THE STATUS OF GENUS NOTHO CYON MATTHEW, 1899 (CARNIVORA): AN ARCTOID NOT A CANID

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ABSTRACT — Dental materials in the Peabody Museum of Yale University recently recognized as Nothocyon geismarianus Cope, 1878, emphasize that the holotype is markedly different from what is commonly regarded as “Nothocyon geismarianus” based on materials referred to that taxon by E. D. Cope. Despite its basined talonid, teeth of Nothocyon geismarianus differ from those of primitive borophagine canids in having a highly compressed trigonid, a reduced paraconid in m2, and a quadrate M1. The form of the m2 in N. geismarianus is uniquely shared with Parictis although the M1 is markedly different between the two. The family level relationship of Parictis, as well as that of N. geismarianus, remains uncertain for lack of knowledge of their basicrania. The history of the genus Nothocyon is reviewed and a new genus and species is proposed for the taxon represented by the material referred to “N. geismarianus.”

INTRODUCTION

The holotype (AMNH 6884) of Canis geismarianus Cope, 1878, is a fragment of left jaw with a single tooth, the m1, from the John Day Formation, central Oregon. The conventional view of this small fox-sized carnivore from the North American Tertiary, however, is based primarily upon a nearly complete skull and mandible (AMNH 6885), and a partial post-craniot skeleton (AMNH 6886) of a canid described slightly later by Cope (1883, 1884). This misconception was further complicated after Matthew (1899) erected, in a peculiar way (see Taxonomic History below), a new genus Nothocyon for C. geismarianus and two other small John Day canids (N. lemur and N. latidens). In Wortman and Matthew’s (1899) view, Nothocyon was supposed to mark a distinct lineage that gave rise directly to two living South American canids (Nothocyon urostitcus Mivart, 1890, and N. parvidens Mivart, 1890, both synonymized with Canis vetulus Lund, 1840, which is now included in the subgenus Lycalopex Burmeister, 1854, of genus Dusicyon Hamilton Smith, 1839 (Cabrera, 1957)). As many as 11 fossil species have since been referred to Nothocyon, primarily on the basis of their tendency to have a basined talonid on m1 as contrasted to the trenchant talonid in the primitive canid Hesperocyon Scott, 1890. All were founded on comparison with the referred skull (AMNH 6885) and post-cranium (AMNH 6886) rather than with the holotype of N. geismarianus (AMNH 6884). The genus “Nothocyon” in the sense of AMNH 6885 and 6886, is now recognized to have played a central role in the basal stock of one of the most diverse radiations within the family Canidae, that of the subfamily Borophaginae (Tedford, 1978; Wang, 1990).

Tooth Measurements — “Length” is defined as the greatest distance along the antero-posterior axis of the tooth, and “width” as the greatest transverse dimension of the tooth, perpendicular to the length measurements; length of parts of the tooth row (e.g., p2–m3) is the greatest distance between the anterior border of the anterior-most tooth and the posterior border of the posterior-most tooth. All measurements are in millimeters.


TAXONOMIC HISTORY OF NOTHO CYON

On November 15, 1878, E. D. Cope read a paper before the American Philosophical Society entitled “On some of the characters of the Miocene fauna of Oregon.” In this paper Cope named a new species of mid-Tertiary fox-sized canid from the John Day Formation, Canis geismarianus, in honor of Philadelphia naturalist Jacob Geismar. Cope’s paper was published in issue number 30 of the Paleontological Bulletin (Cope, 1878:9, republished in 1879), in which a left mandibular fragment with m1 (AMNH 6884, fig. 1) was described. Cope subsequently (1881:180) grouped this species under the European genus Galecyon Owen, 1847, and implied in his discussion of the number of toes in the hindfoot of G. geismarianus that more material than the original single tooth was known. A more complete description by Cope (1883:240) included two figures illustrating a skull and its right lower jaw (AMNH 6885, Cope, 1883:fig. 5) and a partial skeleton.
(AMNH 6886, Cope, 1883:fig. 6), confirming that he had indeed obtained more material since the original description. The label on AMNH 6885 indicates that the specimen was obtained by Cope’s collector J. L. Wortman in 1879, one year after the publication of Canis geismarianus. In his monumental work on “The Vertebrata of the Tertiary formations of the West,” Cope (1884) re-illustrated the material referred to Galecyus geismarianus (plate LXX, fig. 2–3; plate LXXA), and clearly designated the 1878 specimen as the holotype: “It [Galecyus geismarianus] is represented in my collection by the greater part of a skeleton [AMNH 6886] accompanied by a skull with lower jaw complete [AMNH 6885]; by a second skull [AMNH 6887], from which the end of the muzzle and the teeth have been broken; and by a fragment of a mandible which support a sectorial tooth [AMNH 6884]. On the last specimen the species was originally founded” (Cope, 1884:920, italics and material in brackets added here). Notably absent, however, is any illustration of the holotype, AMNH 6884, which has never been figured or even mentioned in the literature since then. Cope’s last mention of this species (1889:233) placed it in the genus Cynodictis.

The true identity of Canis geismarianus was further complicated by W. D. Matthew. In his faunal lists for the “Fresh-water Tertiary of the West,” Matthew (1899:62) listed three species under an “unpublished” (word in his footnote) generic name: Nothocyon (Galecyus) geismarianus, N. lemur, and N. latidens, all from the John Day Formation. In the succeeding article of the same volume, Wortman and Matthew (1899) formally diagnosed the new “genus or subgenus” Nothocyon but listed instead two living South American canids first: Canis urostictus Mivart and C. parvidens Mivart, species that are now synonyms of Dusicyon (Lycalopex) vetulus (Lund), 1840, not Lund, 1842, as cited in Cabrera, 1957. The three John Day fossil species in Matthew’s (1899) original designation were “provisionally” referred to Nothocyon based on the belief that the John Day forms were directly ancestral to these modern South American canids and distinct from the contemporary Canis. Hay (1902) detected the inconsistencies between these two publications and proceeded to elect N. geismarianus as type species. Two years later, Palmer (1904:462) cited Hay and pronounced the “type fixed.”

Allen (1905:151–152), in his report of “Mammalia of southern Patagonia,” seemed to have personally communicated with Matthew about the latter’s original intent of Nothocyon: “Another very distinct group [of living South American canids] is that to which Matthew and Wortman intended to apply the name Nothocyon, but which, through the peculiar circumstances attending the original publication of the name, is not available in this connection. The type of Nothocyon was intended to be Canis urostictus Mivart, as Dr. Matthew informs me, but as first published it did not include this species, . . . .” Allen erected a new genus in recognition of the unavailability of Nothocyon for the living South American foxes: “In allusion to this embroilment I propose for this group [Canis urostictus and C. parvidens], should it be deemed worthy of recognition, the name Eunothocyon, with Canis sladeni Thomas [also Dusicyon (Lycalopex) vetulus] as the type.”

Wortman and Matthew’s (1899) concept of Nothocyon geismarianus was still centered, not on the holotype (AMNH 6884), but on the more complete materials (AMNH 6885, 6886) referred by Cope (1883, 1884), and their comparative descriptions (pp. 127–128) were devoid of any mention of the holotype. This confusion of type concept has persisted and several species have since been recognized under Nothocyon in reference to AMNH 6885 and 6886 rather than to the holotype. Merriam (1906) erected a new variant, Nothocyon geismarianus n. var. mollis (now assigned to the genus Leptocyon), by comparing skull characters only; Peterson (1906) used the P4, instead of m1 of the holotype, of “Nothocyon geismarianus” to distinguish it from his new species N. annectens; Matthew’s (1907) two new species N. gregorii and N. vulgaris (both now assigned to Leptocyon) were based on comparison with the “skull figured by Cope (1884)” and the post-cranium; and Macdonald (1963) clearly indicated his basis of observation when he referred some Wounded Knee materials to N. geismarianus. “A comparison of this material with the lower jaw and dentition of the excellent skull that Wortman collected from Haystack Valley in 1879 (A.M.N.H. No. 6885) and that Cope (1884:920–923, pl. 70, fig. 2) referred to Galecyus geismarianus shows only minor differences. . . .”

In the process of a systematic review of the borophagine canids, Beryl Taylor and Tedford were able to make positive identification of a Yale Peabody Museum specimen (YPM 12733) by comparison with the holotype of Nothocyon geismarianus. The specimen was referred to Cynodictis oreognensis by Thorpe (1922), and, when found in the Yale collection, was mostly embedded in matrix—the reason for Thorpe’s error. Further preparation of this specimen reveals that it consists of partial upper and lower jaws with most of the upper and lower post-canine dentition. With this additional material it became apparent that Nothocyon geismarianus is a hypocarnivorous species distinct from the skull and skeleton (AMNH 6885, 6886) referred to it later by Cope. In fact, N. geismarianus belongs to a taxon that has never been recognized in the literature except in Cope’s (1878) initial brief description of m1. Cope’s later (1883, 1884) mistaken reference of AMNH 6885 and 6886 to N. geismarianus has profoundly changed the perception of the species for more than 100 years. More importantly, N. geismarianus may not even belong to the family Canidae (see discussion below). The popular concept of “Nothocyon geismarianus,” therefore, does not correspond to the original definition of the species. A new genus and species is proposed here for the specimens mistakenly referred to Nothocyon geismarianus.
SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Infraorder CYNODAe Fower, 1869
Family CANIDAE Gray, 1821
Subfamily BOROPHAGINAE Simpson, 1945

CORMOCYON, gen. nov.

Type Species — Cormocyon copei, gen. et sp. nov.

Etymology — "kormos" (Greek) for tree trunk in allusion to phyletic relationships; "cyon" for "canid."

Diagnosis — Cormocyon is a primitive borophagine possessing a bicuspoid talonid with a conical entoconid and consequent broadening of the talonid. There is a corresponding enlargement of the talon of M1 especially the hypocone. These features are synapomorphic with the Caninae and provide evidence for their sister relationship. Borophagine synapomorphies of Cormocyon include weak to nearly absent of the parastyle of M1, large and closely-spaced, strongly cuspidate premolars, large metaconid of m2, often slightly larger than the protoconid, and deep horizontal ramus with expanded angular process. Cormocyon is relatively primitive among borophagine genera, but is distinguished from contemporary hypocarnivorous genera (e.g., Oxetocyon, Cynarctoides) by its elongated m1 with a more open trigonid, better developed entoconid, and posterior cingulum beneath the talonid cusps.

CORMOCYONCOPEI, gen. et sp. nov.

Galecyntus geismarianus: Cope, 1881:180
Galecyntus geismarianus: Cope, 1883:240
Galecyntus geismarianus: Cope, 1884:920
Cynodictis geismarianus: Cope, 1889:233
Nothocyon geismarianus: Matthew, 1899:62
Nothocyon geismarianus: Wortman and Matthew, 1899:127
Nothocyon geismarianus: Hay, 1902:771
Nothocyon geismarianus: Thorpe, 1922:164
Cynodictis geismarianus: Matthew, 1901:381
Nothocyon geismarianus: Merriam and Sinclair, 1907: 184

Holotype — AMNH 6885, skull and mandible with complete dentitions; one cervical, three articulated thoracic vertebrae; articulated last lumber, sacral, and first four caudal vertebrae with partial crushed pelvis; distal right humerus.

Referred Specimens — AMNH 6886, partial postcraniaal skeletons in two blocks of matrix; nearly complete vertebral column from axis to sacrum, most limb bones and vertebrae, exposed on the right side. The holotype (AMNH 6883) could not belong to the same individual as the post-cranial skeleton (AMNH 6886) as Cope (1884) claimed; at least two associated postcranial elements in AMNH 6885 have duplicate counterparts in AMNH 6886—a distal right humerus and a partial pelvis. In addition, the color of preservation is appreciably different between these two specimens.

AMNH 6887, partial edentulous skull with rostrum anterior to P3 broken away.

Type Locality and Age — Haystack Valley, John Day Basin, Oregon. "Diceratherium" zone, Turtle Cove Member(?) of John Day Formation, early Arikareean.

Etymology — In honor of Professor E. D. Cope who first described specimens belonging to this species.

Diagnosis — Same as genus.

Comment — No new description of Cormocyon copei is given here beyond Cope's descriptions (1883:240-241, figs. 5, 6; 1884:920-929, plate LXX, figs. 2, 3, plate LXXa, figs. 1-12). A comprehensive description is outside the purpose of the present paper, which is to clarify the taxonomy of Cormocyon and Nothocyon.

There are two reported occurrences of Cormocyon copei ("Nothocyon geismarianus") outside the John Day Formation: White (1954) described one right ramus from early Arikareean deposits in the Canyon Ferry area, Montana; Macdonald (1963, 1970) listed several specimens, mostly fragments of lower jaws, from the early Arikareean Sharps Formation in the Wounded Knee area, South Dakota. We believe that the Canyon Ferry and Wounded Knee materials, while related to Cormocyon copei, probably belong to different species.

Infraorder ARCTOIDEA Fower, incertae sedis

NOTHO CYON Matthew, 1899

Type Species — Nothocyon geismarianus (Cope, 1878).

Type Locality — Like many of Cope's publications, the locality of AMNH 6884 is only attributed to the John Day Formation, central Oregon. The locality for YPM 12733 is "the Fossil Horse beds on Cottonwood Creek" (Thorpe, 1922), Grant County, Oregon; upper part of John Day Formation (Haystack Valley or Kimberly Member, Fisher and Rensberger, 1972).

Distribution — Late Arikareean and possibly early Hemingfordian of Central Oregon.

Emended Diagnosis — Enamel surface crenulated; premolars robust with lingual cingula; P4 broad relative to its length; M1 hypocone contributes to rectangular occlusal outline, metaconule shifted caudally; m1 trigonid low relative to talonid; m2 trigonid shifted toward the anterior and medio-laterally compressed leaving a wide shelf on the antero-lateral side; great reduction of m2 paraconid.

Etymology — Palmer (1904) had the following interpretation of the generic name: "Nothocyon: notos, spurious; kyon, dog."

NOTHO CYON GEISMARIANUS (Cope, 1878)

Figures 1, 2, Table 1

Canis geismarianus Cope, 1878:9
Cynodictis oregonensis: Thorpe, 1922:163

Holotype — AMNH 6884, fragment of left jaw with worn m1.

Hypodigm — YPM 12733, palate with little worn left
es. Almost all of the upper and lower premolars as well as the left upper and lower carnassials have the labial surface broken off (Fig. 1C). Natural molds of parts of some of the premolars are preserved and epoxy casts were made before preparation to save part of the external morphology of the teeth.

The two upper incisors may be right and left I1s, judging by the curved nature of the root and smooth surface on the lingual side. They have two shallow grooves (especially on the better preserved left I1) on the buccal side, indicating a tricuspid construction. Both left and right upper canines are broken, but their crowns appear to have been short and stout. The premolars are simple and robust.

The right P1 is partly preserved as a cast. The P2 and P3 have small posterior accessory cusps. All premolars have cingula that almost encircle the teeth. Both left and right upper carnassials (P4) are broken on the labial side. The P4 is very broad relative to its length, a situation rarely seen in canids (Fig. 2A). The anterior border of its small protocone is at the same level as the base of the anterior edge of its paracone. A well developed cingulum posterior to the protocone has fine crenulations on its occlusal surface. The shearing surface on the lingual side of the paracone and metacone is very short and heavily crenulated. These cusps are separated by a sharp carnassial notch (Fig. 1D).

The M1 is surrounded by a strong cingulum. Its paracone is slightly higher than the metacone (Fig. 1C, D) but is approximately the same size in occlusal view. The protocone is slightly more posteriorly positioned than the paracone. The paracone is not well differentiated along the preprotoconid. The metacone is well differentiated, much smaller than the protocone, and shifted caudally as in some arctoid carnivorans. The metacone is connected to the hypocone through


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C–M2 and right C–M1, mandible with partial left ramus with c–m3 and right ramal fragment with m1–m2, five isolated upper incisors.

**Type Locality** — Same as genus.

**Emended Diagnosis** — Same as genus.

**Etymology** — In honor of Philadelphia naturalist Mr. Jacob Geismar.

**Description** — *Nothocyon geismarianus* is re-described in light of the newly referred dental materials. Correct assignment of family level affinities cannot be made without knowledge of the basicranial anatomy in the case of *Nothocyon geismarianus* as well as the arctoid *Parictis* with which it is compared in the present paper. We thus make judgements based on dental characters alone.

Much of the bony elements of the upper jaws of YPM 12733 were weathered away except isolated small piec-
a short, transversely oriented ridge and connects with
the posterior cingulum rather than to the metacone.
The large hypocone on the posterolingu al corner gives
the M1 a rectangular appearance, and is the largest
cusp on M1. The M2 is rounded in outline and is
circled by a well developed cingulum that has fine cren-
ulations across its surface (Fig. 2A). M2 cusp construc-
tion is similar to M1 except that the metacone is small-
er, creating a more rounded posterior corner. The
hypocone of M2 is a prominent cusp on the posteriorly
and medially extended lingual cingulum. Occlusal re-
relationships of M2 to m2 and m3 suggest, but do not
prove, that there was no M3.

The isolated left i2 and right i1–i2 have a deep groove
on the lingual side and are so worn on the tips that the
original cusp patterns are difficult to detect. The right
i3 is rather premolar-like in having a principal cusp
and an anterior and posterior cingular cusp. The un-
usual premolariform i3 is also found in certain indi-
iduals of living vulpine foxes (Otocyon, Urocyon, and
Vulpes), but is absent from the living arctoids (Ursidae,
Procyonidae, and Mustelidae). Only a small part of the
lingual side of the left lower canine is preserved; its
crown shows a posterolingu al cingulum and crenu-
lation of the enamel.

The p1 is indicated by the e pyc cast from a partial
natural mold on the right side. All preserved premolars
are strongly built and have cingula on the lingual sides.
The p2 is a simple, conical structure without posterior
accessory cusp, whereas p3 and p4 have a tiny access-
yory cusp about mid-way up the posterior border of
the principal cusp (Figs. 1E, 2B). The enamel of the
premolars is crenulated.

The m1 trigonid is very low and short relative to
the talonid making up 62% of total tooth length (Fig.
1A, B, E, F; Table 1). The shearing blade of m1 is short
with a shallow carnassial notch. The metaconid is po-
itioned slightly behind the protoconid. Both hypo-
conid and entoconid are similar in size, slightly ridge-
like, and are marginally positioned enclosing a broad
talonid valley (Fig. 2B, C). There is a small entocono-
lid between entoconid and metaconid, and a hypocono-
lid between hypoconid and protoconid. There are also two
small accessory cusps between hypoconid and ento-
conid. A tiny protostylid is present on the posterolat-
eral base of the protoconid. The holotype, AMNH
6884, is slightly larger (Table 1) and more worn than
YPM 12733. The mandible of the holotype is also
thicker than that of the latter. The overall morphology
of AMNH 6884 is otherwise very close to the m1 of
YPM 12733. The m2 is perhaps the most distinctive
tooth in this species. The trigonid is composed pri-
marily of the protoconid and metaconid, as the para-
conid is tiny. The protoconid and metaconid are com-
pressed toward the anterior and lingual side, leaving a
large area for an antero-labial cingulum, which is ter-
ninated caudally by a protostylid. This degree of tri-
gonid compression has not been seen in other fossil
and extant canids. The m2 metaconid is slightly larger
than the protoconid and is posterior to it. The talonid
basin occupies about 3/4 of the m2 occlusal surface with
the hypoconid being its dominant cusp. The entoconid,
together with encoconulid, form a shallow rim for the lingual side of the talonid. The m3 is rounded and small, with three low cusps shaped like a trigonid at the postero-labial corner.

Discussion — The fact that Nothocyon geismarianus is significantly different from Cormocyon copei needs no elaboration. The former exhibits some dental characteristics (e.g., shortened P4, enlarged complex M1, and low trigonid and broadened talonid of m1) that parallel such hypocarnivorous canids as Cynarctus, Pliaocyon, and the living raccoon dog Nyctereutes, as well as modern procyonids. Cormocyon, on the other hand, shows a mesocarnivorous dentition, primitive to the caniform carnivorans (see below).

The higher level relationship of Nothocyon geismarianus is far from clear, and it cannot be properly solved without further knowledge of the skull, especially the basicranium. Until then, we are limited to conclusions based on dental characters, many of which are known to be highly susceptible to homoplasy.

On the grounds of dental morphology, Nothocyon geismarianus seems most closely related to Subparicis Clark and Guensburg, 1972, as indicated by comparison with Subparicis dakotensis (AMNH 12244; F:AM 50240; cast of the holotype SDM 2476), Subparicis gilpini (F:AM 50241; 76196; cast of the holotype FMNH PM22405), a maxillary fragment referred by Clark and Guensburg (1972) to Paricis primaevus (FMNH P27157), and an undescribed genus related to Subparicis (F:AM 50392, 63309) (see Tedford, 1976, and Flynn et al., 1988, for the hypothesized relationships of caniform carnivorans, which forms the basis for the assessment of character polarities in this paper). They share the following derived characters: robust but simple conical premolars with cingula around the bases; reduction or loss of the paraconid on m2; lingual-labial compression of the trigonid in m2 associated with a wide antero-labial shelf occupied posteriorly by a protostylid; a tendency for the M1 metaconule to shift posteriorly; low m1 trigonid relative to talonid; and crenulated enamel. Although certain hypocarnivorous canids (e.g., Cynarctus, Pliaocyon, Aletocyon) have parallel developments in some of these characters, few have developed them as far as Nothocyon geismarianus and none has this unique combination of characters. N. geismarianus does, however, possess characters more advanced than Subparicis, such as: the much more posteriorly shifted M1 metaconule and the presence of a hypocone, which imparts a quadrate appearance to the upper first molar; the development of hypoconulid and encoconulid cusps on m1; and the more robust premolars.

We elevate Subparicis Clark and Guensburg, 1972, to generic rank to emphasize that major questions still remain as to the nature of Paricis Scott, 1893. The genotypic species, P. primaevus Scott, 1893, was based on a single left mandibular fragment with p2–p3 and alveoli of p1 and p4–m3 (PUMN 10583). The most distinct features of PUMN 10583 are its simple conical p2–p3 with crenulated enamel and a strong cingulum surrounding the entire base. The holotype is still the only known specimen from the John Day Formation of central Oregon. Several new species have since been referred to Paricis (as the subgenus Subparicis) by Clark and Guensburg (1972), all from the lower White River Group of Chadronian age, considerably older than the John Day deposits. One isolated maxillary fragment with P4–M1 (FMNH 27157) was also unquestionably referred to P. primaevus by Clark and Guensburg (1972:33). This disparity of geological ages and lack of topotype material to more fully characterize the genotypic species calls into question the assignment of the White River Chadronian taxa to Paricis.

Clark and Guensburg (1972), following the suggestion of Hall (1931), advocated a close relationship between Paricis sensu lato and the canid Hesperocyon, but put Paricis in the primitive ursid subfamily Amphicyonodontinae. Evidence cited above indicates that Subparicis and Nothocyon are further removed from canids and probably are related to early arctoids. The new material of Nothocyon, entirely dental in nature, does not resolve this issue.

CONCLUSION

New evidence of Nothocyon geismarianus indicates that the small carnivoran is not a primitive borophagine canid as conventionally perceived. N. geismarianus possesses a dental morphology with some characteristics of the arctoid carnivorans. Further resolution is not possible without basicranial evidence. A new genus and species, Cormocyon copei, includes the borophagine canid specimens from the John Day Formation that Cope incorrectly referred to Nothocyon geismarianus.

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LITERATURE CITED


WANG AND TEDFORD—STATUS OF NOTHOCYON


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