

STRATOCCLADISTIC ANALYSIS OF PALEOCENE CARPOLESTIDAE (MAMMALIA, PLESIADAPIFORMES) WITH DESCRIPTION OF A NEW LATE TIFFANIAN GENUS

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ABSTRACT—“*Carpodaptes*” *jepseni* is a morphologic intermediate between *Carpodaptes* and *Carpolestes*, with the number and position of cusps on p4 more consistent with placement in *Carpodaptes* but relative size of p4 more like *Carpolestes*. The type and only previously known specimen of “*C.*” *jepseni*, a partial dentary with p4–m2, is from Divide Quarry (Tiffanian Land-Mammal Age) in the Fort Union Formation of the Bighorn Basin, Wyoming. New specimens of “*C.*” *jepseni* from Divide Quarry include a nearly complete dentary with p4–m3 and alveoli for all anterior teeth, and the first known upper dentitions with P1–M2 and an alveolus for C1. Specimens of *Carpodaptes cygneus* are also described from Divide Quarry, demonstrating the occurrence of two distinct carpolestid species at the same locality.

Stratocladistic analysis of the thirteen known carpolestid species, using thirty-two morphologic characters and stratigraphic order, produced eight most-parsimonious phylogenetic trees associated with a single cladogram. The topology of the cladogram generated using stratocladistics is identical to that of the single most-parsimonious cladogram from cladistic analysis of the same morphologic data, but stratocladistics allows greater resolution than cladistics at the level of phylogenetic trees. New specimens demonstrate extreme shortening of the anterior jaw of *C. jepseni*, a derived state not present in other carpolestids. This suggests that *C. jepseni* occupies a side-branch close to, but not at, the ancestry of the *Carpolestes* clade (an ancestor-descendant lineage composed of the sequence *C. dubius*, *C. nigridentis*, and *C. simpsoni*, in that order). “*C.*” *jepseni* is here placed in a new genus, *Carpomegodon*.

INTRODUCTION

Carpolestidae are small, primate-like mammals that first appeared in the early Paleocene (Torrejonian North American Land-Mammal Age (NALMA)) of North America and survived through at least the late Paleocene (Clarkforkian NALMA) of North America and possibly into the early Eocene (Bumbanian Asian Land-Mammal Age (ALMA)) of Asia (e.g., Russell and Zhai, 1987; Beard and Wang, 1995; Ting, 1998; see also Beard and Dawson, 1999). The twelve North American species are classified in three genera: *Elphidotarsius*, *Carpodaptes*, and *Carpolestes*. These genera form, broadly, a morphologic sequence of increasing hypertrophy and complexity of posterior premolars (p4 and P3–4). The stratigraphic distribution of carpolestids indicates that these three genera were essentially sequential in time (with short temporal overlap for successive genera): *Elphidotarsius* is present in the Torrejonian through middle Tiffanian NALMA, *Carpodaptes* throughout most of the Tiffanian, and *Carpolestes* is restricted to the late Tiffanian and Clarkforkian (Rose, 1975, 1977; Krause, 1978; Gingerich, 1980a; Fox, 1984, 1994; Bloch and Gingerich, 1998). Two genera have been described as carpolestids from the Bumbanian ALMA of China: *Chronolestes* and *Carpocristes* (Beard and Wang, 1995). While *Carpocristes oriens* is an undoubted carpolestid probably related to North American “*Carpodaptes*” *hobackensis*, *Chronolestes oriens* is a basal plesiadapoid outside the carpolestid clade (Bloch and Fisher, 1996; Silcox et al., 2001).

The northern Bighorn Basin and adjacent Clarks Fork Basin of northwestern Wyoming, have produced the greatest number and diversity of carpolestids found anywhere, spanning almost the entire temporal range of the family. At least seven of the twelve known North American species, ranging in age from the late Torrejonian through the Clarkforkian, are known from this region: *Elphidotarsius florencae*, *Carpodaptes hazelae*, *Carpodaptes cygneus*, “*Carpodaptes*” *jepseni*, *Carpolestes dubius*,

Carpolestes nigridentis, and *Carpolestes simpsoni* (Rose, 1975; Bloch and Gingerich, 1998).

The Paleocene in the Clarks Fork Basin of northwestern Wyoming is represented primarily by the Fort Union Formation. This sequence, which reaches a thickness of about 1,515 m along the southern section of Polecat Bench in the eastern part of the Clarks Fork Basin (Gingerich, 2000), is predominantly fluvial sandstones and drab mudstones. It overlies the Cretaceous Lance Formation and underlies the latest Paleocene to early Eocene Willwood Formation. Vertebrate fossils are sometimes concentrated at the base of channel sandstones and in proximal floodplain sediments (Alexander, 1982). Such concentrations are not common and may be separated by thick stratigraphic sequences that are poorly fossiliferous. Five fossil localities of this kind are known from the Fort Union Formation of the Clarks Fork and northern Bighorn basins (Fig. 1): Puercan Mantua Quarry (Pu-1); Torrejonian Rock Bench Quarry (To-4); and Tiffanian Cedar Point Quarry (Ti-3), Divide Quarry (Ti-4), and Princeton Quarry (Ti-5) (Gingerich, 1980b; Rose, 1981; Gunnell, 1989).

Fossil vertebrates at Divide Quarry are concentrated within a clay-gall conglomerate located at the base of a large channel sandstone (Bartels, 1987). Divide Quarry was first discovered by R. V. Witter and A. C. Silberling who were employed by Princeton University in the late 1940s (Gingerich, 1980b). In the 1980s this quarry was re-opened by University of Michigan field parties and has subsequently yielded over 220 new fossil mammal specimens.

Rose (1975) named a new species of carpolestid, *Carpodaptes jepseni*, from Divide Quarry based on a dentary with p4–m2. Rose regarded generic placement of *C. jepseni* as difficult because it resembled both *Carpodaptes* and *Carpolestes*. He included *C. jepseni* in *Carpodaptes* but noted that the morphologic and stratigraphic intermediacy between *Carpodaptes* and *Carpolestes* indicated that *C. jepseni* might be at or near the ancestry of *Carpolestes*. A new nearly complete lower dentition

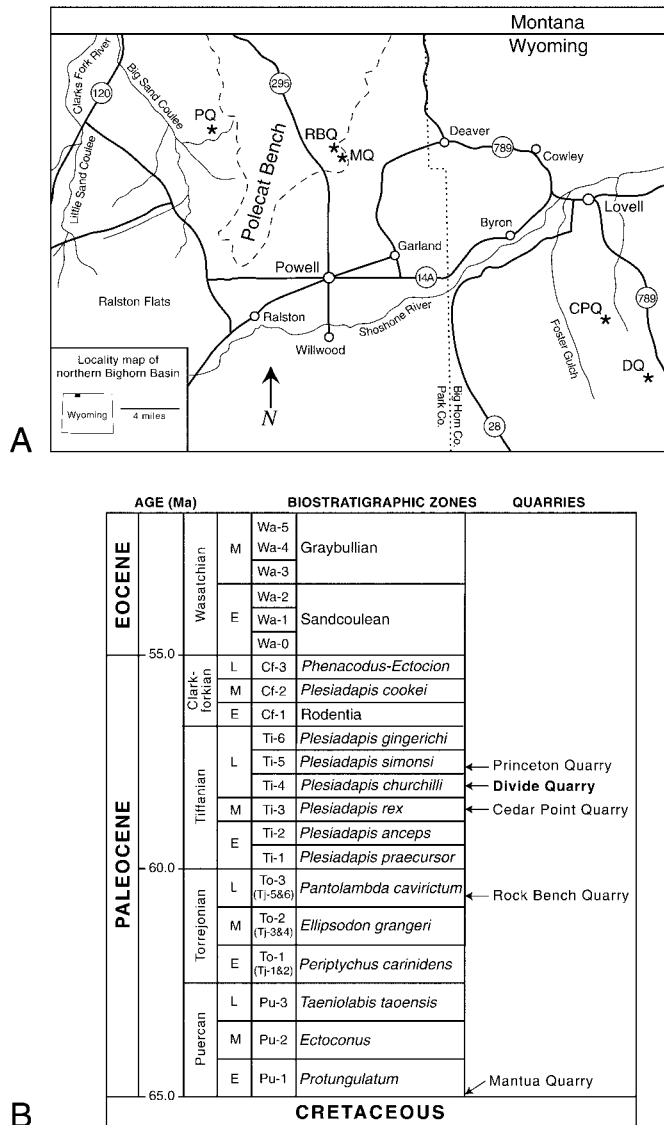


FIGURE 1. **A**, Locality map and **B**, stratigraphic section of the northern Bighorn Basin with Paleocene quarries indicated. **MQ**, Mantua Quarry; **RBQ**, Rock Bench Quarry; **CPQ**, Cedar Point Quarry; **DQ**, Divide Quarry; **PQ**, Princeton Quarry. Figures modified from Bartels (1987). Biostratigraphic zonation after Gingerich (1983, 2000), Archibald et al. (1987), Williamson (1996), and Eberle and Lillegraven (1998).

and several maxillae of *C. jepseni* allow for more extensive comparison of morphology and for re-evaluation of its phylogenetic affinities.

Multiple carpolestid species are rarely found in the same assemblage. Exceptions to this are the co-occurrence of *Elphidotarsius shotgunensis* and *Carpodactes hazelae* in the early Tiffanian (Ti-1) Shotgun local fauna (Rose, 1975), *Elphidotarsius russelli* and *Carpodactes* cf. *C. hazelae* in the early Tiffanian (Ti-1) Cochrane 2 locality of Alberta (Fox, 1990), and *Elphidotarsius wightoni* and *Carpodactes hazelae* in the middle Tiffanian (Ti-3) Hand Hills West and DW-2 localities of Alberta (Fox, 1990). Among other new material from Divide Quarry are several jaws of a small carpolestid with a relatively low-crowned p4, closely resembling that of *Carpodactes cygneus*. These specimens, together with those of *C. jepseni*, document

the occurrence of two distinct carpolestid species at Divide Quarry.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; ROM, Royal Ontario Museum, Toronto; UM, University of Michigan Museum of Paleontology; YPM-PU, Princeton University collection at Yale Peabody Museum, New Haven.

SYSTEMATIC PALEONTOLOGY

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

Discussion—We follow Bloch and Gingerich (1998) in considering Carpolestidae to be Proprimates (Gingerich, 1989), 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 *Chronolestes*, which we consider far removed from the base of the carpolestid clade (Bloch and Fisher, 1996; Silcox et al., 2001).

CARPOMEGODON, gen. nov.

Carpodactes (in part), Rose, 1975, p. 33

Carpodactes (in part), Szalay and Delson 1979, p. 98

Carpolestes (in part), Gingerich, 1980a, p. 412

Type and Only Known Species—*Carpodactes jepseni* Rose, 1975.

Emended Diagnosis—Largest known carpolestid (slightly larger than *Carpolestes dubius*). Differs from other carpolestids in having p4 higher crowned, both absolutely and relative to p4 length and molar size; and medial lower incisor (i1) very robust and anterior teeth between i1 and p4 more compacted. Further differs from *Carpolestes* in having C1 and P1; crown of p4 more pointed (similar to that of *Carpodactes aulacodon*); crown of p4 with 6 distinct apical cusps, with one or two additional cusps variably present (similar to that of *Carpodactes* which has 5–6 apical cusps); unlike that of *Carpolestes* which has 8–9 apical cusps); and crown of P4 wider. Further differs from *Carpodactes* in having the crown of P3 with small anteroexternal extension (like that of *Carpolestes*; unlike that of *Carpodactes* which has no anteroexternal extension); and crown of P3 larger than that of P4 (like that of *Carpolestes*; unlike that of *Carpodactes* which has P3 subequal to or slightly smaller than P4).

Etymology—Greek (masc.): *karpos*, fruit, in analogy with *Carpodactes* and *Carpolestes*; *me-gas*, great; *odon* (*odon*), tooth.

CARPOMEGODON JEPSANI (Rose, 1975)

(Figs. 2–8, Table 1)

Synonymy—*Carpodactes jepseni* Rose, 1975.

Holotype—YPM-PU 20716, right dentary with p4–m2.

Hypodigm—UM 80575: right dentary with p4–m3 and alveoli for anterior teeth. UM 81290: right p4. UM 83264: left p4. UM 85282: right dentary with p4–m2, right P3. UM 85400: right dentary with p4–m3. UM 85918: left maxilla with P1–M2. UM 86241: left maxilla with P3–M2 and alveoli for P2–C1. UM 92257: right maxilla with P2–P3. UM 92261: right maxilla with P3–M2 and alveoli for P2–C1. UM 92279: left dentary with p4–m2. All specimens from UM locality FG-46 (Divide Quarry), Fort Union Formation, North Emblem Reservoir Quadrangle, northern Bighorn Basin, Bighorn County,

TABLE 1. Summary of dental measurements of *Carpomegodon jep-seni* from Ti-4 Divide Quarry. Total sample includes 12 specimens. **Abbreviations:** N, samples size; \bar{x} , mean; s, standard deviation; V, coefficient of variation; L, crown length; W, crown width; and MD, mandibular depth. Measurements in mm.

Tooth position	N	Range	\bar{x}	s	V
<i>Upper dentition</i>					
P3L	5	2.84–3.19	3.08	0.14	4.44
P3W	5	2.77–3.31	2.97	0.21	7.11
P4L	3	2.32–2.38	2.35	0.03	1.30
P4W	3	2.55–2.87	2.72	0.16	5.90
M1L	3	1.74–1.84	1.81	0.06	3.20
M1W	3	2.45–2.52	2.49	0.04	1.52
M2L	1	1.62	—	—	—
M2W	2	2.54–2.70	2.62	0.11	4.32
<i>Lower dentition</i>					
p4L	7	3.51–4.02	3.76	0.19	5.18
p4W	6	2.11–2.56	2.34	0.15	6.47
m1L	5	1.84–2.01	1.95	0.07	3.41
m1W	5	1.61–1.98	1.83	0.16	8.89
m2L	6	1.56–1.87	1.71	0.14	7.95
m2W	6	1.65–1.78	1.73	0.05	2.62
m3L	2	2.28–2.32	2.30	0.03	1.23
m3W	2	1.52–1.53	1.53	0.01	0.46
MD	4	5.38–5.89	5.57	0.22	3.97

Wyoming (detailed locality information is archived at the University of Michigan Museum of Paleontology).

Age and Distribution—*Carpomegodon jep-seni* is known only from Tiffanian faunal zone Ti-4 (late Paleocene) in north-western Wyoming.

Emended Diagnosis—As for genus.

Description—Several new specimens of this species have been found since the original description. One of these, UM 80575, preserves p4–m3 and the alveoli of all anterior teeth (Fig. 2). The anterior part of the dentary (Fig. 3) is very short, with two small alveoli between p4 and a relatively large alveolus for the medial incisor. An additional very small excavation at the posterolateral margin of the large alveolus probably housed another vestigial tooth. There is barely enough room for the large mental foramen between the anterior root of p4 and the large incisor alveolus. The p4 is very large and high crowned. Labially the crown of p4 is strongly exodaenodont, extending well below that of the following molars and overhanging half the depth of the dentary. The anterior border of p4 is angled, giving the apex a pointed appearance. There are six distinct apical cusps, the first five closely spaced and the last one set farther back, midway between the fifth cusp and the talonid. An additional weak cuspule is situated between the fifth and sixth cusps. The talonid of p4 is a well-developed cusp lower than the apical cusps and demarcated from them by a constriction that is more evident in lingual aspect. As in several other species, the posterior half of the lingual surface of p4 is slightly concave. The paraconid of m1 is slightly smaller than the protoconid and is situated anterior and very slightly lingual to it, as in some species of *Carpodaptes*.

The upper dentition of *Carpomegodon jep-seni* is now known from several maxillae (Fig. 4). There are three alveoli anterior to P3 in the maxilla (Fig. 5), with no premaxilla-maxilla suture evident about the anterior-most alveolus. It is therefore assumed that all these teeth were in the maxilla and that the alveoli belonged to single-rooted C1, P1, and P2. The P3 of *C. jep-seni* is larger than P4 and has four prominent buccal cusps, the anterior one slightly separated from the three succeeding cusps, an incipient fifth cusp at the anteroexternal edge, and a modest (somewhat variably expressed) anteroexternal projection. The

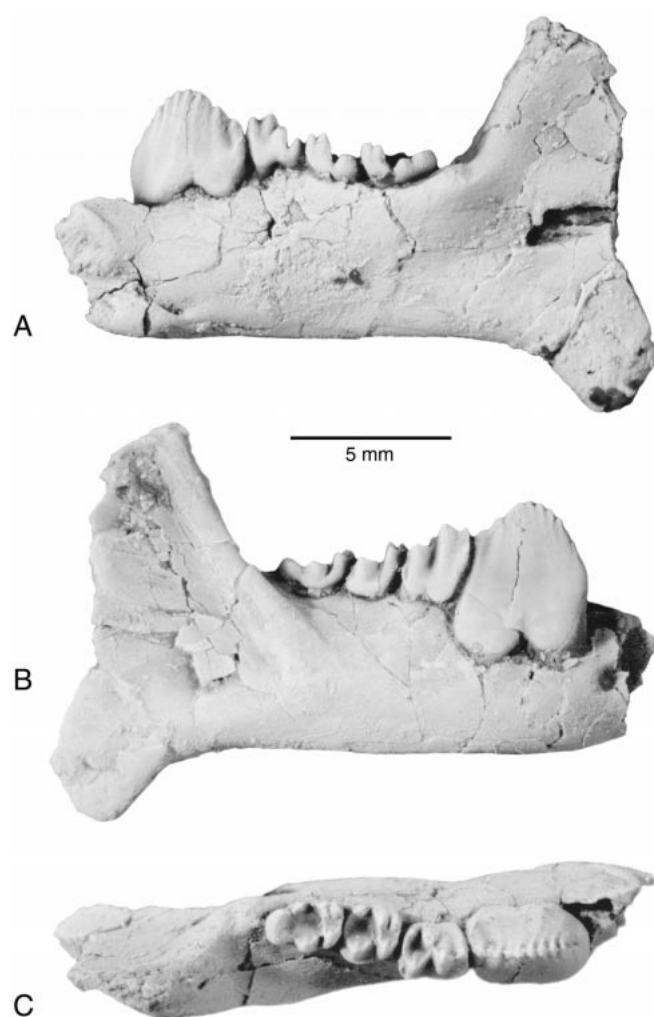


FIGURE 2. A, Lingual; B, buccal; and C, occlusal views of the right dentary of *Carpomegodon jep-seni* (UM 80575) with p4–m3 and the alveoli of all anterior teeth. Note that p4 is very large and high crowned and that there are six distinct apical cusps on p4, the first five closely spaced and the last one set farther back midway between the fifth cusp and the talonid heel. An additional weak cuspule is situated between the fifth and sixth cusp of p4. Scale in mm.

morphology of M1–2 is nearly identical to that of *Carpolestes dubius* (Rose, 1975) and thus is not described here.

Discussion—The anterior part of the dentary (Fig. 3) is much shorter than in any other carpolestid. The alveolus for i1 indicates a much more robust tooth than in *Carpolestes dubius* or *Carpolestes simpsoni* (the i1 is unknown for *Carpolestes nigridens*). Three small alveoli are present between p4 and i1. We interpret these alveoli to have held i2, c1, and p3; hence the lower dental formula of *Carpomegodon jep-seni* is 2.1.2.3, the same as in *Carpodaptes* and *Carpolestes* (except *Carpolestes simpsoni*, which has lost p3), although i2 is clearly more reduced in this specimen.

The more pointed apex of p4 is reminiscent of *Carpodaptes aulacodon* and unlike other species of *Carpodaptes* or *Carpolestes* (Fig. 6). As in *Carpodaptes*, but not *Carpolestes*, the paraconid of m1 is slightly smaller than the protoconid and is situated anterior and very slightly lingual to it. The p4 of *Carpomegodon* is higher crowned in both absolute and relative measurements than that of any other known carpolestid (Fig. 7).

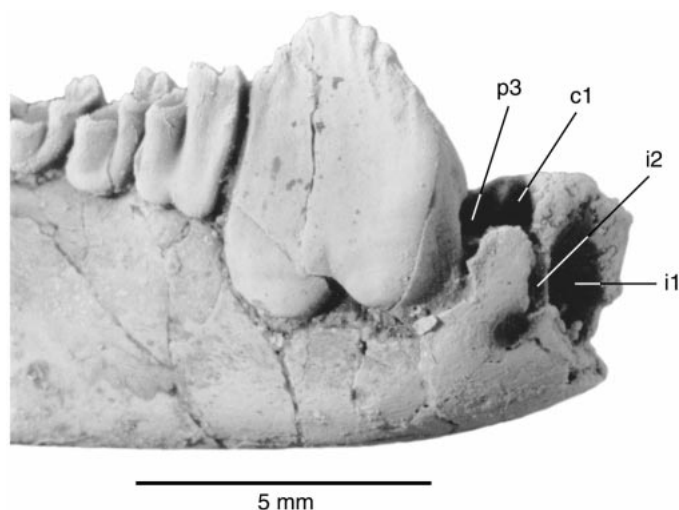


FIGURE 3. Enlarged view of the dentary of *Carpomegodon jepseni* (UM 80575) anterior to p4. Note that the anterior part of the dentary is very short, with two small alveoli between p4 and a relatively large alveolus for the medial incisor. A very small excavation at the posterolateral margin of the large alveolus probably housed a vestigial tooth. We interpret these alveoli to have held i1–2, c1, and p3; hence the lower dental formula of *Carpomegodon jepseni* is 2.1.2.3. Scale in mm.

If our interpretation is correct that the maxillary alveoli anterior to P3 held P2, P1, and C1, *Carpomegodon jepseni* had an upper dental formula of ?3.1.4.3 (the incisor count is unknown, but may be inferred based on specimens of *Carpodaptus* and *Carpolestes*, which have three incisors; Fox, 1984, 1993; Bloch and Gingerich, 1998), the same as earlier-occurring *Elphidotarsius wightoni* but unlike *Carpodaptus hazelae*, which apparently lost C1, and *Carpolestes* species, which have lost C1–P1 (Fox, 1993). Alternatively, the premaxilla-maxilla suture might be obscured (although the specimen is well preserved with no breakage in this area) and the anterior-most tooth could be in the premaxilla, making it an incisor and the tooth just posterior to it C1. *Carpomegodon jepseni* is similar to *Carpolestes dubius* and differs from *Carpodaptus hazelae* in the construction of P3, particularly in having a small anteroexternal extension on P3, and in having P3 larger than P4 (Fig. 8).

CARPODAPTES Matthew and Granger, 1921

CARPODAPTES CYGNEUS (Russell, 1967)

(Figs. 6, 7, 9; Table 2)

Carpolestes cygneus Russell, 1967:19

Carpodaptus cygneus, Krause, 1978:1253, 1267; Rose, 1975:32

Carpodaptus hobackensis, Holtzman, 1978:47 (part)

Carpocristes cygneus, Beard and Wang, 1995:21

Holotype—ROM 05622, right dentary with p4 from Swan Hills, Alberta.

Referred Specimens—UM 77295: left dentary with p4–m3. UM 77321: right dentary with p4–m3. UM 80669: right dentary with p4–m2. UM 83237: left dentary with p4–m2. UM 85236: left dentary with p4. UM 85283: left dentary with p4–m1. UM 85286: left dentary with i1–2, p4. UM 91324: left maxilla with P2–4, M2–3. All specimens are from UM locality FG-46 (Divide Quarry).

Age and Distribution—*Carpodaptus cygneus* is now known from Tiffanian faunal zones Ti-3 and Ti-4 (late Paleocene) of Alberta, Saskatchewan, North Dakota, and northwestern Wyoming.

Discussion—The Divide Quarry sample of *Carpodaptus cyg-*

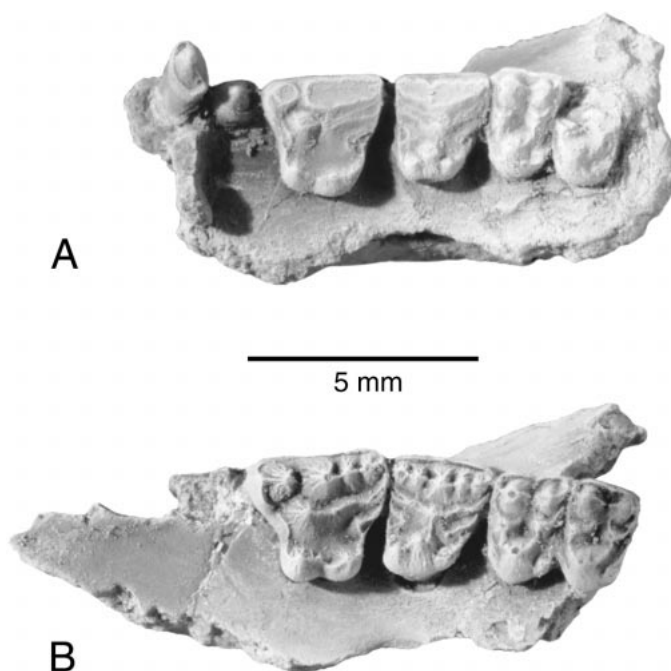


FIGURE 4. Upper dentition of *Carpomegodon jepseni* from Divide Quarry in occlusal view: **A**, P1(C1?)–M2 (UM 85918) and **B**, P3–M2 (UM 86241). Note the presence of three alveoli anterior to P3 in the maxilla, with no premaxilla-maxilla suture evident around the anterior-most alveolus. P1(C1?) and P2 are single-rooted. Scale in mm.

neus includes several well-preserved mandibles and a single maxilla (Fig. 9). The dentaries demonstrate that *C. cygneus* has a lower dental formula of 2.1.2.3. The i1 is similar to those illustrated by Krause (1978) from the Roche Percée local fauna, Saskatchewan, in having a crown that is long and slender, laterally compressed, and apically tapering. The i2 of *Carpodaptus cygneus* is small, single rooted, and often positioned buccally in relation to the other anterior teeth, as in *Carpolestes*. The crown extends anteriorly, making an elongate spur that covers the gap between i1 and the root of i2. The p4 of *C. cygneus* has six apical cusps, as in *C. jepseni* and some *C. hazelae*. It differs from that of *C. jepseni*, however, in having a lower and more rounded crown with a moderate posterolingual excavation. *C. cygneus* further differs from *C. jepseni* in being smaller

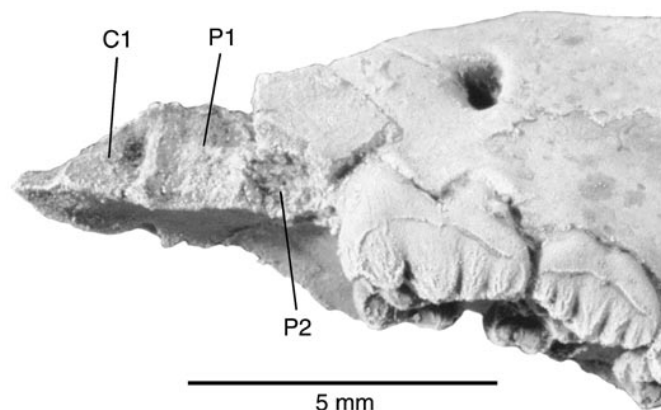


FIGURE 5. Enlarged view of the maxilla (UM 86241) anterior to P3. Note the presence of three alveoli anterior to P3. We interpret these alveoli to have held P2, P1, and C1. Scale in mm.

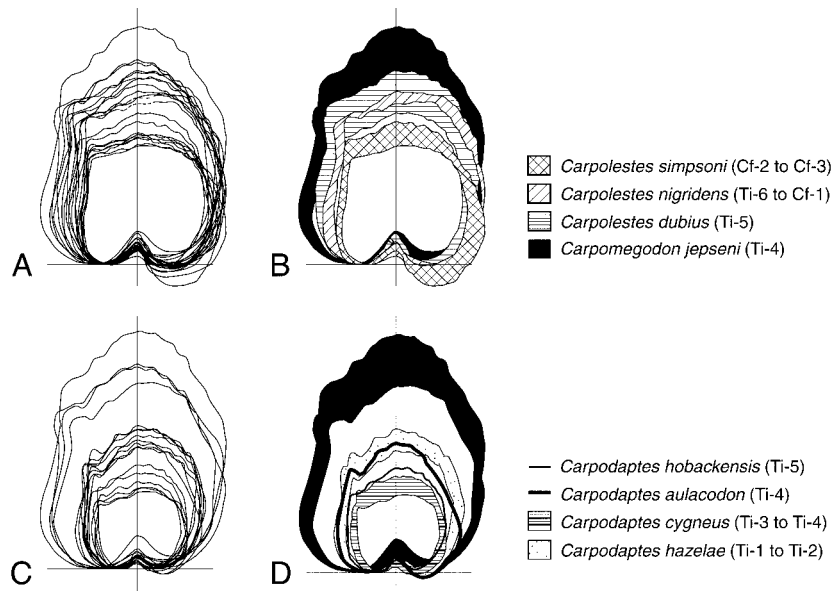


FIGURE 6. Camera lucida drawings of carpolestid p4s. **A–B**, 3 *Carpolestes* and 1 *Carpomegodon* species and **C–D**, 4 *Carpodaptus* species. Outlines are in buccal view with anterior to the right. Shading represents interpretations of p4 outlines with ranges of species variation indicated. The p4s were oriented about a vertical line passing through the highest apical cusp and the ventral notch and a perpendicular horizontal line that touches the base of the posterior lobe. Note that the p4 of *Carpomegodon jepseni*, while mostly higher crowned than that of any of the other species, overlaps somewhat with *Carpolestes dubius* in height and length. The p4 profile of *Carpomegodon jepseni* is very distinct in size from that of any of the *Carpodaptus* species. Note, however, that p4 of *Carpodaptus aulacodon* is similar in shape to that of *C. jepseni*.

(Table 2), having p4 relatively smaller compared to m1, lacking any shortening of the mandible anterior to p4, and having a larger i2. The p4 of *C. cygneus* differs from that of later-occurring *C. hobackensis* and *C. oriens* in having a shallower posterolingual excavation (related to a more developed posterior apical cusp) on p4.

In his diagnosis of *Carpolestes dubius* Jepsen (1930) stated that P2 was "... probably two-rooted." (Jepsen, 1930; p.521). However, Rose (1975) concluded, based on new fossil evidence, that the P2 of *C. dubius* was single-rooted. The P2s of *Elphidotarsius wightoni*, *Carpodaptus hazelae*, and *Carpolestes simpsoni* are thought to be single-rooted (Simpson, 1937; Fox, 1984; Bloch and Gingerich, 1998). The P2 of *Carpomegodon* is also single-rooted (Fig. 4A). Krause (1978) and Holtzman (1978) illustrated P2s of *Carpodaptus cygneus*, but did not describe the number of roots. Unlike that of any carpolestid previously described, the P2 of *C. cygneus* from Divide Quarry (UM 91324; Fig. 9C) is double-rooted. The roots of P2 are clearly divided in lingual view but appear to be partially fused and occupy a single alveolus in buccal view. Otherwise, the upper dentition of *C. cygneus* from Divide Quarry is not markedly different from that described by Krause (1978) from the Roche Percée local fauna.

Beard and Wang (1995) proposed the genus *Carpocristes* for a clade composed of North American *Carpodaptus cygneus* and *Carpodaptus hobackensis*, and Asian *Carpocristes oriens*. As observed by Silcox and Gunnell (in press), the purported synapomorphies (and diagnosis) of this clade are problematic. The following six "unambiguous synapomorphies" of *Carpocristes* were listed by Beard and Wang (1995:24, 32–33): (1) proliferation of median crests on P3–4 (beyond a primitive condition of one); (2) size of upper and lower molars same as in *Carpocristes* spp. (not larger than *Carpocristes* spp.); (3) posterolingual excavation on p4 present (not absent); (4) posterior apical cusp of p4 in posterior position (not in more apical position); (5) strong crest uniting the main shearing blade with the

talonid cusp of p4 (not weak crest); and (6) six or seven apical cusps on p4 (not two, four, five, or eight).

Our observations do not match this characterization. (1) Only *C. oriens* has a proliferation of median crests on P3–4 (*C. cygneus* has two crests as in *Carpomegodon* and *Carpolestes*, not three as in *C. oriens*, and the upper dentition of *C. hobackensis* is unknown). (2) Upper and lower molars of *E. florencae*, *E. shotgunensis*, and *C. hazelae* are as small as those of *Carpocristes* spp. (*E. florencae* and *C. hazelae* were coded as larger in the Beard and Wang data matrix and they did not include *E. shotgunensis*). (3) A posterolingual excavation on p4 is present in *Carpomegodon* and *Carpolestes*, and is variably expressed in *C. cygneus*. (4) *Carpomegodon* and *Carpolestes* also have the posterior apical cusp of p4 in a more posterior position; furthermore, *C. oriens* lacks this cusp altogether (Beard and Wang, 1995:18), although it is coded as being present and in this position in the Beard and Wang data matrix. (5) Relative expression of the crest uniting the main shearing blade with the talonid cusp of p4 is not independent of the position of the posterior apical cusp (number 4 of this list) and, as for that characteristic, *Carpomegodon* and *Carpolestes* also have a strong crest on p4. Not only does including this character give artificially increased weight to the morphology of the crest on p4—it is not even a uniquely derived characteristic of *Carpocristes*. (6) While Beard and Wang code *C. cygneus* as having 6 apical cusps on p4, this taxon is polymorphic for this characteristic and is known to have 5, 6, or 7 apical cusps (Krause, 1978). *C. hazelae* is also variable and is known to have 5 or 6 apical cusps. *C. hobackensis* (excluded from the Beard and Wang data matrix) also has 6 apical cusps. Furthermore, Beard and Wang (1995) treat this character as ordered, thereby assuming that cusps in this position are added (or subtracted) in a step-wise fashion. Because we do not know how the suite of cusps might evolve in a plagiaulacoid tooth (e.g., it is possible that more than one cusp could be added or subtracted in this

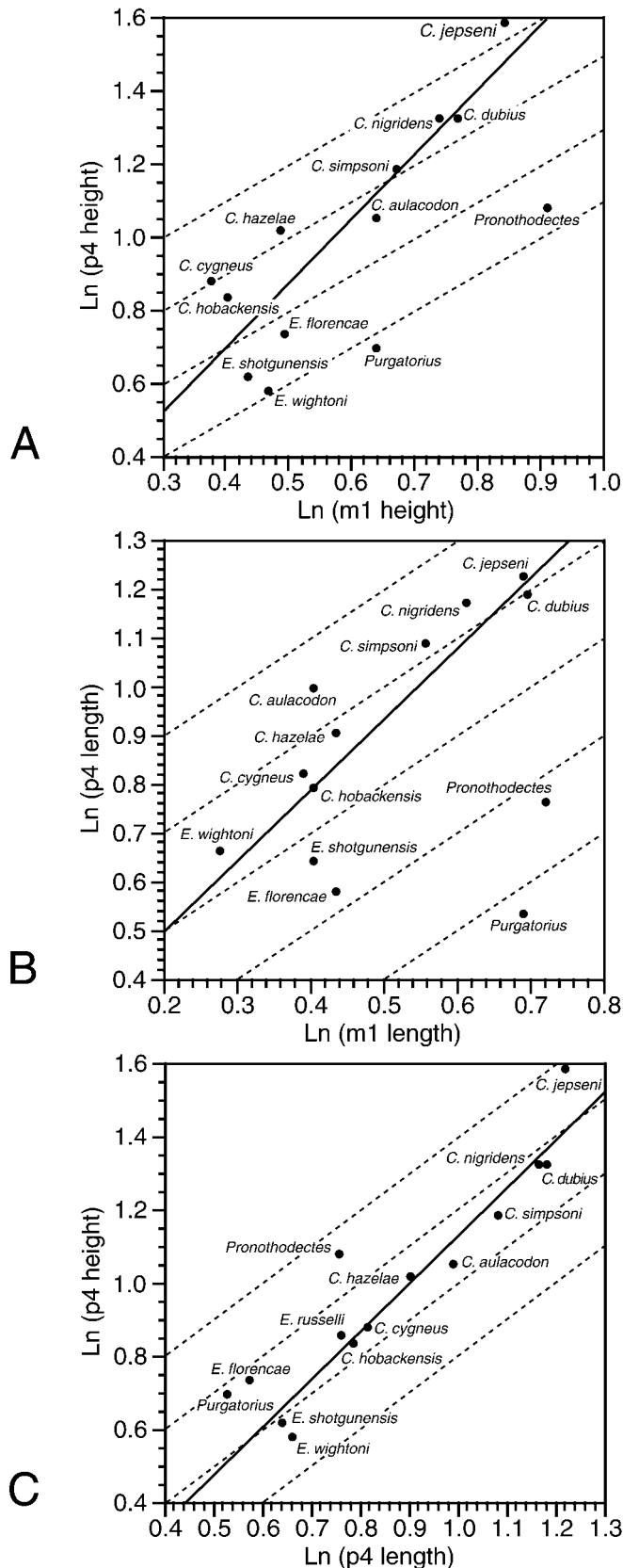


FIGURE 7. Plots of carpolestid p4 size. **A**, p4 height as a function of m1 height; **B**, p4 length as a function of m1 length; and **C**, p4 height as a function of p4 length. The points represent mean sample measurements (in mm). Dashed parallel lines are isoclines of constant difference. Solid line is a least-squares regression through the mean sample

character transformation) we regard this ordering as an unwarranted assumption.

All of the characters Beard and Wang use to diagnose *Carpocristes* are present in other genera or not present in some species included in *Carpocristes*. Results of our phylogenetic analyses (see below) indicate that *Carpodectes cygneus* does not share a special relationship with the *C. hobackensis* + *C. oriens* clade. For these reasons, *Carpodectes cygneus* is here retained in the (certainly paraphyletic) genus *Carpodectes* and the validity of *Carpocristes*, as currently conceived, is doubtful.

CARPOLESTID PHYLOGENY

Previous Hypotheses

When Rose (1975) described the type specimen of *C. jepseni*, he regarded the number and clarity of cusps (six apical cusps) as well as a lower and well separated talonid cusp on p4 to be suggestive of *Carpodectes*. He further regarded the large size, high crown and size of p4 relative to the molars as suggestive of *Carpolestes*. Rose decided to include *C. jepseni* within *Carpodectes* but noted that the morphologic and stratigraphic intermediacy between *Carpodectes* and *Carpolestes* indicated that *C. jepseni* might be in or near the ancestry of *Carpolestes* (also see Rose, 1977). Szalay and Delson (1979) synonymized *Carpodectes* and *Carpolestes*, claiming that recognition of a morphologic intermediate (*C. jepseni*) between the two named genera rendered the later-described genus (*Carpolestes*) invalid. This view, that to be valid these genera must be morphologically discrete, is not widely shared (e.g., Beard and Wang, 1995; McKenna and Bell, 1997; Bloch and Gingerich, 1998). Gingerich (1980a) illustrated the stratigraphic distribution and interpreted phylogenetic relationships of Carpolestidae using a stratophenetic approach. Gingerich 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 ancestral to *Carpolestes dubius*. Beard and Wang (1995), in their paper on the first known Asian plesiadapoids, performed a cladistic analysis of 27 dental characteristics on seven North American and two Asian carpolestid species. In their analysis *C. jepseni* was the sister taxon to the *Carpolestes* clade with *Carpodectes hazelae* the sister taxon of the *C. jepseni*-*Carpolestes* clade.

Cladistic Analysis

New specimens of *C. jepseni* allow for more extensive comparison of its morphology and re-evaluation of its phylogenetic affinities. To help resolve the relationship of *C. jepseni* to other carpolestids, we first performed a cladistic analysis of 32 morphologic characters for the 13 known carpolestid species and two outgroup taxa (Appendices 1 and 2). The Puercan *Purgatorius* and Torrejonian plesiadapid *Pronothodectes* were used as outgroup taxa. The cladistic analysis was rooted with *Purgatorius* because it is the geologically oldest plesiadapiform, is known from both upper and lower dentitions, and is thought to be close to the ancestry of most later plesiadapiforms, including carpolestids (Gunnell, 1989). Contrary to Beard and Wang (1996), Asian *Chronolestes simul* is outside the carpolestid

← measurements. Note that the p4 of *Carpomegodon jepseni* is higher relative to its own length, than is the case for other carpolestids. The length of the *Carpomegodon* p4 relative to that of its m1 is not larger than for other carpolestids, with the exception of *Elphidotarsius shotgunensis* and *Elphidotarsius florenceae*, which seem to deviate from the relationship demonstrated in other species of carpolestids in having a shorter p4 relative to m1 length.

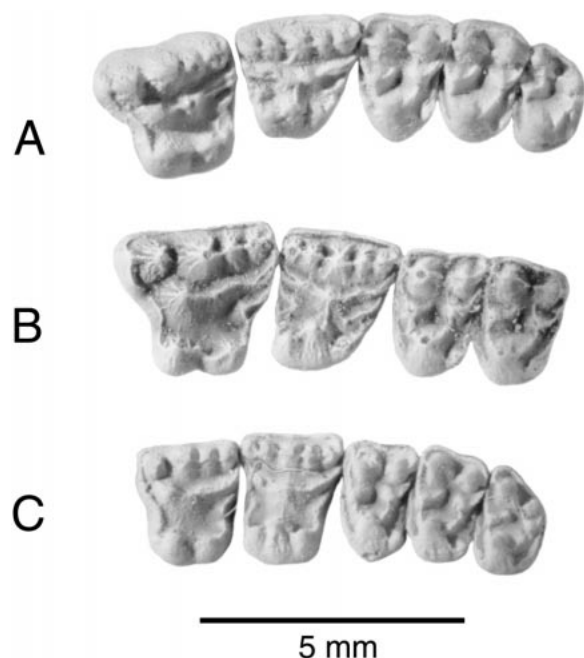


FIGURE 8. **A**, occlusal views of upper dentitions for *Carpolestes dubius* (YPM-PU 19349); **B**, *Carpomegodon jepseni* (UM 86241) and **C**, *Carpodartes hazelae* (AMNH 33980, type). Note that *Carpomegodon jepseni* is similar to *Carpolestes dubius*, and differs from *Carpodartes hazelae*, in having an anteroexternal extension on P3, and in having P4 smaller than P3. Scale in mm.

clade (Bloch and Fisher, 1996) and is likely a basal plesiadapoid (Silcox et al., 2001). As *Chronolestes simul* is derived in aspects of its dentition (e.g., i3 absent, p3 single-rooted), to include it in this analysis, and exclude other plesiadapoid species, might provide misleading information regarding the polarity of these characters. Thus, *Chronolestes simul* is not included in this analysis; the phylogenetic position of this interesting plesiadapiform is beyond the scope of this paper and is discussed in more detail by Silcox et al. (2001).

While certain characters (e.g., body size) may warrant treatment as ordered, to increase phylogenetic resolution (but not necessarily congruence; Slowinski, 1993), such morphoclines are not imposed on any characters coded here. To avoid process assumptions regarding character state transitions, all of the characters in this analysis were treated as unordered (maximally connected; Slowinski, 1993). Morphologic data were assessed through a review of the literature (Rose, 1975, 1981; Gingerich, 1976; Krause, 1978; Fox, 1984, 1994; Gunnell, 1989; Rose et al., 1993; Beard and Wang, 1996; Bloch and Gingerich, 1998) and study of specimens and casts. Although a few specimens preserve cranial and postcranial morphology, most species are known only from teeth. For this reason, all the morphologic data are dental. One character that was variable within species (character 16: number of accessory apical cusps on p4) was coded as polymorphic. Characters not applicable for a species, or simply not known for that species, were coded as missing.

The cladistic analysis was done using PAUP version 3.1.1 (Swofford, 1993). A branch-and-bound search using the 32 morphologic characters yielded a single most-parsimonious cladogram (Fig. 10A) with a tree length of 68 steps (65, excluding autapomorphies), a consistency index of 0.93 (0.92, excluding autapomorphies), and a retention index of 0.94. The cladogram shows the thirteen carpolestids as monophyletic with the plesiadapid *Pronothodectes* as the sister taxon to this clade.

TABLE 2. Summary of dental measurements of *Carpodartes cygneus* from Ti-4 Divide Quarry. Total sample includes 8 specimens. Abbreviations as in Table 1. Measurements in mm.

Tooth position	N	Range	\bar{x}	s	V
<i>Upper dentition</i>					
P2L	1	0.67	—	—	—
P3W	1	0.57	—	—	—
P3L	1	1.67	—	—	—
P3W	1	1.60	—	—	—
P4L	1	1.45	—	—	—
P4W	1	1.70	—	—	—
M2L	1	1.10	—	—	—
M2W	1	1.73	—	—	—
M3L	1	1.07	—	—	—
M3W	1	1.63	—	—	—
<i>Lower dentition</i>					
p4L	7	1.94–2.30	2.09	0.13	5.96
p4W	6	1.16–1.30	1.22	0.05	4.06
m1L	5	1.39–1.44	1.42	0.06	4.35
m1W	5	1.02–1.32	1.21	0.12	9.71
m2L	4	1.22–1.44	1.30	0.10	7.51
m2W	4	1.09–1.24	1.17	0.07	5.80
m3L	2	1.71–1.72	1.72	0.01	0.41
m3W	2	1.01–1.09	1.05	0.06	5.39
MD	6	3.06–3.37	3.18	0.11	3.38

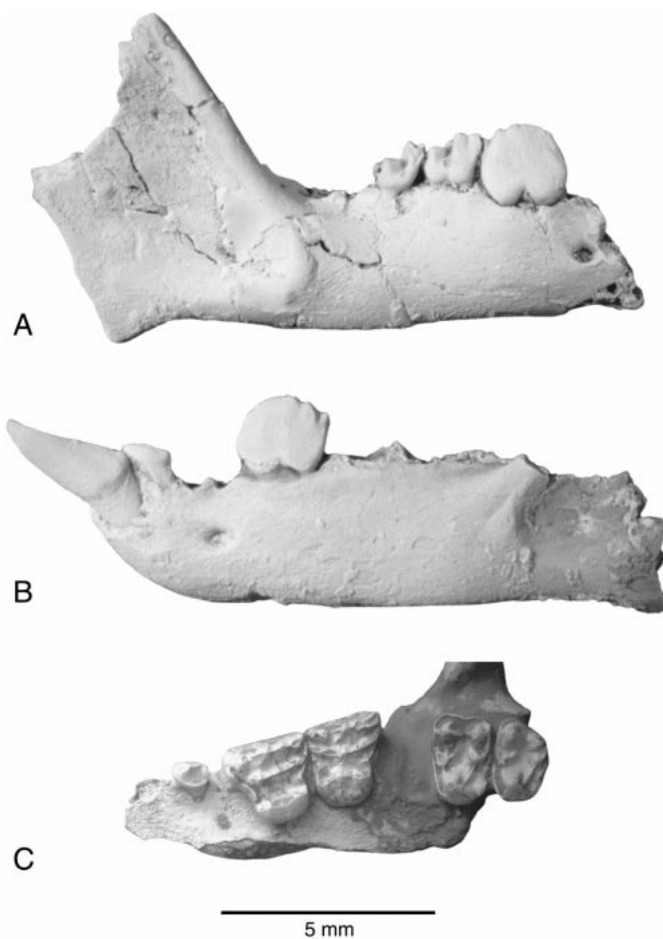


FIGURE 9. **A**, buccal view of right dentary (UM 80669); **B**, buccal view of left dentary (UM 85286); and **C**, occlusal view of left maxilla (UM 91324) of *Carpodartes cygneus* from Divide Quarry. The i1 is similar to those illustrated by Krause (1978) from the Roche Percée local fauna, Saskatchewan, in having a crown that is long and slender, laterally compressed, and apically tapering. Scale in mm.

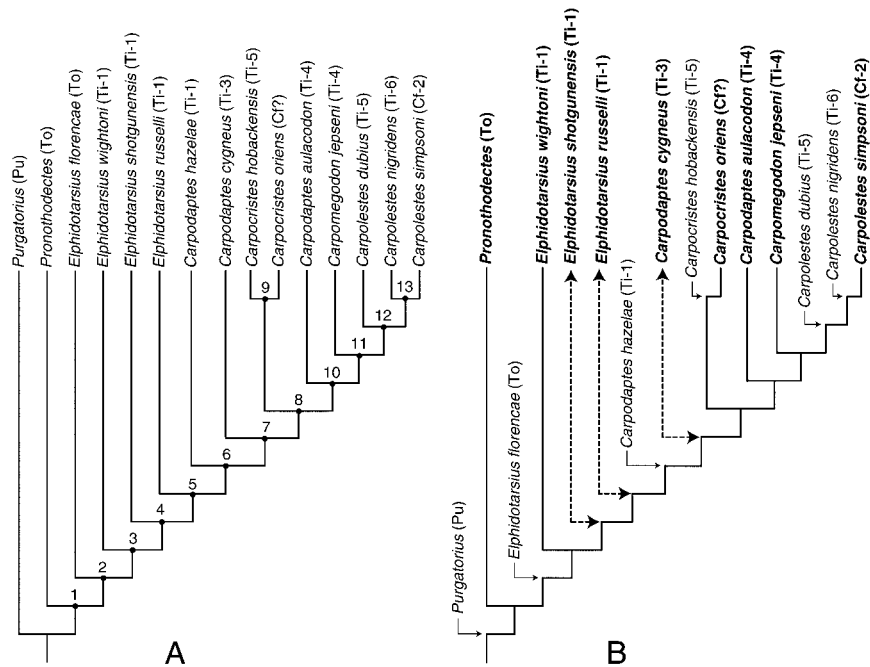


FIGURE 10. Hypotheses of phylogenetic relationship among North American carpolestids based on dental characters (Appendices 1 and 2). **A**, cladistic analysis yielded a single most-parsimonious cladogram generated by a branch-and-bound algorithm (Swofford, 1993) and rooted with *Purgatorius*: tree length = 65 (68, with autapomorphies), consistency index = 0.92 (0.93, with autapomorphies), retention index = 0.94. All characters were unordered. Unambiguous synapomorphies supporting each node are as follows (change is from 0 to 1 for binary characters; state indicated for multistate characters) node 1–2, 6, 7(1), 9(1), 30(1); node 2 (Carpolestidae)-10(1), 11, 13, 14(1), 16(1), 21, 24(1), 25(1), 26(1), 28(1), 29(1); node 3–3(1), 22(1), 23(1), 25(2), 27(1); node 4–24(2); node 5–14(2); node 6–9(2), 12, 16(2), 17(1), 22(2), 27(2), 28(2), 29(2), 30(2), 31, 32; node 7–19(1); node 8–27(3); node 9–20; node 10–18(2), 22(3); node 11–17(2), 23(2), 25(3); node 12 (Carpolestes)-3(2), 7(2), 8, 16(5), 18(1), 20, 28(3). **B**, stratocladistic analysis yielded eight overall most-parsimonious trees associated with a single topology, identical to the most-parsimonious cladogram generated by PAUP. Terminal taxa are shown in bold type with heavy lines, while ancestral taxa are shown in light type with arrows pointing to their correct position on the tree. *E. shotgunensis*, *E. russelli*, and *C. cygneus* are equivocal in their placement as terminal taxa or at ancestral nodes.

This result differs from Beard and Wang's (1995) cladistic analysis in that *Carpodaptes hazelae* does not share a special relationship with the *C. jepseni* + *Carpolestes* clade but falls out as the sister taxon to the taxa grouped at node 7 of our cladistic hypothesis (Fig. 10A). Also, *Carpodaptes cygneus* does not share a special relationship with the "*Carpodaptes*" *hobackensis* + *Carpocristes oriens* clade but falls out as the sister taxon to the taxa grouped at node 8 of our cladistic hypothesis (Fig. 10A). Otherwise, for those taxa common to the two analyses, relationships are the same.

The results of our cladistic analysis differ from those of Beard and Wang (1995) because we: (1) included all of the known carpolestid species (Beard and Wang excluded *Elphidotarsius shotgunensis*, *Elphidotarsius russelli*, *Carpodaptes aulacodon*, and treated the species of *Carpolestes* as one taxonomic unit); (2) used a different set of dental characteristics to form our data matrix; (3) had different interpretations of morphology for many of the taxa, leading to different coding of morphology for characters in common between the two analyses; (4) chose not to treat certain multi-state characters as ordered where we had no basis for restricting hypotheses of character transformation to linear morphoclines; (5) had more complete material for two of the known taxa (*Carpolestes* species and *C. jepseni*); and (6) used *Purgatorius* to root the analysis (Beard and Wang used a hypothetical morphotype based on *Purgatorius*, *Paromomys*, and *Micromomys*).

To compare our cladistic result quantitatively with that of Beard and Wang (1995) we calculated morphologic tree length of the two cladograms (theirs and our 'reduced' result) using

only taxa included in both analyses, evaluated using our character matrix. Our modified cladistic result had a morphologic tree length of 65 (RI = 0.91) and the Beard and Wang result had a morphologic tree length of 68 (RI = 0.85). To accept the Beard and Wang cladogram over the one presented here, one must accept three additional instances of homoplasy associated with the position of the posterior apical cusp on p4 (character 19), number of median crests on P3 (character 26), and number or position of buccal cusps on P3 (character 27). The specific taxa associated with these homoplasies, and whether the homoplasies represent reversal or convergence, depend on whether the character is analyzed using the ACCTRAN or DELTRAN options in MacClade.

Stratocladistic Analysis

Stratocladistics (Fisher, 1991, 1992, 1994) is a phylogenetic method that incorporates stratigraphic data into a parsimony-based phylogenetic analysis by minimizing ad hoc hypotheses of both homoplasy and non-preservation in the fossil record. Stratocladistics allows for hypotheses of ancestry, operating at the level of phylogenetic trees, not just cladograms. Because ancestor-descendant pairs are to be expected in the fossil record (Foote, 1996), a method that tests for these relationships, such as stratocladistics, is preferable to a method that excludes them a priori (as does conventional cladistics). However, regardless of whether hypotheses of ancestry are being entertained, accurate reconstructions of cladistic relationship are important to all phylogeneticists. With respect to accuracy, Fox et al. (1999)

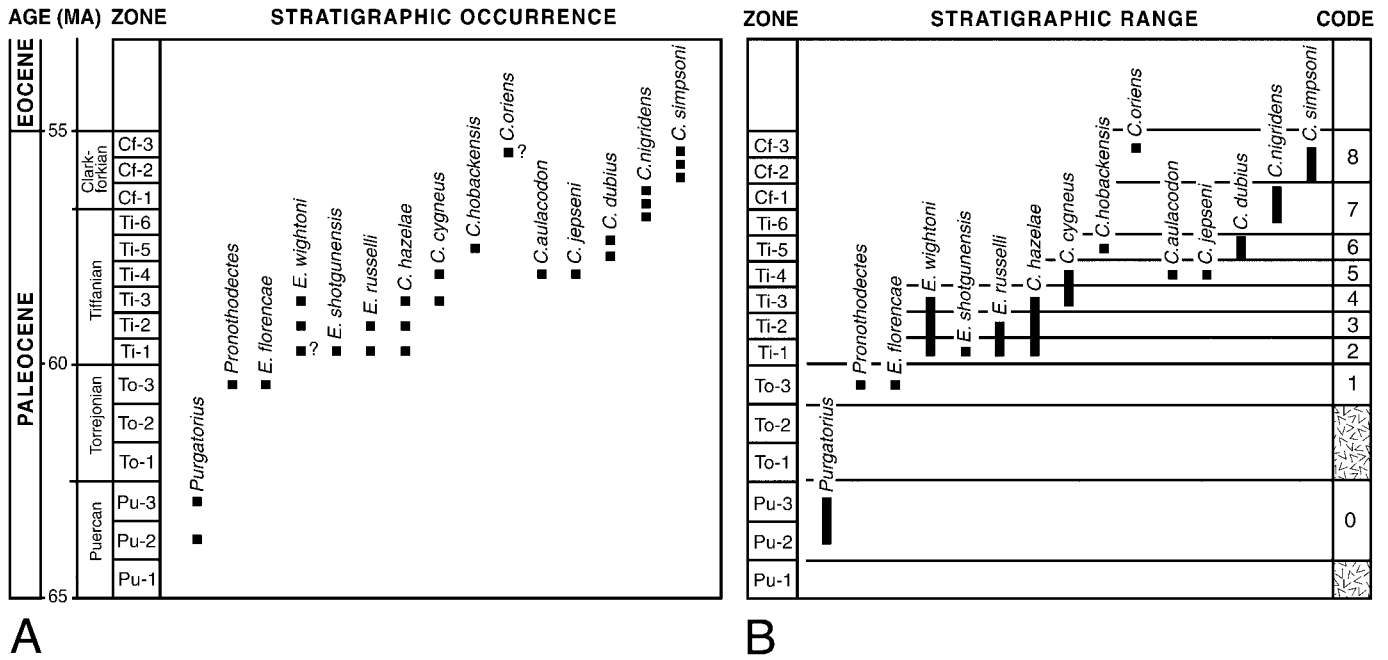


FIGURE 11. **A**, stratigraphic occurrence and **B**, ranges for the thirteen carpolestids. *Purgatorius* was used to root the trees in the cladistic analysis and *Pronothodectes* was included as an outgroup taxon. Stratigraphic position of samples is shown at the greatest resolution allowed by interbasinal correlations. Samples known from a faunal zone are plotted (arbitrarily) as being from the middle of that zone. In the plot of stratigraphic ranges (B) the stratigraphic character is coded in 9 states, all of which are subdivisions of the Paleocene. The first occurrence of *Elphidotarsius wightoni* is in either Ti-1 or Ti-2 (Fox, 1990). To allow for the possibility that *E. wightoni* is known from Ti-1, it was coded as occurring in that interval. Resolution of this issue could affect the conclusions of this analysis, as a later first occurrence of *E. wightoni* would provide support for different hypotheses of ancestry. Stratigraphic occurrence of *C. oriens* is here plotted as mid-to-late Clarkforkian, but it is possibly early Eocene in age (see text). Resolution of this issue will not affect the results of this analysis.

found, working with simulated evolutionary histories, that stratocladistics, using temporal and morphologic data, performed better than conventional cladistics, which excluded temporal data. Stratocladistics recovered the true phylogeny in over twice as many cases as cladistics, and even when neither method recovered the true phylogeny, stratocladistics usually did better than cladistics at selecting a hypothesis close to it.

Stratigraphic data (Appendix 2; last column) were assembled from the literature (Rose, 1975, 1977; Gingerich, 1976, 1980a; Krause, 1978; Fox, 1984, 1990; Archibald et al., 1987). The stratigraphic resolution chosen for the analysis was determined by the precision with which occurrences had been reported, the precision of correlation among the different stratigraphic sequences over which the record was being summarized, and the observed pattern of occurrences of samples that we could confidently associate as “taxa” in this analysis. For the outgroup taxa and most carpolestid species, the limiting resolution was that of the faunal zones shown in Figure 11. These occurrences are recorded in Figure 11A as single blocks positioned midway through the indicated zone. In principle, each such occurrence could have been treated as a separate taxon, but we recognize several sequences of occurrences in successive intervals as species-level lineages (e.g., *C. hazelae* in Ti-1 through Ti-3). Each of these sequences was recorded as a single taxon observed in multiple zones. To code the stratigraphic character (Fig. 11B), we used the minimum number of intervals necessary to represent the temporal ordering of unit taxa. Intervals in which none of these taxa occurred were left uncoded, to clarify that no hypothesis would be disadvantaged by this lack of data. Occurrences of *C. nigridentis* and *C. simpsoni* are known to much greater resolution than shown in Figure 11A, but recognition of

additional intervals in this portion of the column would not have improved resolution of the relationships of unit taxa.

One of the uncertainties involving *C. oriens* is whether the Wutu fauna, from which it comes, is early Eocene (e.g., Russell and Zhai, 1987; Beard and Wang, 1995; Ting, 1998) or late Paleocene (Beard and Dawson, 1999). We believe that an early Eocene age is more likely (Wutu has perissodactyls and artiodactyls, both considered indicative of the Eocene). However, to simplify this discussion we treat *C. oriens* as occurring in the mid-to-late Clarkforkian (Fig. 11) as suggested by Beard and Dawson (1999). The phylogenies selected by the stratocladistic analysis are unaffected by whether we place this taxon in the Clarkforkian or the early Eocene. Including this derived Asian taxon in the stratocladistic analysis did have the effect of changing relationships among some of the taxa (*C. cygneus* and *C. hobackensis*) where character support was least secure.

The first stage in the stratocladistic analysis was to import the single most-parsimonious cladogram generated by PAUP (see above) to MacClade version 3.0 (Maddison and Maddison, 1992) and include the stratigraphic character (not included in the cladistic analysis; PAUP does not recognize the stratigraphic character). Autapomorphies were retained in the stratocladistic analysis as they affect hypotheses of ancestry. Once the stratigraphic character is included, MacClade calculates a new tree length that includes both morphologic and stratigraphic debt. Without yet moving beyond PAUP’s resolution of relationships, assessment of stratigraphic data implicitly converts PAUP’s cladogram to the phylogenetic tree isomorphic to it (68 morphologic steps + 11 stratigraphic steps = 79 steps overall). To determine whether this represents a stratocladistic solution, two additional investigations are required. The first uses the

“make-ancestor” tool in MacClade to search for the most stratigraphically parsimonious tree(s) associated with PAUP’s cladogram. Trying combinations of ancestors, we found eight shortest trees, four with 68 morphologic steps + 4 stratigraphic steps = 72 steps overall, and four with 69 morphologic steps + 3 stratigraphic steps = 72 steps overall. The second additional investigation is to determine whether alternative topologies of relationship allow further reduction of overall tree length. We undertook this using the “debt ceiling” approach of Fisher (1992). Having discovered trees with an overall length as low as 72, and given that the number of stratigraphic steps cannot go below zero, trees with a chance of improving on those already discovered cannot have morphologic lengths greater than 71 steps, and trees with a chance of equaling the most parsimonious overall cannot have morphologic lengths greater than 72 steps. Rerunning the PAUP analysis to save cladograms longer than minimum (morphologic) length, we found 42 at 69 steps, 468 at 70 steps; 2,713 at 71 steps, and 10,595 at 72 steps. At this point, as the number of cladograms under the “debt ceiling” became prohibitively high (13,819) we abandoned the approach. Instead, we used the more heuristic approach of manual branch swapping to search for alternative topologies of shorter or equal overall tree length. The shortest trees remained the eight originally discovered at 72 steps overall, associated with the single cladogram at 68 morphologic steps. These eight trees constitute our stratocladistic solution (Fig. 10B). This set of hypotheses represents a considerable reduction in number relative to the 18,432 phylogenetic trees compatible with our single cladogram.

The eight trees selected by stratocladistics differ because of equivocal ancestorization of three species, *E. shotgunensis*, *E. russelli*, and *C. cygneus*. In the case of *C. cygneus*, an equivocal ancestor resulted because the stratigraphic “savings” of ancestorization was exactly offset by the morphologic “cost” of reversing a morphologic transition that could otherwise be interpreted as an autapomorphy. However, in the cases of *E. shotgunensis* and *E. russelli*, stratigraphic resolution was simply not adequate to demonstrate precedence of possible ancestors relative to putative descendants. No morphologic evidence refuted ancestral status, but neither did stratigraphic evidence support it.

There are 11 stratigraphic steps associated with our cladistic result and 3–4 stratigraphic steps associated with our stratocladistic result. To accept the phylogenetic tree isomorphic to our cladogram over our stratocladistic trees requires acceptance of 7–8 additional instances of non-preservation in sediments known to preserve similar mammalian taxa. In the carpolestid clade, 6–7 stratigraphic steps are caused by ghost lineages or taxa: (1) between nodes 2 and 3 (Fig. 10A) in the Torrejonian NALMA; (2) between nodes 5 and 6 in Ti-1 and Ti-2; (3) ancestral to *C. oriens* in Ti-5 or the Gashatan ALMA; (4) between nodes 7 and 8 in Ti-3 (this step is common to four of our eight shortest trees, but not the other four); (5) between nodes 12 and 13 in Ti-5; and (6) ancestral to *C. simpsoni* in Cf-1. Although our eight shortest trees avoid most of this debt, they still include some stratigraphic incongruities. For example, the gap between *C. hobackensis* and *C. oriens* requires explanation, no matter when ancestors of *C. oriens* dispersed to Asia. If they dispersed relatively late, they should be preserved in Ti-6 and Cf-1 faunal zones in North America, but if they dispersed earlier, they should occur in the equivalent interval in Asia (Gashatan-Bumbanian ALMA). In either case, our stratocladistic result accepts one unit of stratigraphic debt associated with *C. oriens* because other mammals (and in North America, even carpolestids) occur within this interval.

Clyde and Fisher (1997) used Farris’ (1989) Retention Index to compare the fit of stratigraphic data to the fit of morphologic data for a given phylogenetic hypothesis. For the phylogenetic

tree isomorphic to the morphologically most-parsimonious cladogram generated by PAUP, the morphologic retention index, 0.94, is much larger than the stratigraphic retention index, 0.76. For the stratocladistic results the morphologic and stratigraphic retention indices are more similar to each other, at 0.93–0.94 and 0.91–0.93 respectively. Thus, for little-to-no increase of morphologic debt, the stratocladistic analysis gives large savings in stratigraphic debt.

In this study, cladistic and stratocladistic results differ only in the recognition of ancestors, not in cladistic ordering. The results of both methods provide support for the monophyly of Carpolestidae. The stratocladistic phylogenies (Figs. 10B, 12) show Torrejonian *Elphidotarsius florencae* giving rise to the clade that includes the remaining carpolestids. *Carpodartes hazelae* gave rise to the clade that includes *Carpodartes cygneus*, *C. hobackensis* and its descendant *C. oriens*, and the clade that includes *Carpodartes aulacodon*, *Carpomegodon jepseni* and the *Carpolestes* clade. *Carpodartes aulacodon* is the sister taxon to the clade that includes *Carpomegodon jepseni* and the *Carpolestes* clade. *Carpomegodon jepseni* is the sister group to the ancestor-descendant *Carpolestes* lineage, composed of the ordered sequence *C. dubius*, *C. nigridens*, and *C. simpsoni*.

DISCUSSION

New specimens from late Tiffanian Divide Quarry clearly demonstrate the co-occurrence of two carpolestid species. *Carpodartes cygneus* is represented by a small sample of exceptionally well preserved specimens. The much larger *Carpomegodon jepseni* is represented by a nearly complete mandible and several maxillae.

The lower dentition of *Carpomegodon jepseni*, as has been previously stated (Rose, 1975), is similar to those of both *Carpodartes* and *Carpolestes*. One specimen of *C. jepseni* preserves alveoli of four teeth anterior to p4. The degree of reduction of i2 and foreshortening of the dentary, and the hypertrophy of p4, are more derived in *Carpomegodon jepseni* than in any other carpolestid. At the same time, p4 has fewer apical cusps than *Carpolestes*, and resembles advanced *Carpodartes* in this respect. The p4 of *C. jepseni* is similar in absolute length to some larger specimens of *Carpolestes dubius* and seems to have a similar shape to that of *Carpodartes aulacodon*.

The maxilla of *Carpomegodon jepseni* shows overall similarities to that of *Carpolestes dubius*. This is especially true in the morphology of P3, which has an anteroexternal elongation, a feature considered diagnostic of the *Carpolestes* clade and not present in any *Carpodartes* species. A larger P3 than P4 is also a character shared with *Carpolestes*. Two specimens of *C. jepseni* demonstrate that this species retained a C1 and maybe a P1. Thus *C. jepseni* may have had an upper dental formula of 3?.1.4.3, a condition shared by *Elphidotarsius* and *Carpodartes* and considered primitive for Carpolestidae (Fox, 1993). Later species of *Carpolestes* have lost C1–P1.

Assuming the foreshortening of the jaw in UM 80578 is typical of *Carpomegodon jepseni*, this species is autapomorphic with respect to this character. This derived state, together with a similarly derived reduction in the size of i2, provides evidence that *C. jepseni* did not give rise to *Carpolestes dubius* or any other *Carpolestes* species that have more elongate anterior mandibles and larger i2s. Therefore, despite the fact that the stratigraphic position of *C. jepseni* is consistent with it being ancestral to *Carpolestes*, it seems to represent a separate lineage that is more primitive than *Carpolestes* in some respects but more derived in others.

A stratocladistic analysis of 32 morphologic characters and stratigraphic data for the 13 known carpolestid species yields a well-constrained set of hypotheses of relationship among species. One surprising result (supported by both our cladistic and

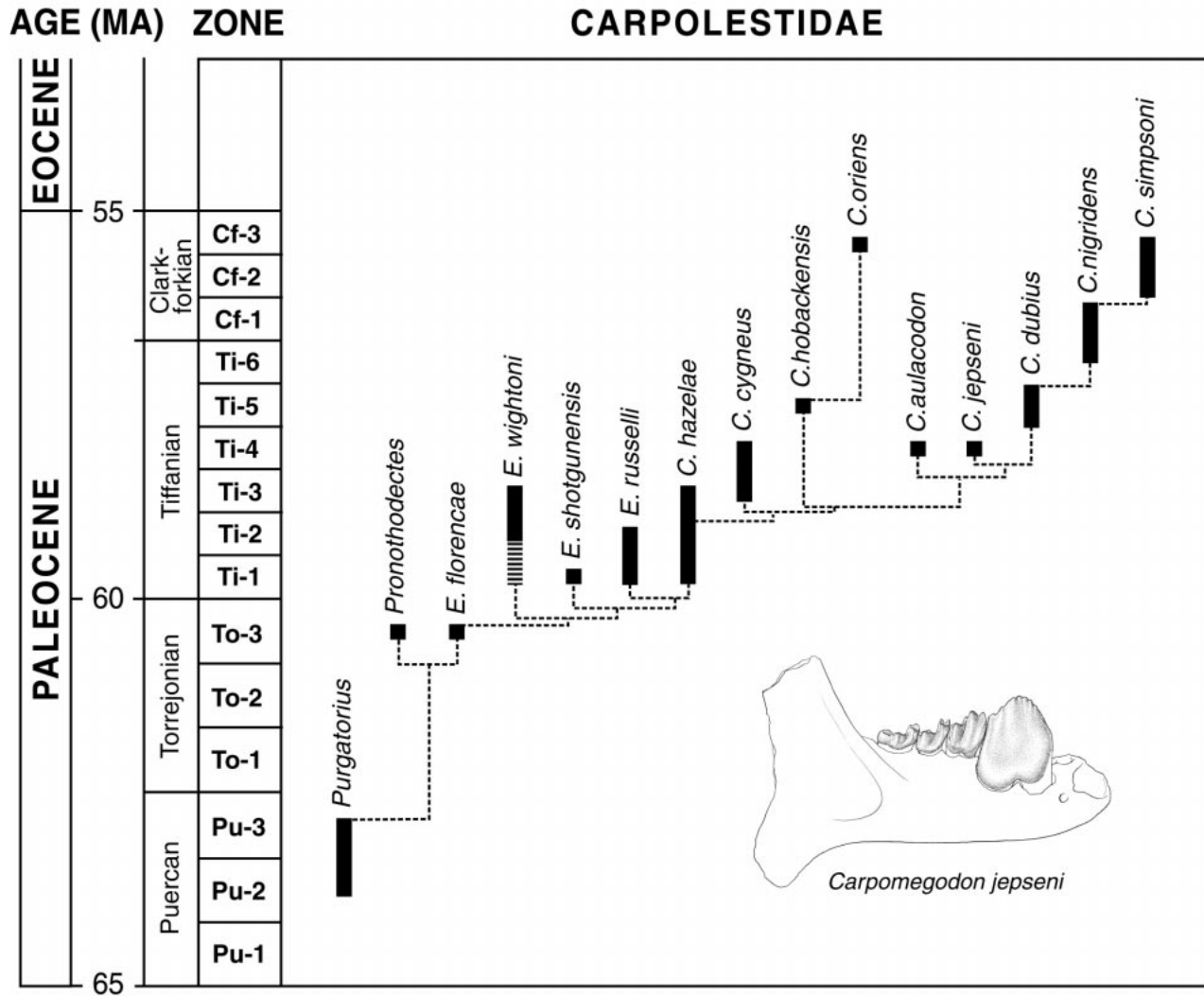


FIGURE 12. One of the phylogenetic trees (with equivocal ancestors as sisters only) resulting from the stratocladistic analysis (Fig. 10B). Divergences of sister taxa are shown schematically, with no implied knowledge of the exact timing of cladogenesis. Note that *Carpomegodon jepseni* (Ti-4) is the sister taxon to the clade that includes *Carpolestes dubius*, *C. nigridens*, and *C. simpsoni*, which represent an ancestor-descendant lineage spanning the late Tiffanian (Ti-5) through Clarkforkian NALMAS.

stratocladistic hypotheses) was that p2 appears to have “re-evolved” in *C. oriens*. In support of this is a suite of derived characteristics that would preclude *C. oriens* from branching lower down in the clade (thereby rendering the presence of p2 a shared-primitive condition). As is always the case in phylogenetic analysis, we recognize that our understanding of this particular relationship might change as more carpolestids are discovered.

Gingerich’s (1980a) stratophenetic analysis yielded results similar to those of the stratocladistic analysis. As recognized previously (Fisher, 1991) the two methods often converge in their interpretations of relationship for groups with a dense and continuous fossil record. Comparing our analysis with the cladistic analysis of Beard and Wang (1995) there is also substantial agreement. Our few differences are mostly driven by our different reading of morphologic data. In addition, stratocladistics’ view of carpolestid relationships is more highly resolved at the level of phylogenetic trees, with explicit consideration of hypotheses of ancestry and descent, supported by stratigraphic as well as morphologic data.

ACKNOWLEDGMENTS

We thank K. C. Beard, G. F. Gunnell, P. D. Polly, D. L. Fox, M. T. Silcox, R. Secord, H. L. Severson, R. C. Hulbert, and one anonymous reviewer for improvements to the manuscript. We especially thank W. Ryan and W. Sanders for preparation of specimens, B. Miljour for help in preparation of figures, and J. Trapani for assisting with scanning electron microscopy. C. Henderson provided access to the SEM at the University of Michigan Electron Microbeam Analysis Lab (EMAL). The EMAL scanning electron microscope used in this study was funded in part by National Science Foundation Grant EAR-9628196. Field and laboratory research was supported by National Science Foundation grant BSR-8607841 to P. D. G.

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Received 13 February 2000; accepted 25 August 2000.

APPENDIX 1

Description of characters used in phylogenetic analyses. Outgroup taxa were *Purgatorius* and *Pronothodectes*. The cladistic analysis used

Purgatorius to root the preferred cladogram. All characters except character 33 (the stratigraphic character, not used in the cladistic analysis) were unordered. Those characters that were variable within a species were coded as polymorphic. Autapomorphic characters (characters 1, 5, and 15) were included in the stratocladistic analysis, as they can affect hypotheses of ancestry; cladistic results are reported with and without them.

1. Mandible anterior to p4—not foreshortened, with substantial to moderate space both anterior and posterior to the mental foramen (0), or foreshortened, with barely enough room for a mental foramen between the anterior root of p4 and the alveolus of i1 (1).
2. i1—subequal in size to c1 and not strongly procumbent (0), or enlarged relative to c1 and strongly procumbent (1).
3. i1 crown—short and lanceolate (0), moderately long and lanceolate (1), or long and slender (2).
4. Basal cusp on lingual cingulum of i1—absent (0), or present (1).
5. i2—present and aligned with other anterior teeth (0), or vestigial and displaced buccally in relation to other anterior teeth (1).
6. i3—present (0), or absent (1).
7. c1—larger than i2 (0), slightly smaller than i2 (1), or distinctly smaller than i2 (2).
8. c1 anterior projection—weak (0), or strong and touching the crown of i2 (1).
9. p2—present with two roots (0), present with one root (1), or absent (2).
10. p3—subequal in size relative to p4 (0), reduced in size relative to p4 (1), or absent (2).
11. p3—double-rooted, occupying two alveoli (0), or with partially or wholly fused roots, occupying a single alveolus (1).
12. Crown of p3—premolariform and unreduced(0), or button-like and reduced (1).
13. Crown of p4—premolariform, not hypertrophied and not exodaenodont (0), plagiaulacoid, hypertrophied and exodaenodont (1).
14. Metaconid on p4—absent (0), present and posterolingual to protoconid (1), or present and in line with other cusp(s) in the trigonid (2).
15. Paraconid on p4—present (0), or absent (1).
16. Number of accessory apical cusps on p4—none (0), one which, together with the three trigonid cusps, forms a blade with four longitudinally arranged cusps (1), two which, together with the three trigonid cusps, form a blade with five longitudinally arranged cusps (2), three which, together with the three trigonid cusps, form a blade with six longitudinally arranged cusps (3), four which, together with the three trigonid cusps, form a blade with seven longitudinally arranged cusps (4), or five to six which, together with the three trigonid cusps, form a blade with eight to nine longitudinally arranged cusps (5).
17. Labial height of p4 relative to that of m1—low (0), intermediate (1) or high (2).

18. Outline of plagiaulacoid p4 in labial view—gently rounded (0), somewhat pointed (1), or very pointed (2).
19. Posterior apical cusp on crest uniting main shearing blade with talonid cusp of plagiaulacoid p4—near penultimate apical cusp (0), or roughly equidistant between penultimate apical cusp and talonid cusp (1).
20. Posterior apical cusp of plagiaulacoid p4—cuspsate and above a strong vertical rib on lingual face (0), or weak, with slight to no expression of a vertical rib on lingual face(1).
21. Lower molars—not exodaenodont (0), or somewhat exodaenodont (1).
22. Trigonid of m1—triangular, with paraconid in a lingual position (0), subtriangular, with paraconid in a more anterior position (1), anteroposteriorly aligned, with the paraconid directly anterior to the protoconid (2), or anteroposteriorly aligned, with the paraconid directly anterior to the protoconid and trigonid more elongate anteroposteriorly (3).
23. P3—smaller than P4 (0), subequal to or slightly larger than P4 (1), or much larger than P4 (2).
24. P3 protocone—a single, distinct cusp (0), a single weak cusp (1), or accompanied by a hypocone to form two lingual cusps (2).
25. Lingual basin on P3—absent (0), weakly present (1), well developed (2), or well developed and anteroposteriorly enlarged (3).
26. Number of median crests on P3—None (0), one, represented by pre- and postconule cristae (1), two or three, represented by pre- and postconule cristae and one or two more posterolingual crests not continuous across the tooth crown (2).
27. Buccal side of P3—with two cusps, a major cusp followed by a smaller posterior cusp (0), three cusps with anterior cusp separated somewhat from two posterior cusps (1), four cusps with an anterior cusp separated somewhat from three posterior cusps (2), five cusps with an anterior cusp separated somewhat from three posterior cusps and an anterior fifth cuspsule forming a short anteroexternal spur (3), or five cusps with anterior one fully as developed as others, resulting in an elongate anteroexternal spur (4).
28. Occlusal view of P4—triangular (0), subtrapezoidal (1), trapezoidal (2), or square (3).
29. Number of cusps on buccal row of P4—two (0), four (1), or five to six (2).
30. Number of median crests on P4—none (0), one with a distinct central conule (1), two, with the more buccal crest showing a distinct central conule and the more lingual crest represented by pre- and postconule cristae (2), or two, with as many as five nearly equal cusps on the more buccal crest and the more lingual crest represented by pre- and postconule cristae (3).
31. Number of lingual cusps on P4—one (0), or three (1).
32. Preprotocrista on P4—present (0), or absent (1).
33. Stratigraphic Range—Puercan (0), Torrejonian (1), Tiffanian₁ (2), Tiffanian₂ (3), Tiffanian₃ (4), Tiffanian₄ (5), Tiffanian₅ (6), Tiffanian₆ to Clarkforkian₁ (7), Clarkforkian₂₋₃ (8).

APPENDIX 2.

Character matrix used for phylogenetic analyses. Characters that are either not known for a particular taxon, due to incomplete fossil material, or that are not applicable, are treated as missing (“?”).

	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3			
<i>Purgatorius</i>	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0	0	0	0	0	0		
<i>Prionhodectes</i>	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	?	?	0	0	0	0	0	0	0	1	0	0	1	0	0	
<i>Elphidotarsius florencae</i>	0	1	0	0	0	1	1	?	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	0	0	1
<i>Elphidotarsius shotgunensis</i>	0	1	?	?	0	1	1	?	1	1	1	?	1	1	0	1	0	0	0	0	1	1	1	2	2	1	1	?	?	?	?	?	?	2	
<i>Elphidotarsius russelli</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2&3	
<i>Elphidotarsius wightoni</i>	0	1	1	0	1	1	0	1	1	1	?	1	1	0	1	0	1	0	0	0	1	1	1	2	1	1	1	1	1	0	0	2&3&4	0		
<i>Carpodaptes aulacodon</i>	0	1	?	?	0	1	1	?	2	1	1	1	1	2	0	2	1	2	0	0	1	3	?	?	?	?	?	?	?	?	?	?	5		
<i>Carpocristes hobackensis</i>	0	1	1	0	0	1	1	0	2	1	1	1	1	2	0	2	1	0	1	1	2	?	?	?	?	?	?	?	?	?	?	?	6		
<i>Carpodaptes cygneus</i>	0	1	1	0	0	1	1	?	2	1	1	1	1	2	0	2&3&4	1	0	1	0	1	2	1	2	2	2	2	2	2	1	1	4&5			
<i>Carpodaptes hazelae</i>	0	1	?	?	0	1	1	?	2	1	1	1	1	2	0	2&3	1	0	0	1	2	1	2	2	1	2	2	2	1	1	1	2&3&4			
<i>Carpomegodon jepseni</i>	1	1	?	?	1	1	1	?	2	1	1	1	1	2	0	3	2	2	1	0	1	3	2	2	3	2	3	2	3	1	1	5			
<i>Carpolestes dubius</i>	0	1	2	0	0	1	2	1	2	1	1	1	1	2	0	5	2	1	1	1	3	2	2	3	2	3	3	2	3	1	1	6			
<i>Carpolestes nigridentis</i>	0	1	2	?	0	1	2	1	2	1	1	1	1	2	0	5	2	1	1	1	3	2	2	3	2	4	3	2	3	1	1	7			
<i>Carpolestes simpsoni</i>	0	1	2	0	0	1	2	1	2	2	?	?	1	2	0	5	2	1	1	1	3	2	2	3	2	4	3	2	3	1	1	8			
<i>Carpocristes oriens</i>	0	1	?	?	0	1	1	?	1	1	1	1	1	2	0	4	1	0	2	1	1	2	1	2	2	3	3	2	2	3	1	1	8		