CARPOLESTES SIMPSONI, NEW SPECIES (MAMMALIA, PROPRIMATES) FROM THE LATE PALEOCENE OF THE CLARKS FORK BASIN, WYOMING

BY

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CARPOLESTES SIMPSONI, NEW SPECIES (MAMMALIA, PROPRIMATES) FROM THE LATE PALEOCENE OF THE CLARKS FORK BASIN, WYOMING

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Abstract — *Carpolestes* is a small North American late Paleocene mammal with distinctively specialized premolar teeth. P^3 is polycuspate with a distinct anteroexternal extension, and P_4 is high-crowned, bladelike, and multicuspate. *Carpolestes* is now known from at least 180 specimens representing four morphologically and stratigraphically distinct species. Fossils from freshwater limestones of the Clarks Fork Basin include complete dentitions of a new species, *Carpolestes simpsoni*, from Clarkforkian faunal zones Cf-2 and earliest Cf-3. This is the youngest known species, and it differs from older species in having a more reduced dental formula of 3.0.3.3/2.1.1.3 with P_3 absent. It differs in being smaller (ca. 100 g) and in having P^3 and P_4 of unique size and shape. New specimens show that the three teeth anterior to P^2 are rooted in the premaxilla, meaning that *Carpolestes* retained three upper incisors (as has been reported for certain species of *Elphidotarsius* and *Carpodaptes*). I^1 of *Carpolestes* resembles *Carpodaptes* in having a strong laterocone.

The *Carpolestes* lineage decreased in size over time from the middle Tiffanian through the middle Clarkforkian land-mammal ages. Analysis of this evolutionary time series shows the average base rate of change of tooth size (M_1 area) to have been about 0.002 standard deviations per generation. The temporal scaling slope is -0.52, which is close to expectation for random change and significantly different from expectation for either stasis or simple directional change.

INTRODUCTION

Carpolestidae are small, primate-like mammals that first appeared in the middle Paleocene and survived through the late Paleocene in North America. They are distinctive in having enlarged central incisors, a reduced anterior dentition (posterior to I_1), and a plagiaulacoid structure of P_4, with correlated specializations of P^{3-4} (Simpson, 1935; Szalay, 1972; Rose, 1975; Szalay and Delson, 1979).

Twelve species are recognized in North America that are usually classified in three genera: *Elphidotarsius*, *Carpodaptes*, and *Carpolestes* (Simpson, 1935; Rose, 1975, 1977; Holtzman, 1978; Krause, 1978; Gingerich, 1980; Fox, 1984, 1993; Bloch and Gingerich, 1994). Szalay and Delson (1979) recognized only *Elphidotarsius* and *Carpodaptes* as valid genera. The three genera have been thought to form a morphologic and stratigraphic sequence indicating that they were representatives of a single rapidly-evolving clade (Rose, 1975, 1977).

The oldest carpolestid, *Elphidotarsius*, first appeared in faunal zone To-3 of the Torrejonian land-mammal age, along with several other proprimates including the picrodontid *Picrodus*, the plesiadapid *Pronothodectes*, and the paromomyid *Ignacius* (Archibald et al., 1987). The youngest of North American carpolestids, *Carpolestes simpsoni* (sp. nov.), is found in Clarkforkian faunal zones Cf-2 and the earliest part of Cf-3, with and just after the last occurrence of the largest known species of *Plesiadapis*, *Plesiadapis cookei* (Rose, 1981; Gingerich, 1980; Gingerich, 1983; Archibald et al., 1987). The only carpolestid from Asia is from the early Eocene, and no Paleocene proprimates are known from the Asian continent (Beard and Wang, 1995).

Fossils representing the genus *Carpolestes* have more than doubled in number since the last revision of the family (Rose, 1975). These include many recovered from freshwater limestones of the middle Clarkforkian (Cf-2) faunal zone of the Clarks Fork Basin, Wyoming. The new material includes complete mandibles, two skulls, several fragmentary rostra, and some possibly-associated postcrania. Such complete preservation is exceptional for small fossil mammals, which are usually represented by fragmentary jaws and isolated teeth.

Several publications describing material from Paleocene-Eocene freshwater limestones of the Clarks Fork Basin have appeared in the past decade (Gingerich, 1987; Gunnell and Gingerich, 1987; Rose and Gingerich, 1987; Houde, 1988; Beard and Houde, 1989; Beard, 1989a, 1990a; Kay et al., 1990, 1992; Houde and Olson, 1992, Rose et al., 1993; MacPhee et al., 1995; Bloch et al., 1998). These fossils have had a significant impact on the study of birds, insectivores, and plesiadapiform proprimates of the Paleocene and early Eocene.

Dental terminology follows that of Van Valen (1966) and Szalay (1969) in general, and Gingerich (1976) for cusp and crest nomenclature used to describe the incisors. Dimensions of the teeth and mandible have been measured as illustrated in Figure 1 using calipers and a binocular microscope.

INSTITUTIONAL ABBREVIATIONS

UM   — Museum of Paleontology, University of Michigan, Ann Arbor
YPM-PU   — Princeton University collection at Yale Peabody Museum, New Haven

HISTORY OF STUDY

Carpolestes ("fruit stealer") was first described by Simpson (1928), based on *Carpolestes nigridens* from Bear Creek Montana. Simpson (1929) named *Carpolestes aquilae*, also from Bear Creek, and Jepsen (1930) described *Carpolestes dubius* from Princeton Quarry, Wyoming

Rose (1975) revised the family Carpolestidae, reviewing previous literature and including emended diagnoses for all known taxa. Rose placed Carpolestidae (Simpson, 1935) in the infraorder Plesiadapiformes (Simons, 1972), superfamily Plesiadapoidea (Trouessart, 1897), and order Primates (Linnaeus, 1758). Rose (1975) recognized three genera and nine species of Carpolestidae. He confirmed the position of *E. florencae* (Gidley, 1923) and *E. shotgunensis* (Gazin, 1971) in *Elphidotarsius* (Gidley, 1923). He placed *C. aulacodon* (Matthew and Granger, 1921), *C. hazelae* (Simpson 1936), *C. hobackensis* (Dorr, 1952), *C. cygneus* (Russell, 1967), and new species *C. jepseni* in *Carpodaptes* (Matthew and Granger, 1921). He also confirmed the positions of *Carpolestes dubius* (Jepsen, 1930) and *Carpolestes nigridens* (Simpson, 1928) in *Carpolestes* (Simpson, 1928).

Rose (1975) synonymized *C. aquilae* (Simpson, 1929) with *C. nigridens* in an emended diagnosis of *C. nigridens*, noting that distinguishing features cited by Simpson (1935) were typical of intraspecific variation while no characters consistently separated the two species. Rose (1975) followed Van Valen (1969) in removing European *Saxonella* from Carpolestidae but, instead of placing it in Plesiadapidae, as Van Valen had, suggested putting it in its own family Saxonellidae.

Rose (1975) described the first known upper teeth of *Elphidotarsius*, and the first lower incisors of *Elphidotarsius* and *Carpolestes*. He inferred a dental formula of 2?.1?.3?.3/2.1.2-3.3 for
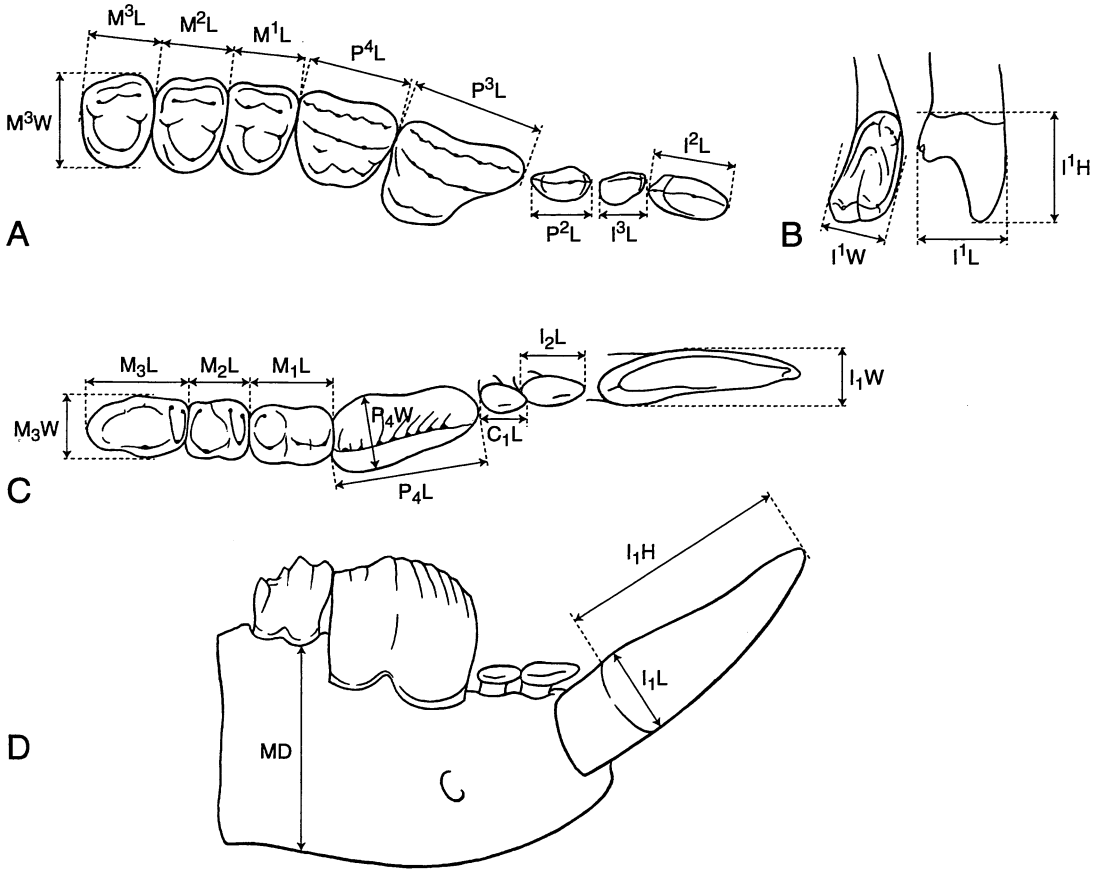
FIG. 1 — Measurements taken on teeth and mandibles of *Carpolestes*, following, in part, Rose (1975: 4). A, I^2-M^3 in occlusal view; B, I^1 in occlusal and lateral views; C, I_1-M_3 in occlusal view; and D, I_1-M_1 and part of dentary in lateral view. Lengths (*L*) are maximum anteroposterior crown dimensions, as shown. Widths (*W*) are maximum crown dimensions measured perpendicular to length. Height (*H*) is measured from the base of the enamel-dentin boundary to the tip of the crown. Mandibular depth (*MD*) is measured beneath the anterior root of M_1. Measurements are summarized in Table 1 and listed individually in Appendix tables A1-A4.

Carpolestidae, with P_1 absent and P_2 reduced or lost in *Carpodaptes* and *Carpolestes*. Rose (1975) pointed out that the three carpolestid genera are restricted temporally, with *Elphidotarsius* in the Torrejonian, *Carpodaptes* in the Tiffanian, and *Carpolestes* in the Clarkforkian. Rose further considered that these genera formed a morphologic and stratigraphic sequence indicating that they were representatives of a single generic lineage. Rose cited morphological similarities between plesiadapids and carpolestids as an indication that the two families are closely related through a common ancestor that was possibly similar to *Pronothodectes*.

Rose (1977) emphasized that Carpolestidae are useful for determining the sequence and correlation of North American Paleocene faunas because they are "rapidly evolving, morphologically distinctive, common and widespread, and found in all major lithofacies" (Rose, 1977: 536). Rose noted that individual taxa were of short duration and could be used for estimation of the age of vertebrate assemblages.

Krause (1978) described carpolestids from five localities in western Canada and used the primate evidence for biostratigraphic correlation with Paleocene sites in the western interior of the

United States. Krause described *Carpodaptes cygneus* specimens from Roche Percee (Ravenscrag Formation), Canyon Ski Quarry (Paskapoo Formation) and Swan Hills (Paskapoo Formation), which he assigned to a late (but not latest) Tiffanian age, and *Carpodaptes* cf. *C. cygneus* from Police Point (Ravenscrag formation), which he assigned to a middle Tiffanian age. Krause illustrated previously unknown M_{1-3}, P_2, M^{1-3} and I_1 of *C. cygneus*. Krause also illustrated and described the first known carpolestid I^1, of *C. cygneus*. In a reconstruction of the palate of *C. cygneus*, Krause illustrated the presence of a large and undivided palatal fenestra. Krause also illustrated a P_4 and described P_4, M_{2-3} of a new species, *Elphidotarsius russelli* from Cochrane site 11 (Porcupine Hills Formation), which he tentatively assigned to a late Torrejonian age. Krause stated that *E. russelli* was the dental intermediate between *Elphidotarsius* and *Carpodaptes*.

Szalay and Delson (1979) synonymized *Carpodaptes* and *Carpolestes*, placing *C. aulacodon*, *C. hazelae*, *C. hobackensis*, *C. jepseni*, *C. nigridens*, and *C. dubius* in *Carpodaptes*. Szalay and Delson reasoned that, because a morphological intermediate was known between *Carpodaptes* and *Carpolestes* (in the form of *C. jepseni*), *Carpolestes* was no longer a valid genus. Szalay and Delson also synonymized *C. hobackensis* and *C. cygneus*, and proposed a dental formula of 2.1.3.3/2.1.3.3 for *Elphidotarsius* and a dental formula of 2.1.3.3/2.1.2.3 for *Carpodaptes*.

Gingerich (1980) illustrated the stratigraphic distribution and interpreted phylogenetic relationships of Carpolestidae using a stratophenetic approach. Contrary to Szalay and Delson (1979) and in support of Rose (1975), Gingerich recognized three genera of Carpolestidae, and recognized the validity of *Carpodaptes hobackensis* and *Carpodaptes cygneus* as distinct species. Gingerich hypothesized that *E. florencae* gave rise to *E. shotgunensis* through reduction in body size. Gingerich hypothesized that *E. shotgunensis* gave rise to *Carpodaptes hazelae*, which gave rise to *Carpodaptes cygneus* and *Carpodaptes hobackensis* in a trend of decreasing body size. Gingerich further hypothesized that the *Carpolestes* lineage began with the first appearance of *C. jepseni* in the Tiffanian land-mammal age (Ti-4), based on similarity in body size and the idea that it was phylogenetically ancestral to *Carpolestes dubius*, an idea at least partially supported by an undescribed upper dentition of *C. jepseni* (Bloch et al., in preparation). *C. jepseni*, according to Gingerich, co-occurs with *Carpodaptes cygneus* and is much larger in body size than any previously known carpolestid. Gingerich hypothesized that *C. jepseni* gave rise to *C. dubius* and *C. nigridens* in a second trend of decreasing body size.

Rose (1981) described and illustrated new material of *Carpolestes nigridens* and a *Carpolestes dubius-nigridens* intermediate from the Clarks Fork Basin, north central Wyoming. A partial premaxilla-maxilla of *Carpolestes nigridens* was the most complete anterior upper dentition of a carpolestid to be described. The specimen, UM 71002, included $?I^2$-$?C$-P^{2-3}, with the premaxillary-maxillary suture, seen in lateral view, meeting the back of the alveolus for the ?canine. Rose reasoned that the ?canine was held primarily in the premaxilla, although he suggested, as an alternative interpretation, that the tooth might be I^3 "...but no other plesiadapiform is known to have more than two upper incisors" (Rose, 1981: 63). Rose noted the presence of *C. nigridens* in all three zones within the Clarkforkian (as defined by *Plesiadapis gingerichi*, *Plesiadapis cookei*, and *Phenacodus-Ectocion*) and noted the usefulness of *C. nigridens* as an index fossil for the Clarkforkian land-mammal age.

Rose and Fleagle (1981) proposed a dental formula of 2.1.3.3/2.1.2.3 for the genus *Carpolestes*. This differed from other, more ambiguous, interpretations of the homology of the tooth in the premaxilla-maxilla suture (which had been called either ?canine or I^3; Rose, 1981).

Fox (1984) described and illustrated a new species of *Elphidotarsius*, *E. wightoni*, from the Paskapoo Formation of central Alberta. The sample of this new species included an incomplete left dentary with I_{1-2}, C, P_{3-4} and M_{1-3}, with an alveolus for a missing P_2, as well as maxillae preserving P^1-M^3. Fox also described a premaxilla of *?Carpodaptes hazelae* from the Paskapoo Formation that contained I^1 and alveoli for two posterior teeth identified as I^{2-3}. Based on this, Fox proposed a dental formula of 3.?.4.3/2.1.3.3 for *E. wightoni* and regarded the presence of three upper incisors and four upper premolars as primitive for Carpolestidae. Fox stated that the ?canine identified by Rose (1981) was an I^3, with the canine and P^1 being lost in *C. nigridens*. Fox regarded *E. wightoni* as an evolutionary transition between *Elphidotarsius* and *Carpodaptes*, and of middle Tiffanian age (as determined by the presence of *Plesiadapis rex*).

Fox noted the co-occurrence of *E. wightoni* and *C. hazelae,* and questioned the biostratigraphic utility of the succession of carpolestid species for zonation of the nonmarine upper Paleocene of North America.

Biknevicius (1986) used microwear and morphometric analysis to assess dental function in the Carpolestidae. Biknevicius determined that carpolestids used P^4 and the trigonid of M^1 to wedge foods apart in a slicing-crushing cycle, a cycle which has only been identified in one other extinct taxon, Multituberculata. Biknevicius also noted extensive phase I shearing. The combination of these features led Biknevicius to conclude that carpolestids ate foods of combined textures, particularly food with a soft interior covered by either a brittle or ductile coat. Biknevicius further concluded that carpolestids were probably omnivorous, eating insects, nuts and seeds with a shift to include more fruit in the later occurring forms.

Schwartz (1986) included *Elphidotarsius* (Gidley, 1923), *Carpodaptes* (Matthew and Granger, 1921), *Carpolestes* (Simpson, 1928), *Tinimomys* (Szalay, 1974), and *Azibus* (Sudre, 1975) within the Carpolestidae. Schwartz stated that many of the premolar and molar characters of *Tinimomys* are distinctive of carpolestids and not paromomyids, the group in which it was more traditionally placed. Furthermore, Schwartz cited features of *Azibus* that reflected the apomorphies of carpolestids and not adapids (Gingerich, 1977a).

Gingerich (1987) included a photograph of the lateral view of the first known skull of a carpolestid. The specimen was recovered from a freshwater limestone, interpreted as having been deposited in a rotting tree or vertebrate burrow. The specimen came from faunal zone Cf-3 in the Clarks Fork Basin, and Gingerich referred the specimen to *Carpolestes cf. C. nigridens* with no description of the material.

Beard and Houde (1989) commented on Schwartz's idea of affinity of carpolestids with *Tinimomys* based on exceptionally complete new material of *Tinimomys* removed from a freshwater limestone from locality SC-4 in faunal zone Wa-1 of the Clarks Fork Basin. They concluded that there was no evidence for any special relationship between carpolestids and *Tinimomys*, and that a number of derived characters supported nesting *Tinimomys* within Micromomyini, with familial affinities uncertain.

Beard (1989b) described what he called the first postcranial bone of a carpolestid, proximal and distal fragments of a small humerus. Tentative assignment to *Carpolestes nigridens* was made "...on the basis of size, morphology, and provenance" (Beard, 1989b: 133), though he gave no measurements nor a scale in his illustrations. Beard noted that the humerus was similar to humeri of plesiadapids and paromomyids, with some distinguishing features. He also noted that a humerus described by Szalay and Dagosto (1980) as an "archontan" might represent the species *Carpodaptes aulacodon*. Beard further stated that the Plesiadapidae, Paromomyidae, and Micromomyidae shared a more recent common ancestry with *Cynocephalus* (Order Dermoptera) than they did with primates (Beard, 1989a, 1989b, 1990). Beard (1993a, 1993b) specifically included the Carpolestidae within Dermoptera.

Fox (1990) documented the occurrence of five species of carpolestids from at least nine different localities in Alberta. These included: *Elphidotarsius russelli* and *Carpodaptes* cf. *C. hazelae* from early Tiffanian (Ti-1); *Elphidotarsius* cf. *E. wightoni, Elphidotarsius wightoni,* and *Carpodaptes hazelae* from early Tiffanian (Ti-1 or Ti-2); *Elphidotarsius wightoni, Carpodaptes hazelae, Carpodaptes cygneus*, and *Carpodaptes* cf. *C. cygneus* from middle Tiffanian (Ti-3); and *Carpodaptes cygneus* and *Carpodaptes* cf. *C. hobackensis* from late Tiffanian (Ti-4).

Fox (1993) stated that new evidence from *Elphidotarsius* and *Carpodaptes* indicates that the primitive dental formula for the Carpolestidae is 3.1.4.3/3.1.3.3, which differs from that of primitive eutherians only in the loss of P_1. Fox suggested, in light of the new evidence, that the upper dental formula of *Carpodaptes* differs from the primitive form only in the loss of C^1. He also suggested that the upper dental formula of *Carpolestes nigridens* (Rose and Fleagle, 1981) be reinterpreted as 3.0.3.3 with the loss of C^1 and P^1 and not I^3 and P^1. Fox concluded that if the Carpolestidae and Plesiadapidae are sister groups, then carpolestids are more primitive than known plesiadapids in having three upper incisors and having C^1-P^1. Fox further concluded that there is no anatomical evidence that carpolestids are dermopterans (Kay et al., 1990; Beard, 1991, 1993a, 1993b).

Rose et al. (1993) described new dentitions of *Tinimomys* and *Niptomomys*, the former of which was removed from a freshwater limestone from University of Michigan locality SC-26 in the early Wasatchian of the Clarks Fork Basin, Wyoming, with an extensive comparison of upper incisors of Plesiadapiformes. Rose et al. discussed the morphology of I^1 of *Carpodaptes cygneus* (Krause, 1978) and ?*Carpodaptes hazelae* (Fox, 1984) and noted that they are distinct in having a strong laterocone, a low crest mesioproximal to the anterocone, no mediocone, and a double posterocone. Rose et al. commented on the I^1 of *Carpolestes nigridens* illustrated, in lateral view, in Gingerich (1987). They noted that *C. nigridens* appears to differ from other Plesiadapiformes, including *Carpodaptes,* but resembles *Tinimomys* in lacking a laterocone. Rose et al. tentatively referred an I^1 ascribed to *Palaechthon minor* (Gidley, 1923) as possibly belonging to *Elphidotarsius florencae* and an I^1 illustrated by Simpson (1928, Fig. 13) as possibly belonging to *Carpolestes nigridens*. Rose et al. added that both of these incisors could, alternatively, belong to non-plesiadapiformes such as erinaceid or nyctitheriid insectivores, or plagiomenids.

Beard and Wang (1995) described and illustrated the first known Asian Plesiadapiformes from the early Eocene Wutu Basin of China. Beard and Wang called *Chronolestes simul,* known from partial upper dentitions with a dental formula of 3?.0?.4.3 and complete lower dentitions with a dental formula of 2.1.3.3 , a primitive carpolestid and sister taxon to the Torrejonian (To-3) *Elphidotarsius florencae.* Beard and Wang called *Carpocristes oriens,* known from P^4-M^3 and P^3-M^3, a more derived carpolestid most closely allied with Tiffanian (Ti-5) *Carpodaptes hobackensis.* Furthermore, Beard and Wang moved *Carpodaptes cygneus* (Russell, 1967; Rose, 1975; Krause, 1978) and *Carpodaptes hobackensis* (Dorr, 1952; Rose, 1975; Holtzman, 1978, in part) to the new genus *Carpocristes.* Beard and Wang concluded that the relationships implied in their phylogenetic analysis suggest two Paleocene episodes of trans-Beringian dispersal of carpolestids, one from North America to Asia in the middle Torrejonian and one from North America to Asia in the latest Tiffanian or earliest Clarkforkian. All of their specimens were restricted to early Eocene coal beds and no Paleocene carpolestids are known from Asia.

SYSTEMATIC PALEONTOLOGY

Order PROPRIMATES Gingerich, 1989
Infraorder PLESIADAPIFORMES Simons, 1972
Superfamily PLESIADAPOIDEA Trouessart, 1897
Family CARPOLESTIDAE Simpson, 1935

Carpolestidae Simpson, 1935, p. 9. Rose, 1975, p. 10-11.

Type genus. — *Carpolestes* Simpson, 1928.
Included genera. — *Carpodaptes* Matthew and Granger, 1921; *Elphidotarsius* Gidley, 1923; *Carpolestes* Simpson, 1928; and *Carpocristes* Beard and Wang, 1995.
Age and distribution. — Early Paleocene (Torrejonian) through the latest Paleocene (Clarkforkian) in North America. Early Eocene in Asia.

Discussion. — Classification of Paleocene "Primates," specifically that of Carpolestidae, has changed many times since the first carpolestid was described by Matthew and Granger (1921). They noted that "this form cannot be definitely assigned to any family or order; it may be a primate, a menotyphlan insectivore, or neither" (Matthew and Granger, 1921: p. 6). Carpolestids were classified within the primate family Tarsiidae (Gidley, 1923; Simpson, 1928) until Simpson (1935) named a new primate family Carpolestidae. Simons (1972) placed most of the Paleocene "primates," including Carpolestidae, within the primate infraorder Plesiadapiformes. More recently, classification of Carpolestidae has become unstable, with inclusion in order Primates as Plesiadapiformes (Gingerich, 1976; Bown and Rose, 1976) or Tarsiidae (Dashzeveg and McKenna, 1977, McKenna and Bell, 1997), order Proprimates (Gingerich, 1989; 1990a), and order Dermoptera

(Beard, 1991, 1993a, 1993b; Kay, 1990, 1992). Carpolestidae are here considered to be Proprimates following Gingerich (1989) and not tarsiiform Euprimates as suggested by McKenna and Bell (1997). Diagnosis of Carpolestidae follows Rose (1975). The content of the family Carpolestidae is equivalent to that of the subfamily Carpolestinae of Beard and Wang (1995) and does not include the Asian genus *Chronolestes*, which may be far removed from the base of the carpolestid clade (Bloch and Fisher, 1996).

Genus *Carpolestes* Simpson, 1928

Carpolestes Simpson, 1928, p. 7. Jepsen, 1930, p. 520. Rose, 1975, p. 36.
Litotherium Simpson, 1929, p. 9.
Carpodaptes (in part), Szalay, 1972, p. 23. Rose, 1975, p. 33. Szalay and Delson, 1979, p. 98.

Type species. — *Carpolestes nigridens* Simpson, 1928.
Included species. — *Carpodaptes jepseni* Rose, 1975; *Carpolestes dubius* Jepsen, 1930; *Carpolestes nigridens*, Simpson 1928; and *Carpolestes simpsoni*, new species.
Distribution. — Late Paleocene (Tiffanian-4 through Clarkforkian-3 faunal zones) of Montana and Wyoming.

Carpolestes simpsoni, new species
Figs. 2-6

Carpolestes nigridens (in part), Rose, 1975, p. 36, 43: fig. 27a; 1981, p. 62: fig. 27b-f.
Carpolestes cf. *C. nigridens*, Gingerich, 1987, p. 312, 283: fig. 6.

Holotype. — UM 86273, compressed skull with: left; I^1 (broken), I^{2-3}, P^2 (broken), P^3-M^3; right I^1 (broken), I^2 (broken), I^3-M^3 (Fig. 2a). Complete left dentary with I_1-M_3 (Figs. 2b-d).
Referred Specimens. — UM locality **SC-19**: UM 65033. **SC-29**: UM 65254, 101994. **SC-53**: UM 69338, 85179, 98199, 101923, 104032. **SC- 62**: UM 82615, 82670, 82672, 82673, 82688, 85177, 85178, 98450, 101780, 101963. **SC-116**: UM 81693, 98437, 98443, 98444. **SC-117**: UM 95859, 95860, 98084, 101974. **SC-127**: UM 66909. **SC-143**: UM 81429. **SC-188**: UM 71002-71005, 71644, 71778, 73566, 75460, 77624, 101964-101973, 101975. **FG-6**: UM 77583 (3 spec.), 77586 (3 spec.), 77561. "Clark Fork" beds, Bighorn Basin: PU 19543.
Type locality. — UM locality SC-29 "*Carpolestes* skull site," near the center of the eastern edge of Section 35, T56N, R101W, Park County, Wyoming. Detailed locality information has been published elsewhere (Gingerich, 1987, p. 277).
Age and distribution. — *Carpolestes simpsoni* is known from middle and late Clarkforkian faunal zones Cf-2 and Cf-3 (latest Paleocene) in northwestern Wyoming.
Diagnosis. — Smallest species of *Carpolestes* known. Dental formula 3.0.3.3/2.1.1.3. *C. simpsoni* differs from *C. dubius* in having P^2 narrower and slightly higher-cusped; a pronounced anterolateral projection on P^3 that makes the breadth somewhat less than the length; P^4 with the lingual side longer relative to the buccal side (giving it a more square outline); and less pronounced curvature toward the midline at the tip of I_1. *C. simpsoni* differs from *C. nigridens* in having a smaller P^3 with a narrower anterolateral projection, pinching toward the midline at the anterior and posterior edges of P^3 (which results in an hour-glass shape lingual to the buccal row of cusps); smaller P^4 that is slightly more square in outline; and narrower and lower crowned P_4. *C. simpsoni* differs from all species of *Carpolestes* in being smaller, as determined from M_1 area; in having a uniquely shaped P^3; in having a near-vertical protocone on M^1; in having a broader shelf of the hypocone on M^2; and in having a lower dental formula of 2.1.1.3 (i.e., it differs from other species in lacking P_3).
Etymology. — Named for George Gaylord Simpson in recognition of his many contributions to vertebrate paleontology, including recognition and naming of the family Carpolestidae.
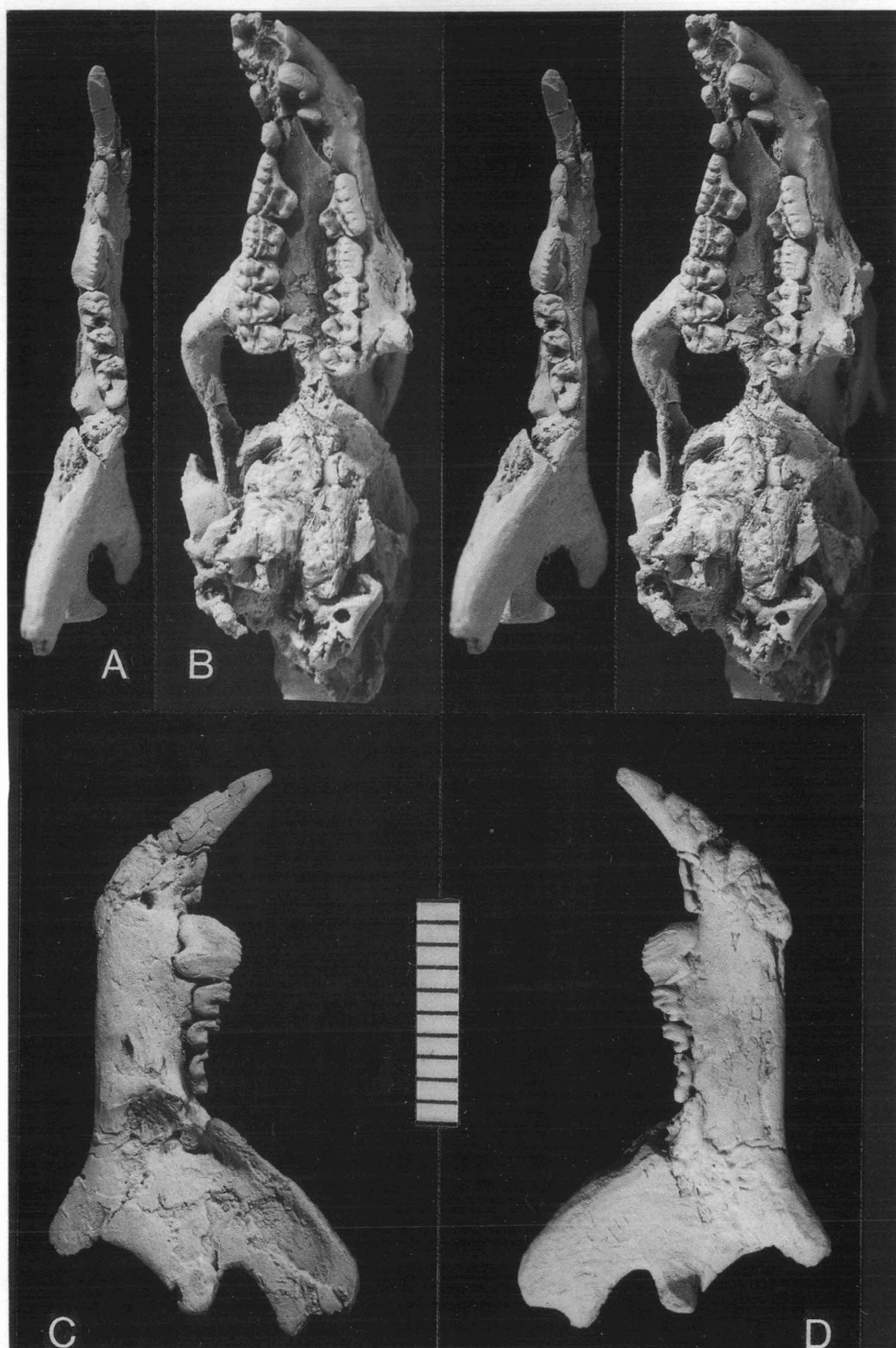
FIG. 2 — Type specimen of *Carpolestes simpsoni* (UM 86273). A-B, stereophotographs of left mandible with I_1-M_3 and skull with left I^1 (broken), I^{2-3}, P^2 (broken), and P^3-M^3 and right I^1 (broken), I^2 (broken), and I^3-M^3, in occlusal view. C-D, left mandible in lateral and medial views. Note the presence of two tiny teeth posterior to the enlarged I_1. All other species of *Carpolestes* have three reduced teeth posterior to I_1, giving *Carpolestes simpsoni* a unique lower dental formula of 2.1.1.3. Scale is in mm.

Description. — Fifty-six specimens, including several complete upper and lower dentitions, are known for the new species. Measurements of these specimens are summarized in Table 1 and listed in Appendix tables A1-A4. The palate with complete upper dentition is illustrated in Figure 3. The dentary with complete lower dentition is illustrated in Figure 4.

I^1 (Fig. 5): I^1 has a strong laterocone, even larger than the anterocone, a low crest mediodorsal to the anterocone (but no mediocone), an interstitial wear facet on the mesial face of the mesioapical cusp, and a double posterocone with the lateral cusp substantially larger. The anterocone, together with the laterocone, forms an apical ridge running mediolaterally. Strong apical wear facets are present on all specimens of I^1. The I^1 often has the laterocone and anterocone distinct but worn almost completely away, with the anterocone being the slightly less worn of the two.

I^2: I^2 is single rooted and about 20% smaller than the I^1. It is fairly high crowned and mitten-shaped and has an apical ridge running mediolaterally, but this is oriented almost perpendicular to the apical ridge on I^1. The apical ridge has a single lateral cusp similar to the laterocone on the I^1, and it slopes slightly dorsolaterally away from the central cusp, giving the tooth a procumbent profile. There is a low cusp, like the posterocone on I^1, at the base of the I^2 dorsolingual to the laterocone. I^2 has a crest that runs dorsally from the medial edge of the apical ridge until it reaches the base of the crown, where it turns laterally to wrap around the lingual face of the posterocone forming a strong basal cingulum. I^2 has similar apical wear to that observed on the I^1. In an extreme case the laterocone of the I^2 is completely worn away, with some wear on the rest of the apical ridge as well as wear on the apex of the posterocone.

I^3: I^3 is the smallest tooth in the upper dentition. It has a high apical cusp with a small cusp posterodorsal to the apical cusp. There is an even smaller cuspule higher on the crown, on the anterodorsal side of this somewhat compressed tooth. There is a lingual cingulum running from the anterior cuspule to the posterior cusp.

P^2: P^2 is slightly larger than I^3. As with I^3, P^2 is laterally compressed with one prominent cusp and low accessory cuspules in front and back. The anterior cuspule is set more apically than the posterior cusp, with a weak lingual cingulum running from the posterior cuspule, along the base of the crown, up to the anterior cuspule. P^2 has a single undivided root, which is stout and oval in cross section.

P^3: P^3 has three parallel rows of cusps that run anteroposteriorly across the crown of the tooth, with the buccal row extending to form a pronounced parastyle. The buccal row is comprised of five cusps with an incipient sixth anterior cuspule, that, together with two large cusps, makes up the parastyle. The lingual row, which is half the length of the buccal row, is comprised of two cusps, although a third anterior cusp is sometimes present. The mid-row is comprised of four cusps, of which the anterior-most cusp is distinct and more lingually situated than the rest. The outline of the tooth, lingual to the buccal row of cusps, is hour-glass shaped with the midpoints of the anterior and posterior edges of the tooth slightly pinched toward the mid-line (Fig. 7a-b). The enamel of this tooth is somewhat crenulated in its unworn state.

P^4: P^4, like P^3, is polycuspate with three longitudinal rows of cusps. The buccal row has five equally spaced cusps and lacks a strong parastyle. The median row has five low cuspules. A low, faint crest runs from the lingual face of the central cusp of the buccal row to the buccal face of the central cusp of the median row. The lingual row has three distinct cusps, with the central cusp the largest. The central cusp of the lingual row is positioned more buccally than the other two lingual cusps and is closer to the anterior lingual cusp ("twinned"). A low crest runs from the lingual face of the central cusp of the median row to the buccal face of the central cusp of the lingual row. Two small cuspules are located between the median and lingual rows. These cuspules are lingual to the space between the two anterior-most cuspules and the posterior-most cuspule of the median row. They are joined to the base of the anterior and posterior extremes of the median crest, respectively, by low crests. The lingual side of P^4 is longer relative to the buccal side, giving it a square outline. As on P^3, the enamel is somewhat crenulated in its unworn state.

M^1: The crown of M^1 is rectangular and the paracone, metacone, and protocone are nearly equal in height. A small hypocone is connected to the protocone by a postprotocingulum. A
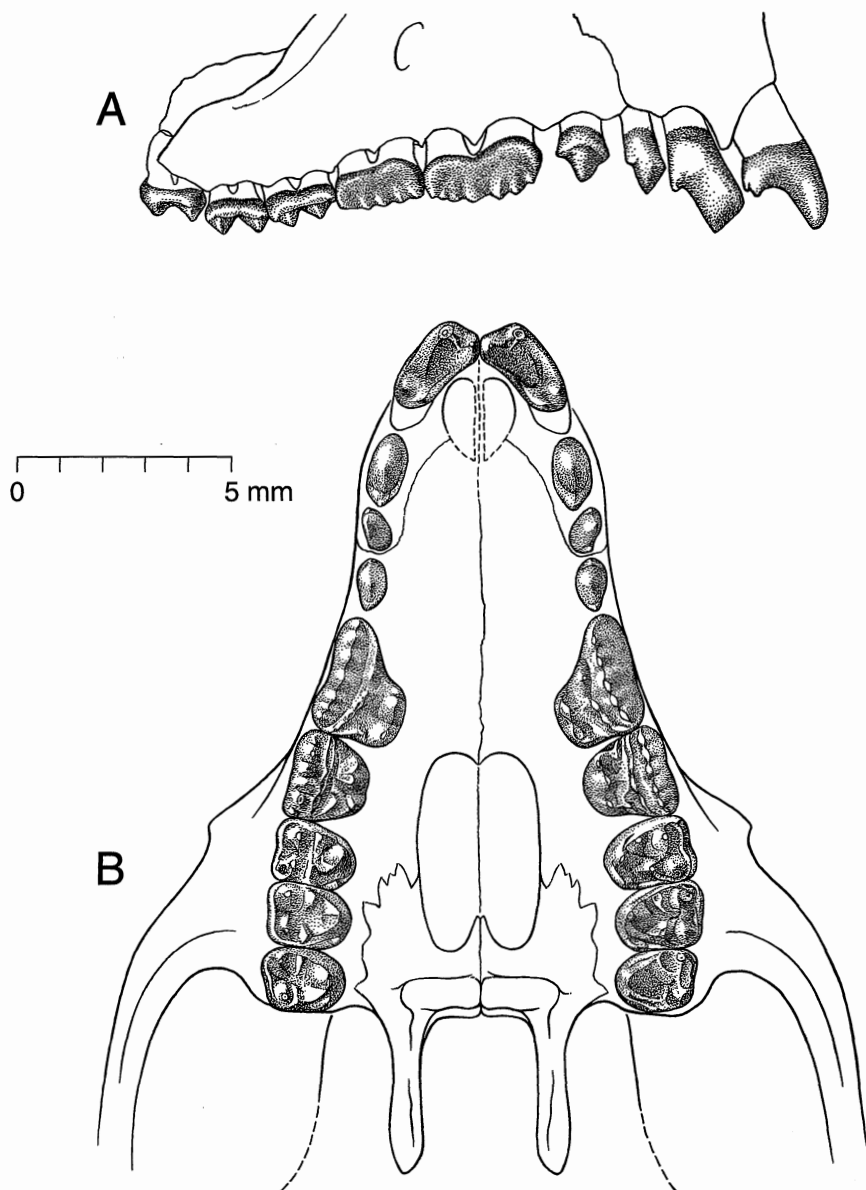
FIG. 3 — Composite drawings of palate and upper dentition of *Carpolestes simpsoni* based on UM specimens 82670, 82688, 85177, 86273, 71002, 101923, 101963, and 101994. A, right I^1-M^3 in lateral view; and B, palate with left and right I_1-M_3 in occlusal view. Note that the premaxillary-maxillary suture intersects and runs behind the posterior root of the tooth interpreted as I^3 (see photograph in Fig. 6). Note too, in occlusal view, the large palatal vacuity separating maxillae from palatines along the midline. This window appears to be divided into paired fenestrae by a thin midline process of the vomer. Such palatal fenestrae are not known in any other proprimate. Scale is in mm.

prominent paraconule is connected to the protocone by a strong preprotocrista, with an equally prominent metaconule connected to the protocone by a strong postprotocrista.

M^2: M^2 is similar to M^1, although it has a weak hypocone and only the faintest traces of a postprotocingulum.
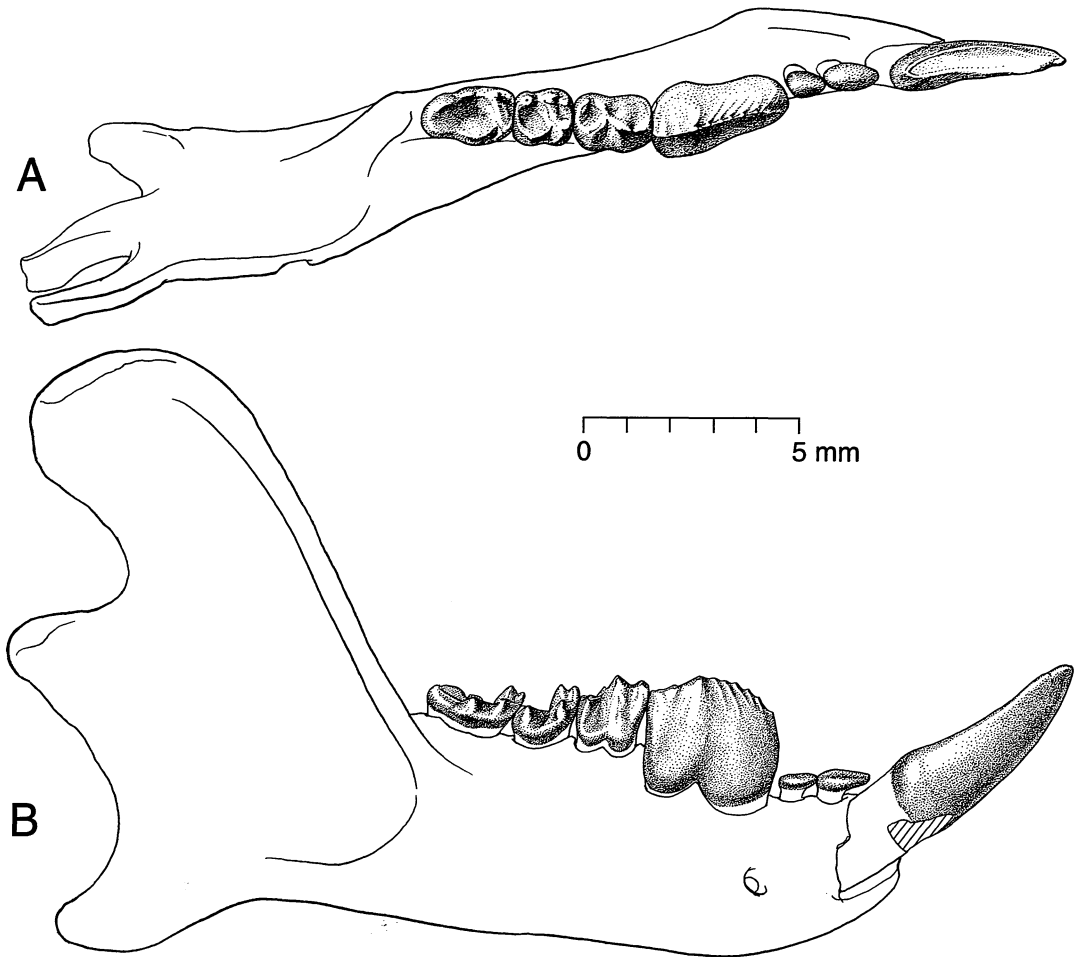
FIG. 4 — Composite drawing of dentary with I_1-M_3 of *Carpolestes simpsoni* based on UM 82615 and 82672, in occlusal (A) and lateral (B) views. Note presence of only two small single-rooted teeth between enlarged I_1 and P_4. Scale is in mm.

M^3: M^3 is different from the other molars in having a narrow shelf in place of the hypocone.

Palate: Several specimens preserve most of the morphology of the hard palate of *Carpolestes simpsoni* (Fig. 3b). The palatines of *Carpolestes* are restricted to small, subtriangular horizontal laminae medial to the molars. The contact between the palatines and the maxilla is manifest in a very distinct, jagged suture. Posteromedial to M^3, a process of the palatine forms a contact between the left and right palatine. At this contact the posterior margin of the palate is nearly straight and is buttressed by a strong, rounded postpalatine torus with wings extending posteriorly onto the basicranium. The area anterior to the palatine contact is open, forming a large palatal fenestra. This opening appears to be divided by a thin process of bone interpreted as the vomer. Anteriorly, the palatal fenestrae are closed by the contact between left and right maxillae. In one specimen (UM 85177) there is evidence for the presence of moderate incisive foramina at the anterior contact between the premaxilla and the maxilla.

I_1: I_1 is enlarged, procumbent, laterally compressed, and has no basal cusp on the lingual cingulum. A ridge forms the lateral border of the dorsal face of the tooth. At the base of the crown the ridge meets a weak internal cingulum. I_1 has a strong dorsal curvature, with the tip of the crown curving towards the midline.
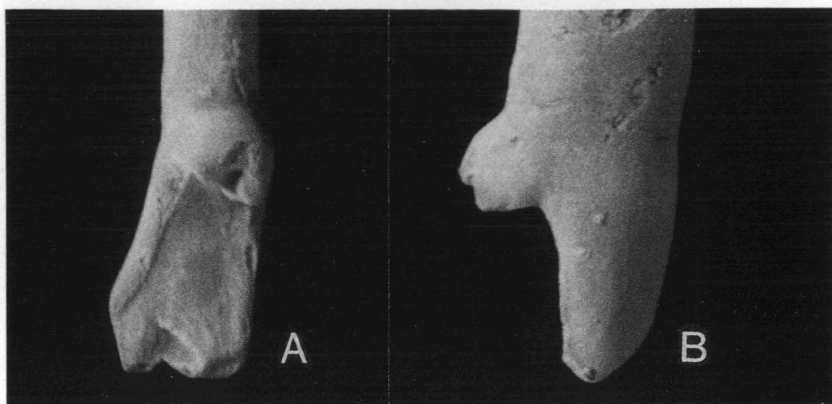
FIG. 5 — Photograph of upper central incisor of *Carpolestes simpsoni*. Right I^1 (UM 101994) in lateral (A) and occlusal (B) views. Note that while I^1 appears to have only one apical cusp when seen in lateral view, two apical cusps (anterocone and laterocone) are clearly visible in occlusal view. Scale is in mm.
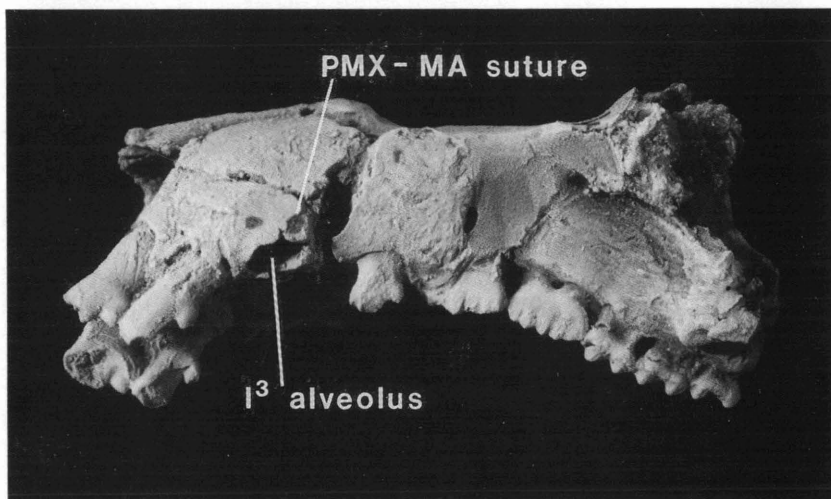
FIG. 6 — Rostrum of *Carpolestes simpsoni* (UM 85177) in lateral view. The premaxilla is dislodged from the maxilla, showing that the premaxillary-maxillary suture runs behind the alveolus for I^3. The maxilla overlaps onto the premaxilla to giving the impression that it makes up part of the wall of the alveolus. The tooth behind the suture is interpreted as P^2, and there is thus no canine in the upper dentition. Scale is in mm.

I_2: I_2 is small, single rooted, and often placed buccally in relation to the other anterior teeth. The crown extends anteriorly, making an elongated spur, almost completely covering the gap between I_1 and the root of I_2.

C_1: C_1 is small and single rooted, with the enamel of the crown forming an anteriorly-elongate spur about half as long as the spur on I_2. The spur fills the gap between the root of C_1 and I_2.

P_4: P_4 is large, high crowned and blade-like, with 8-9 apical cusps (Fig. 7c-d). The blade merges posteriorly with the trigonid of M_1.

TABLE 1 — Summary of dental and mandibular measurements for *Carpolestes simpsoni* from Clarkforkian zones Cf-2 and Cf-3. Total sample includes 56 specimens. Abbreviations: N, sample size; $\bar{x}$, mean; s, standard deviation; V, coefficient of variation; L, crown length; W, crown width; and H, crown height (see Fig. 1 for explanation). Measurements are in mm.

| Tooth position		N	Range	$\bar{x}$	s	V
Upper dentition						
	L	6	1.81 - 1.96	1.85	0.06	2.98
I^1	W	6	1.10 - 1.27	1.16	0.06	5.42
	H	5	2.25 - 2.48	2.34	0.09	3.75
	L	6	1.38 - 1.58	1.49	0.07	4.62
I^2	W	6	0.77 - 0.88	0.84	0.04	4.82
	H	5	1.73 - 2.18	1.99	0.20	9.85
	L	4	0.84 - 1.09	0.95	0.10	10.82
I^3	W	4	0.54 - 0.65	0.58	0.05	8.33
	H	4	1.30 - 1.46	1.38	0.08	5.92
P^2	L	5	1.23 - 1.28	1.25	0.02	1.85
	W	5	0.66 - 0.74	0.72	0.03	4.48
P^3	L	13	2.40 - 2.87	2.63	0.15	5.59
	W	13	1.86 - 2.31	2.05	0.15	7.34
P^4	L	9	1.90 - 2.15	2.02	0.08	3.80
	W	8	1.63 - 1.97	1.78	0.12	6.99
M^1	L	9	1.35 - 1.57	1.49	0.06	4.04
	W	9	1.86 - 2.16	2.04	0.11	5.23
M^2	L	9	1.28 - 1.50	1.42	0.06	4.35
	W	9	1.79 - 2.02	1.91	0.07	3.89
M^3	L	6	1.37 - 1.53	1.47	0.06	4.13
	W	6	1.76 - 1.87	1.81	0.04	2.36
Lower dentition						
	L	4	2.00 - 2.19	2.08	0.09	4.27
I_1	W	4	0.96 - 1.12	1.07	0.07	6.81
	H	2	5.06 - 5.85	5.46	0.56	10.24
I_2	L	4	1.42 - 1.61	1.53	0.09	5.59
	W	4	0.72 - 0.87	0.79	0.06	7.94
C_1	L	4	0.85 - 1.04	0.93	0.08	8.64
	W	4	0.55 - 0.64	0.59	0.04	7.00
P_4	L	27	2.69 - 3.22	2.96	0.15	4.96
	W	26	1.39 - 1.84	1.60	0.12	7.56
M_1	L	20	1.58 - 1.85	1.75	0.08	4.77
	W	17	1.20 - 1.46	1.32	0.08	4.87
M_2	L	10	1.31 - 1.58	1.48	0.09	5.88
	W	10	1.22 - 1.38	1.31	0.06	4.60
M_3	L	10	2.02 - 2.26	2.12	0.09	4.31
	W	9	1.20 - 1.36	1.30	0.05	4.06
Mandibular depth						
	MD	13	4.50 - 5.17	4.84	0.26	5.38
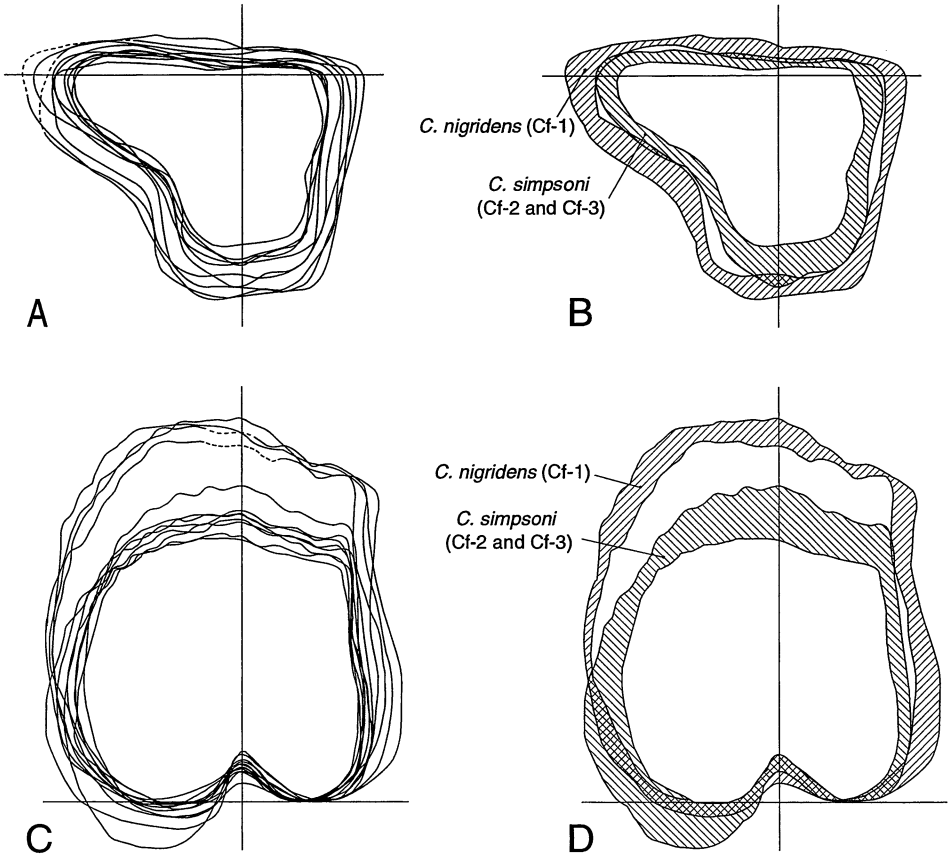
FIG. 7 — Size and shape of P³ and P₄ in *Carpolestes nigridens* and *Carpolestes simpsoni*. A, P³ outlines in occlusal view (N = 10); and B, interpretation of same with ranges of species variation indicated by hatching. C, P₄ outlines in lateral view (N = 12); and D, interpretation of same with ranges of species variation indicated by hatching. Dotted lines show reconstructed profiles. P³s were oriented for drawing by aligning a vertical through the third cusp from the posterior side of the buccal row with the notch between the two cusps on the lingual row; a perpendicular horizontal line runs through the anterior-most cusp of the buccal row. P₄s were oriented for drawing by aligning a vertical through the highest apical cusp and the ventral notch; a perpendicular horizontal line runs through the base of the posterior lobe of the crown. Note that the ranges of variation in P³ occlusal outlines for *C. nigridens* and *C. simpsoni* are virtually non-overlapping. Note too that P₄s of *C. simpsoni* are lower-crowned and anteriorly more projecting (exodaenodont) than those of *C. nigridens*.

M₁: M₁ trigonid is slightly higher than the talonid of P₄. The paraconid is situated directly anterior to the protoconid, with the protoconid being slightly more prominent. A small metaconid sits posterolingual to the protoconid. A small talonid basin is present posterior to the trigonid, with a distinct hypoconid and entoconid but no hypoconulid.

M₂: M₂ is shorter than M₁, but similar in width. The lingual part of the trigonid of M₁, made up of the paraconid and metaconid, is a little higher than the posterior end of the talonid of M₁. The protoconid is considerably shorter than the other two cusps of the trigonid. The talonid of M₂ is larger and broader than on M₁, with a distinct hypoconid and entoconid, but no hypoconulid.

M₃: M₃ is longer than both M₁ and M₂, but of equal width. It has a pronounced third lobe bearing two cusps (twinned hypoconulid).

Dentary: There is a moderately large mental foramen present below P_4. The mandibular symphysis is unfused. The coronoid process is high and broad. The angular process is recurved, and tapers posteriorly forming a hook-like process. The condyle is roughly half-way between the angular process and the top of the coronoid process. The articular surface of the articular condyle covers both the dorsal and posterior surfaces of the condyle. A large mandibular foramen is present on the medial side of the jaw below the anterior portion of the coronoid process and about two-thirds of the way down the ascending ramus.

Discussion. — Complete upper and lower dentitions are known for *Carpolestes simpsoni*, with at least 56 specimens from 11 different Clarkforkian localities. The fossils representing this species are the most complete of any member of the family. The best specimens were dissolved from limestone lenses, many of which are found at UM locality SC-62. The type skull and mandible were removed from a limestone lens found at UM locality SC-29.

A photograph showing the lateral view of UM 86273 containing a worn I^1 was published by Gingerich (1987: fig. 6). Rose et. al. (1993) described this tooth as differing from other Plesiadapiformes, including other carpolestids, but resembling *Tinimomys*, in lacking a laterocone. New fossils show that *Carpolestes*, like *Carpodaptes* (Fox, 1993,1984; Krause, 1978; Rose et. al., 1993), actually has a prominent laterocone. Both the anterocone and laterocone are very worn on the specimen illustrated in Gingerich (1987), creating a lateral profile superficially like that of *Tinimomys*. In fact, the anterocone is so worn that it is hidden behind the more prominent laterocone.

The I^1 of *Carpolestes simpsoni* is most similar to that of *Carpodaptes cygneus* among described incisors (Rose et. al. 1993) in having a strong laterocone, even larger than the anterocone, a low crest mediodorsal to the anterocone but no mediocone, an interstitial wear facet on the mesial face of the mesioapical cusp, and a double posterocone, with the lateral cusp substantially larger. The I^1 of both *Carpolestes simpsoni* and *Carpodaptes cygneus* differs from that of *Carpodaptes hazelae* (Fox, 1993,1984) in lacking a mediocone. I^1 of *Carpolestes simpsoni* differs from that of *Carpodaptes cygneus* in having a crown that is deeper relative to breadth and lower relative to both depth and breadth. Furthermore, the anterocone is situated considerably more lingual on the I^1 of *Carpolestes simpsoni* and, together with the laterocone, forms an apical ridge running mediolaterally. This is different from the I^1 of *Carpodaptes*, which has an anterocone situated labial to the laterocone, forming an apical ridge running in a much more labiolingual direction. As a result, *Carpolestes*, in both labial and lingual views, has a distally wider crown than that of *Carpodaptes*. While both *Carpodaptes* and *Carpolestes* have a low crest mediodorsal to the anterocone, it is considerably less prominent in *Carpolestes*. The two cusps making up the posterocone of the *Carpolestes* I^1 appear to be lower and closer together than in *Carpodaptes*.

The I^2 of *Carpolestes* is similar to that of *Carpodaptes* (Fox 1993) in having a single root, a high central cusp, a small posterior cusp situated at the base, a strong basal cingulum developed lingually, a short diastema between I^1 and I^2, and in being substantially smaller than I^1. The I^2 of *Carpolestes* is different in lacking a well developed "heel" and, while the basal cingulum does develop lingually into a small anterior ridge approaching the crown of I^1 at the apex of the tooth, it does not form a broad shelf as described for *Carpodaptes* (Fox 1993).

The tooth behind I^2 is interpreted here as I^3. The premaxilla-maxilla suture is present in several specimens. In lateral view, the suture intersects the middle of the alveolus of the I^3 (Fig. 3a). In viewing the suture from the palate, it appears to run almost to the back of the I^3 alveolus (Fig. 3b). With this information alone, using conventional definitions (Gingerich 1976), the tooth is a canine. However, a new specimen of *Carpolestes simpsoni* (Fig. 6) shows that the alveolus for the tooth posterior to I^2 is in the premaxilla, as in *Carpodaptes* (Fox 1984), with the maxilla overlapping onto the premaxilla to give the impression that it makes up part of the wall of the alveolus. Thus, contrary to Rose and Fleagle (1981) and Bloch and Gingerich (1994), but as suggested by Fox (1984, 1993), the tooth in front of P^2 is probably a third incisor, with the canine absent in the upper dentition.

The P^2 of *Elphidotarsius wightoni* (Fox, 1984) and *Carpodaptes hazelae* (Simpson, 1937) is similar to that of *Carpolestes simpsoni* in having a single undivided root that is stout and oval in

cross section and in having a main cusp, a posterior heel, and a basal cingulum that extends anterolingually around to the buccal side of the tooth. P^2 of *Carpolestes simpsoni* differs from those of *Elphidotarsius wightoni* and *Carpodaptes hazelae* in having a higher central cusp and in being more compressed buccolingually, with a more elongate oval cross-section. P^2 of *Carpolestes dubius* (Rose, 1975) is not as narrow or high-cusped as that of *Carpolestes simpsoni*.

The P^3 of *Carpolestes simpsoni*, like *Carpolestes nigridens* (Rose, 1975), has three parallel rows of cusps running anteroposteriorly across the crown of the tooth, with the buccal row extending to form a pronounced parastyle. In the past, because the P^3 of *Carpolestes simpsoni* was morphologically similar to the P^3 of *Carpolestes nigridens*, and because so few specimens of *Carpolestes* were known from the later Clarkforkian land-mammal age, variation in P^3 morphology was attributed to variation within a single species of *Carpolestes nigridens* (Rose, 1975: PU 19543; Rose, 1981: UM 71002). With a much larger sample of *Carpolestes simpsoni* it has become apparent that the P^3, while similar in morphology to that of *Carpolestes nigridens*, is significantly smaller. The length of P^3 in *Carpolestes simpsoni* is shorter relative to its breadth and the anterolateral projection is narrower than in *Carpolestes nigridens*. The outline of the tooth, lingual to the buccal row of cusps, is square in *Carpolestes nigridens* and more hour-glass shaped in *Carpolestes simpsoni*, with the midpoints of the anterior and posterior edges of the tooth being slightly pinched toward the mid-line (Fig. 7a-b).

Also polycuspate with five buccal cusps, the P^4 lacks a strong parastyle in both *Carpolestes nigridens* and *Carpolestes simpsoni*. P^4 is considerably smaller in *Carpolestes simpsoni* than it is in *Carpolestes nigridens*. The lingual side of P^4 is longer relative to the buccal side in *Carpolestes simpsoni*, giving it an outline closer to a square than the more trapezoidal outline seen in *Carpolestes nigridens*, and *Carpolestes dubius*. P^4 of *Carpolestes* differs from that of *Carpodaptes* in having an outline more closely resembling a square than the buccolingually elongated, rectangular, P^4 of *Carpodaptes*.

The upper molars of *Carpolestes simpsoni*, having a primitive plesiadapiform morphology, are similar to all other species of Carpolestidae. The upper molars of *Carpolestes dubius* (Rose, 1975) and *Carpolestes simpsoni* are well represented in the fossil record, but only a few upper molars of *Carpolestes nigridens* are known.

The M^1 of both *Carpolestes nigridens* and *Carpolestes dubius* (Rose, 1975) is different in being buccolingually longer, and larger in crown area, than the M^1 of *Carpolestes simpsoni*. Also, unlike the near-vertical nature of the protocone of *Carpolestes simpsoni*, the M^1 protocone is tilted buccally in *Carpolestes nigridens* and *Carpolestes dubius*. On M^2 the shelf of the hypocone seems to be slightly broader in *Carpolestes nigridens* and *Carpolestes dubius*. While the M^3 is not known for *Carpolestes nigridens*, the M^3 of *Carpolestes simpsoni* is almost identical to that of *Carpolestes dubius*, differing only in molar area.

The hard palate of *Carpolestes simpsoni* (Fig. 3b) is very similar to that of *Carpodaptes cygneus* (Krause 1978). As in *Carpodaptes*, the palatines of *Carpolestes* are restricted to small, subtriangular horizontal laminae medial to the molars. Posteromedial to M^3, a process of each palatine forms a contact between the left and right palatines, a condition also seen in *Carpolestes dubius* (Jepsen 1930). At this contact, as in *Ignacius* (Kay et. al. 1992), the posterior margin of the palate is nearly straight and buttressed by a strong, rounded postpalatine torus with wings extending posteriorly onto the basicranium, a condition also seen in *Leptictis* (Novacek 1986). Similar to *Carpodaptes cygneus* (Krause 1978) and *Carpolestes dubius* (Rose 1975), the area anterior to the palatine contact is open, forming a large palatal fenestra. Unlike the condition described for *Carpodaptes*, this opening appears to be divided in *Carpolestes* by a thin blade of bone interpreted to be the vomer.

The I_1 is more laterally compressed and longer from base to tip than that of *Elphidotarsius* (Rose, 1975) as it is in *Carpolestes dubius* (Rose, 1975), the only other *Carpolestes* species for which the central incisor is known. I_1 of *Carpolestes*, as in *Carpodaptes*, does not have a basal cusp that arises from a lingual cingulum like that of *Elphidotarsius wightoni* (Fox, 1984). The ridge forming the lateral border of the dorsal face of I_1 is situated more mesially than in I_1 of *Elphidotarsius*, giving it a more central, lingually-oriented position. This is similar to the I_1 morphology of

Carpolestes dubius and *Carpodaptes* (Dorr, 1952; Krause, 1978). At the base of the crown, in both *Carpolestes dubius* and *Carpolestes simpsoni*, the lateral ridge meets a weak internal cingulum. I_1 of *Carpolestes* has a stronger dorsal curvature than that in *Carpodaptes* and *Elphidotarsius*, with the tip of the crown curving toward the midline in both *Carpodaptes* and *Carpolestes* but not in *Elphidotarsius*. Furthermore, the amount of curvature at the tip of the I_1 in *Carpolestes simpsoni* is about equivalent to that in *Carpodaptes cygneus*, with *Carpolestes dubius* having a much more pronounced curvature toward the midline.

The small single-rooted I_2 of *Carpolestes simpsoni* is often placed buccally in relation to the other anterior teeth, similar to the I_2 of *C. dubius*.

The canine of *Carpolestes simpsoni*, like that of *Carpolestes dubius*, is small and single rooted, with the enamel of the crown forming an anteriorly-elongate spur about half as long as the spur on I_2.

There is a gap between C_1 and P_4, but there is no P_3, which is present as a small, peg-like, single rooted tooth in *Carpolestes dubius* and *Carpolestes nigridens*. The blade-like P_4 is typical of the genus *Carpolestes* in being relatively large, high crowned, and having 8-9 apical cusps. It is, however, different from that of *Carpolestes nigridens* in being smaller in surface area and having a slightly lower crown (Fig. 7c-d).

As is typical for carpolestids, the paraconid of M_1 is situated directly anterior to the protoconid with both cusps being equally prominent. The M_1 area of *Carpolestes simpsoni*, which is used as a proxy for body size (Gingerich, 1977b, 1981; Gingerich et al., 1982; Conroy, 1987; see below), is smaller than for any earlier *Carpolestes* species. Unlike that of *Carpolestes nigridens*, the trigonid of M_1 of *Carpolestes simpsoni* is slightly higher than the talonid of P_4.

The dentary for *C. simpsoni* is shallower than that of earlier *C. nigridens*. As is true for all known Plesiadapiformes, the mandibular symphysis is unfused, and the posterior part of the mandible is similar to that of *Plesiadapis*. The coronoid process, like that of *Carpodaptes* (Rose, 1975), is high and broad. The angular process, like those of early *Plesiadapis*, *Phenacolemur* and *Carpodaptes*, is recurved and tapers posteriorly, forming a hook-like process. The condyle, like those of *Plesiadapis* and *Carpodaptes*, is roughly half-way between the angular process and the top of the coronoid process. It is, however, slightly higher (above the tooth row) than in *Carpodaptes*. The articular surface of the articular condyle covers the entire dorsal and posterior surfaces of the condyle, although the transverse diameter of the articular condyle (1.94-2.54 mm, $n = 2$) is larger than in *Carpodaptes* (1.6 mm, $n = 1$; Rose, 1975).

BODY MASS ESTIMATION

Body size is one of the most important factors influencing behavioral and ecological adaptations in mammals, and it can be used to infer aspects of the physiology and ecology of fossil mammals (Schmidt-Nielsen, 1984; Damuth and MacFadden, 1990). The distribution of size of Paleocene plesiadapiform Proprimates is different from that of modern primates (Fleagle, 1978), suggesting that they may have had somewhat different behaviors and ecology. While it is premature to carry interpretation of body size in Proprimates too far, it is interesting to have some understanding of the body sizes of species discussed here.

Body size is generally predicted from teeth (e.g., Gingerich et al., 1982; Conroy, 1987; Legendre, 1989) or long bones (e.g., Gingerich, 1990b). Different teeth and bones do not always scale isometrically with each other, which makes it important that size be predicted independently from as many different skeletal elements as possible. At present this is only possible to a limited extent in *Carpolestes*, but femur length and diameter yield an estimate close to that predicted from M_1 size, lending credibility to both.

A carpolestid femur (UM 101963) is known, with a well preserved diaphysis but lacking proximal and distal epiphyses. It was found in association with a skull of *Carpolestes simpsoni* in a limestone setting that commonly preserves skeletal associations. The femur is small, but otherwise closely resembles femora of *Plesiadapis*. Considering both its association and form, there is
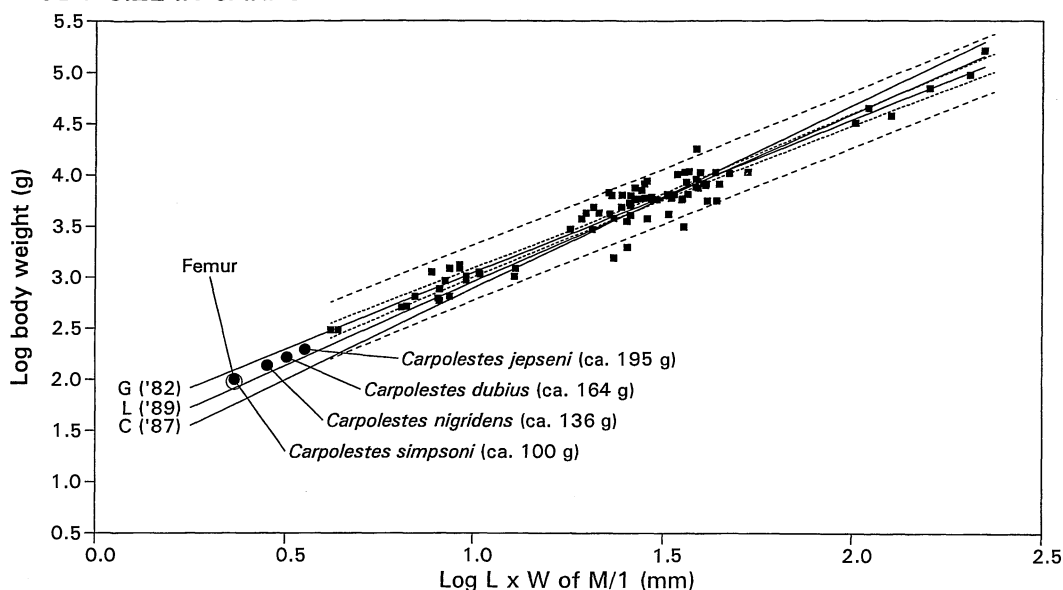
BODY SIZE IN *CARPOLESTES*

FIG. 8 — Estimation of body weight in the four species of *Carpolestes*. Solid squares show the relationship of body weight to tooth size in 83 male and female samples of 43 living primate species (Gingerich et al., 1982). Solid line is least-squares regression of log body weight on log crown area of M_1: narrow dotted lines are 95% confidence limits for the relationship and broader dashed lines are 95% prediction limits. Two alternative regression lines are shown, one from Conroy (1987) and the other from Legendre (1989). Body weight estimated from the midshaft diameter of a femur of *Carpolestes simpsoni* (UM 101963) falls between the Gingerich et al. (1982) and Legendre (1989) regressions (open circle; see text). Consequently, we averaged pairs of estimates of body weight calculated from the Gingerich et al. and Legendre regressions for all four carpolestid species (solid circles). These range from a high of 195 g in the earliest species *Carpolestes jepseni* to a low of about 100 g in the latest species *C. simpsoni*, indicating that body size decreased by approximately 50% in the evolution of this lineage.

little question that it represents *C. simpsoni*. Furthermore, because the skull it was found with has all permanent teeth erupted, it is possible to infer that the diaphysis is that of a virtually fully-grown young adult. Other proprimates (UM 87990, a nearly complete skeleton of *Plesiadapis cookei*, for example) have all teeth erupted but femoral epiphyses unfused when they reach adulthood.

It is possible, by comparing the femoral diaphysis to those of more complete proprimate femora, to estimate the length of UM 101963 in life as having been 27.5 mm. The diaphyseal midshaft measures 2.0 mm in diameter anteroposteriorly. These two numbers, substituted in the BODYMASS program of Gingerich (1990b), yield body weight estimates of 117 and 77 g, respectively, with a geometric mean of 95 g.

The mean log length × width of M_1 in *Carpolestes simpsoni* is 0.36. Substituting into the generalized-primate regression (*Tarsius* and other small insectivores removed) of Gingerich et al. (1982, p. 92) yields a body weight estimate of 122 g. Alternatively, substituting into the all-primate regression of Conroy (1987) yields an estimate of 57 g. Substituting into the generalized-primate regression of Legendre (1989) yields an intermediate estimate of 82 g. All three regression lines are plotted in Figure 8. The body weight of 95 g estimated from femur size is intermediate between the two estimates based on Gingerich et al. and the Legendre regressions. Thus we averaged body weight estimates based on these two regressions, yielding results in Figure 8: av-

CLARKS FORK BASIN *CARPOLESTES*

FIG. 9 — Pattern of change of M_1 size in late Paleocene *Carpolestes* from northwestern Wyoming. Measure plotted is natural logarithm of M_1 area. Solid circles and diamonds (type specimens) represent specimens of known meter level in the Polecat Bench-Sand Coulee stratigraphic section. Open circles and diamonds are specimens from nearby localities interpolated on the basis of faunal comparisons. Rates of change shown here, between paired samples and for the lineage as a whole, are well within the range of rates calculated for the same scales of time in other studies (see Fig. 13). Body mass, in grams, was estimated using mean M_1 area and the regression equations of Gingerich (1982) and Legendre (1989; see Fig. 8).

erage weights of about 195 g for *Carpolestes jepseni*, 164 g for *C. dubius*, 136 g for *C. nigridens*, and 100 g for *C. simpsoni*. Body size decreased by approximately 50% in the evolution of the *Carpolestes* lineage (see below).

TRENDS IN *CARPOLESTES* TOOTH SIZE AND SHAPE AND RATES OF EVOLUTION

Sediments in the Clarks Fork Basin provide a continuous and well-sampled late Paleocene stratigraphic section that has yielded many specimens of *Carpolestes* from many intervals. The *Carpolestes* lineage shows a trend of decreasing body size through time (Fig. 9). Upper and lower cheek teeth exhibit increasing amounts of change from back to front, with most change happening
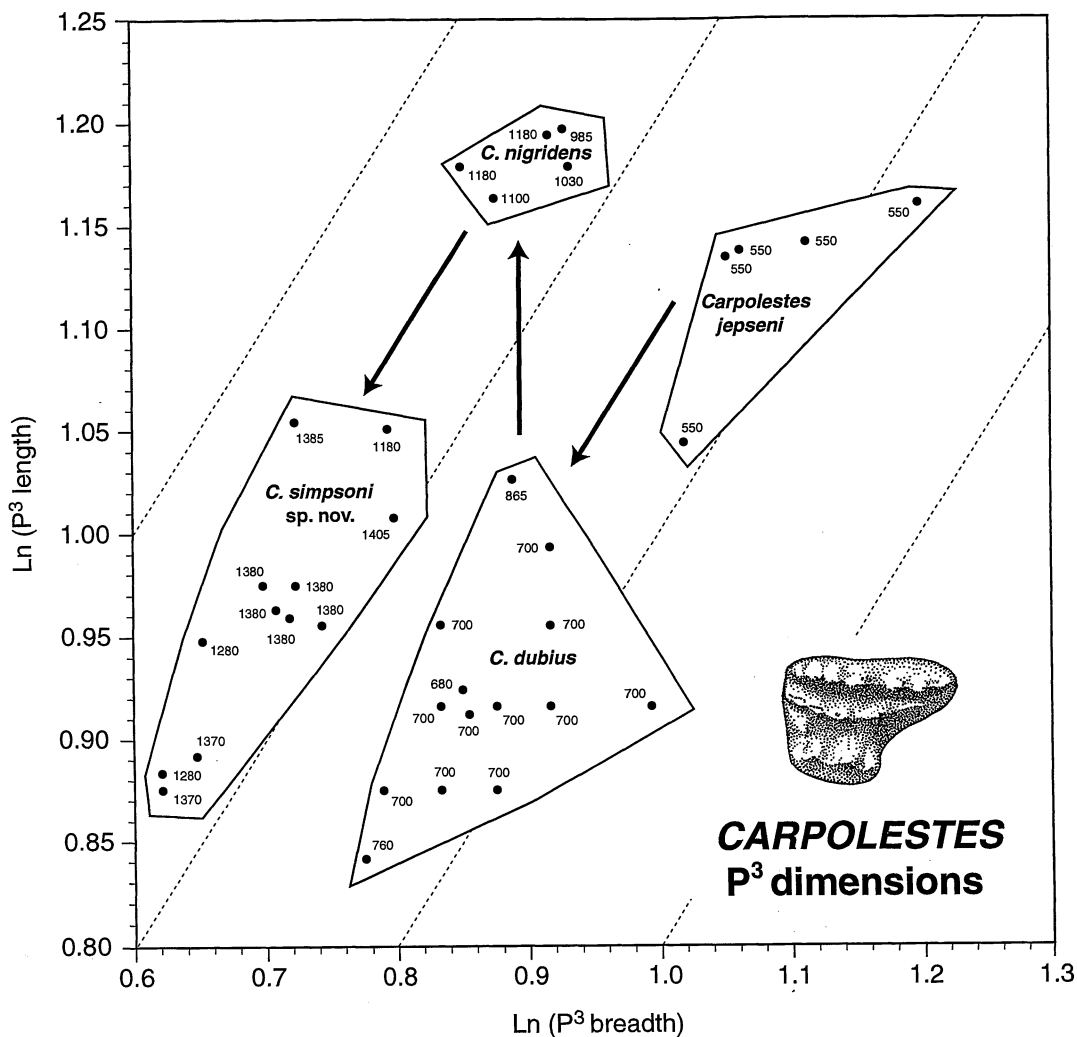
FIG. 10 — Evolution of P[3] shape in the four species of late Paleocene *Carpolestes* from northwestern Wyoming. Numbers within species clusters indicate stratigraphic levels for individual specimens. Dashed parallel lines are isoclines of constant log length-log breadth difference (specimens on the same isocline are isomorphs of similar shape). The four species are easily separated when size and shape are both considered. Arrows show hypothesized ancestor-descendent relationships. Note that new species *C. simpsoni* has a P[3] similar in shape to that of *C. nigridens*, but it differs in being significantly smaller.

in the more anterior premolars. P[3] is unique in that it appears to follow a different pattern through time than that of the other teeth (Figs. 10 and 11), including P$_4$ (Fig. 12) which shows a pattern similar to that of M$_1$. Change in P[3] is clearly influenced by something more than just a change in body size. As *Carpolestes jepseni* gave rise to *Carpolestes dubius*, P[3] remained a similar shape and decreased in size, following the overall trend as exhibited by the other teeth of *Carpolestes*. As *C. dubius* gave rise to *C. nigridens*, P[3] increased in size and changed shape, deviating from the overall trend of decreasing body size. Finally, as *C. nigridens* gave rise to *C. simpsoni*, P[3] retained a similar shape and decreased in size, again following the overall trend of decreasing body size.

In order to get some idea of rates of change within the *Carpolestes* lineage, the mean length and mean width of M$_1$ were determined for each stratigraphic level. Rates were then calculated be-
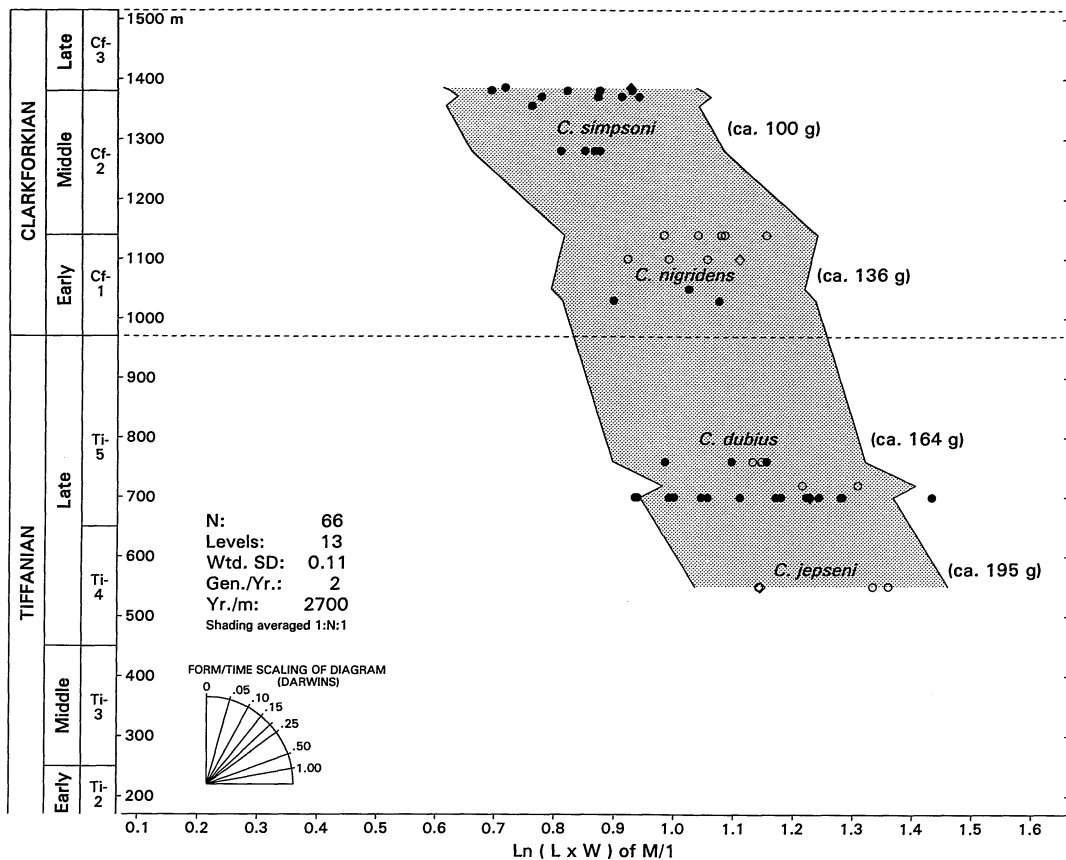
CLARKS FORK BASIN *CARPOLESTES*

FIG. 11 — Pattern of change of P3 size in late Paleocene *Carpolestes* from northwestern Wyoming. Measure plotted is natural logarithm of P3 area. Solid circles and diamonds (type specimens) represent specimens of known meter level in the Polecat Bench-Sand Coulee stratigraphic section. Open circles and diamonds are specimens from nearby localities interpolated on the basis of faunal comparisons. Rates of change shown here, between paired samples and for the lineage as a whole, are well within the range of rates calculated for the same scales of time in other studies.

tween each pair of mean lengths or mean widths representing a range of different time scales (Gingerich, 1993, 1996). The *Carpolestes* lineage decreased in size over time from the middle Tiffanian through the middle Clarkforkian land-mammal ages, with an average base rate of change of tooth size derived from M_1 area on the order of about 0.002 standard deviations per generation and a temporal scaling slope of -0.52 that is little different from expectation for a random walk (Fig. 13).

BIOSTRATIGRAPHY

The late Paleocene of North America includes the Tiffanian and Clarkforkian land-mammal ages. The Tiffanian is recognized as the time between the first appearance of *Plesiadapis* and the first appearance of Rodentia (Archibald et al., 1987). The Clarkforkian is recognized as the time between the first appearance of Rodentia and the first appearance of Artiodactyla (Archibald et al., 1987). The Tiffanian is subdivided into five faunal zones based on different time-successive spe-
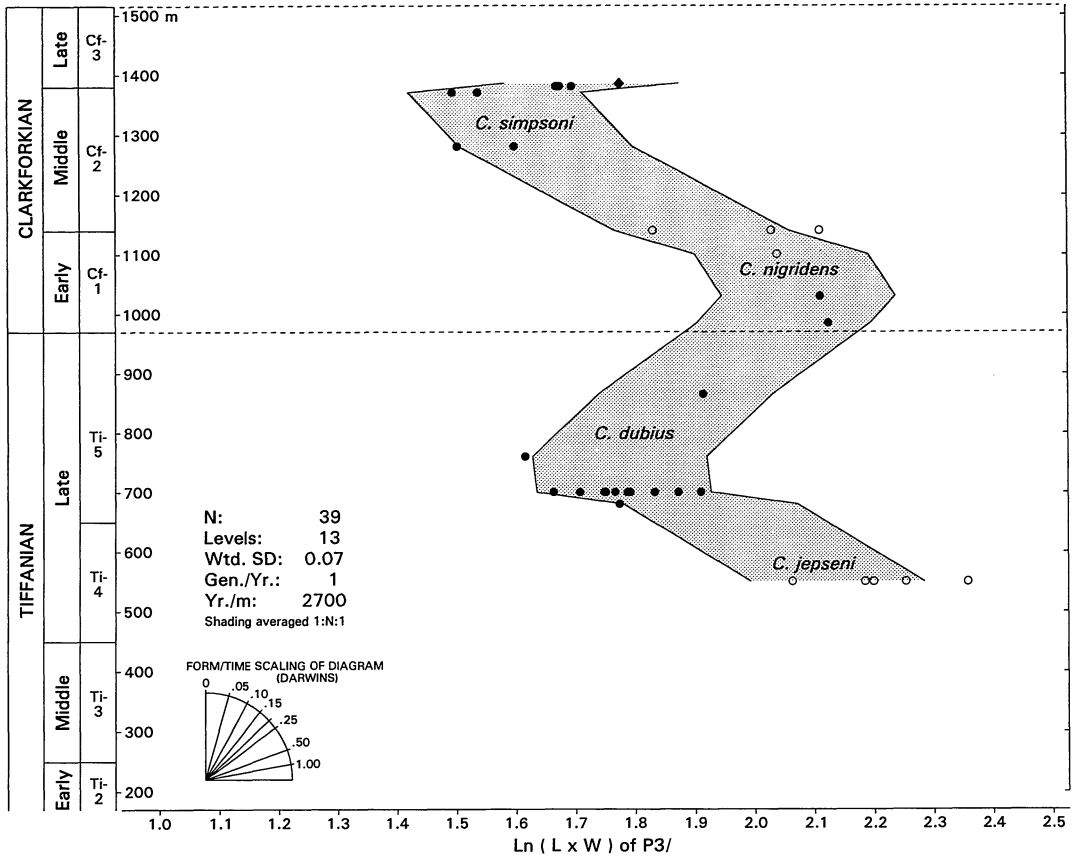
CLARKS FORK BASIN *CARPOLESTES*
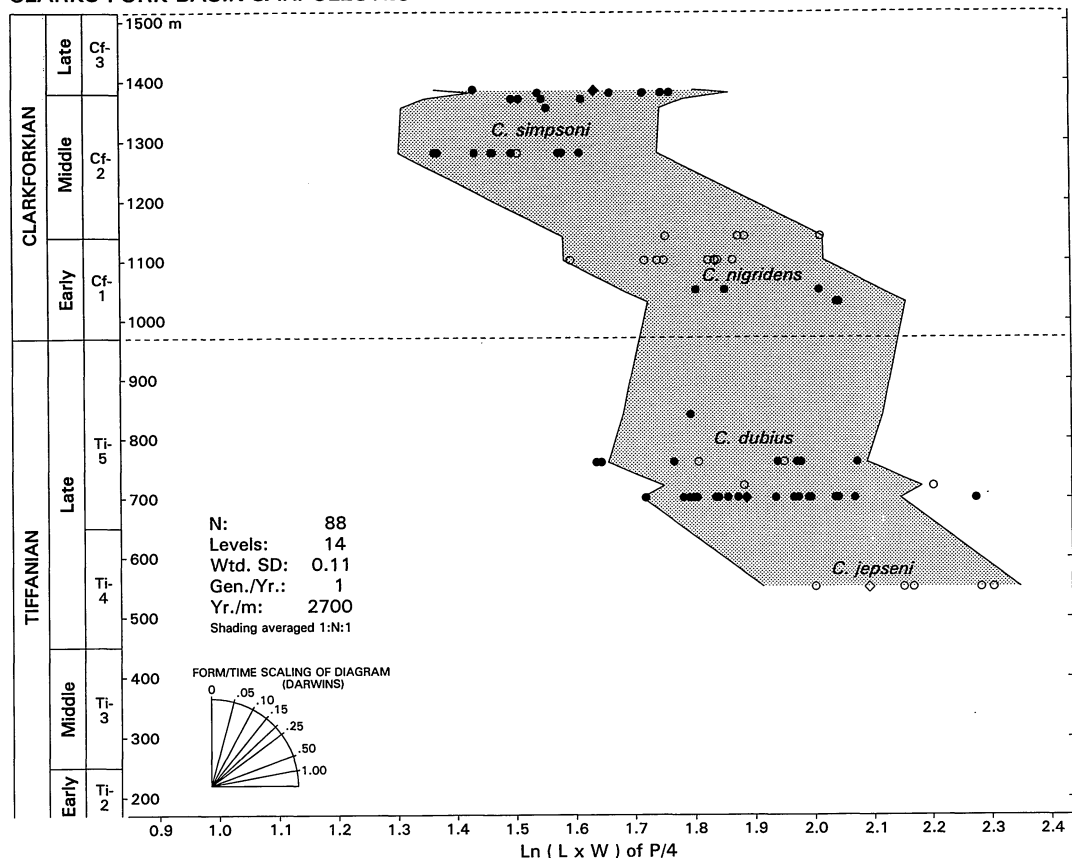
FIG. 12 — Pattern of change of P4 size in late Paleocene *Carpolestes* from northwestern Wyoming. Measure plotted is natural logarithm of P4 area. Solid circles and diamonds (type specimens) represent specimens of known meter level in the Polecat Bench-Sand Coulee stratigraphic section. Open circles and diamonds are specimens from nearby localities interpolated on the basis of faunal comparisons. Rates of change shown here, between paired samples and for the lineage as a whole, are well within the range of rates calculated for the same scales of time in other studies.

cies of *Plesiadapis* (Gingerich, 1975, 1976). The Clarkforkian is subdivided into three faunal zones with the first two defined by the first appearance of *Plesiadapis gingerichi* and *Plesiadapis cookei* respectively, and the third by the absence of a large species of *Plesiadapis* and abundance of the condylarths *Phenacodus* and *Ectocion* (Rose, 1980, 1981; Gingerich, 1983).

Carpolestidae have long been thought to be useful biostratigraphic indicators of the terrestrial upper Paleocene of North America (Rose, 1977, 1981; Gingerich, 1980). However, Fox (1984) questioned this biostratigraphic utility because of the co-occurrence of *Elphidotarsius* and *Carpodaptes* in the Paskapoo Formation of central Alberta. More detailed study of all North American carpolestid specimens should help to clarify these issues and allow for improved chronological resolution for the late Paleocene.

In this study we have chosen to restrict our analysis to species of North American *Carpolestes*. Results demonstrate that species of *Carpolestes* are useful biostratigraphic tools for subdividing the late Tiffanian and Clarkforkian land-mammal ages. *"Carpodaptes" jepseni* is known only from a single locality whose fauna includes *Plesiadapis churchilli* and is late Tiffanian (Ti-4) in

Log₁₀ Evolutionary Rate (haldanes : std.dev./gen.) vs Log₁₀ Time Interval (generations [0.50 yr.])

Carpolestes

Dir. change
Random
Stasis (Dyn. equil.)

N = 10
Residuals
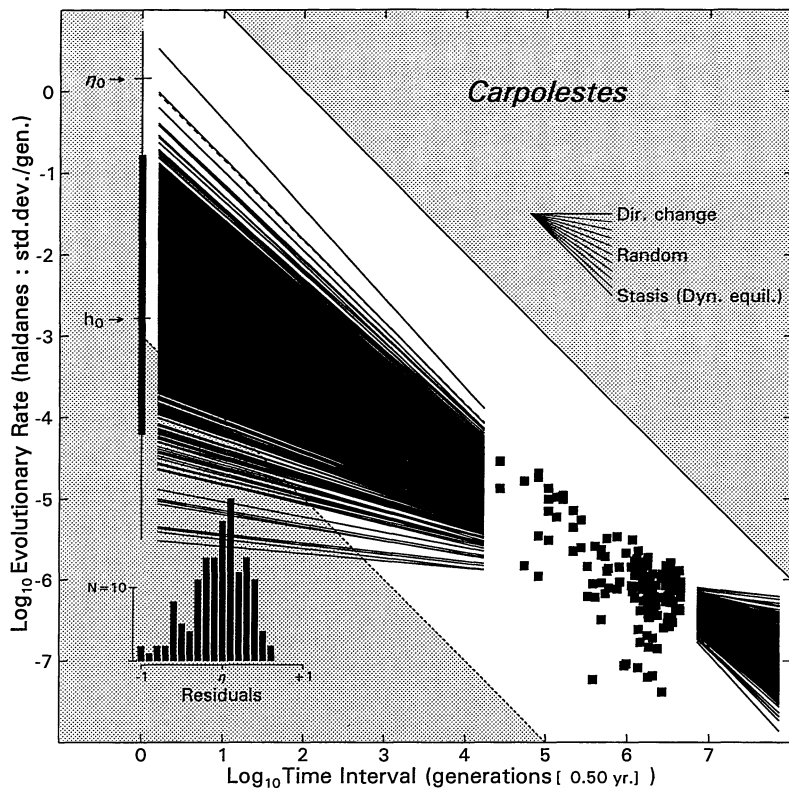
Carpolestes		M/1 - Clarks Fork Basin			Bloch & Gingerich (1998)	
Total rates	156	MAX. LIKELIHOOD (M.Abs.Dev.: 0.283)				
NONZERO RATES	155		Minimum	Median	Maximum	Fractal D
			(0.025)	(0.500)	(0.975)	1.520
Min. log int.	4.431					
Max. log int.	6.654	SLOPE		-0.520		Interpret.
MEDIAN LOG INT.	6.241	CI*	-0.291	-0.624	-0.850	R
Min. log rate	-7.386	T. INTERCEPT		0.164		Theoretical η_0
Max. log rate	-4.541	CI*	0.058	0.165	0.214	1.4591
MEDIAN LOG RATE	-6.035	C. INTERCEPT		-2.780		Calculated h_0
POSITIVE rates	21	CI*	-4.206	-2.133	-0.780	0.0017
Med. log int.	5.364	TEST POINT (Log int. = 0.000)				
Med. log rate	-5.648	CI*	-4.206	-2.133	-0.780	
NEGATIVE rates	134	PI*	-4.482	-2.220	-0.606	
Med. log int.	6.261	*Confidence and prediction		N = 155		
Med. log rate	-6.076	intervals, bootstrapped with		B = 1000		

HALDANE2.EXE P. Gingerich University of Michigan 09-07-1998 11:18:09 Run time: 00:13:42

FIG. 13 — Log rate versus log interval [LRI] distribution for 155 non-zero rates of change in the *Carpolestes pseni-C. simpsoni* lineage. Rates of change are calculated in phenotypic standard deviations per generations (haldanes) for intervals between all pairs of specimens. Intervals range from $10^{4.431} \approx 26{,}915$ to $10^{6.654} \approx 4{,}508{,}167$ generations. A total of 21 rates are positive and 134 are negative, reflecting the overall decrease in size of this lineage. The temporal scaling slope of the LRI distribution is -0.52, meaning that the fractal dimension of the original time series is 1.520. Bootstrapped 95% confidence interval for the slope ranges from -0.292 to -0.868, which excludes purely directional change (slope of -0.0), includes random change or a random combination of directional change and stasis (slope of -0.5), and excludes stasis (slope of -1.0). Null expectation of random change cannot be rejected on this evidence, and interpretation is thus 'random' (*R*). Theoretical base rate η_0 is $10^{0.164} \approx 1.4591$ haldanes, which falls within the available sample of comparable base rates (Gingerich, 1996). The calculated base rate h_0, based on the location of the sample rates and their temporal scaling slope, is $10^{-2.780} \approx 0.002$ haldanes: the observed change can be explained by directional and random change at the rate of only about 0.002 standard deviations per generation on a generational time scale.
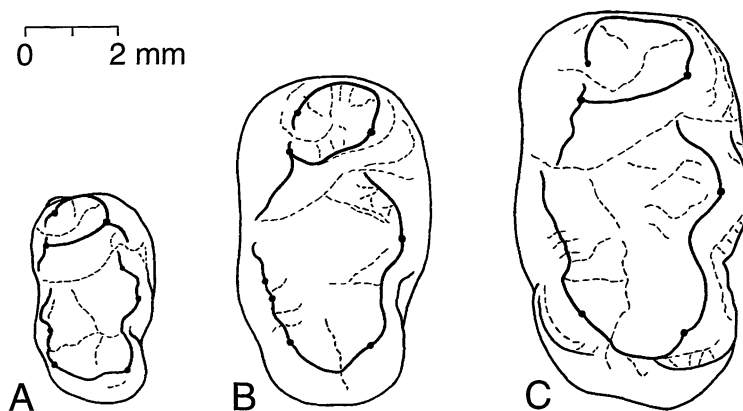
FIG. 14 — Drawing of M₃s of *Plesiadapis* species from the Paint Creek locality (SC-143) in northwestern Wyoming. A, small *P. dubius* (UM 67244); B, large *P. gingerichi* (UM 104033); and C, large *P. cookei* (UM 71016), all in occlusal view. Three distinct species of *Plesiadapis* appear to be represented at Paint Creek. *P. gingerichi* and *P. cookei* are generally considered to be ancestor and descendant species indicative of Clarkforkian faunal zones Cf-1 and Cf-2, respectively. On this evidence the Paint Creek locality either (1) samples both large species and both faunal zones, (2) samples a highly variable transitional population, or (3) samples a unique basin-margin environment in which both large species co-occurred. A similar overlap of *Carpolestes nigridens* and *C. simpsoni* is suggested by specimens reported here (see Fig. 15 and text). Scale is in mm.

age. *Carpolestes dubius*, as now known, is restricted to the Tiffanian Ti-5 faunal zone, co-occurring with *Plesiadapis fodinatus* and *Plesiadapis simonsi*. *Carpolestes nigridens* is restricted to the Cf-1 faunal zone, co-occurring with *Plesiadapis dubius* and *Plesiadapis gingerichi*. *Carpolestes simpsoni* is almost completely restricted to the Cf-2 faunal zone, co-occurring with *Plesiadapis dubius* and *Plesiadapis cookei*.

An exception occurs at University of Michigan locality SC-29. SC-29, which yielded the type specimen of *Carpolestes simpsoni*, is in the earliest Cf-3 faunal zone (recognized by an absence of *Plesiadapis cookei*). It is possible, because SC-29 is the only Cf-3 locality known to have *Carpolestes*, that it actually belongs to the Cf-2 faunal zone and *Plesiadapis cookei* is present at this locality but has not yet been found. However, the relatively large sample of Paleocene mammals from the locality and the fact that *Plesiadapis* is otherwise a fairly common part of most Cf-2 faunas seems to indicate that this is not the case (but a Cf-2 diagnosis of the SC-29 fauna cannot be completely ruled out). Nearly complete restriction of *C. simpsoni* to Cf-2 makes it a useful biostratigraphic tool, however the presence of *C. simpsoni* in one possible Cf-3 locality indicates that its presence alone is not yet enough to resolve a fauna to a precise biostratigraphic zone.

One of the most productive Clarkforkian localities in the Clarks Fork Basin is the "Paint Creek locality", SC-143. The stratigraphic level of SC-143 relative to others in the Clarks Fork Basin has never been established because of its position on the western margin of the basin and its isolation from other Clarks Fork Basin localities. Due to poor provenience data for some specimens, Jepsen (1930) believed that this locality was of Wasatchian age, while more recently Gingerich (1976) and Rose (1981) demonstrated that SC-143 is Clarkforkian, diagnosed by the presence of Cf-2 *Plesiadapis cookei*. A new M₃ found by G. F. Gunnell in 1998 (UM 104033; L = 7.71 mm, W = 4.52 mm) is larger than that of *Plesiadapis dubius* (L = 4.55-5.00, W = 2.70; Rose, 1981) and smaller than that of *Plesiadapis cookei* (L = 8.50-10.00, W = 4.75-5.55; Rose, 1981), and is very similar in size to that of *Plesiadapis gingerichi* (L = 7.40, W = 4.35-4.60; Rose, 1981). Together with other specimens from SC-143 (UM 67244, 71016), UM 104033 clearly demonstrates that *Plesiadapis dubius*, *Plesiadapis gingerichi*, and *Plesiadapis cookei* are all found at Paint Creek (Fig. 14).
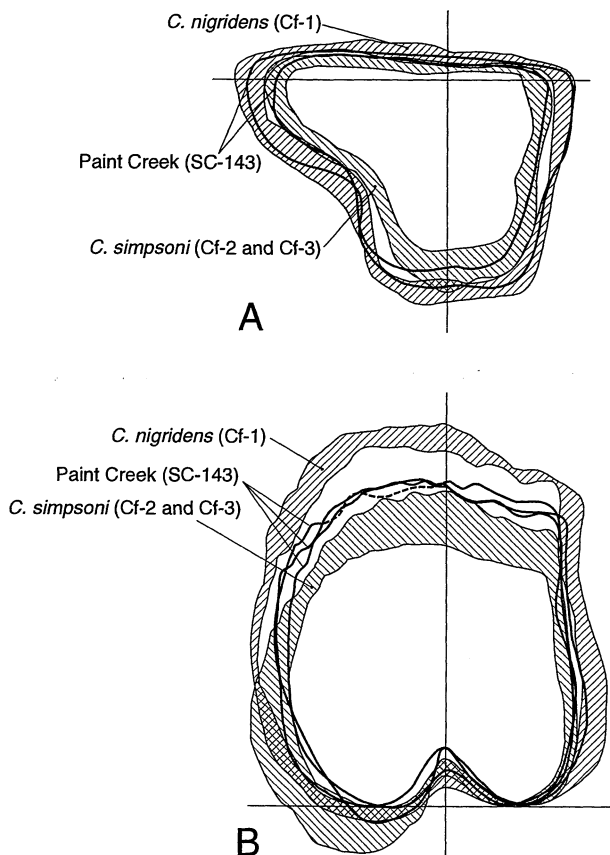
FIG. 15 — Camera lucida outlines of P^3 (A) and P$_4$ (B) for *Carpolestes* from the Paint Creek locality (SC143) in northwestern Wyoming (heavy lines). Paint Creek specimens are shown in relation to other *C. nigridens* and *C. simpsoni* (hatched; see Fig. 7). Note that Paint Creek P^{3}s and P$_4$s are intermediate in most respects between early Clarkforkian *C. nigridens* and middle Clarkforkian *C. simpsoni*. On this evidence the Paint Creek locality either (1) samples both species and both faunal zones, (2) samples a highly variable transitional population, or (3) samples a unique basin-margin environment in which both species co-occur. Distinguishing these possibilities will require further investigation.

It is surprising that SC-143 would have both Cf-1 and Cf-2 faunal zones represented given its small size and seemingly continuous deposition. However, the *Carpolestes* fauna at SC-143 further supports this interpretation in that it seems to have *C. simpsoni* and *C. nigridens* co-occurring. The evidence for this co-occurrence (Figs. 10 and 15a) is the presence of a single P^3 that seems to represent the morphology of *C. simpsoni*. All of the other specimens known from the locality ($n =$ 15) are those of *C. nigridens*.

One alternative explanation for the co-occurrence of *P. gingerichi-C. cookei* and *C. nigridens-C. simpsoni* is that these are highly-variable transitional populations. In support of this explanation one P$_4$ of *Carpolestes* seems to represent an intermediate morphology (Fig. 15b), however no such evidence exists for any of the *Plesiadapis* specimens. Another possibility is that, on the basin margin, we are sampling from a slightly different environment in which otherwise ancestral-descendent species co-occur, an argument that has been made by Gunnell (1997) studying the origin of genera at the Wasatchian-Bridgerian boundary in the Green River Basin. This idea is reinforced by the fact that paleosols at SC-143 are of greater maturity than contemporary deposits in the basin

depocenter, indicative of a high floodplain with better-drained sediments. Whatever the case, it seems likely that SC-143 is at or near the boundary between the Cf-1 and Cf-2 faunal zones.

DISCUSSION

New specimens of *Carpolestes*, more than twice the number known when the genus was last revised (Rose, 1975), add considerably to our knowledge of this latest-occurring North American genus of Carpolestidae. *Carpolestes simpsoni* from Clarkforkian faunal zone Cf-2 and earliest Cf-3 of the Clarks Fork Basin can be distinguished from earlier species by having a dental formula of 3.0.3.3/2.1.1.3 with P_3 absent, smaller body size, and P^3 of unique shape and size. Specimens of *Carpolestes simpsoni* show that it had three upper incisors, a primitive condition shared by other Carpolestidae but not known in other plesiadapiformes. *Carpolestes simpsoni* is most closely related to and probably evolved from *Carpolestes nigridens* of Clarkforkian faunal zone Cf-1 in the Clarks Fork Basin, Wyoming, and Bear Creek, Montana.

Contrary to Rose et al. (1993) and Beard and Wang (1995), who suggested that the I^1 of *Carpolestes* illustrated by Gingerich (1987) was similar to that of *Tinimomys* and *Chronolestes* respectively, the I^1 of *Carpolestes* is very similar to that of *Carpodaptes* in having a strong laterocone and a double posterocone. The palate of *Carpolestes* has large fenestrae, a primitive character probably shared by Carpolestidae but not yet known in other plesiadapiformes.

Body masses for *Carpolestes* species were calculated using measured M_1 area and predictive equations of Gingerich et al. (1982) and Legendre (1989). Averaged body weight estimates based on these two regressions yield a result that is close to estimates from femur length and diameter (Gingerich, 1990b). Results indicate that *C. jepseni* weighed about 195 grams, *C. dubius* 164 grams, *C. nigridens* 136 grams and *C. simpsoni* 100 grams. All of the *Carpolestes* species have body weights well below "Kay's threshold" of 500 grams (Kay, 1975; Gingerich, 1981) indicating, in support of Biknevicius (1986; see above), that *Carpolestes* was not folivorous.

The *Carpolestes* lineage decreased in size, as illustrated by M_1 area, from the late Tiffanian through the middle Clarkforkian. P^3, however, followed a different trend of changing shape as well as size. It is possible that some dietary shift occurred at this time with the migration of rodents into North America and subsequent competition between non-paromomyid plesiadapoids, such as carpolestids, and rodents (Maas et al., 1988), but this is far from proven. The *Carpolestes* lineage decreased in size over time from the middle Tiffanian through middle Clarkforkian land mammal ages, with an average base rate of change of tooth size derived from M_1 area of about 0.002 standard deviations per generation, and a temporal scaling slope of -0.52 that is little different from expectation for a random walk.

Species of *Carpolestes* are useful biostratigraphic tools in subdividing the late Tiffanian and Clarkforkian land-mammal ages. *"Carpodaptes" jepseni* occurs with *Plesiadapis churchilli* in the late Tiffanian (Ti-4). *Carpolestes dubius* occurs in the Tiffanian Ti-5 faunal zone with *Plesiadapis simonsi*. *Carpolestes nigridens* is restricted to the Cf-1 faunal zone, co-occurring with *Plesiadapis gingerichi*. Nearly complete restriction of *C. simpsoni* to Cf-2, with *Plesiadapis cookei*, makes it a useful biostratigraphic indicator, however the presence of *C. simpsoni* in one possible Cf-3 locality indicates that its presence alone is not yet enough to resolve a fauna to a precise biostratigraphic zone.

ACKNOWLEDGMENTS

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APPENDIX

TABLE A1 — Dimensions of premaxillary teeth of *Carpolestes simpsoni*. Abbreviations: *L*, crown length; *W*, crown width; *H*, crown height. Measurements are in mm.

Specimen	I¹			I²			I³		
	L	W	H	L	W	H	L	W	H
UM 71002	—	—	—	1.38	0.84	1.73	0.84	0.54	1.32
UM 77583	—	—	—	1.52	0.88	—	—	—	—
UM 82688	1.84	1.16	2.32	1.44	0.77	2.08	—	—	—
UM 85177	1.96	1.27	2.48	1.58	0.83	1.84	1.09	0.56	1.44
UM 85178	1.81	1.12	2.35	1.50	0.88	2.13	0.94	0.57	1.30
UM 86273	1.84	1.10	—	1.49	0.84	2.18	0.94	0.65	1.46
UM 101966	1.82	1.12	2.25	—	—	—	—	—	—
UM 101994	1.83	1.19	2.29	—	—	—	—	—	—

TABLE A2 — Dimensions of maxillary teeth of *Carpolestes simpsoni*. Abbreviations as in Table A1. Measurements are in mm.

Specimen	P²		P³		P⁴		M¹		M²		M³	
	L	W	L	W	L	W	L	W	L	W	L	W
UM 71002	1.28	0.66	2.58	1.92	—	—	—	—	—	—	—	—
UM 77583	—	—	—	—	—	—	1.50	2.10	—	—	—	—
UM 77583	—	—	—	—	2.08	1.97	—	—	—	—	—	—
UM 77586	—	—	—	—	2.15	—	—	—	—	—	—	—
UM 77586	—	—	—	2.31	—	—	—	—	—	—	—	—
UM 81693	—	—	2.40	1.86	—	—	—	—	—	—	—	—
UM 82670	1.26	0.73	2.61	2.05	1.96	1.70	1.35	2.09	1.28	2.02	1.37	1.79
UM 82688	1.23	0.74	2.60	2.10	1.97	1.64	1.45	2.02	1.44	1.87	1.46	1.76
UM 85177	1.23	0.73	2.65	2.01	1.99	1.88	1.52	2.16	1.40	1.98	1.53	1.80
UM 85178	—	—	2.62	2.03	2.06	1.78	1.49	1.90	—	—	—	—
UM 85179	—	—	2.78	—	—	—	—	—	—	—	—	—
UM 86273	1.23	0.72	2.87	2.06	1.90	1.63	1.50	1.86	1.44	1.90	1.53	1.80
UM 101923	—	—	2.74	2.22	2.08	1.89	1.57	2.13	1.50	1.99	1.45	1.87
UM 101963	—	—	2.65	2.06	2.01	1.74	1.50	2.10	1.46	1.90	1.50	1.86
UM 101965	—	—	—	—	—	—	1.50	1.96	—	—	—	—
UM 101967	—	—	—	—	—	—	—	—	1.40	1.85	—	—
UM 101968	—	—	—	—	—	—	—	—	1.40	1.88	—	—
UM 101971	—	—	—	—	—	—	—	—	1.45	1.79	—	—
UM 101972	—	—	2.42	1.86	—	—	—	—	—	—	—	—
UM 101974	—	—	2.44	1.90	—	—	—	—	—	—	—	—
YPM-PU 19543	—	—	2.80	2.30	—	—	—	—	—	—	—	—

TABLE A3 — Dimensions of anterior mandibular teeth of *Carpolestes simpsoni*. Abbreviations as in Table A1. Measurements are in mm.

Specimen	I_1 L	W	H	I_2 L	W	C_1 L	W
UM 82615	2.00	1.12	—	1.42	0.72	0.91	0.60
UM 82672	2.02	1.10	5.85	1.50	0.80	—	—
UM 82673	—	—	—	—	—	0.85	0.56
UM 85178	2.12	1.09	—	1.58	0.87	0.91	0.55
UM 86273	2.19	0.96	5.06	1.61	0.77	1.04	0.64

TABLE A4 — Dimensions of posterior mandibular teeth of *Carpolestes simpsoni*. Abbreviations as in Table A1. Measurements are in mm.

Specimen	P_4 L	W	M_1 L	W	M_2 L	W	M_3 L	W	MD
UM 65033	—	—	1.79	1.22	—	—	—	—	—
UM 65254	2.91	1.44	1.58	1.30	1.31	1.24	—	—	—
UM 66909	3.04	1.56	1.79	1.20	—	—	—	—	4.94
UM 69338	2.80	1.76	—	—	—	—	—	—	—
UM 71003	3.06	1.46	—	—	—	—	—	—	—
UM 71004	3.18	1.52	1.78	1.34	1.58	1.36	—	—	—
UM 71005	2.94	1.52	1.79	1.26	—	—	—	—	—
UM 71644	2.76	1.57	—	—	—	—	—	—	—
UM 71778	3.08	1.58	1.82	1.29	—	—	—	—	—
UM 73566	2.78	1.51	—	—	—	—	—	—	—
UM 75460	3.19	1.57	—	—	—	—	—	—	4.57
UM 77024	—	—	1.85	1.30	1.54	1.23	—	—	5.16
UM 77561	—	—	1.66	—	—	—	—	—	—
UM 77586	2.82	1.60	—	—	—	—	—	—	—
UM 82615	3.22	1.73	1.64	1.39	1.44	1.38	2.21	1.36	4.56
UM 82672	3.12	1.84	1.84	1.38	1.41	1.33	2.02	1.26	—
UM 82673	3.20	1.82	1.77	1.36	1.44	1.29	2.10	1.26	4.86
UM 85177	—	—	1.66	1.21	1.42	1.36	2.02	1.35	5.02
UM 85178	3.01	1.75	—	—	—	—	—	—	4.63
UM 85179	2.98	—	1.80	—	—	—	2.02	—	4.62
UM 86273	2.90	1.77	1.76	1.44	1.58	1.36	2.18	1.34	4.50
UM 95859	2.87	1.64	1.85	1.35	—	—	—	—	—
UM 95860	3.03	1.66	—	—	—	—	—	—	4.64
UM 98084	2.94	1.54	—	—	—	—	—	—	—
UM 98199	—	—	1.61	1.23	1.54	1.22	—	—	—
UM 98437	—	—	1.79	1.34	—	—	2.20	1.31	5.17
UM 98443	—	—	1.76	1.46	—	—	—	—	—
UM 98444	2.76	1.62	—	—	—	—	—	—	—
UM 98450	—	—	—	—	—	—	2.26	1.33	5.16
UM 101780	2.92	1.60	—	—	—	—	—	—	—
UM 101923	3.05	1.64	1.84	1.32	1.49	1.31	2.10	1.28	5.08
UM 101964	2.84	1.39	—	—	—	—	—	—	—
UM 101969	—	—	1.68	—	—	—	—	—	—
UM 101970	2.69	1.46	—	—	—	—	—	—	—
UM 101973	—	—	—	—	—	—	2.04	1.20	—
UM 101975	2.94	1.47	—	—	—	—	—	—	—