves to specialists the evaluation of relationships in suprafamilial classification.

Family CYMAPRIMATONTIDAE, new family

Known age and geographic distribution:—Early to ? Middle Oligocene, South Dakota.

Type genus:—*Cymaprimadon*, new genus.

Family characters:—Large for insectivores, about the size of modern *Lutra* or *Lynx*, mandible low, thick, extremely massive; posterior mental foramen very large, postero-ventrally directed, beneath the P_4 - M_1 inter-alveolar partition; a curved, longitudinal groove on the latero-ventral side of the dental ramus; mandibular symphysis small and narrow; symphyseal surfaces unsutured and almost flat; inferior cheek-tooth row strongly arched into an open sigmoid; one lower incisor enlarged, procumbent, with enamel distribution restricted and a prominent median groove; other incisors reduced or absent; canine reduced; P_1 absent; P_2 reduced, P_3 larger, P_4 the

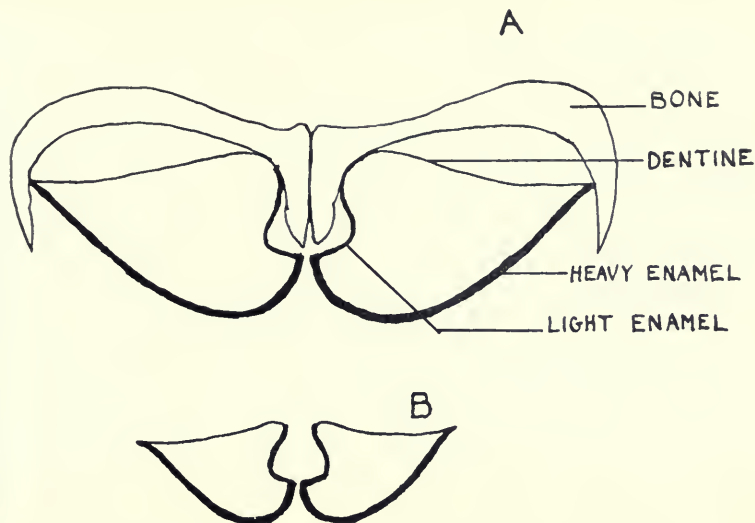


FIG. 1. Cross-sections of incisor of *Cymaprimadon kenni*: A, Slightly behind alveolar rim. B (Hypothetical), near tip of tooth.

longest of the cheek-tooth series; M_1 - M_3 progressively smaller; posterior roots of cheek teeth large, round; anterior roots smaller, flattened antero-posteriorly; molar paraconids reduced but present; hypoconid large, developing toward a blade; entoconid and hypoconulid greatly reduced; root of enlarged incisor extended back to beneath posterior root of P_3 ; mandibular canal high in jaw.

Genus *Cymaprimadon*,¹ new genus

Type species:—*Cymaprimadon kenni*,² new species.

Type specimen of species:—Field Museum no. PM 9567, a right mandibular ramus with M_3 and the greater portion of an enlarged incisor.

Since only this one specimen of the genus species is known, generic and specific characters are not separable.

Geologic horizon:—Top of Crazy Johnson Member, Chadron Formation, Lower Oligocene.

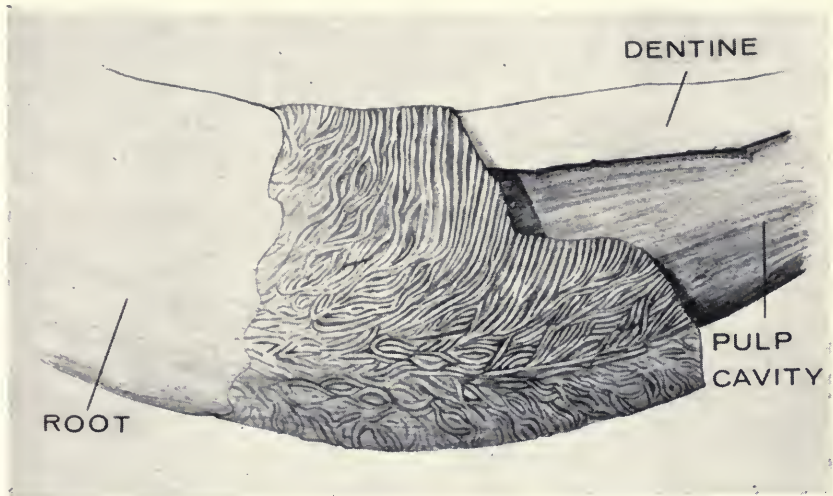
Locality:—NW $\frac{1}{4}$ of NE $\frac{1}{4}$, sec. 25, T 3S, R 10E, Pennington Co., South Dakota. Northeast face of the Finney Breaks.

¹ From *κυμα*, a wave or furrow; *primus*, first; *ὄδων*, a tooth, in reference to the groove in the enlarged incisor.

² Named in honor of Mr. Kenneth Kietzke, who found the type specimen.

GENERIC AND SPECIFIC CHARACTERS:

1. Measurements as in Table 1.
2. Dental formula = $\frac{?3}{1} - \frac{1}{1} - \frac{3}{3} - \frac{3}{3}$.
3. I_1 reduced, probably absent; I_2 greatly enlarged, procumbent; I_3 reduced, probably absent.
4. I_2 enamel distributed as in Figure 1, and very thin. A complex pattern of fine, vermiform crenulations developed on the enamel surface (fig. 2).
5. Alveolus for I_2 extending back to beneath the anterior alveolus for P_4 .
6. Cheek-tooth series continuous, crowded, without diastemata, from I_2 to M_3 .
7. M_3 trigonid low, less than twice the height of talonid, measured from the enamel border.
8. Protoconid largest, paraconid medial and smallest; trigonid cusps slightly compressed at points, to enclose a tiny basin.
9. Talonid a very shallow, flat-bottomed basin, sloping strongly mesio-anteriorly. The large hypoconid rises but little higher than this basin, standing almost on the midline of the tooth with a ridge extending forward to the postero-internal base of the protoconid. The entoconid and hypoconulid are reduced to tiny nubbins on the posterior part of the low ridge which forms the postero-internal rim of the basin.
10. Tiny accessory cuspule on the postero-external side of the hypoconid.
11. Tiny accessory cuspule on the mesio-posterior wall of the metaconid.
12. Small but definite anterior cingulum at base of protoconid; obscure cingular prominence at base of paraconid; internal cingulum at base of metaconid; the three cingula separated from each other.
13. A prominent shelf around the alveoli of the molars and P_4 , and heavy crests at the ends of the premolar interalveolar partitions.
14. Posterior mental foramen large, as a family character; anterior to this a row of smaller foramina, probably individually variable in detail.
15. Protuberant muscle scars on ventral border of ramus below M_3 and below P_1 .



A

B



FIG. 2. A, Drawing of enamel pattern of incisor, greatly enlarged. B, Photograph of same.

16. Rugose area on side of chin.
17. Bone surface generally marked by widely spaced, tiny, posteriorly directed pores, from which grooves 1-5 mm. long extend backward, roughly parallel to the elongation of the bone on which they occur.

New But Unnamed Genus and Species

Specimen upon which description is based:—Field Museum specimen UC 349 (formerly in the collection of the Walker Museum, University of Chicago).

The known stratigraphic occurrence is Oligocene; probably the specimen is from the Scenic Member of the Brule Formation, but possibly it is from the Peanut Peak Member of the Chadron Formation. The locality is "White River Badlands, South Dakota." Since this expression was used by early collectors to mean "Badlands of the White River Formation" (now group), rather than "Badlands in the drainage area of the White River," the locality data should not be interpreted to exclude Cheyenne River and Bad River drainage basins.

TABLE 1

Dimension	<i>C. kenni</i> , PM 9567	UC 349
Depth of mandible below anterior root of M ₁	12.6	15.6
Thickness of mandible below anterior root of M ₁	8.5	10.5
Anterior rim of temporal fossa to posterior rim of posterior mental foramen	20.0	23.1
Cheek-tooth series, C-M ₃ alveoli	41.4	
Cheek-tooth series, P ₄ - M ₃ alveoli	30.5	35.4
M ₁ - M ₃ alveoli	20.6	24.3
P ₄ alveolus, antero-posterior	9.5 ¹	10.2
M ₁ , alveolus, antero-posterior	7.5	7.5
M ₂ alveolus, antero-posterior	6.8	6.9
M ₃ , length	5.6	7.8
M ₃ , breadth	4.4	5.8
M ₃ , height, enamel rim-top of protoconid	4.9	6.4 ²
M ₃ , height, enamel rim-top of metaconid	4.0	5.6
M ₃ , height, enamel rim-top of hypoconid	3.3	4.7

¹ Slightly too large, due to breakage and laboratory repair.

² Estimated,—tip broken.

Table 1 reveals that this specimen represents an animal much larger than *Cymaprimadon kenni*. The individual had, apparently, lived to a very slightly more advanced age than had the type of *C. kenni*, because M₃ is fully erupted. M₃ of *C. kenni* has the enamel

border a little below the alveolar rim. In neither case is there any trace of wear. Both individuals had apparently attained approximately full size shortly before their death. The similarity of growth stage makes it probable that, with the exceptions noted below, differences between the two specimens are individual or generic rather than developmental.

SIGNIFICANT CHARACTERISTICS OF SPECIMEN UC 349:

1. Measurements as in Table 1.
2. Dental formula = $\frac{\quad}{1 \quad 0 \quad 2 \quad 3}$
3. Enlarged incisor alveolus extends back to beneath posterior root of P₃; posterior wall consists of spongy bone apparently formed shortly before the individual's death.
4. Cheek-tooth series crowded, continuous. Little or no room for C₁, P₁₋₂, between the enlarged incisor and P₃; probably these teeth were missing.
5. P₃ reduced relative to the corresponding tooth in *Cymaprimadon kenni*.
6. M₂ and M₃ of equal size; M₄ slightly longer. P₁ longest in the cheek-tooth series but proportionally shorter than in *C. kenni*.
7. M₃ trigonid low; height 62% of the length of the tooth, compared with 83% in *C. kenni*.
8. M₃ protoconid very slightly larger than metaconid. Paraconid reduced to a sloping prominence connected to the anterior ridge of the protoconoid; a deep, medio-ventrally trending groove between the paraconid and metaconid. Protoconid and metaconid cusps slightly compressed at tips, but form no basin due to the reduction of the paraconid.
9. M₃ talonid consists of a heavy, blunt blade, rising posteriorly to the hypoconid as its cone-shaped terminus. The remaining conules form a denticulated posterior portion of a heavy internal rim which does not enclose a basin because it is not appreciably higher than the area within it. A heavy, low ridge extends down the linguo-posterior wall of the hypoconid to a denticle on the rim, but does not directly join it.
10. There is a small accessory cuspule on the mesio-posterior wall of the metaconid, as in *C. kenni*, but none on the hypoconid.
11. A very broad, low, heavy cingulum forms a straight wall across the anterior face of M₃. Unlike *C. kenni*, no other cingula occur.

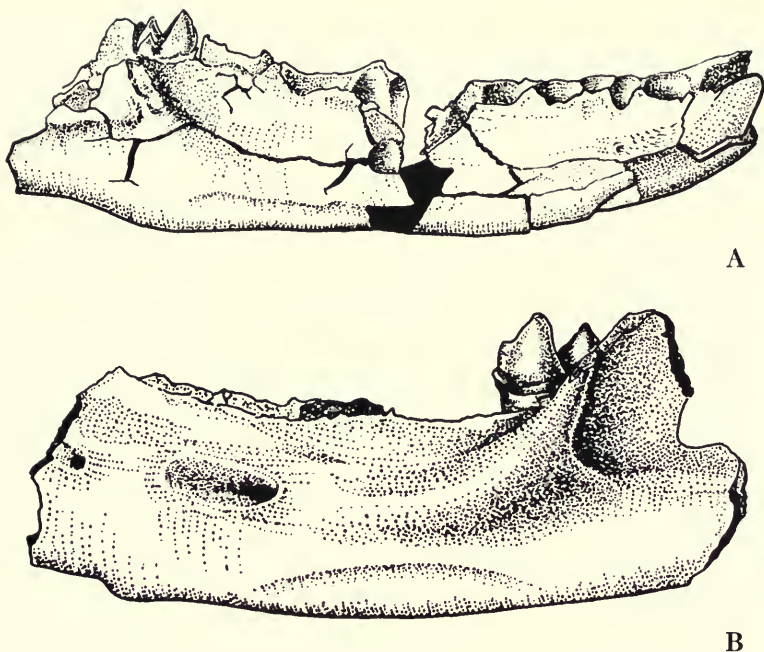


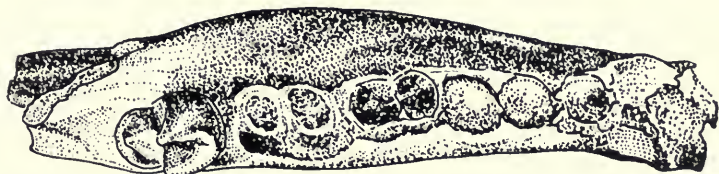
FIG. 3. Lateral view of jaws: A, *C. kenni*. B, UC 349.

12. The shelf and crests around the alveolar borders are even more prominent than in *C. kenni*.
13. The protuberant muscle scars of *C. kenni* are absent in UC 349; otherwise the foramina and jaw characters preserved resemble those of *C. kenni*.

In most respects, this animal represents a genus evidently more advanced along the generic trend of the family than is *Cymaprimadon*. The increase in overall size and weight, further reduction of the paraconid, further alteration of the talonid to a shearing blade based upon the hypoconid, and apparent further reduction of the anterior cheek-tooth series may all be regarded as changes carrying the Cymaprimadontidae further from whatever was their ancestral group. The development of a heavy anterior cingulum and suppression of the other two partial cingula presumably have the same significance. The degree of specialization suggests, as does the type of preservation, that UC 349 represents a genus later in time (probably Orellan) than the middle Chadronian *Cymaprimadon*.



A

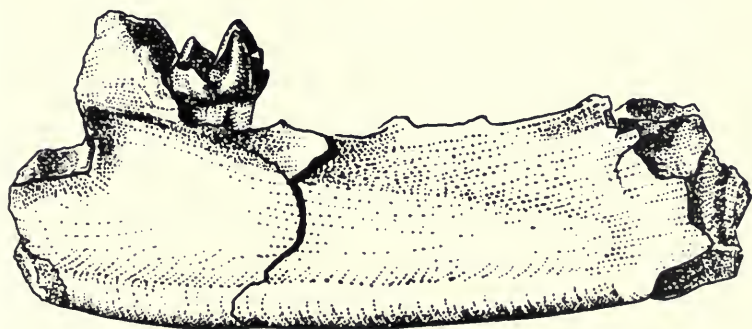


B

FIG. 4. Vertical view of jaws: A, *C. kenni*. B, UC 349.



A



B

FIG. 5. Lingual view of jaws: A, *C. kenni*. B, UC 349.

III. Soft anatomy and probable way of life of *Cymaprimadontids*

The symphysis in *C. kenni* makes a 30° angle with the axis of the mandible. The skull must have been approximately 45-50 mm. wide at the mandibular condyles. Judging from the weight of the bone and the massive muscle scars, the head was probably a great deal wider. The general head proportions were probably nearly those of an otter or lynx, with large temporal and masseter muscles compensating by their bulk for the undoubtedly narrower calvarium of *Cymaprimadon*.

Strong outward angulation of M_1 and the lower premolars suggests that the anterior part of the palate was broad. Some sort of active, well-muscled labial apparatus is indicated by the rugose area on the anterior surface of the jaw; adequate blood was supplied through the large mandibular canal and short, wide-diameter mental foramina. Whatever the labial apparatus was, it presumably functioned in connection with the use of the unique I_2 .

I_2 poses a real problem. Great enlargement, high specialization in shape, and the development of a unique enamel decoration all indicate that the tooth functioned in a distinctive manner extremely important to the animal. The tooth must have tapered distally to a long, sharp, triangular point with an internal groove and a rounded external side. The right and left incisors together probably produced a sharp, procumbent point with a cross-section as shown in Figure 1,B, rounded ventrally and marked by a tube with a dorsally open slot.

Such a dental structure, with thin, discontinuous enamel areas, is obviously designed for only one purpose—piercing a soft, non-abrasive object. Any normal masticatory function is impossible for it. The tube is designed for the passage of liquids, either into or out of the animal's mouth.

The first alternative, that the tube is part of a suction apparatus, requires that the animal use it to suck in either vegetable juices or blood. The only vegetable juices available to teeth so delicate would be the juice of soft-fleshed fruits. A tube so narrow would be of little use, and would almost certainly become plugged with fiber. Furthermore, the cheek-tooth dentition and heavy jaw musculature are not those of an innocently frugivorous animal. Judging from the size and alignment of the alveoli, P_4 functioned as a reasonably



A



B

FIG. 6. Vertical view of M_3 : A, *C. kenni*. B, UC 349.

efficient carnassial tooth, and even M_3 is constructed for effective dissectorial mastication.

Vampirism offers an even less satisfactory alternative utilization of these teeth. The two together would form a sharp-pointed but very short half-cone-shaped weapon, with a base at least 20 mm. broad. No animal could possibly sit quietly unnoticed while such an object was rammed into its body, and the open tube could not possibly function during the ensuing struggle.

Since this dental apparatus would not effectively ingest liquid food, the remaining possibility is that it served to inject something. *Solenodon*, the only other known mammal with a similarly grooved tooth, has been shown to be venomous (Rabb, 1959), and to use its grooved but heavily-enamelled incisors as fangs for insertion of its venom. In *Cymaprimadon*, the particular gland specialized for venom was probably either the sublingual or the submaxillary, both of whose ducts discharge appropriately at the base of the incisors.

Use of the incisor tube to transmit venom to its victims would be effective. Corollary to this use would be the development of a heavy maxillary root of the zygomatic arch, probably accompanied by an eversion of the arch to a feloid position. The masseter would then occupy an almost fore-and-aft position, and would drive the mandible forward. Heavy scars along the base of the mandible, presumably in part for the insertion of the digastric, suggest that *Cymaprimadon* was also able to withdraw its weapon with some vigor. These musculoskeletal adaptations are, of course, conjectural. Confirmation must await discovery of a skull.

If *Cymaprimadon* was venomous, it must also have been an active carnivore. Such an apparatus would be entirely wasted on beetles and grasshoppers. The cheek-tooth dentition also suggests a carnivorous habit. Whether *Cymaprimadontids* preyed chiefly upon fish and amphibians, or upon forest-dwelling terrestrial mammals, or on birds and arboreal mammals, is largely conjectural. The paleogeographic location of the type of *C. kenni*, and the matrix of UC 349, suggest that they lived away from the stream channels proper but close enough that they certainly inhabited forests rather than savannah plains or prairies. Their rarity as fossils might be a function of arboreal existence, or might simply indicate that they were rare elements of the fauna.

In any event, a carnivorous insectivore weighing at least several pounds, with a head as big as an otter's and a highly effective toxic

fang, must have been a frightening member of the predatory community.

IV. Relationships

Determination of the relationships of the Cymaprimadontidae is attended by the difficulties usual to insectivore classification: fragmentary materials plus the difficulty of distinguishing genetically related characters from parallel or convergent characters.

A search for earlier related or ancestral forms leads at once to the Pantolestidae. Both families are large for insectivores, with massive mandibles. More significantly, both have cheek teeth small in proportion to the jaw, molars with reduced paraconids and relatively short trigonids, P_4 the longest tooth in the series, and a large, short posterior mental foramen. The large canines and small incisors of the Pantolestidae obviously exclude them from a directly ancestral position, but the two families might well represent successive divergences from a common stem.

Possible descendants are unknown as fossils. However, comparison with *Solenodon*, which has been drawn earlier on a purely functional basis, reveals a fair number of resemblances and no single conclusive difference.

Both are large for insectivores. In both, the mandibular canal is large and placed high in the jaw. The symphysis in both extends back to a position beneath P_3 . In both, the canine is greatly reduced and an incisor (I_2 in *Solenodon* and probably in *Cymaprimadon*) is grooved and enlarged. In both, apparently, venom was developed and used for predation.

An equal number of equally impressive differences also becomes apparent. *Solenodon* has an exceedingly long, narrow skull rather than a massive one. I_3 is present. P_4 is not quite so long as M_1 . The molars do not decrease in length posteriorly. The paraconids of the molars almost equal the metaconids in height, and lie on the lingual side of the tooth rather than in the middle. The talonid consist of a ridge and an open basin, as in *Cymaprimadon*, but in *Solenodon* the ridge connects to the metaconid and the basin is labial to it, whereas in *Cymaprimadon* the ridge connects to the protocoid and the basin is lingual to it.

The relationship, if any, is distant. Tentatively, I believe that there is a relationship, but that the line leading to *Solenodon* separated

from the ancestral stock of the other two before they differentiated from each other.

It seems improbable that venom, absent from all other mammalian groups, would develop absolutely independently in three families of Insectivora (Soricidae—Pearson, 1942; Solenodontidae—Rabb, 1959; Cymaprimadontidae—this publication). For this reason I tend to regard the three as somewhat more closely related to each other than they are to some other families of insectivores.

The anatomy of the mandibular canal seems to be a solid line of evidence linking the Pantolestidae, Cymaprimadontidae, and Solenodontidae.

The three would all fall, probably, within the suborder Soricomorpha of the order Lipotyphla of Butler (1956). They would occupy the same position in McDowell's (1958) classification, but the Pantolestidae and Cymaprimadontidae might properly be excluded from the superfamily Soricoidea. Van Valen's (1966) "group M" is stated on p. 104 to include the Pantolestidae and on p. 108 to be ancestral to the primates, which in turn are ancestral to the rodents; "group M" is also, apparently, ancestral to the lagomorphs. Since "group M" is not a formal taxonomic designation, it cannot be properly considered. However, it seems very clear that the Cymaprimadontidae are related at an ordinal level to the Pantolestidae, and that they are not ordinally related to primates, rodents, or rabbits.

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