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SMALL LIMNOCYONINES (HYAENODONTIDAE, MAMMALIA) FROM THE BRIDGERIAN MIDDLE EOCENE OF WYOMING: *THINOCYON*, *PROLIMNOCYON*, AND *IRIDODON*, NEW GENUS

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MICHAEL MORLO[1] AND GREGG F. GUNNELL[2]

Abstract — The fossil record of small Limnocyoninae from the Bridgerian land-mammal age is reviewed and new specimens are described. Among 120 examined specimens of *Thinocyon*, 96 represent the type species, *T. velox*, with the other 24 representing *T. medius*. The relatively large sample size of *T. velox* demonstrates the great size and morphological variability of this species. Sexual dimorphism affects skull morphology slightly in over-all size differences, but this is not reflected in tooth morphology. Only two of up to eight previously described species of *Thinocyon* are recognized as valid: *T. velox*, known from Bridgerian biochrons Br-1 through early Br-3, and *T. medius*, known only from Br-3. Both species of *Thinocyon* are small (500-1800 g), hypercarnivorous, and semifossorial. Their mode of life was probably similar to that of recent *Mustela vison*. No other known creodont utilized weasel-like ecomorphospace.

Two additional limnocyonine taxa are recognized from biochron Br-1a, both of which are more primitive than *Thinocyon*. One represents the latest known occurrence of *Prolimnocyon antiquus*. The second represents a new genus and species, *Iridodon datzae*. *Iridodon* differs from other limnocyonines in being smaller. It further differs from *Prolimnocyon* in lacking M_3, from *Limnocyon* in having more slender premolars, from *Oxyaenodon* in having basined molar talonids, and from *Thinocyon* in lacking a bowed dentary and in having a narrower M_1. *Iridodon* represents the sister-group to all other Bridgerian Limnocyoninae except *Prolimnocyon*.

INTRODUCTION

Limnocyoninae are relatively small hyaenodontid creodonts characterized by reduction and loss of upper and lower third molars. They first appear in the earliest Eocene of North America, Europe, and Asia, and are best represented by a modest radiation in the western interior of North America. Limnocyonines disappear from the fossil record at the end of the middle Eocene in North America (Uintan land-mammal age) and Asia (Irdanmanhan land-mammal age). This paper examines the evolutionary history and paleobiology of small Bridgerian limnocyonine creodonts.

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Thinocyon is by far the most common Bridgerian limnocyonine and is the most abundant Bridgerian creodont genus besides "*Sinopa*", a genus generally placed in Proviverrinae. Marsh (1872) established *Thinocyon* based on the genotype species *T. velox*, but generic separation from the larger *Limnocyon* was not widely accepted (Wortman, 1902). Matthew (1909) reintroduced *Thinocyon* and included the species *T. velox* and *T. medius* in it. He also described two new species, "*T. mustelinus*" and "*T. cledensis*". McKenna et al. (1962) placed a single tooth, described by Marsh (1872) as "*Entomodon comptus*", in *Thinocyon* as a fifth valid species. All subsequent authors have followed Matthew (1909) in regarding *Thinocyon* as being distinct from *Limnocyon*.

The last detailed discussion of North American *Thinocyon* was provided in an unpublished Ph.D. thesis (Ivy 1993). Ivy split *Thinocyon* into six species, two of them described as new. Up to seven different species have been referred to North American *Thinocyon*, but only two are recognized as valid here. The last overview of North American creodonts was provided by Gunnell (1998b) who synonymized "*T. mustelinus*" with *T. velox*. His taxonomic list contained four North American *Thinocyon* species: *T. velox*, *T. medius*, "*T. cledensis*", and "*T. comptus*".

The only report of *Thinocyon* outside of North America was by Chow (1975), who established the species "?*Thinocyon*" *sichowensis* based on a specimen from the middle Eocene of China originally described as "?*Pterodon*" by Young and Bien (1935).

In recent years, the number of specimens attributable to *Thinocyon* has increased to around 120, principally by field work conducted by the American Museum of Natural History, the Milwaukee Public Museum, and the University of Michigan Museum of Paleontology. This new material allows, for the first time, a detailed examination of the variability of this genus, and sheds new light on the evolution and systematics of the related species. Moreover, some extremely well preserved specimens provide information that allows a better reconstruction of the paleobiology of this small creodont. Only two small Bridgerian limnocyonine specimens are known that do not belong to *Thinocyon*, both coming from the early Bridgerian Biochron Br-1a (Gunnell and Yarborough, 2000; Clyde et al., 2001). The large Bridgerian and Uintan limnocyonine genera *Limnocyon* and *Oxyaenodon* are included in phylogenetic analyses in this paper, but are otherwise not discussed in detail.

INSTITUTIONAL ABBREVIATIONS

AMNH — American Museum of Natural History, New York
BMUW — Burke Museum, University of Washington, Seattle
CM — Carnegie Museum of Natural History, Pittsburgh
FMNH — Field Museum of Natural History, Chicago
GMUW — Geological Museum of the University of Wyoming, Laramie
IVPP — Institute for Vertebrate Paleontology and Paleoanthropology, Beijing
UM — University of Michigan Museum of Paleontology, Ann Arbor
USNM — U. S. National Museum of Natural History, Washington D.C.
USGS — U. S. Geological Survey (Bridger collection housed in USNM)
YPM — Yale University, Peabody Museum, New Haven
YPM-PU — Princeton University collection, housed in the Yale Peabody Museum

BRIDGER FORMATION STRATIGRAPHY

Matthew (1909) divided the Bridger Formation into five parts (horizons A-E) based on sediments in the southern Green River (Bridger) Basin (Fig. 1). Bridger A includes the lowest 200 m

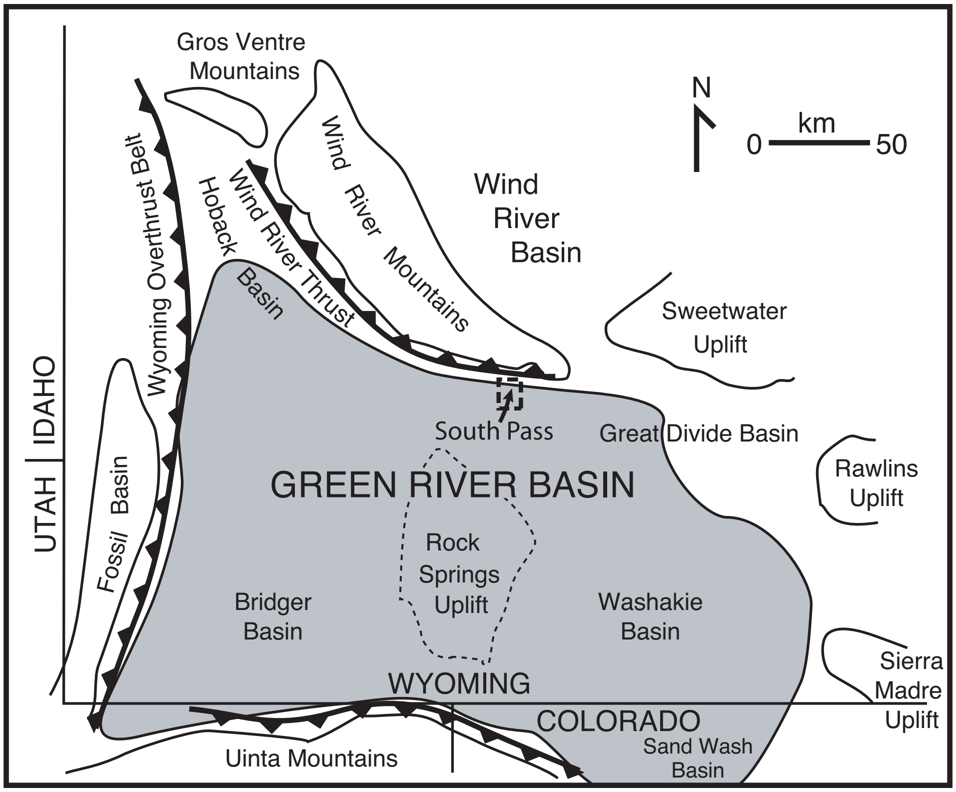

FIG. 1 — Map of greater Green River Basin in southwestern Wyoming. Main areas that have produced fossil specimens studied in this report are the Bridger Basin and South Pass.

of the Bridger Formation (Gunnell and Bartels, 1994). Bridger B includes the succeeding 150 m of the Bridger Formation and is abundantly fossiliferous. A thin ostracodal limestone (Evanoff *et al*, 1998; McGrew and Sullivan, 1970) separates Bridger A and B. Bridger B is separated from Bridger C by a calcareous limestone, the Sage Creek White Layer, while Bridger D is separated from Bridger C by the Lone Tree White Layer. Bridger C and D together include 300 m. Bridger E includes the top 50 m of the Bridger Formation.

Wood (1934) grouped Bridger A and B into the Blacks Fork "Member" of the Bridger Formation, based on faunal differences between this interval and Bridger C and D, together called the Twin Butte "Member" by Wood. Evanoff *et al*. (1998) have added the Turtle Bluff Member for Bridger E sediments.

Gunnell (1998a) proposed a biochronological subdivision of the Bridgerian, recognizing Br-0, Br-1a, Br-1b, Br-2 and Br-3 biochrons. Br-0 is the lower Gardnerbuttean, Br-1a includes the middle and upper Gardnerbuttean, and Br-1b is based on the faunal assemblage from Bridger A. Together biochrons Br-0 through Br-1b represent the early Bridgerian North American land-mammal age (NALMA). The early-middle Eocene boundary occurs at or near the Br-1b to Br-2 boundary (Gunnell and Yarborough, 2001; Clyde et al., 2001). The Br-2 faunal assemblage (middle Bridgerian) includes Matthew's Bridger B horizon, while Br-3 includes the Bridger C and D horizons (late Bridgerian). Bridger E may represent a separate biochron (Br-4) but the faunal assemblage has not yet been fully studied.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linneaus, 1758
Order CREODONTA Cope, 1875
Family Hyaenodontidae Leidy, 1871
Subfamily Limnocyoninae Wortman, 1902

Emended diagnosis.— Differs from Proviverrinae in having M^3 and M_3 reduced or absent. Differs from Oxyaenidae in overall smaller size, having P_1 double-rooted except in the most primitive species, having lower molars with relatively larger basined talonids with reduced entoconids, and in having M_1 relatively large.

Included North American genera.— *Limnocyon* Marsh, 1872, *Thinocyon* Marsh, 1872, *Oxyaenodon* Wortman, 1899, *Prolimnocyon* Matthew, 1915, *Iridodon* n. gen.

Discussion.— Questionably included in Limnocyoninae is the Chinese *Prolaena parva* (Xu et al., 1979), known only by the poorly preserved holotype (IVPP V5361). This taxon was described as an oxyaenid, but was later transferred to Limnocyoninae by Tong and Lei (1986). It differs from oxyaenids not only in having M_1 and the talonid of M_2 relatively enlarged (Tong and Lei 1986), but also in having a double-rooted P_1, a character state otherwise completely unknown in oxyaenids. It resembles Uintan *Oxyaenodon* in the outline of P_1 and P_3 and in reduction of the talonids, although they are relatively much smaller than in the Uintan form, especially in M_1. The specimen comes from the Hetaoyuan Formation of Honan Province of China and is probably contemporary with the Irdin Manha middle Eocene assemblage (Russell and Zhai, 1987). It may be temporally older than the highly derived Uintan *Oxyaenodon*, but is even more derived than that North American taxon. It remains unclear whether or not this taxon belongs in Limnocyoninae (if it is a creodont at all), and how it is related to North American hyaenodontids.

The Oligocene European *Thereutherium thylacodes* Filhol, 1876 was discussed in detail by Lange-Badré (1979) and placed in Limnocyoninae mainly because it lacks M_3 and M^3. According to Lange-Badré, *Thereutherium* further resembles *Thinocyon* in the posteriorly shifted I_2, the reduced single-rooted P_1, the reduced paraconule and metaconule in the upper molars, the fusion of paracone and metacone, the presence of a parastylid on P_4, having M_1 about as long as M_2, the outline of the occipital, the absence of a sagittal crest, and a short palatinum. As will be demonstrated below, evidence for a single-rooted P_1 in *Thinocyon* is equivocal, while sizes of upper molar conules and P_4 parastylid, posteriorly shifted alveolus of I_2, relative length of lower molars, and Lange-Badré's cranial characters are highly variable and partly reflect sexual dimorphism in *Thinocyon*.

Other than the reduction of the third molar, fusion of the upper molar paracone and metacone remains as the only shared character state between *Thereutherium* and *Thinocyon*. The paracone and metacone of M^1 in *Thereutherium*, however, are nearly completely fused, with the paracone clearly being the larger cusp (see Lange-Badré, 1979: pl. 30 fig. 1). In M^1 of *Prolimnocyon*, *Limnocyon*, and *Thinocyon*, the metacone is only slightly smaller than the paracone and they are only fused at their base. The paracone and metacone of M^1 are completely fused only in the much larger Uintan *Oxyaenodon* and the doubtful Asiatic limnocyonine *Prolaena*. Independently, fusion of the paracone and metacone as a larger cusp is also known in Hyainailourinae and Apterodontinae (see Morlo and Habersetzer, 1999, for the most recent high level taxonomy of Hyaenodontidae).

Thereutherium also differs in several other respects from all Limnocyoninae, including: it is much smaller than all other genera, has a highly reduced single-rooted P_1 and P^1, has very strong cingulids surrounding $P_{3\text{-}4}$, metaconids are small to absent, paracone and metacone are fused in M^2, and M^2 has three roots. Only Uintan *Oxyaenodon* and the Asiatic *Prolaena* have highly reduced metaconids and talonids on $M_{1\text{-}2}$, but both lack strong premolar cingulids. Furthermore, among limnocyonines, only the extremely primitive early Eocene (Wa-1 to Wa-3) "*Prolimnocyon*" *haematus* is known to have single-rooted P^1 and P_1, but even these are much less reduced than they are in *Thereutherium*.

The character state combination of strong premolar cingulids together with reduction of the metaconid and metacone are also known in *Apterodon* (Szalay 1967) and *Quasiapterodon* (Lavrov 1999), the former of which is co-occurring with *Thereutherium* in biozone MP 22 (Lange-Badré, pers. comm.). We therefore exclude *Thereutherium* from Limnocyoninae and suggest that the genus might have immigrated to Europe together with *Apterodon*, implying a phylogeny separate from Limnocyoninae.

Gunnell (1998b) raised the taxonomic level of Limnocyoninae to family status. The oldest genus, *Prolimnocyon*, is now known as one of the earliest non-oxyaenid creodonts. It is present in Wa-0 of the Clarks Fork Basin (Gingerich, 1989) and the Bumbanian of China (Meng et al., 1998). A recently reported Paleocene (Clarkforkian) occurrence of *Prolimnocyon* in North America (Bloch and Bowen, 2001) is incorrect: the specimen represents a juvenile *Tytthaena* instead (Bloch, pers. comm.). *Prolimnocyon* differs from contemporary proviverrines mainly in the reduced M_3 and M^{2-3}, but its M_{1-2} show the same type of talonid with a reduced entoconid and an elongated basin as are seen in the North American and partly European 'proviverrine' genera *Acarictis*, *Arfia*, *Galecyon*, *Gazinocyon*, *Prototomus*, *Proviverroides*, *Pyrocyon*, "*Sinopa*", and *Tritemnodon*, in the Asian taxon *Paratritemnodon*, and in a new taxon from Pondaung (Egi and Tsubamoto, 2000; MM, unpublished data), all formerly placed in 'Proviverrinae.' As in Limnocyoninae, a single-rooted P_1 and P^1 are primitive for this group. 'True' Proviverrinae (the European genera *Alienetherium*, *Allopterodon*, *Cynohyaenodon*, *Leonhardtina*, *Lesmesodon*, *Paracynohyaenodon*, *Parvagula*, *Protoproviverra*, *Proviverra*, '*Proviverra*' *eisenmanni*, and *Quercitherium*, as well as the African genera *Anasinopa*, *Masrasector*, and *Metasinopa*) primitively have a tricuspid talonid with a broad basin (which may be reduced, as in *Eurotherium*, *Matthodon*, and *Prodissopsalis*). Moreover, double-rooted P_1 and P^1 are primitive for this group. Based on these data, Limnocyoninae might well be a sister-taxon to the first group of "Proviverrinae" with both being separate from Proviverrinae *sensu stricto* (which would then require a new name). A revision of proviverrines is beyond the scope of this paper, therefore we tentatively retain the old use of Limnocyoninae as a subfamily of Hyaenodontidae.

Thinocyon Marsh, 1872

Thinocyon Marsh, 1872, p.204.
Thinocyon, Matthew, 1909, p. 448; Thorpe, 1923, p. 33; Denison, 1938, p. 179; McGrew et al., 1959, p. 169; Gazin, 1976, p. 10; Gunnell, 1998a, p. 114; Gunnell, 1998b, p. 99.
Limnocyon (in part), Wortman, 1902, p. 113.
Thinocyon (in part), West, 1973, p. 91.

Type species.— *Thinocyon velox* Marsh, 1872.

Included species.— *T. velox, T. medius.*

Emended diagnosis.— Dental formula 3.1.4.2 / 3.1.4.2. P^3/P_3 always lower than P^2/P_2. *Thinocyon* differs from *Prolimnocyon* in lacking M_3. *Thinocyon* differs from *Limnocyon* in its overall smaller size and in generally being more gracile; further differs from *Limnocyon* in having M^2 with a small metacone and a small to absent metaconule; the paracone-metacone blade is the anteroposteriorly longest part of M^2, while in *Limnocyon* lingual length is as long as the blade. *Oxyaenodon*, the other Bridgerian and Uintan limnocyonine genus, lacks a metacone on M^2.

Age and distribution.— Bridgerian biochrons Br-1 to Br-3 (middle Eocene), Wyoming.

Specimens Erroneously Referred to *Thinocyon*

Certain specimens referred to *Thinocyon* in the past can be excluded from this genus. "*Thinocyon*" *comptus* (Marsh, 1872) is based on a single, isolated, right dP_4 (YPM 13506; Fig. 2C-D) with a confusing taxonomic history. The tooth comes from Henrys Fork, Twin Buttes Member, Bridgerian Biochron Br-3. Marsh (1872: 214) originally described YPM 13506 as the last lower molar of a new genus and species, "*Entomodon comptus*," which he regarded as an "insectivore". However, Marsh further confused the issue by noting that a specimen he described earlier in the same paper (1872: 205) as ?*Viverravus nitidus* (YPM 11888), new species, might pertain to *Entomodon* as well, but was probably a different species than *E. comptus* because it was smaller.

Matthew (1909) regarded YPM 11888 as a dP_4 of a leptictid and Thorpe (1923) referred to it as an M_1 of a questionable *Viverravus*, but noted that it did not differ from Marsh's *E. comptus* except in size. McKenna et al. (1962) regarded YPM 11888 as a P_4 of a leptictid similar to *Hypictops*. These authors also felt that YPM 13506 was not related to YPM 11888 and was more likely to be an M_1 of a small *Thinocyon* species. Ivy (1993: 259) felt that YPM 13506 was a dP_4 of "a carnivorous mammal and maybe a *Thinocyon*" without offering any morphological grounds for recognizing it as such.

YPM 13506 differs from M_1 of *Thinocyon* in lacking a labial cingulid, having a lower paraconid, a relatively higher metaconid that is placed more posteriorly, a higher hypoconid and steeper cristid obliqua, a more basined talonid, and a better developed hypoconulid. The tooth lacks roots, but shows a wear facet on the protoconid. Following Ivy (1993), we interpret it as a dP_4.

There is only one dP_4 known for *Thinocyon*, UM 101320 (Fig. 2A-B), associated with two dentary fragments containing P_2 and M_2, both nearly completely erupted. The morphology of these associated teeth confirms that UM 101320 represents *T. velox*. While overall tooth size is nearly the same, "*T.*" *comptus* differs from UM 101320 in having a more bulbous and less anteriorly leaning paraconid, a more bulbous and rounded metaconid, a shorter and more labially angled talonid, and a lower lingual talonid margin lacking cuspules. These character states seem to exclude YPM 13506 from *Thinocyon*, as well as from creodonts generally.

YPM 13506 also differs from viverravid dP_4's in being much broader and less trenchant. Morphologically, it is similar to the dP_4 of FMNH PM 3869 (a miacid), but it differs in having the paraconid leaning less anteriorly and a much narrower talonid. It is therefore very unlikely that YPM 13506 belongs to any carnivorous group. The non-trenchant character of its paraconid suggests that it may be a leptictid or a pantolestid, but there are no dP_4's of either of these groups known to us for comparison. However, in the short talonid and the high hypoconulid, YPM 13506 resembles dP_4 of an undescribed paroxyclaenid from Messel (SMF Me2620). Paroxyclaenidae are considered to be the sister group to Pantolestidae (Russell and Godinot, 1988; Clemens and Koenigswald, 1993), suggesting that a relationship with pantolestids is possible for YPM 13506.

"?*Thinocyon*" *sichowensis* Chow, 1975, the only taxon referred to the genus outside of North America, is based on a right maxillary fragment, depicted in Young and Bien (1935: 227, fig. 1) as "?*Pterodon* sp." The specimen comes from the middle Eocene Guanzhuang Formation, Hsi-Kou locality, Xintai District, Shandong Province and is mentioned in several papers summarizing the mammalian record of Asia (Li and Ting, 1983; Russell and Zhai, 1987; Tong et al., 1996; Beard 1998).

Young and Bien (1935) describe the specimen as preserving "P^4", "M^1", and the alveolus of "M^2". Without having access to the specimen we can only judge from their drawing, which shows that "P^4" has no metastyle, but only a posterior accessory cusp and a protocone leaning posteriorly. In no other known hyaenodontid does the protocone of P^4 point posterolabially, but instead is always directed labially or anterolabially. This is, however, the case for the protocone of P^3 of several different hyaenodontid taxa. "M^1" has a very short metastyle that runs directly posteriorly, and a labial crest extends from the paracone to the labial cingulum. These character states are not present in hyaenodontid M^1s, but are typical of hyaenodontid P^4s. The paracone is worn which led Chow (1975) to concluded that two major cusps were present (contra Young and Bien, 1935). However, the occlusal view shows the typical wear pattern of a hyaenodontid P^4 with only one major cusp. There is no evidence for the presence of a metacone. We interpret the preserved teeth as $P^{3\text{-}4}$ instead of P^4-M^1, and the alveolus therefore belongs to M^1 instead of M^2.

Chow (1975) referred this fragment to *Thinocyon*, but it differs from that taxon in possessing a strong protocone on P^3. Hyaenodontid dP^3s have large protocones and this might be true for *Thinocyon* as well. However, the straight, dorsally extended posterior root of this tooth suggests that it is not deciduous. Even if our interpretation of tooth homology is incorrect and the preserved teeth belong to P^4-M^1 as the previous authors believed, the specimen would still differ from

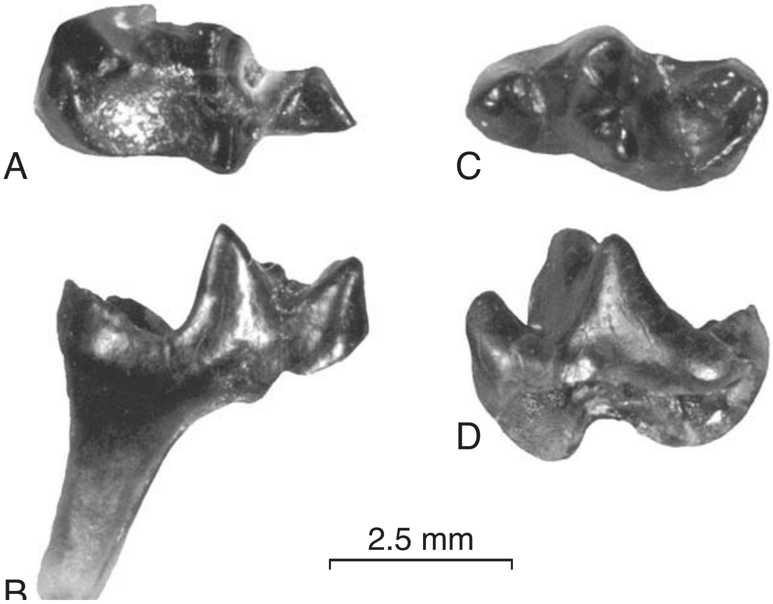

FIG. 2 — UM 101320, left dP_4 of *Thinocyon velox*, in occlusal (A) and lingual (B) views; YPM 13506, right dP_4 of "*Entomodon comptus*," in occlusal (C) and lingual (D) views. Note higher and more anteriorly leaning paraconid and longer talonid in *T. velox*.

Thinocyon in having a posterolabially leaning "P^4" protocone and only one major cusp on "M^1". We therefore exclude the specimen from *Thinocyon*. This restricts the known geographic occurrence of *Thinocyon* to North America only.

The taxonomic relationships of "?*Thinocyon*" *sichowensis* remain unclear, but it appears unlikely that it is a limnocyonine. The strong protocone on P^3 differentiates it from all known limnocyonines except the much larger Bridgerian *Oxyaenodon*.

FMNH PM 15858, figured in West (1973: pl. 3, fig. e) as "*Thinocyon* cf. *velox*", does not belong to *Thinocyon*. Anterior to the tooth West described as "P_2", two complete alveoli are visible, and also the posterior border of an additional premolar alveolus is present. This tooth therefore is not P_2 but P_3. Additionally, the posterior alveolus of "P_4" is elongated in comparison to the anterior one, as is typical for hyaenodontid M_1 alveoli. Finally, M_2 (= "M_1" of West, 1973) has an entoconid clearly separated from the hypoconulid by a deep notch. Since this specimen had three molars we exclude it from *T. velox*. A separated entoconid is extremely rare in North American proviverrines, but some specimens of *Sinopa minor* Matthew, 1909 (UM 33466) have a cuspate lingual talonid margin. We refer FMNH PM 15858 to this species, which was regarded as a probable junior synonym of *S. rapax* Leidy, 1871, in Gunnell (1998b).

Thinocyon velox Marsh, 1872
Figs. 2A-B, 3-12

Thinocyon velox Marsh, 1872, p. 204.
Thinocyon velox, Matthew, 1909, p. 449; Thorpe, 1923, p. 33; Denison, 1938, p. 179; Gazin, 1976, p. 10; Gunnell, 1998b, p. 99.
Limnocyon velox, Wortman, 1902, p. 118.
Thinocyon cledensis Matthew, 1909, p. 460.
Thinocyon cledensis, Denison, 1938, p. 180; Gunnell, 1998b, p. 99.

FIG. 3 — Holotype of *Thinocyon velox*. YPM 11797, left mandible in occlusal (A) and labial (B) views. Note low and bowed mandibular body and absence of an anterior cusp on P_4.

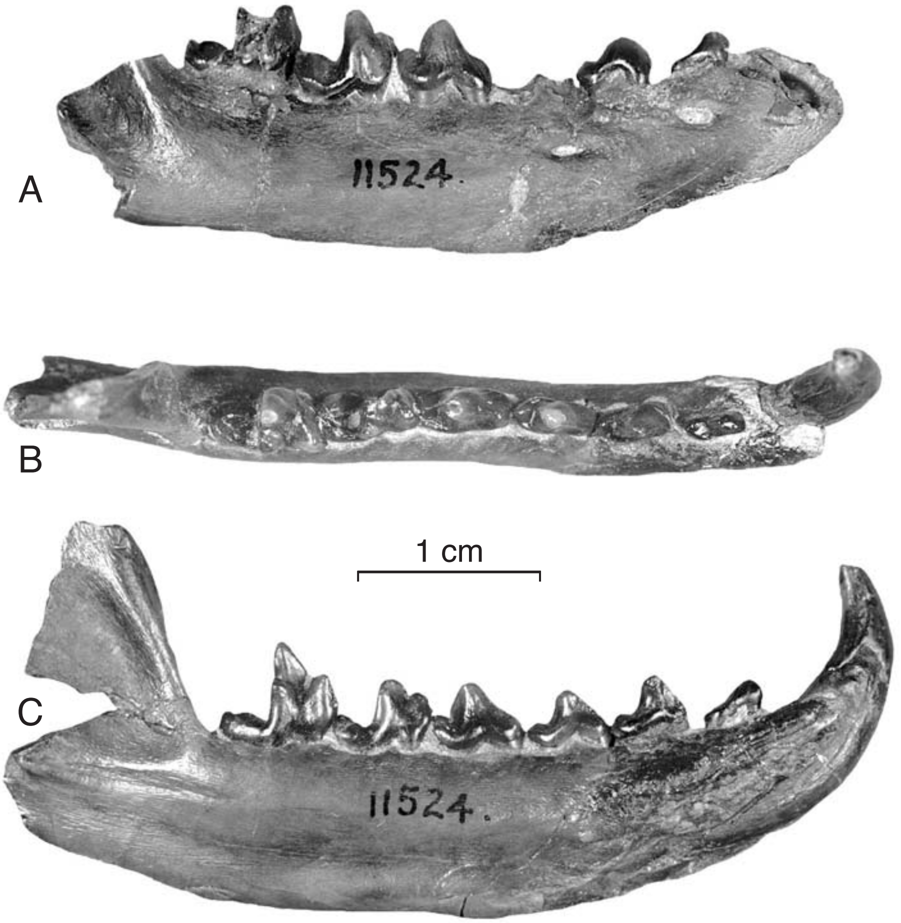

FIG. 4 — *Thinocyon velox*. AMNH 11524, right dentary in labial (A) view, left dentary in occlusal (B) view, left dentary in lingual (C) view.

Thinocyon mustelinus Matthew, 1909, p. 461.
Thinocyon mustelinus, Thorpe, 1923, p. 35; Denison, 1938, p. 179; Gazin, 1976, p. 10; Gunnell, 1998b, p. 99.
Thinocyon cf. *T. velox* (in part), West, 1973, p. 91.
Thinocyon sp., cf. *T. velox*, Gunnell, 1998a, p. 114.

Holotype.— YPM 11797, left mandible with C_1, P_1, broken $P_{2\text{-}3}$, P_4, roots of M_1, and M_2 talonid (Fig. 3; Wortman 1902: fig. 76).

Type locality.— Grizzly Buttes, Blacks Fork Member, middle Bridger Formation (Br-2).

Age and distribution.— Bridgerian biochrons Br-1b through Br-2, northern and southern Green River Basin, and Br-3, Washakie Basin, Wyoming.

Referred specimens.— AMNH 1728, 1731, 1742 (holotype of "*T. cledensis*" Matthew, 1909; Fig. 12), 11524 (Figs. 4, 11), 11528, 11553, 12157, 12631 (endocast figured in Radinsky, 1977, as "*T. velox*"), 12632, 12633, 12635 (holotype of "*T. mustelinus*" Matthew, 1909; Fig. 6A), 13080, 13081 (Fig. 8A, 9A; Matthew 1909, txt.-fig. 59-61, pl. 44, fig. 2-4), 13082, 13140, 14574, 19201, 55660, 83670 (Fig. 8B), 91061, 91131, 98735, 131831, 140007 (Fig. 7), BMUW 60641, FMHN PM 15860, PM 15083 (West 1973: pl. 3, fig. f), PM 55534, PM 60215, GMUW 3059 (Figs. 5D, 6B, 10), UM 32792, 32796, 32797, 32809, 33474, 33477, 33479, 33661, 95486, 95748, 98794 (Fig. 5A-C), 99738, 100050, 100523, 100639, 100690, 100830, 100882, 101320 (Fig. 2A-B), USNM 5915 (= AMNH 11525), 13329, 13330, 13331, 22479, 361374, 361375, 361376, 361377, 361378, 361379, 361380, 361381, 361382 (two individuals), 361383, 361384, 361385, 361386, 361387, 361389, 361390, 361391, 361392, 361395, 361396, 361397, 361398, 361400, 362786, 362777, 362778, 362780, 362783, 362785, 362784, 362781, 362782, 362787, YPM 12877a-c, 12870 (Wortman 1902: 77-80; Thorpe 1923), 12879, 13006a, 13026, 16101.

Emended diagnosis.— The type of *T. velox* differs from *T. medius* in being smaller and having the mandibular body less robust, lower, and more bowed. In some specimens of *T. velox*, the posterior mental foramen is placed under P_2 instead of P_3. In *T. velox*, P_1 is relatively larger (Fig. 14A), P_4 has a weak to absent anterior cusp and is much lower, the hypoconid of M_1 is less massive and the cristid obliqua is relatively longer. P^4 mostly lacks a parastyle and has a weaker protocone, the metastyle of M^1 is slightly more angled and less posteriorly directed, and the protocone is small. M^2 has a much more labially directed parastyle, the metacone is directly posterior to the paracone instead of being shifted lingually, the metaconule generally is larger, and the cingula of the protocone and parastyle are weak. The latter does not surround the protocone except in the most derived individuals.

Description.— Due to great variability both in size and morphology we first give a detailed redescription of the holotype in order to have a basis for discussion of this variability. Tables 1 and 2 summarize tooth measurements for *Thinocyon velox* and *Thinocyon medius*.

Holotype of *Thinocyon velox*

The holotype of *T. velox* (Fig. 3) has a very shallow dentary (height = 6.2 mm under M_2), as do other specimens (AMNH 12632, UM 32796, 32797, 99738, 100639, YPM 12870), but not all (AMNH 11524 [Fig. 4], 12157, 12633, YPM 12877a). The dentary is slightly bowed near P_3. The symphysis extends to the anterior root of P_3, but is often shorter in smaller specimens (AMNH 11528, 12635, 13140, 19201, UM 95748). Two mental foramina are present, the anterior one under the posterior root of P_1 and the posterior one under P_2. There are diastemata separating C_1-P_1, P_1-$P_{2,}$ and P_2-P_3.

Incisor alveoli indicate that I_2 was placed farther posteriorly than either I_1 or I_3. In larger specimens (FMNH PM 60215) I_1 may align with the other incisors. The lower canine is simple and shows some lingual and labial striations. A small wear facet produced by I^3 is present lingually. P_1 is longer than high, is posteriorly enlarged, has a very small accessory cuspule on the postprotocristid, and has the protoconid slightly angled lingually. P_2 is broken but shows that it was posteriorly enlarged. P_3 is broken anterior to the posterior enlargement, which is surrounded by a cingulid, and there is a small basal posterior cusp developed. P_4 has a very small anterior

TABLE 1 — Lower tooth measurements of *Thinocyon velox* and *Thinocyon medius*.

Thinocyon velox	C_1L	C_1W	P_1L	P_1W	P_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W	M_2L	M_2W
AMNH 11524			3.45	1.75	3.85	2.00			5.15	2.80	5.50	3.20	6.50	
AMNH 11528			3.20	1.35										
AMNH 11553							4.20	2.30						
AMNH 12157							3.85	2.25	5.25	3.05				
AMNH 12632			3.35	1.50										
AMNH 12633									5.40	2.80				
AMNH 13080	4.00	3.20							4.50	3.20				
AMNH 13081			2.70	1.60	3.70	1.85	3.85	1.85	4.00	2.30	5.60	3.15	6.30	3.80
AMNH 14574									5.15	2.40				
AMNH 1742									5.25	2.40	6.15	3.35		
AMNH 19201			2.90	1.45	3.70	2.10	3.70	2.10	4.40	2.40				
AMNH 83670	4.30	3.40	3.90	1.60	4.20	2.00	4.25	2.10	5.45	2.85	6.00	3.35	6.65	3.85
AMNH 9106						1.85	4.00	1.90	4.70	2.60	5.25	3.15		3.60
AMNH 91131							4.70	2.20			6.10	3.40		
AMNH 96393													5.85	3.25
FMNH 55534	4.55	4.00	3.55	1.85	4.25	2.00	4.45	2.30	5.30	3.00	6.15	3.50		
FMNH 60125					4.45		4.70		5.45					
GMUW 3059			3.50	1.60	4.30	1.90			5.00	2.20	5.95	3.00		
UM 100690									5.05	2.15				
UM 100882			3.50	1.75										
UM 101320	2.45	2.25	3.35	1.30										
UM 101526											4.65	2.90		
UM 32797									4.80	2.70	5.60	3.60	6.20	4.00
UM 32809	4.20	3.55							5.20	3.20				
UM 33474									5.00	2.35				
UM 33661							4.50	2.00						
UM 95486									4.55	2.05				
UM 95748											5.35	3.10	6.10	3.15
UM 98653											6.40	3.30		
UM 98794	3.10	2.90	3.40	1.65	3.80	1.90			4.20	2.15	5.30	2.95	5.70	3.15
UM 99738	3.60	2.80	3.75	1.50										
USNM 13329			3.50	1.70	4.50	2.15	4.60	2.10						
USNM 13331											5.90	3.25		
USNM 361276											4.95	3.45	6.00	3.30
USNM 361284			3.25	1.65	3.85	2.25	4.20	2.15	5.50	2.80				3.85
USNM 361374							4.85	2.20	5.20	2.50	6.60	3.30		
USNM 361378											5.20	2.90	5.30	3.45
USNM 361379											5.35	2.95		
USNM 361380							4.00	1.70	4.00	2.15	5.45	3.10	5.90	
USNM 361381					3.50	1.80	3.95							
USNM 361383									4.40	2.50	5.80	3.60		
USNM 361385									5.20	3.10	5.50	3.50	6.05	3.90
USNM 361387											5.70		6.70	3.80
USNM 361389									4.95	2.75			6.75	3.80
USNM 361390													6.30	3.70
USNM 361391											7.15	4.20		
USNM 361396			3.35	1.45	3.55	1.70								
USNM 362777									4.90	3.00	6.20	3.70		
USNM 362780											5.90	3.05		
USNM 362781											5.65			
USNM 362783									4.90	2.40				
USNM 362784									4.40	2.40				
USNM 362786											6.60	3.90		
USNM 5915	4.25	3.15			4.10	2.05	4.20	2.15	5.30	2.90	6.40	3.35	7.05	3.80

TABLE 1 — Lower tooth measurements of *Thinocyon velox* and *Thinocyon medius (continued)*.

Thinocyon velox	C$_1$L	C$_1$W	P$_1$L	P$_1$W	P$_2$L	P$_2$W	P$_3$L	P$_3$W	P$_4$L	P$_4$W	M$_1$L	M$_1$W	M$_2$L	M$_2$W
YPM 11797 (type)			3.00	1.35					4.60	2.55				
YPM 12877									5.70	2.70				
YPM 12877a									5.45					
YPM 12877b									5.50	2.70				
YPM 12879									4.70	2.50	6.30	3.40		
YPM 13005									4.75	2.10				

Thinocyon medius	C$_1$L	C$_1$W	P$_1$L	P$_1$W	P$_2$L	P$_2$W	P$_3$L	P$_3$W	P$_4$L	P$_4$W	M$_1$L	M$_1$W	M$_2$L	M$_2$W
AMNH 11529							4.30	1.95	4.45	2.50			6.60	
AMNH 12076			3.50	1.70	4.50	2.40			5.50	2.80				
AMNH 12154			3.35	1.55		2.40	4.25	2.10	5.10	2.60		3.50	6.50	3.90
USNM 361373			3.90	1.90	5.20	2.45	5.40	2.45			6.50	4.80	8.00	4.55
USNM 362776			3.80	1.80	4.90	2.45	5.50	2.60	5.70	3.20	7.15	3.50		
YPM 11798 (type)	5.60	4.10	4.05		5.30	2.50	5.40		6.20	3.20	6.40	4.35	7.80	4.50
YPM 12874a							5.55	2.45						
YPM 12881					5.30	2.50								

cusp, a high and sharp protoconid, and a posterior heel that is half the height of the protoconid and separated from it by a notch. A lingual cingulid extends from the anterior cusp to the posterior heel, and is much stronger than a very weak labial cingulid. A tiny cuspule forms the posterior cingulid.

M$_1$ is represented only by its roots, the anterior root being broader than long and only half the size of the posterior one. Only the talonid of M$_2$ is preserved. The cristid obliqua is anteroposteriorly oriented and rises in height posteriorly. The hypoconulid is only slightly smaller than the hypoconid and both cusps are indistinct. The talonid is basined slightly and not open lingually.

Upper Teeth of *T. velox*

Upper incisors are preserved in FMNH PM 60215, and these increase in size from I^1 to I^3. They are heavily worn in this specimen, but the left I^2 shows that they are tricuspid, with the highest cusp in the center. Like C$_1$, C^1 has low ridges on its labial and anterior sides.

P^1 is similar to P$_1$ in being double-rooted and low. The same is true for P^2, which differs from P$_2$ only in being a little broader. Like P$_2$, P^2 may develop a very small posterior cingulum cuspule that can vary within a single individual, as in USNM 361381 where the right P^2 lacks this cuspule while it is present on left P^2.

P^3 is lower than P^2 and normally possesses a small parastyle, but this varies (FMNH PM 60215 has a typically small parastyle on left P^3 while it is very strong on right P^3). Occasionally P^3 has a small posterior cusp, but all specimens have a small posterolingual swelling or vestigial protocone.

P^4 has a prominent paracone that leans posteriorly, an anteriorly placed, large protocone, and a short metastyle which is lower than the protocone. A parastyle is mostly lacking, but this varies independent of stratigraphic position, as a small one is present in the relatively late occurring AMNH 11524 while larger ones are found in AMNH 12631, GMUW 3059 (Fig. 6B), and UM 100690 from Br-1 as well as UM 98794 from Br-2. A relatively strong cingulum surrounds the tooth.

TABLE 2—Upper tooth measurements of *Thinocyon velox* and *Thinocyon medius*.

Thinocyon velox	C^{1}L	C^{1}W	P^{1}L	P^{1}W	P^{2}L	P^{2}W	P^{3}L	P^{3}W	P^{4}L	P^{4}W	M^{1}L	M^{1}W	M^{2}L	M^{2}W
AMNH 11524													4.00	7.60
AMNH 12631	4.05				3.60				5.65		5.35			
AMNH 12635 (type)											4.80	4.70		
AMNH 13081			3.45	1.70	3.60	1.80	4.30	2.05	4.75	4.00	6.15	5.50	3.60	6.70
AMNH 131831											6.00	5.30	4.40	7.00
AMNH 19201									4.70	3.90	5.40			
AMNH 55660											5.85	5.30		
AMNH 83670	4.40	3.30	3.90	1.85	4.15	2.00	4.70	2.30	5.85	5.20	6.70	6.00	4.15	
AMNH 98735											6.35	5.00		
FMNH 15083									3.85		4.40	4.35		
FMNH 60125	4.55		3.90		4.55		4.10		5.40		6.50		3.70	
GMUW 3059	3.40	2.70	3.50	1.80	4.20	1.75			5.30	4.10	6.50	5.25	2.95	6.40
UM 100523	3.80	2.70			3.55	1.85			5.65	3.80				
UM 33477									6.25	4.45	6.25	6.05	3.55	6.30
UM 98794	3.05	2.45	3.20	1.40	3.55				5.30	3.70	5.55	5.10	3.50	5.40
USNM 361375											5.90	4.95	3.40	5.70
USNM 361377									5.55	4.10	5.80	5.40		
USNM 361381			3.30		3.50		3.50		4.60		5.50			
USNM 361382	3.45	2.85	2.85	1.20	3.85	1.65	3.80	2.00	5.00	4.30				
USNM 361386			3.35						5.55		6.00			
USNM 361396											5.80	5.15		
USNM 362787									5.60	4.70	5.80			
USNM 5915							4.65	2.10	5.95	4.85	6.40	6.00	2.85	7.45

Thinocyon medius	C^{1}L	C^{1}W	P^{1}L	P^{1}W	P^{2}L	P^{2}W	P^{3}L	P^{3}W	P^{4}L	P^{4}W	M^{1}L	M^{1}W	M^{2}L	M^{2}W
AMNH 12154			3.40	1.65	4.60	2.10	4.30	2.30	6.00	4.25	6.20	6.00	3.60	7.00
USNM 361373					5.00	2.35	5.35	2.60	7.40	6.30	7.60	7.10	3.50	8.45
YPM 11798 (type)									7.00	5.00	7.50			

The paracone and metacone of M^1 are of equal height, but the metacone often may appear smaller because of wear (GMUW 3059). The cusps are fused at their base. A small parastyle is present, the edge of which protrudes nearly labially in smaller specimens (AMNH 12635; Fig. 6A), but more anteriorly in larger individuals. A metaconule and paraconule are normally well developed but the paraconule may be obscured by wear (USNM 361375). The metastyle is separated from the metacone by a notch that broadens with wear (FMNH PM 15083 in West, 1973: pl. 3, fig. f). The protocone of M^1 is fairly strong, and its anterior cingulum is much stronger than the posterior one.

M^2 is a very short tooth with an extended parastylar blade that is mostly surrounded by a cingulum. This cingulum is larger in more derived specimens of *T. velox* (AMNH 83670, FMNH PM 60215, UM 33479), as it is in *T. medius*. There is a relatively weak to absent lingual cingulum. All *T. velox* have the M^2 metacone lying directly posterior to the paracone. It is much weaker than the paracone and can be extremely reduced. However, a small metaconule is always developed, as is a paraconule.

Deciduous Teeth of *T. velox*

The dP$_4$ of UM 101320 (Fig. 2A-B) resembles M$_1$, but is relatively narrower with a more anteriorly placed paraconid. The hypoconulid is higher than the hypoconid, but the main difference between the talonids of dP$_4$ and M$_1$ is in the cristid obliqua which is much more sloping in the

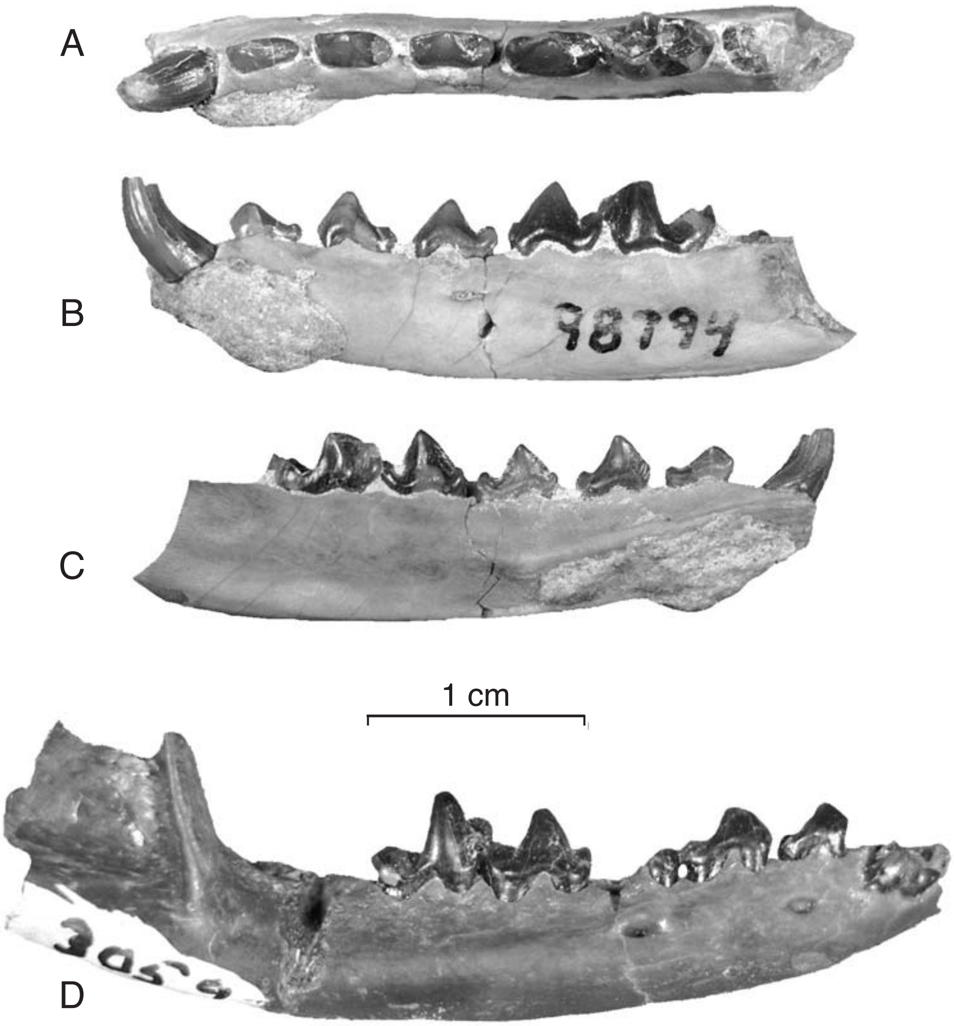

FIG. 5 — Variability in *Thinocyon velox*. A-C, UM 98794 in occlusal, labial, and lingual views showing relatively small P_4 anterior cusp and relatively deep dentary; D, GMUW 3059 in labial view showing extremely large P_4 anterior cusp and relatively shallow dentary.

former. Additionally, UM 101320 includes two left dentary fragments with $P_{1\text{-}2}$ and M_2, a right dentary fragment with dC_1 and $P_{1\text{-}2}$, a fragmentary skull with M^1, and the posterior right dentary with $M_{1\text{-}2}$ still in occlusion. Of these teeth, P_2 and M_2 are nearly completely erupted, while dP_4 shows no sign of resorption.

UM 100050 is another juvenile *Thinocyon*. It consists of a left dentary fragment preserving the posterior half of P_1, the anterior margin of the alveolus of P_2 or dP_2, and the tip of the permanent canine still deep in its crypt. A third non-adult specimen of *Thinocyon* is BMUW 60641, which has P_4 and lower canine not fully erupted.

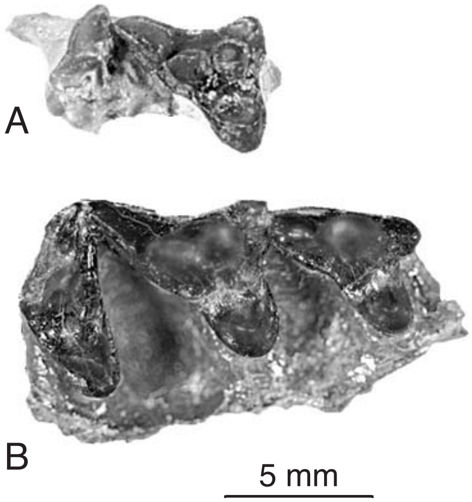

FIG. 6 — Variability in *Thinocyon velox*. A, AMNH 12635, holotype of "*T. mustelinus*", right $M^{1\text{-}2}$ in occlusal view; B, GMUW 3059, right P^4-M^2, in occlusal view. Note the size difference and the anterolabially extended preparastylar wing on M^1 of AMNH 12635.

Lower Teeth of *T. velox*

AMNH 13081 (Matthew 1909: txt.-fig. 59-61, pl. 44, fig. 2-4) preserves a complete skull, both dentaries, and a partial skeleton. The dentaries are very similar to the holotype, but differ in possessing a small diastema between P_3 and P_4, having P_1 slightly higher, and showing some variation in the placement of mental foramina.

FMNH PM 60215 preserves I_3, the crown of which is divided by a low groove with wear facets on either side. It therefore is unclear whether this tooth was bicuspid, as is usually the case in European proviverrines (Morlo and Habersetzer, 1999). In contrast to the holotype, the alveolus of I_2 is not shifted posteriorly, but lies in the same plane as the alveoli of I_1 and I_3.

In general, P_1 rarely varies much from that seen in the holotype except in size. The same is true for P_2, but it occasionally may have a very small basal posterior cusp. P_3 is never as high as P_2 but is longer, and in most specimens has a tiny anterior cingulid cuspule and a posterior basal cusp. P_4 is normally as in the holotype, but often there is a slightly to moderately larger anterior cusp present (AMNH 11524 [Fig. 4], UM 98794 [Fig. 5A-C], GMUW 3059 [Fig. 5D], YPM 12877b or YPM 12879). YPM 12877b and YPM 12879 have this cusp placed anterolingually in addition to being larger. Similar variability of more complicated occlusal crown surfaces in the posterior premolars has been documented in extant *Vulpes* by Szuma (2000, 2002), interpreted as being related to increasing dietary opportunism (Szuma 2003). Premolar variability in *T. velox* is not clearly related to stratigraphic position, which suggests a similar interpretation for this Eocene creodont.

AMNH 13081 has an M_1 talonid length that is 47% of total tooth length, but relative talonid length may differ as in YPM 13006a where the talonid is very short relative to the trigonid. The metaconid is normally as high as the paraconid, but may also be higher (AMNH 91131), and normally lies lingual to the paraconid and posterior to the protoconid. The talonid of M_1 is worn in AMNH 13081, but the hypoconid is clearly smaller than the hypoconulid. The M_1 entoconid of AMNH 11524 (Fig. 4) and AMNH 12635 is reduced and incorporated into the entocristid, while in FMNH PM 55534 the entoconid is still visible and separated from the hypoconulid by a tiny notch. The talonid basin is deep but narrow in most individuals.

In M_2, the metaconid normally is lower than the paraconid and placed directly lingual to the protoconid. The talonid is lower than in M_1 because the hypoconulid and hypoconid are of equal

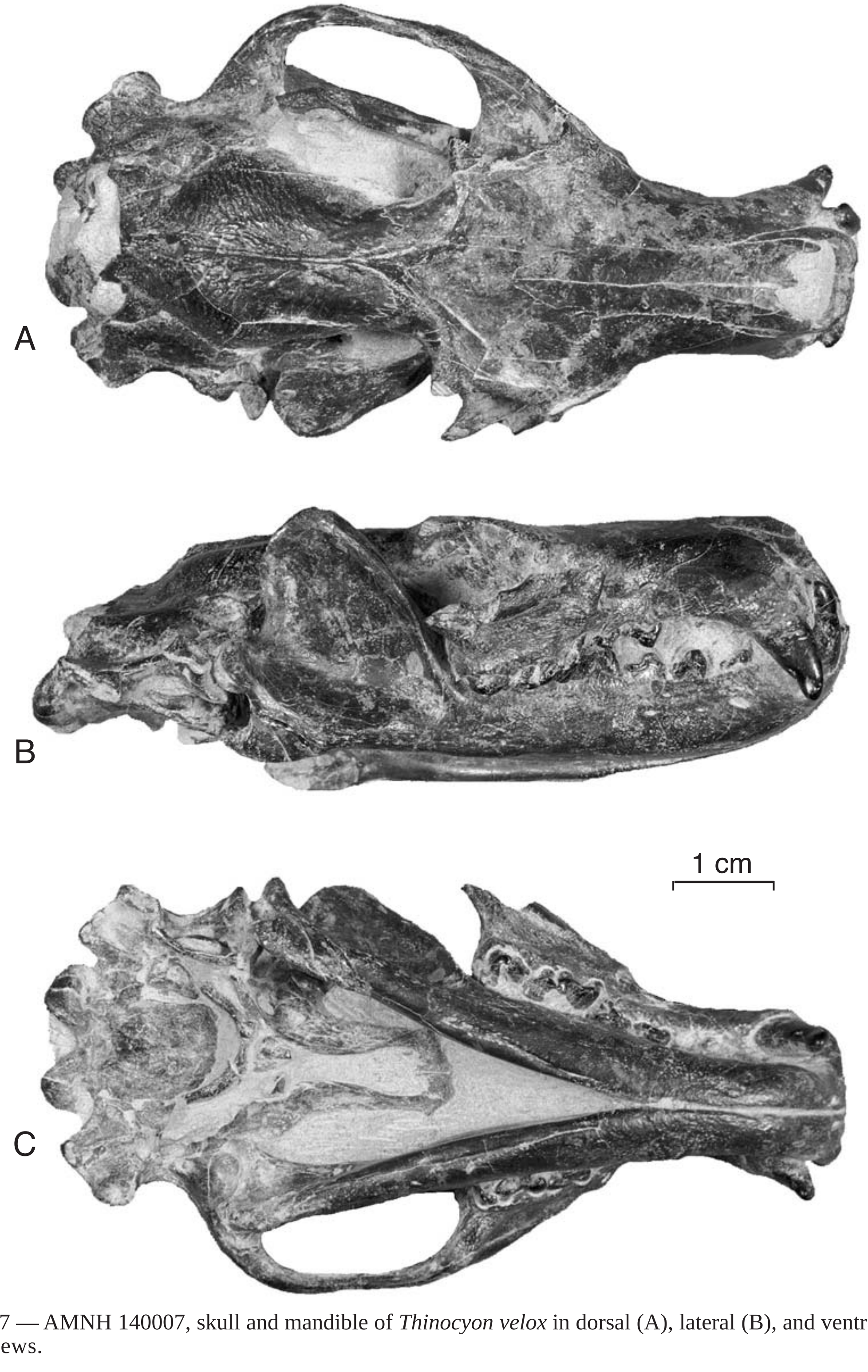

FIG. 7 — AMNH 140007, skull and mandible of *Thinocyon velox* in dorsal (A), lateral (B), and ventral (C) views.

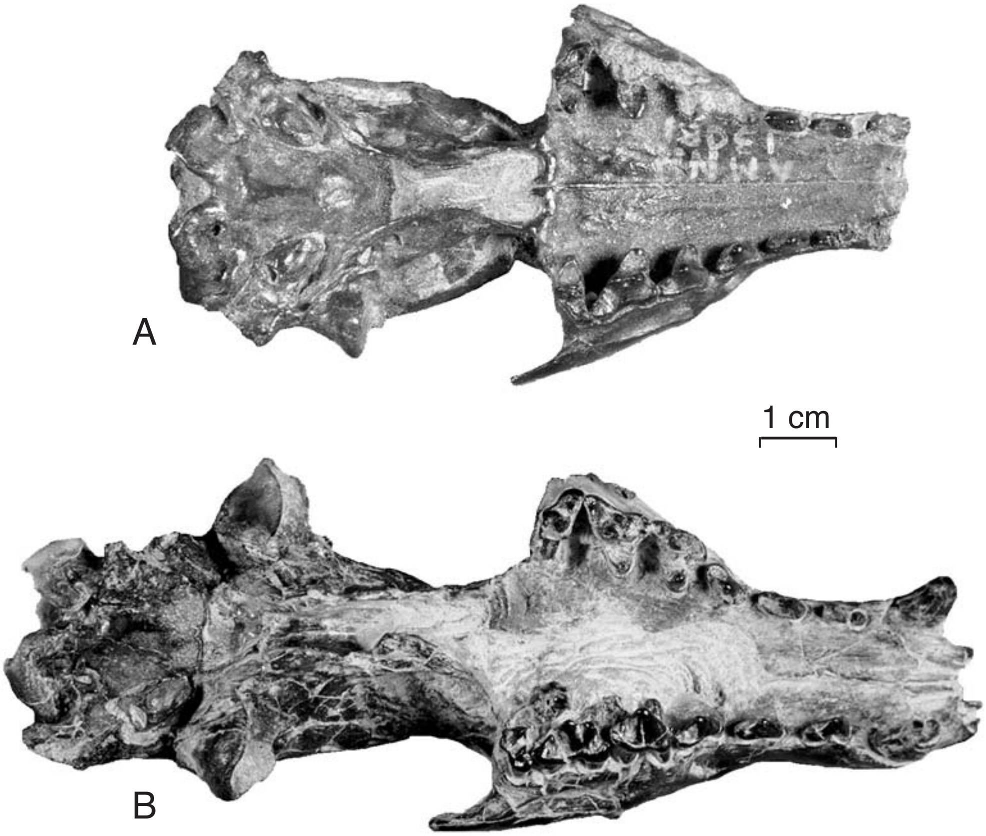

FIG. 8 — Cranial sexual dimorphism in *Thinocyon velox*. A, AMNH 13081, female skull; and B, AMNH 83670, male skull, in ventral views. Note much longer skull of male, but similar tooth sizes in both sexes.

height. The entoconid is reduced to a slight swelling along the lingual talonid margin and may be lacking completely (AMNH 11524; Fig. 4). The cristid obliqua may be straight (holotype, USNM 361389, USNM 361392, 362781) or more posterolabially directed (UM 32796, 99738, USNM 362777, 362778, YPM 13026, 12877b, 13026).

Skull of *T. velox*

This description is based on AMNH 140007 (Fig. 7), AMNH 13081 (Fig. 8A, 9A), AMNH 83670 (Fig. 8B), FMNH PM 60215, UM 33479, and UM 100523, the two last of which come from the same locality (BRW-15). The premaxilla is relatively short, with a small diastema between C^1 and I^3. The nasals extend from the middle of the premaxilla posteriorly to a point above the contact between P^4 and M^1. The point where the nasal, maxillary, and frontal bones meet lies above the metastyle of P^4 in AMNH 13081 (Fig. 8A), but also may lie above the P^4 parastyle (UM 100523, FMNH PM 60215) or even above P^3 (YPM 16101). The large maxillary foramen lies directly above P^3. The lacrimal extends anteriorly to a point above the anterior root of P^4, and posteriorly to the posterior edge of the coronoid fossa.

A sagittal crest is developed, but variable in height, corresponding to the height of the occipital. If the occipital is as high as it is broad, then the sagittal crest is high. Specimens with this configuration are interpreted as males (AMNH 83670, 91061, 131831, FMNH PM 60125, UM

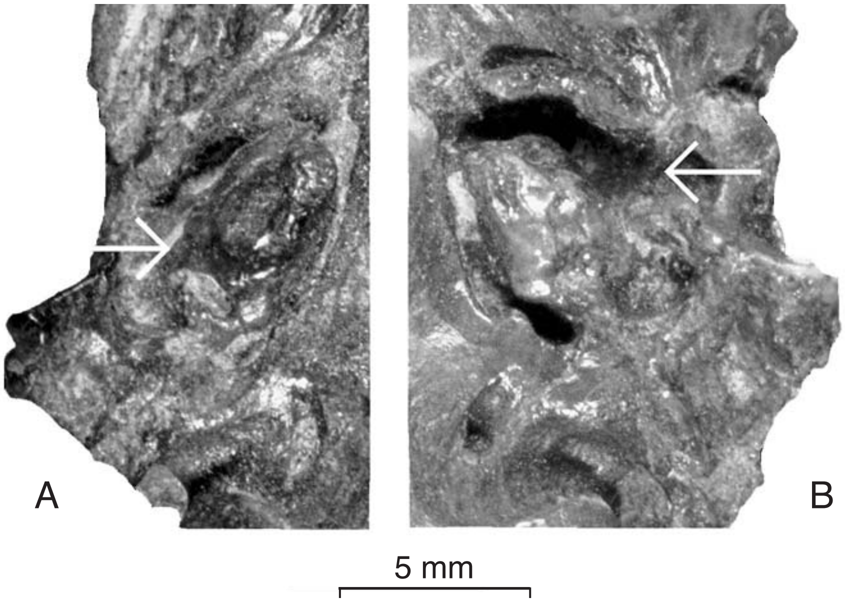

FIG. 9 — Basicrania of *T. velox*, female AMNH 13081 (A), and male AMNH 12631 (B). Arrow in A indicates small, bony ridge extending from promontorium. Arrow in B indicates relatively larger tympanic recess in this male specimen.

33479, YPM 16101). Known dentaries that accompany these skulls are large with relatively deep horizontal rami, differing substantially from the holotype. Moreover, the pterygoid region differs in being much longer in males (Fig. 8B). Other specimens with occipital heights only about 2/3 the width and without sagittal crests are interpreted as females (AMNH 13081, UM 100523, YPM 12870). YPM 12870 is accompanied by dentaries with very shallow horizontal rami. These differences are not correlated to differences in tooth morphology and there is no simple relationship with size, because some of the females get very large, but the largest specimens appear to be males. With respect to the cheek teeth, *Thinocyon* is convergent on extant *Vulpes* in which only canine size is sex-dependent (Szuma 2002).

The basicranium (Figs. 8-9) is generally broad and flat as described by Matthew (1909), quite similar to *Prolimnocyon* (Polly, 1996). There is no evidence of an ossified auditory bulla. The promontorium is ovoid, being slightly broader posteriorly. There is a shallow yet distinct groove for the promontory artery extending across the lateral portion of the promontorium. There is also a faint, small groove for the stapedial artery leading to the fenestra ovale. The fenestra rotundum is large and round, the fenestra ovale smaller and ovoid. The stylomastoid foramen is larger than the fenestra rotundum and is separated from the tympanic recess by the post-tympanic process of the squamosal, which extends to the lateral surface of the promontorium. The epitympanic recess is relatively shallow, but deeper than the mesotympanic recess located directly anterior to the former. The tympanic recess is apparently somewhat larger in males (Fig. 9) and there may be a small, bony ridge extending from the promontorium posterolaterally, although this is not present in every specimen.

Postcrania of *T. velox*

Postcranial descriptions are based on UM 33479, GMUW 3059 (Fig. 10), AMNH 11524 (Fig. 11), AMNH 13081, and AMNH 140007. Only a few elements of the axial skeleton are preserved.

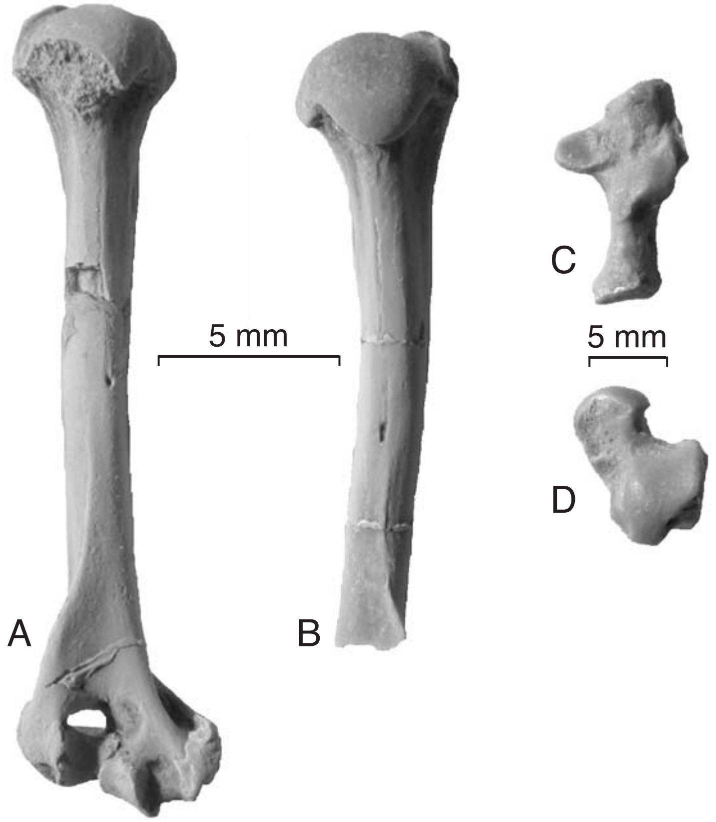

FIG. 10 — Postcrania of *T. velox,* GMUW 3059. A-B, left and right humeri in posterior view; C-D, right calcaneum and astragalus in dorsal view.

The sacrum is formed by three fused vertebrae that have fairly high and long dorsal spines. The third sacral vertebra has a large postzygapophysis, suggesting a mobile tail.

The appendicular skeleton is much better represented. The scapula is not well preserved in any of these specimens so its shape is unclear, but the acromion reaches far over the flat glenoid fossa, implying a very mobile shoulder. The clavicle is slender, but no more so than in proviverrines (Morlo and Habersetzer, 1999). All long bones are slender, the humeral head is hemispherical, and the greater tuberosity is relatively low. The deltapectoral crest is very weak (GMUW 3059, Fig. 10), having no clear distal end as in similar-sized proviverrines found in Europe (Morlo and Habersetzer, 1999). The supracondylar crest is moderate (UM 33479) but relatively larger than in proviverrines. An entepicondylar foramen is present and the entepicondyle is relatively broad. Large specimens like GMUW 3059 have a weaker supracondylar crest but still have a broad entepicondyle.

The olecranon of the ulna is long and slightly bowed internally, but is neither protruding anteriorly (which would suggest arboreal locomotion), nor posteriorly (which would imply cursorial locomotion). The ulna has a large proximal surface, a shallow radial facet, and a relatively broad and flat humeral facet. The radial head is ovoid, but not very deep and has only a small capitular eminence.

The manus is relatively large with metacarpal III being about 30% as long as the humerus. Digits I and V are reduced and digit II is shorter than digit IV, which is only slightly shorter than digit III. Distal phalanges are not very curved, but are fissured as in North American Proviverrinae but unlike middle Eocene proviverrines of Europe (Morlo and Habersetzer 1999).

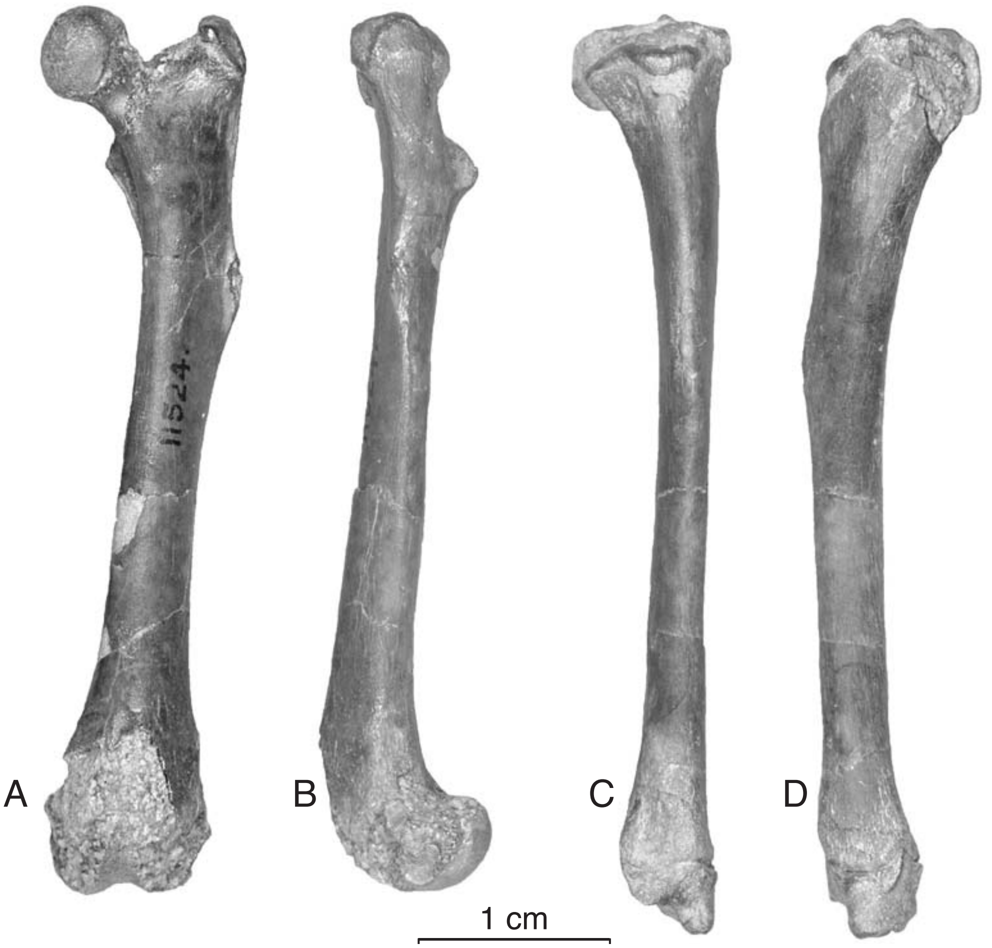

FIG. 11 — Postcrania of *T. velox*, AMNH 11524. A-B, left femur in anterior and lateral views; C-D, left tibia in anterior and lateral views.

The pelvis has a very long ilium with a broad dorsal flange and the ischium is narrow (GMUW 3059, UM 33479). The femoral head is round and is equal in height to the medially curved greater trochanter. The lesser trochanter is large and laterally grooved in AMNH 11524 (Fig. 11) and UM 33479, but not in GMUW 3059. A very small third trochanter is present. Distally, the femoral condyles are broad, corresponding to broad femoral facets on the tibia. The distal tibial fossa is relatively short.

Discussion

Specimens of different sizes and stratigraphic horizons (large AMNH 12631, GMUW 3059 and UM 100690 from Br-1, and small UM 98794 from Br-2) differ from the holotype of *T. velox* in having strong anterior cusps on P_3 and P_4 and/or a strong parastyle on P^4. However, they otherwise lack character states typical of *T. medius* and instead resemble *T. velox* in their bowed and slender dentary body, low P_1, low P_4, high metaconid on M_1, relatively long talonids on $M_{1\text{-}2}$, strongly angled metastyle on M^1, thin parastyle cingulum and incomplete protocone cingulum on M^2, and metacone posteriorly placed relative to the paracone on M^2. We therefore interpret these

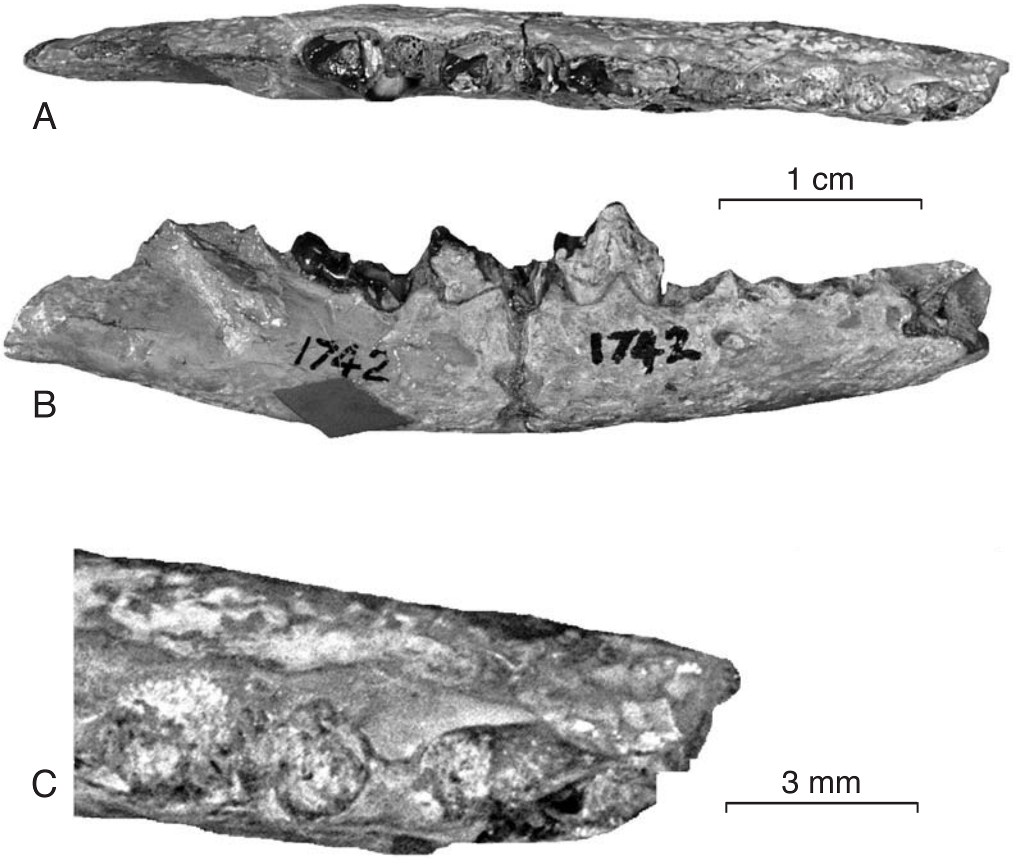

FIG. 12 — Holotype of "*T. cledensis*," AMNH 1742. A-B, occlusal and, labial views; and C, close-up occlusal view showing alveoli for $P_{1\text{-}2}$.

specimens as belonging to *T. velox*. Very large specimens also are known from Br-3 (AMNH 121578, AMNH 12633) that morphologically correspond to *T. velox*.

"*T. mustelinus*" Matthew, 1909 (Fig. 6A) was distinguished from *T. velox* by its smaller size. Other characters used to distinguish these two taxa are partly size dependent including the smaller symphysis (AMNH 12635, AMNH 11528), the more bowed dentary, the more labially pointing parastyle, the more concave labial outline of M^1, and the straight lingual margin of P^4. There are, however, specimens intermediate in size as well as morphology, between these two taxa. As was suggested by Gunnell (1998b), we regard *T. mustelinus* as a subjective junior synonym of *T. velox*.

"*T. cledensis*" Matthew, 1909 (Fig. 12) is only represented by the holotype, AMNH 1742, from Br-3, La Clede Meadows, Lower Adobe Town Member, Washakie Formation in the Washakie Basin. It contains fragments of both dentaries, with right C_1-P_4, $M_{1\text{-}2}$ talonids, and left $P_{1\text{-}3}$, broken P_4, and M_1. It differs from *T. medius* in being smaller, having a much less robust dentary, lacking an anterior cusp on P_4, and lacking a notch separating the entoconid and hypoconid. AMNH 1742 has a posterior mental foramen under P_3, but this is also the case in some specimens of *T. velox* and may even differ within a single individual (AMNH 13081). "*T. cledensis*" was diagnosed as having a single-rooted P_1 (Matthew, 1909), however, this is far from clear, because in the left dentary only the posterior border of the supposed single P_1 alveolus is visible, while the right dentary is broken labially and does not show the posterior border of the canine alveolus.

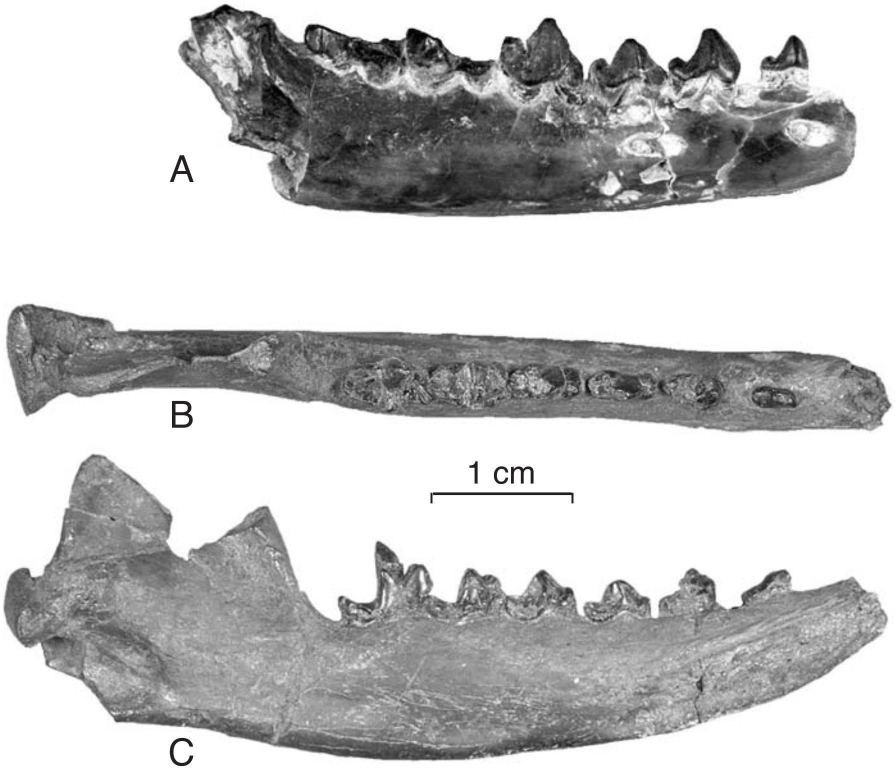

FIG. 13 — Lower dentitions of *T. medius*. A, YPM 11798, holotype, in labial view. B-C, AMNH 12154, in occlusal and lingual views. Note size differences of teeth, size of anterior cuspules of P_{3-4}, and dentary depth. AMNH 12154 represents the smallest and most primitive known specimen of *T. medius*.

Therefore it is possible that the holotype had a small alveolus for the anterior root of P_1. Such small anterior alveoli are known from specimens that definitely belong to *T. velox* (UM 32797). Given the similarity of the dentary, P_4, and the molar talonids, we interpret "*T. cledensis*" as a subjective junior synonym of *T. velox*. USNM 361374 is the only other known specimen of *T. velox* from Br-3 preserving P_1 and this tooth is clearly double-rooted.

Given the relatively large number of specimens, it is very surprising that only three juveniles are known for *T. velox*. UM 101320 represents a complete juvenile skull with part of the dentition. The lack of any resorption in the associated dP_4 verifies a very late eruption of P_4. In the semiadult BMUW 60641, P_4 and C_1 are the only teeth not fully erupted. The canine apparently started to erupt when P_2 and M_2 were nearly completely erupted. This late eruption of the canine is also seen in UM 100050, which shows only the tip of the lower canine while the anterior edge of the alveolus of P_2 is perfectly formed. An eruption of P_4 after $M_{2,}$ as shown in BMUW 60641, might be derived for Limnocyoninae, because this is also documented in UM 68637, a left mandible fragment of the early Wasatchian *Prolimnocyon haematus* Gingerich and Deutsch, 1989. The known eruption sequence in *Thinocyon* is: P_2 and M_2 start to erupt before P_3, which starts to erupt before P_4 and C_1; P_2 and M_2 finish eruption before P_3, which finishes eruption shortly after P_2 and M_2, while P_4 and C_1 finish eruption much later. A delayed eruption of P_4 is also known in palaeoryctids and some lipotyphlans (Morlo and Nagel, 2002), but in proviverrines P_4 erupts shortly after P_3, while P_2 does not start to erupt until M_2 is nearly in place (Morlo and Habersetzer, 1999), not together with M_2 as in *Thinocyon*. It is therefore not possible to regard this character as a synapomorphy for all hyaenodontids.

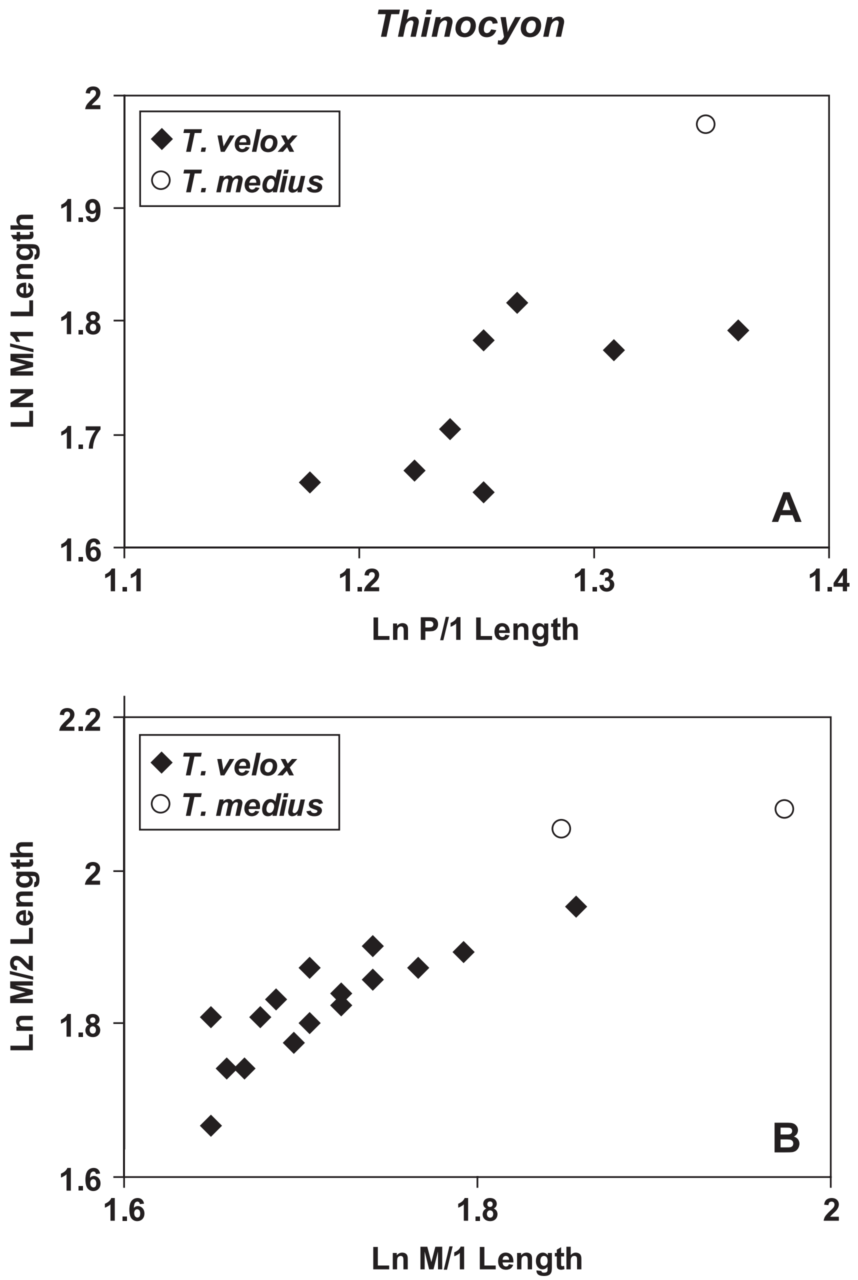

FIG. 14 — Size variability in *Thinocyon velox* and *T. medius*. A, length of P_1 relative to M_1; B, length of M_2 relative to M_1.

Thinocyon medius (Wortman, 1902)

Figs. 13, 15, 16

Limnocyon medius Wortman, 1902, p. 120.

Thinocyon medius, Matthew, 1909, p. 459; Thorpe, 1923, p. 34; Denison, 1938, p. 179; Gazin, 1976, p. 10; Gunnell, 1998b, p. 99.

Thinocyon sp., McGrew et al., 1959, p. 169.

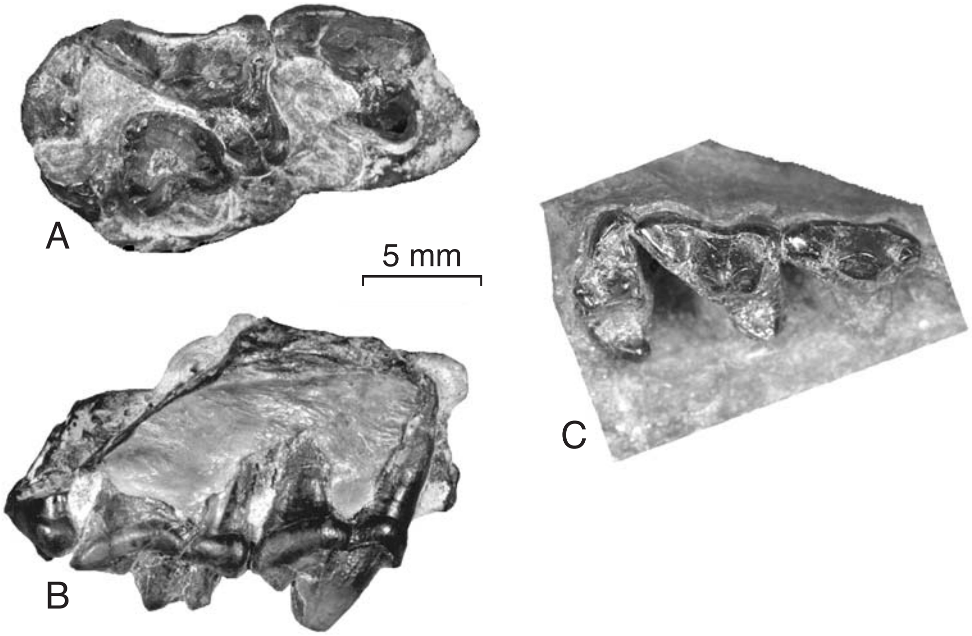

FIG. 15 — Variability of upper dentition of *T. medius*. A-B, YPM 11798, holotype, in occlusal and labial views. C, AMNH 12154, in occlusal view. Note similar morphology but large size differences between teeth.

Holotype.— YPM 11798, left and right dentaries and fragments of both maxillae, partially in occlusion (Figs. 13A, 15A-B; Wortman, 1902, figs. 81-82). Figure 82 in Wortman (1902) is inaccurate in showing the metacone lacking on M^2. Actually, this region is very worn. Other specimens show that M^2 has a metacone, but lacks a metaconule.

Type locality.— Henrys Fork, Twin Buttes Member, Upper Bridger Formation.

Age and Distribution.— Type and all known specimens are from Br-3, Bridger Formation, southern Green River Basin, Wyoming.

Referred specimens.— AMNH 11529, 12075, 12076, 12077, 12154 (Figs. 13B-C, 15C; Matthew 1909: figs. 62-70), 12630, 13082, USNM 361373, 361393, 361394, 361400, 362776, YPM 12872, 12874a-b, 13006b.

Emended diagnosis.— *T. medius* is larger than *T. velox*, has a higher and unbowed dentary, and has the posterior mental foramen always positioned beneath P_3. P_1 is relatively smaller, large anterior cusps are always developed on $P_{3\text{-}4}$, and P_4 is relatively taller resulting in a steeper preprotocristid. The entoconid is always clearly recognizable on M_1, and the M_2 cristid obliqua extends posterolabially. P^3 has a slightly weaker lingual swelling, and P^4 always has a strong parastyle and a much more prominent protocone. The M^1 metastyle is more posteriorly oriented and the metaconule is reduced or absent. M^2 has a concave labial outline because of an extremely broad cingulum and a small metacone, which is lingually shifted instead of being placed directly posterior to the paracone as in *T. velox.*

Description.— *T. medius* is dentally quite similar to *T. velox*. Lower dentaries, however, can be easily distinguished by the shallower and bowed dentary of *T. velox*. *T. medius* never has the posterior mental foramen under P_2, but always under P_3 (occasionally true of some derived specimens of *T. velox* as well). The symphysis extends to the anterior border of P_3 (YPM 12874a).

As in *T. velox*, *T. medius* shows considerable variability, especially in size of the anterior cusps of $P_{3\text{-}4}$ and the parastyle of P^4. The anterior cusps of $P_{3\text{-}4}$ are always present (sometimes on P_2 as well) and the cristid obliqua always extends posterolabially on M_2. These character states seem to be the only ones other than size that consistently separate the two taxa.

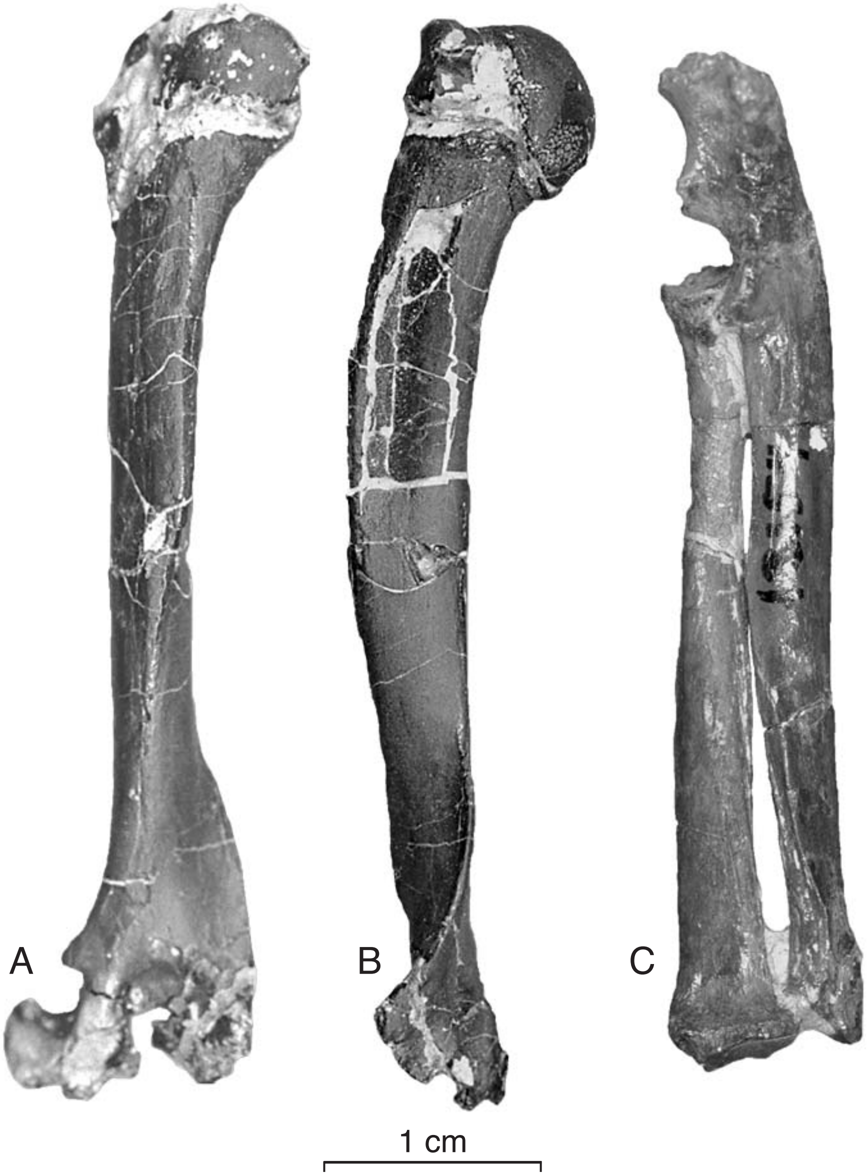

FIG. 16 — Postcrania of *T. medius*. A, AMNH 12154, left humerus in anterior view, showing relatively weak supracondylar crest and small entepicondyle; B, left humerus in lateral view showing weak deltopectoral crest; C, left ulna and radius in lateral view.

Among upper teeth, the M^1 metastyle is oriented more posteriorly and is less angled, and the protocone is much stronger than in *T. velox*. More derived specimens of *T. medius* have reduced metaconules, paraconules, and protocone cingula. M^2 has a strong lingual cingulum, a broader parastyle cingulum, and has the metacone placed more lingually than the paracone. The M^2 metacone of the holotype is broken (Fig. 15A-B), however, AMNH 12154 (Fig. 15C) shows this cusp clearly was present. It also has a reduced metaconule, which is absent in some specimens. Derived specimens of *T. velox* often have a broad parastyle cingulum on M^2 but always have a much weaker lingual cingulum.

Postcrania of *T. medius*

Many specimens referred to *T. medius* have postcranial remains associated with teeth. The most complete information comes from AMNH 12154 (Fig. 16; Matthew, 1909) and AMNH 13082. *T. medius* differs postcranially from *T. velox* in having a more rounded humeral head with a lower tubercle, a weaker supracondylar crest, a relatively narrower entepicondyle, a more oval radial head, a higher femoral greater trochanter, a weaker lesser trochanter, a stronger third trochanter, and a relatively smaller tibial platform. The distal tibia is narrow but has a relatively broad astragalar facet. The fibula is widely separated from the tibia. The foot is relatively large, with digit V being only slightly shorter than digit II, and with digits III and IV being the longest. Metatarsal III length is 45% of femur length.

Discussion.— *T. medius* resembles *Limnocyon verus* in the presence of a strong parastyle on P^4, but P^4 of the latter species is a little larger, possesses a weaker labial cingulum, and has a less curved lingual cingulum.

The *T. medius* lineage shows change through the later Bridgerian including relative shortening of P_1, shortening of the talonid of M_1, separation of the labial walls of hypoconulid and entoconid on M_1, loss of M^1 metaconules and paraconules, and increase in size. The stratigraphically lowest specimens of *T. medius* are generally smaller and much more similar to *T. velox* than are later occurring specimens.

Some of these more primitive individuals of *T. medius* were placed in a separate species ("*T. submedius*") by Ivy (1993). We see no reason to create a species distinct from *T. medius* and instead prefer to view these specimens as showing expected transitional character states within an evolving lineage.

Iridodon, new genus

Type species.— *Iridodon datzae*, new species

Included species.— Genotype only.

Diagnosis.— *Iridodon* differs from *Prolimnocyon* in lacking M_3, from *Limnocyon* in being much smaller and having much more slender premolars, from *Oxyaenodon* in having basined molar talonids, and from *Thinocyon* in lacking a bowed dentary, in having the $M_{1\text{-}2}$ cristid obliqua angled about 30° labially, and in having a narrower M_1.

Etymology.— Named for Iris, the Greek goddess of the rising sun and messenger of Hera, in reference to the early occurrence of the genus relative to other Bridgerian limnocyonines lacking M_3, and '*odous*, *odon*', Gr., masc., tooth.

Iridodon datzae, new species

Fig. 17

Holotype.— UM 103465, left dentary fragment with root of I_3, alveoli of C_1 and P_1, P_2, fragment of P_3, and P_4-M_2. Only known specimen, found by J. Trapani, July 16, 1997.

Age and horizon.— UM locality SP-5, Sweetwater County, South Pass, Green River Basin, Wyoming; Wasatch Formation, Cathedral Bluffs Tongue, Gardnerbuttean, Bridgerian biochron Br-1a.

Diagnosis.— As for genus, only known species.

Etymology.— datzae, for the generous financial support provided for this study by Mrs. Erika Datz, head of the Erika and Walter Datz Fund.

Description.— The dentary is dorsoventrally shallow but labiolingually thick, a character state Matthew (1909) cited as typical for *Thinocyon*. In posterior view, the dentary forms a half-circle, with its lingual border being straight and labial border convex. The anterior mental foramen is beneath P_1, the posterior one under P_2. The symphysis is very long, extending to P_3.

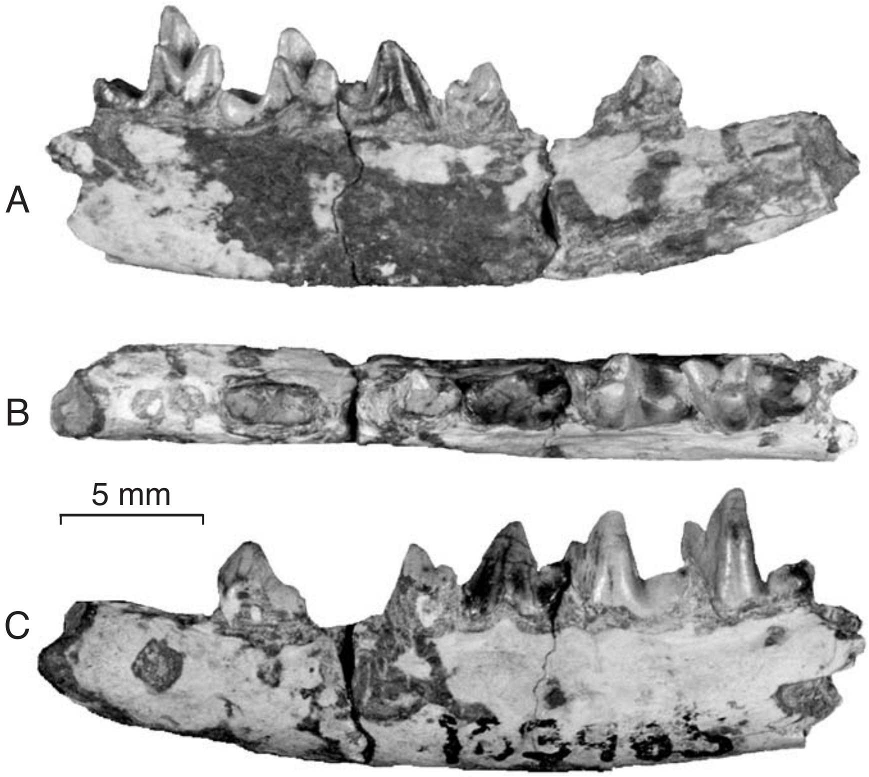

FIG. 17 — Holotype of *Iridodon datzae* n. gen., n. sp. UM 103465, in lingual (A), occlusal (B), and labial (C) views.

The canine is broken at its root, and the crown is not preserved. The root measures 3.2 mm in length and 2.4 mm in breadth. The double-rooted P_1 is only represented by its alveoli (2.4 mm in length). P_2 (3.25 x 1.95 mm) is relatively shorter than in *T. velox*, lacks the posterior enlargement typical of that species, and also completely lacks accessory cuspules. Only the posterior part of P_3 is preserved, consisting of a posterior cingulid cusp that ends in a notch that separates it from the postprotocristid.

P_4 (3.7 x 2.4 mm) is completely preserved. It is a very narrow tooth and much more gracile than in either species of *Thinocyon*. The protoconid of P_4 leans posteriorly more than in *T. velox*, and a tiny anterior cuspule is developed. Posteriorly, a strong posterior cingulid cusp is developed that lies along the midline of the tooth. The posterior heel extends anterolabially and has a lingual cingulid.

M_1 (4.6 x 2.5 mm) is a compact tooth with the talonid being as long as the trigonid. The metaconid is slightly higher than the paraconid and the talonid basin is deep and closed. The cristid obliqua runs posterolabially and ends in a robust and broad hypoconid which is slightly lower than the hypoconulid.

M_2 (4.5 x 2.75 mm) is similar to M_1, but differs in having a higher trigonid and an elongated talonid outline instead of being quadrangular as in M_1. The metaconid is as high as the paraconid. The hypoconulid is broken, but the entoconid is higher than the hypoconid, implying a still higher hypoconulid. The cristid obliqua of M_2 runs posterolabially at an angle of about 30° and parallel to the lingual border, thereby producing a parallelogram-like talonid basin.

Discussion.— Characters useful for differentiating small hyaenodontids at the species level generally are size, premolar morphology, and detailed morphology of molar talonids (Gingerich and Deutsch, 1989; Morlo and Habersetzer, 1999). *I. datzae* is about the size of the smallest

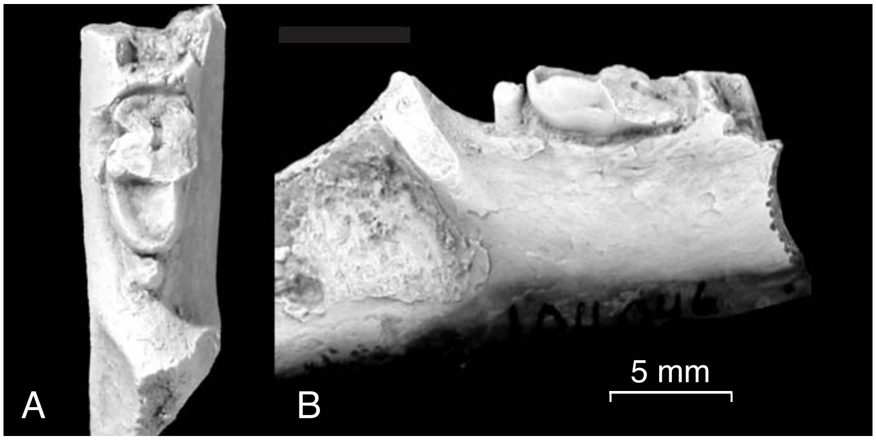

FIG. 18 — Bridgerian *Prolimnocyon antiquus* from South Pass. A-B, UM 104046, right dentary with M_2 talonid-M_3 in occlusal and labial views.

specimens of *T. velox*, but the entoconid of M_2 is clearly higher than the hypoconid and the premolars are slender. In premolar morphology, *I. datzae* differs from more primitive *Prolimnocyon* in having a double-rooted P_1.

Iridodon datzae is the only limnocyonine species known from Br-1a that lacks M_3. It has several primitive character states including narrow premolars, high metaconids on M_{1-2}, and elongated molar talonids with a very high entoconid and entocristid on M_2. It is also one of the smallest known species of Bridgerian limnocyonines.

There are some Br-1b and Br-2 specimens of *T. velox* that have some character states similar to *I. datzae*. YPM 13026 has relatively large entoconids on the talonid edges of both M_1 and M_2, and has a labially extended cristid obliqua on M_2. The cristid obliqua of M_1, however, extends far less labially than in the much smaller *I. datzae*. Other specimens of *T. velox* like UM 100690 and GMUW 3059 appear to have relatively narrow P_4s, but this is mainly due to the presence of an anterior cusp.

Prolimnocyon antiquus Matthew, 1915
Fig. 18

Prolimnocyon antiquus Matthew, 1915, p. 70.
Prolimnocyon antiquus, Gunnell, 1998b, p. 99.
Prolimnocyon elisabethae Gazin, 1952, p. 51.
Prolimnocyon elisabethae, Kelley and Wood, 1954, p. 348; Gazin, 1962, p. 53; Van Valen, 1966, p. 72; Guthrie, 1967, p. 14; Gingerich and Deutsch, 1989, p. 364; Gunnell, 1998b, p. 99.
Prolimnocyon cf. *antiquus*, Gazin, 1962, p. 53.

Holotype.— AMNH 14768, right dentary with C_1, M_1, M_2 talonid, and alveoli for P_{1-4}, M_3.

Type locality.— Lost Cabin beds, Wind River Basin, Wyoming.

Referred specimen.— UM 104046, right dentary fragment with talonid of M_2 and complete M_3, found by J. L. Tetreault at UM locality SP-5, Wasatch Formation, Cathedral Bluffs Tongue, Bridgerian biochron Br-1a, Sweetwater County, Green River Basin, Wyoming.

Age and distribution.— Late early Eocene, Wasatchian through early Bridgerian, Lysitean (Wa-6) through Gardnerbuttean (Br-1a), Bighorn, Green River, and Wind River basins, Wyoming.

Description.— UM 104046 (Fig. 18) is slightly larger than YPM 27573, a specimen of *P. atavus* from the Lysitean (Wa-6) that also has a single-rooted M_3. UM 104046 differs morphologically in

TABLE 3 — Characters used in phylogenetic analyses (bold indicates ordered character).

1. P_2 posteriorly short (0), or elongate (1)
2. P_3 with posterior heel absent (0), or present (1)
3. P_3 with posterior cingulid cusp absent (0), or present (1)
4. P_3 as high or higher than P_2 (0), P_3 not as high as P_2 (1)
5. P_4 preprotocristid bowed posteriorly (0) or protoconid more lanceolate (1)
6. M_1 with tricuspid talonid (0), entoconid/hypoconulid merged into talonid edge (1)
7. **M_1 metaconid higher (0), equal (1), smaller (2) than paraconid or fused (3)**
8. M_1 hypoconulid highest talonid cusp (0), or hypoconid highest (1)
9. M_1 shorter than M_2 (0), longer (1)
10. M_1 cristid obliqua extends labiad at > 30° (0) or < 30° and more posteriad (1)
11. M_2 cristid obliqua extends labiad at > 30° (0) or < 30° and more posteriad (1)
12. **M_2 metaconid higher (0), equal (1) or smaller (2) than paraconid**
13. M_2 hypoconulid highest talonid cusp (0), or hypoconid highest (1)
14. **M_2 larger than M_3 (0), much larger (1), M_3 absent (2)**
15. P^3 posterior accessory cusp absent (0), or present (1)
16. P^3 protocone vestigial (0), absent (1)
17. P^3 as high or higher than P^2 (0), P^3 lower than P^2 (1)
18. P^4 parastyle small (0), parastyle strong (1)
19. P^4 paracone sloped posteriorly (0), not sloped posteriorly (1)
20. **P^4 protocone weak (0), strong (1), enlarged (2)**
21. M^1 metacone as high as paracone (0), lower (1)
22. M^1 metacone fused with paracone higher than half height (0), completely fused (1)
23. M^1 metaconule present (0), absent (1)
24. **M^1 with strong cingulae at protocone (0), weak (1), lacking (2)**
25. M^2 metacone posterior to paracone (0), lingual (1), or fused (2)
26. M^2 metaconule present (0), vestigial to absent (1)
27. M^2 with strong cingulae at protocone (0), expanded (1), weak or lacking (2)
28. M^2 width < twice length (0), width > twice length (1)
29. **M^3 present (0) reduced (1) or lacking (2)**
30. Stratigraphic character. Wa-1 (1), Wa-2 (2), Wa-3 (3), Wa-4 (4), Wa-5 (5), Wa-6 (6), Wa-7 (7), Br-0 (8), Br-1 (9), Br-2 (a), early Br-3 (b), late Br-3 (c), Uintan (d)

having a lower and longer M_2 talonid and a more reduced M_3. The first of these character states is found in YPM-PU 19357, while the second is present in CM 22504, both representing *P. antiquus* (Guthrie, 1971). We therefore assign UM 104046 to *P. antiquus* which extends its range into the Gardnerbuttean (Br-1a). UM 104046 differs from *I. datzae*, known from the same locality, not only in retaining M_3, but also in being much larger and having a much deeper dentary.

Discussion.— *P. antiquus* was previously known only from the late Wasatchian (Lysitean and Lostcabinian). UM 104046 is the only record of *Prolimnocyon* from the Bridgerian. Its occurrence in the same locality as *I. datzae* validates the coexistence of *Prolimnocyon* with more derived members of Limnocyoninae, a phenomenon typical in the basin margin assemblage at South Pass (Gunnell and Bartels, 2001).

PHYLOGENETIC ANALYSIS

Cladistic analysis of a character matrix consisting of 10 hyaenodontid taxa and 29 morphological characters (see Tables 3 and 4 for character state list and character matrix) resulted in three equally parsimonious cladograms with a tree length of 63 steps, consistency index (CI) of 0.70, and retention index (RI) of 0.62. A stratocladistic analysis (Fisher, 1994) resulted in a single shorter tree (Figs. 19-20) having 71 morphological and 12 stratigraphic steps, a CI of 0.64, and a

TABLE 4 — Character state matrix based on Table 3 for Wasatchian and Bridgerian Limnocyoninae.

	Character																												
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
Thinocyon velox	1	1	1	1	1	1	1/2	0	0	1	1	2	0	2	0	0	1	0/1	0	1	0	0	0	1	0	0	0/1	1	2	9/a/b
Thinocyon medius	1	1	1	1	1	1	1	0	0	1	1	2	0	2	0	1	1	2	0	2	0/1	0	0/1	1	1	1	1	1	2	b
Iridodon datzae	1	1	1	?	0	1	0	0	1	0	0	1	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	2	2	8
Limnocyon verus	1	0	1	0/1	1	1	0	0	0	1	1	2	0	2	1	1	1	1	0	2	?	0	1	1	0	0	0	1	2	9/a/b
Limnocyon potens	0	0	1	1	1	1	0	0	0	1	?	?	?	2	1	1	1	2	0	2	?	0	1	0	1	1	0	1	2	c
Prolimnocyon atavus	0	0	1	1	1	1	0	0	0	1	1	1	1	1	?	?	?	1	0	0	1	0	0	1	0	1	0	1	1	3/4/5/6/7
Prolimnocyon haematus	1	0	1	?	0	0	0	0	0	1	0	1	1	1	0	?	0	1	0	0	1	0	0	1	0	1	0	1	1	1/2
Oxyaenodon dysodus	0	0	0	0	1	1	3	1	0	1	1	2	0	2	0	0	0	2	1	2	1	1	0	2	2	1	2	1	2	c
Galecyon mordax	1	1	?	0	0	0	?	0	0	0	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1/2
Prototomus phobos	0	0	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	2/3

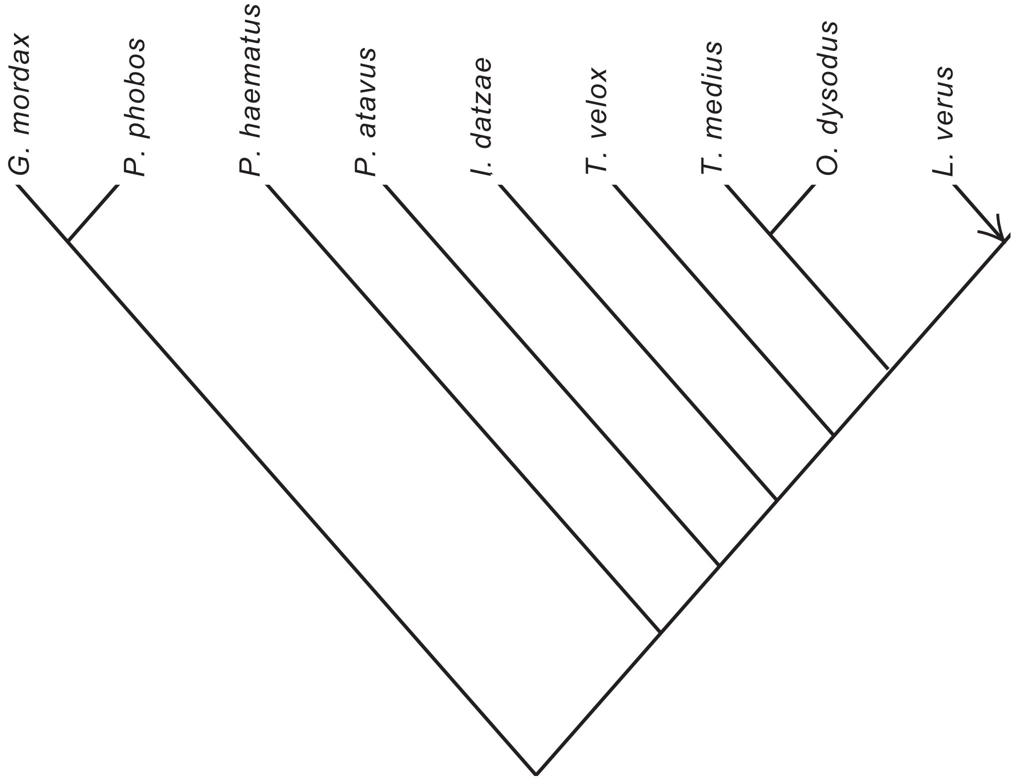

FIG. 19 — Shortest tree derived from stratocladistic analysis based on 10 taxa, 29 morphological characters, and one stratigraphic character (see Tables 3-4, Fig. 20). This tree has 71 morphological steps, 12 stratigraphic steps, CI = 0.64 and RI = 0.58. *Limnocyon verus* is ancestral to *Limnocyon potens*. Limnocyoninae is monophyletic, *Thinocyon* is a probable paraphyletic taxon.

RI of 0.58. In this analysis *Iridodon* is the sister taxon to all later occurring Bridgerian limnocyonines, and *Prolimnocyon* (two species) is the sister taxon to the Bridgerian clade. *Limnocyon verus* is ancestral to *Limnocyon potens*. *Oxyaenodon* is a sister taxon to *Thinocyon medius* in this analysis but also can be a sister taxon to the *Limnocyon* clade with only one additional morphological step. If the relationship between *T. medius* and *Oxyaenodon* is substantiated this would necessitate *Thinocyon* being a paraphyletic taxon. *Prolimnocyon* and the Bridgerian clade is a sister group to an earlier-occurring Wasatchian group consisting of *Galecyon* and *Prototomus*.

ECOMORPHOLOGY

Body mass estimates for *Thinocyon* were reported recently by Egi (2001), based on limb proportions. Applying the regressions and methods described by Morlo (1999), gives body mass estimates of between 0.6 and 1.2 kg for *T. velox,* and 1.8 kg for *T. medius*. These are in concordance with the results of Egi (2001).

Postcrania of *Thinocyon* have been used for comparisons with other creodonts (Gebo and Rose, 1993). However, the only detailed description of *Thinocyon* postcrania was that provided for *T. medius* by Matthew (1909). Postcrania of *T. medius* and *T. velox* are very similar. They share important characters of the forelimb such as: strong scapular spine, long acromion, shallow

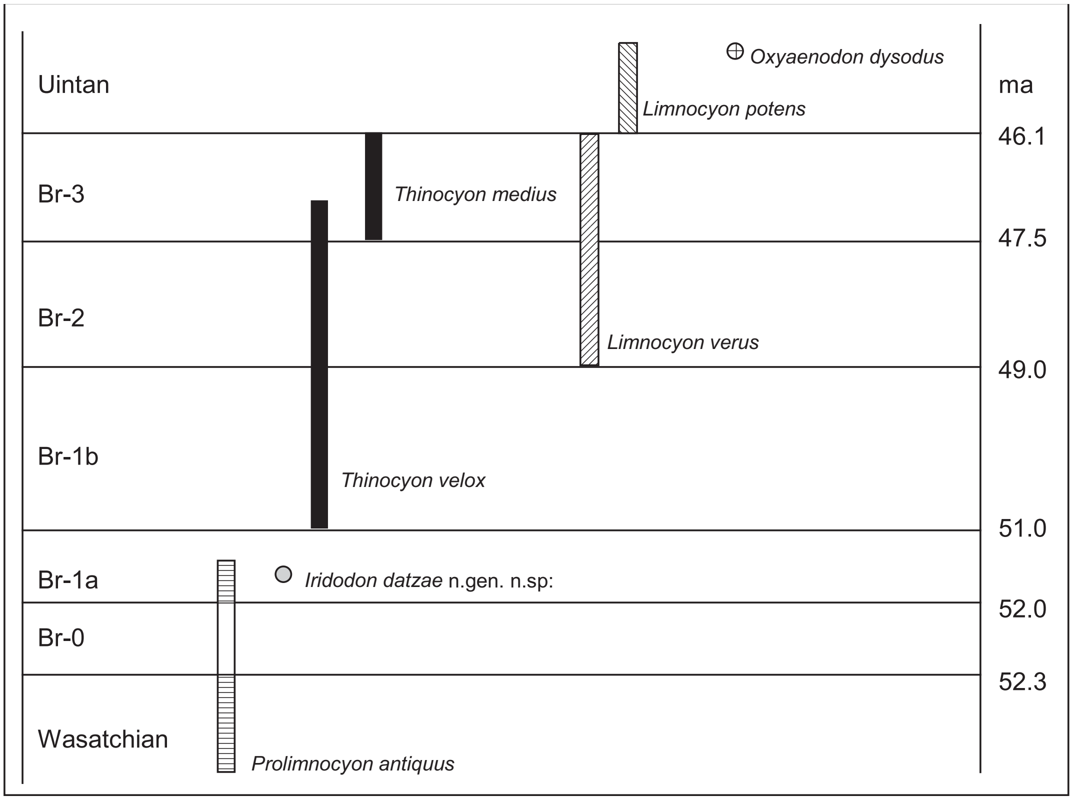

FIG. 20 — Stratigraphic distribution of Bridgerian and Uintan Limnocyoninae. Br-1a: *I. datzae*, *P. antiquus*. Br-1b: *T. velox*. Br-2: *T. velox*, *L. verus*. Early Br-3: *T. velox*, *T. medius*, *L. verus*. Late Br-3: *T. medius*, *L. verus*. Uintan: *L. potens*, *O. dysodus*.

glenoid fossa, round humeral head, weak deltopectoral crest, strong supracondylar crest, broad entepicondyle, shallow humeral and radial fossae of the ulna, and a semi-oval radial head with a small capitular eminence. All of these characters indicate that *Thinocyon* had a very mobile forelimb (Gebo and Rose, 1993; Morlo and Habersetzer, 1999).

The weak deltopectoral crest suggests that *Thinocyon* was not arboreal, the broad entepicondyle indicates that it was not cursorial, and the relatively long humerus suggests that it was not semi-aquatic. The relatively straight distal phalanx resembles that of semi-fossorial species. The humerus/metacarpal III and femur/metatarsal III indices are very low, implying relatively large hands and feet, which are typical for terrestrial carnivores. Relatively long digits IV and V in both the fore and hind foot indicate that *Thinocyon* was plantigrade.

A relatively elongated ulnar olecranon process, which is slightly angled medially, is found in semi-fossorial carnivores (Van Valkenburgh, 1987). This fits well with the enlarged supracondyloid crest that separates *Thinocyon* from small proviverrines. Olecranon shape, the pronounced supracondylar crest, and the outline of the distal phalanges all indicate that *Thinocyon* was a terrestrial, semi-fossorial animal. Its relatively small size and mobile forelimb suggest that it was probably a capable climber as well.

Despite their similarity, *T. medius* as well as some larger specimens referred to *T. velox* (GMUW 3059) differ from smaller specimens of *T. velox* in some small details that imply less mobility of the forelimb and the hind limb. Among these character states are a relatively smaller supracondylar crest, a less round radial head, a less grooved lesser femoral trochanter, a relatively smaller

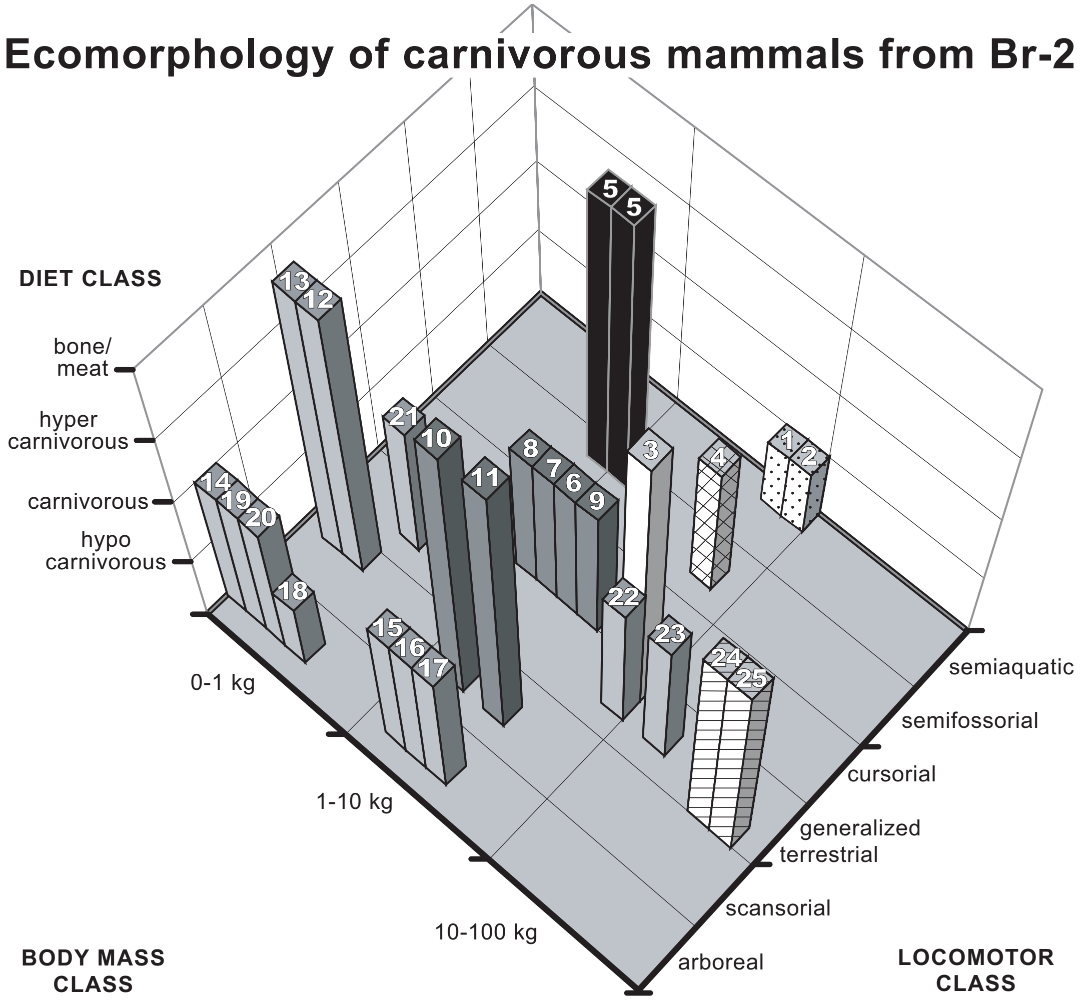

FIG. 21 — Body mass, locomotor type, and diet class of Br-2 carnivorous mammals showing *Thinocyon velox* (5) to be the only semi-fossorial hypercarnivore with a body mass less than 3 kg. Pantolestidae: 1, *Pantolestes elegans*; 2, *Pantolestes longicaudus*. Oxyaenidae: 3, *Patriofelis ulta*. Hyaenodontidae: 4, *Limnocyon verus*; 5, *Thinocyon velox*; 6, *Sinopa rapax*; 7, *Sinopa grangeri*; 8, *Sinopa minor*; 9, *Sinopa major*; 10; *Tritemnodon agilis*; 11, *Machaeroides eothen*. Viverravidae: 12, *Viverravus gracilis*; 13, *Viverravus minutus*. Miacidae: 14, *Miacis parvivorus*; 15, *Vulpavus palustris*; 16, *Vulpavus profectus*; 17, *Vulpavus ovatus*; 18, *Palaearctonyx meadi*; 19, *Öodectes herpestoides*; 20, *Öodectes proximus*; 21, *Uintacyon edax*; 22, *Uintacyon vorax*; 23, *Uintacyon major*. Mesonychidae: 24, *Mesonyx obtusidens*; 25, *Harpagolestes macrocephalus*.

knee joint, and a larger and more closely articulating tibial/astragalar joint. The humeral entepicondyle of GMUW 3059 is as broad as in smaller specimens, but it is reduced in *T. medius*.

These differences between smaller and larger specimens of *Thinocyon* mirror the situation in two contemporary proviverrine species of *Lesmesodon* from the middle Eocene of Europe (Morlo and Habersetzer, 1999). Greater mobility might be expected for the smaller of two closely-related terrestrial species because topography is relatively more complex for the smaller form. This is less true for arboreal species. The differences between the two *Thinocyon* species support the interpretation of *Thinocyon* as a terrestrial mammal. *T. medius* does not differ from *T. velox* in relative foot size, or olecranon and distal phalanx shape, suggesting that it too was as a capable digger.

Matthew (1909) and Gebo and Rose (1993) suggested that the postcranial skeleton of *Thinocyon* was very similar in structure and size to that of extant *Mustela vison*. This species is considered to be terrestrial (Taylor, 1989) but opportunistic, often even competing with otters on some islands (Clode and MacDonald, 1995). A similar eclectic lifestyle was probably the case for *Thinocyon*.

The only paper dealing with a (semi-)quantitative analysis of diet in small creodonts is that of Morlo (1999), in which methods developed for carnivorans (Van Valkenburgh, 1996) were adapted. While useful, application of these methods was not without problems and produced uncertainty concerning the diet class of some species (Morlo, 1999). Tooth parameters employed in this method include relative M_{1-2} blade length, shape of P_4, and relative M_{1-2} talonid size. *Thinocyon* was not included in the 1999 analysis, but applying the method of Morlo (1999) to *T. velox* and *T. medius* shows that both can be confidently assigned to the meat/invertebrate dietary class.

The greatest number of *Thinocyon* specimens come from Br-2 and all belong to *T. velox*. As was demonstrated above, this species is a very small to small, hypercarnivorous, and semi-fossorial creodont. When examining carnivore guild structure in Br-2 (Fig. 21) it becomes clear that this ecomorphology is unique, not only among Br-2 creodonts, but also other carnivorous taxa. In the contemporaneous European locality of Messel, the only semi-fossorial carnivore yet known is the pantolestid *Buxolestes minor*, while all known Messel creodonts are generalized terrestrial carnivores (Morlo and Habersetzer, 1999). Other semi-fossorial, hypercarnivorous creodonts have been reported from the Wasatchian of North America and the late middle Eocene of Geiseltal, but all had body masses greater than 10 kg (Morlo, 1999). The known species of the European proviverrine *Allopterodon* also had small body size and were hypercarnivorous, but no postcranial material is known (see Morlo 1999). *Thinocyon* is the only Eocene example of a small, semi-fossorial, hypercarnivorous mammal, which may be the reason for its success in the Bridgerian.

CONCLUSIONS

Our reinvestigation of all genera formerly placed in Limnocyoninae leads to the exclusion of several taxa from this subfamily. Character states shared between *Thereutherium* and *Apterodon*, along with the co-occurrence of both genera in the same biozone (MP 22), suggests that *Thereutherium* may have had an African origin and may be more closely related to Apterodontinae than to any other hyaenodontid subfamily.

The poorly preserved holotype specimen of *Prolaena parva* from the middle Eocene Hetaoyuan Formation of Honan Province, People's Republic of China does not provide enough information to make any definitive taxonomic statements. It is most similar to North American Uintan *Oxyaenodon* among known creodonts. *Prolaena* is regarded as the only known middle Eocene possible limnocyonine outside of North America.

The only known Asian record of a possible *Thinocyon*, "?*T.*" *sichowensis*, can be excluded from the genus because of the presence of a large P^3 protocone. *Thinocyon*, as presently known, is restricted to Br-1b through Br-3 in North America.

The oldest known limnocyonine lacking M_3 is *I. datzae* from the South Pass assemblage (Br-1a). This new taxon is characterized by its small size, slender teeth, highly angled M_{1-2} cristid obliqua, and non-bowed dentary. In the same faunal assemblage is the latest known occurrence of *Prolimnocyon*, presumably belonging to *P. antiquus*. Phylogenetic analysis supports *I. datzae* as the sister-group to all other Bridgerian limnocyonines, while Wasatchian *Prolimnocyon* is the ancestor of all Bridgerian taxa.

Thinocyon first appears in Br-1b represented by *T. velox*. *T. velox* specimens exhibited large morphological variability, some retaining primitive character states known in *I. datzae* while others had character states foreshadowing *T. medius*. There was considerable tooth size variation present in *T. velox,* with some tooth characters being size dependent.

Average tooth size of *T. velox* increased into Br-2. Both the holotypes of *T. velox* and "*T. mustelinus"* come from Br-2. Because most specimens of *T. velox* are from Br-2 , morphologic variability is best documented in this biochron. This documented variability encompasses both

"*T. mustelinus*", as well as "*T. cledensis*" from early Br-3, making both subjective junior synonyms of *T. velox*.

In addition to size and morphologic variation, *T. velox* exhibits sexual dimorphism in cranial characteristics. Males have elongated pterygoids and basicrania, a higher sagittal crest and an occipital that is as high as it is broad. Females have shorter pterygoids and basicrania, sagittal crests less well developed, and an occipital broader than high. Tooth size was not affected by dimorphism, even in canines that often reflect sexual dimorphism in other mammals (e.g., felids, many primates). However, dentary shape was affected, with males having less rounded and much deeper dentaries than are typically found in females.

Thinocyon medius first appears in Br-3 but there are some specimens present in early Br-3 that represent *T. velox*. Diagnostic character states of *T. medius* include the lingually shifted metacone and strong cingulae on M^2, retention of a paraconule and metaconule on M^1, presence of a small metaconule on M^2, and presence of small anterior cusps on lower premolars. More derived specimens have $P_{3\text{-}4}$ with larger anterior cusps. The latest documented occurrence of *T. medius* is from Br-3.

Iridodon datzae and *Thinocyon velox* represent the smallest creodonts known from the Bridgerian, with body masses at or below 1.2 kg, and both species belonged to the hypercarnivorous diet class (Morlo, 1999). An analysis of postcranial remains of *T. velox* indicates that it was terrestrial and semi-fossorial. Following Matthew (1909), Gebo and Rose (1993) suggested that extant *Mustela vison* is a good analogue for *Thinocyon*. We corroborate this result and interpret *Thinocyon* as a Bridgerian ecomorph of this carnivoran.

T. medius was slightly larger than *T. velox* (1-3 kg) but resembled the smaller species in diet and overall postcranial morphology. It may have had slightly less mobile limbs. Both species had relatively short long bones, long bodies, and large hands and feet. In these features, as well as in body size and diet class, they resembled modern weasels, a life style hither to undocumented among Eocene carnivorous mammals.

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