

## 41 Hyracodontidae

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### INTRODUCTION

The hyracodonts were a group of rhinocerotoids that flourished during the middle and late Eocene and Oligocene of Eurasia and North America (Radinsky, 1967; Prothero, Guérin, and Manning, 1989; Prothero, 1996). Their most distinctive feature is their elongate limbs. Primitive hyracodonts were about the size of sheep (Figure 41.1) and quite cursorial. One group of hyracodonts, the paraceratherines, grew to gigantic size. An Oligocene hyracodont from Asia, *Paraceratherium* (= *Indricotherium*, *Baluchitherium*) reached 6 m (18 feet) at the shoulder and weighed up to 20,000 kg (Lucas and Sobus, 1989). It was the largest land mammal that ever lived, and probably browsed on the tops of trees. Smaller hyracodonts, however, were among the most cursorial animals of their time. They had relatively simple browsing dentitions, and large herds of them probably roamed the mixed forest-grasslands of the Oligocene, browsing on low vegetation. The hyracodont *Triplopus* was very common in the middle Eocene. Together with the small primitive paraceratherine *Forstercooperia*, it migrated freely between Eurasia and North America. In the late Eocene of North America, there were two genera of hyracodonts. By the late Chadronian, the group was reduced to the small cursorial genus *Hyracodon*, whose last occurrence is in the lowermost Sharps Formation in South Dakota (earliest Arikarean), about 30 Ma (Tedford et al., 1985, 1996).

### DEFINING FEATURES OF THE FAMILY HYRACODONTIDAE

#### CRANIAL

In most features of the skull and skeleton, hyracodonts differ little from more primitive rhinocerotoids, such as *Hyrachyus*. The skull has a well-developed sagittal crest, slender but flaring zygomatic arches, an unretracted nasal notch and elongate nasal bones,

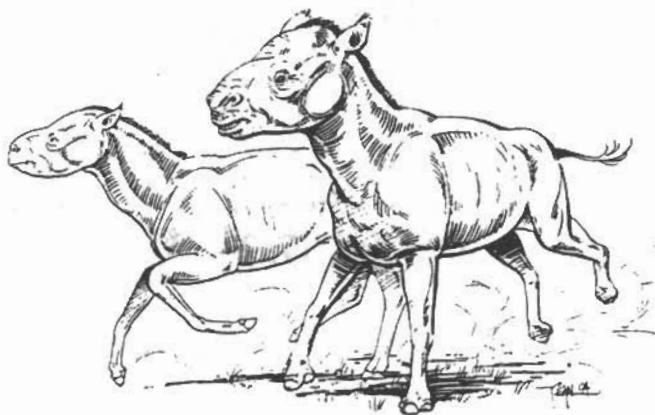


Figure 41.1. Restoration of *Hyracodon*, by Brian Regal.

and a deep mandible with an upward-curved symphysis (Figure 41.2A).

#### DENTAL

Most genera had a full complement of incisors and canines, which were small spatulate or conical teeth. A few of the more specialized forms lost incisors and developed other anterior teeth into tusks. There is typically a short diastema between the anterior and cheek teeth, and in some taxa, both the rostrum and the symphysis are laterally constricted. The upper molars show the characteristic rhinocerotoid pi pattern formed by are were not fully molarized, and there are various combinations of crests uniting the protocone and hypocone. The most characteristic tooth is the M3, which has a highly reduced, lingually deflected metacone, not the large, labially deflected ridge of amynodonts or the triangular M3 without a metastyle of rhinocerotids. Most hyracodont molars also have reduced parastyles. The lower dentition shows the stereotyped rhinocerotoid pattern of L-shaped paralophids and metalophids connecting the cusps of the trigonid and talonid, and are not diagnostic of the group.

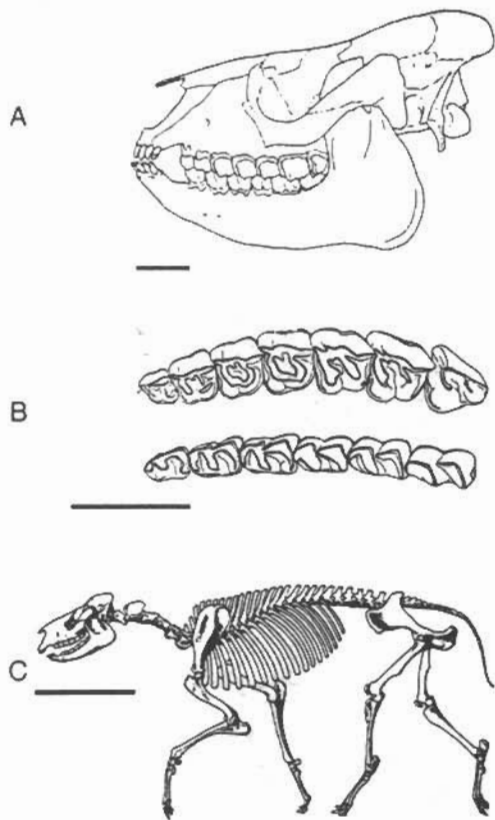


Figure 41.2. Osteology of *Hyracodon nebraskensis*. A. Skull and mandible (scale bar = 5 cm). B. Upper and lower dentitions in crown view (scale bar = 5 cm). C. Articulated skeleton (scale bar = 50 cm). (After Scott, 1941.)

### POSTCRANIAL

The skeleton is generally primitive in overall proportions and not very different from that of *Hyrachyus*, except in one area. Hyracodont limbs and particularly the feet are much more elongate and gracile than those found in any other group of rhinocerotoids. All hyracodonts have a tridactyl pes, unlike amynodonts and primitive rhinocerotids. The metapodials are long and slender (or laterally compressed), a sure indication of a more cursorial habit. The family Hyracodontidae is primarily diagnosed by its limb proportions. Ironically, these proportions persist even when individual taxa become gigantic. The largest indricotheres still had long limbs and toes, even though they were larger than graviportal elephants, titanotheres, rhinocerotids, and even most dinosaurs, whose metapodials are greatly compressed dorsoventrally. The gigantic indricotheres are a clear example of how inherited patterns can persist in a group, even after they have moved to a completely different adaptive niche. Anatomy is not infinitely adaptive and plastic, but subject to inherited constraints.

### SYSTEMATICS

#### SUPRAFAMILY

The family Hyracodontidae was last fully revised by Radinsky (1967). Although I disagree with some of his conclusions and his use

of shared primitive characters, I agree with his choice of inclusion of North American taxa in this family (Figure 41.3). The relationships of the Rhinoceroidea have been discussed by Prothero, Manning, and Hanson (1986). Hyracodontids are clearly the sister group of the Rhinocerotidae, and the Amynodontidae are a more primitive sister taxon. The family Hyracodontidae is defined by the shared derived presence of elongate limbs and metapodials, a tridactyl manus (i.e., metacarpal V greatly reduced), and also by a reduced, lingually deflected metacone on M3.

#### INFRAFAMILY

Two monophyletic subfamilies can be recognized. The subfamily Indricotheriinae includes all the gigantic forms of Eurasia, plus their smaller sister taxon *Forstercooperia* from the middle Eocene of both Eurasia and North America (Lucas, Schoch, and Manning, 1981). They are recognized by their greatly enlarged size, enlarged p1, and reduced M3 metacone (paralleling the rhinocerotids). The subfamily Hyracodontinae includes the smaller, more cursorial forms of the late Eocene and Oligocene of Eurasia and North America. They are defined by their flattened premolar ectolophs and greatly reduced parastyles. Of these, only *Triplopus* is common in the middle Eocene, and *Hyracodon* in the late Eocene and Oligocene; the other two taxa are known only from a few localities.

#### INCLUDED NORTH AMERICAN GENERA IN THE FAMILY HYRACODONTIDAE

The locality numbers listed for each genus refer to the list of unified localities in Appendix I. The acronyms for museum collections are listed in Appendix III.

The locality numbers may be listed in a couple of alternative ways. Parentheses around the locality (e.g., [CP101]) mean the taxon in question at that locality is cited as an "aff." or "cf." the taxon in question. Parentheses are usually used for individual species, thus implying the genus is firmly known from the locality, but the actual species identification may be questionable. Question marks in front of the locality (e.g., ?CP101) mean the taxon is questionably known from that locality, thus implying some doubt that the taxon is actually present at that locality, either at the genus or the species level.

#### INDRICOTHERIINAE

##### *Forstercooperia* Wood, 1939

Type species: *Forstercooperia totadentata* (Wood, 1938).

Type specimen: AMNH 20116.

Characteristics: As discussed by Lucas, Schoch, and Manning (1981), *Forstercooperia* is a small indricothere found in the middle and late Eocene of both Asia and North America. It is the primitive, small sister taxon of all the giant Oligocene indricotheres. The nasal incision is above the canine, and the upper incisors are conical and pointed. Unlike most indricotheres, it has a full dentition with unmolarized P3. The M3 metacone is variable, but usually absent. Its crown height index is about 0.6. The manus is fully tridactyl.

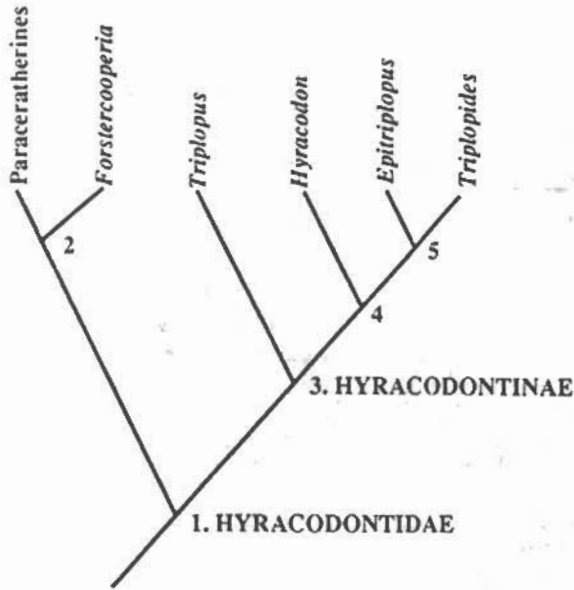


Figure 41.3. Interrelationships of the Hyracodontidae (after Prothero, Manning, and Hanson, 1986). Characters at the nodes are as follows: (1) HYRACODONTIDAE: tridactyl manus; long limbs and metapodials; laterally compressed carpus and tarsus. (2) INDRICOTHERIINAE: Large size; enlarged p1; M3 metacone reduced. (3) HYRACODONTINAE: flattened premolar ectolophs; parastyles further reduced. (4) Increased hypsodonty (crown height index greater than 0.75); labial cingulum on P3–4; P1 replaces dP1; p1 rarely present; paracone folded toward parastyle on M1–2; p2–4 labial cingula; high paralophids and metalophids; sharply constricted symphysis and rostrum. (5) Lower canine reduced; elongate narrow M2; oblique cross lophs; M1–2 metacones deflected labially with sharp crease; trace of M3 metacone lost.

Average length of M2: 19.0–26.0 mm.

Included North American species: *F. grandis* (known from localities CP6A, CP38C); *F. minuta* (localities SB25B, CP36B).

Comments: In a paper published after this manuscript was submitted, Holbrook and Lucas (1997) claim that the North American specimens of *Forstercooperia* do not belong to this taxon, but to a new taxon, *Uintaceras radinskyi*, that forms the sister taxon of the Rhinocerotidae. If their assertions are correct, Indricotheriinae are confined to the Asian subcontinent.

### HYRACODONTINAE

#### *Triplopus* Cope, 1880

Type species: *Triplopus cubitalis* Cope, 1880.

Type specimen: AMNH 5095.

Characteristics: *Triplopus* is the commonest rhinocerotoid from the Uintan of North America. It was once greatly oversplit taxonomically, but most of the invalid genera and species have been eliminated by Radinsky (1967). *Triplopus* has almost no derived characters of its own, but is diagnosed by its size (slightly larger than *Hyrachyus* and smaller than later rhinocerotoids), its equal-sized spatulate

incisors, and a very faint metacone on M3. As the name implies, the manus is tridactyl.

Average length of M2: 11.0–17.3 mm.

Included species: *T. cubitalis* (known from locality CP38C); *T. obliquidens* (= *T. amararum*) (localities CP6A, CP6B, CP38D); *T. woodi* (localities CC9C, CC9BB); *T. implicatus* (localities [SB44A], CP6B, CP38C); *T. rhinocerinus* (localities [SB43A], [NP22]).

*Triplopus* sp. is also known from localities SB43B, CP65.

#### *Hyracodon* Leidy, 1856

Type species: *Hyracodon nebraskensis* (Leidy, 1850).

Type specimen: USNM 336207.

Characteristics: *Hyracodon* is diagnosed as a medium-sized hyracodontid, with pointed incisors and small canines. The dP1 is replaced by P1, and p1 is usually lost. Premolar and molar paracones are not separated posteriorly from the ectolophs. M1–M2 have a large antecrochet and protocone set off with vertical grooves. M3 has a persistent small metacone.

Average length of M2: 15.0–25.0 mm.

Included species: *H. nebraskensis* (known from localities CP40A, CP40B, CP41A, CP41B, CP68B, CP68C, CP68D, CP84A, CP84B, CP84C, CP85C, CP98B, CP98C, CP99A, CP99B, CP99C, NP10B, NP50C); *H. primus* (localities SB44B, SB44C, SB44D, CP7C, CP42A); *H. petersoni* (= *H. selenidens*) (localities SB43E, SB44E, CP39IIA, CP42A, CP98A, NP10A, NP10B); *H. priscidens* (localities [CP39B], CP39C, [CP39F], CP39G, CP42A, [CP83A], [CP83B], CP83C, NP10B, NP24C, NP25C); *H. leidyanus* (localities CP68D, CP84B, CP84C, CP85C, CP99B).

*Hyracodon* sp. is also known from localities ?SB52, (CP43), ?CP45A, CP83C, CP85A, CP86A, CP99C, NP9A, NP24E, (NP25B), NP27C, NP32B.

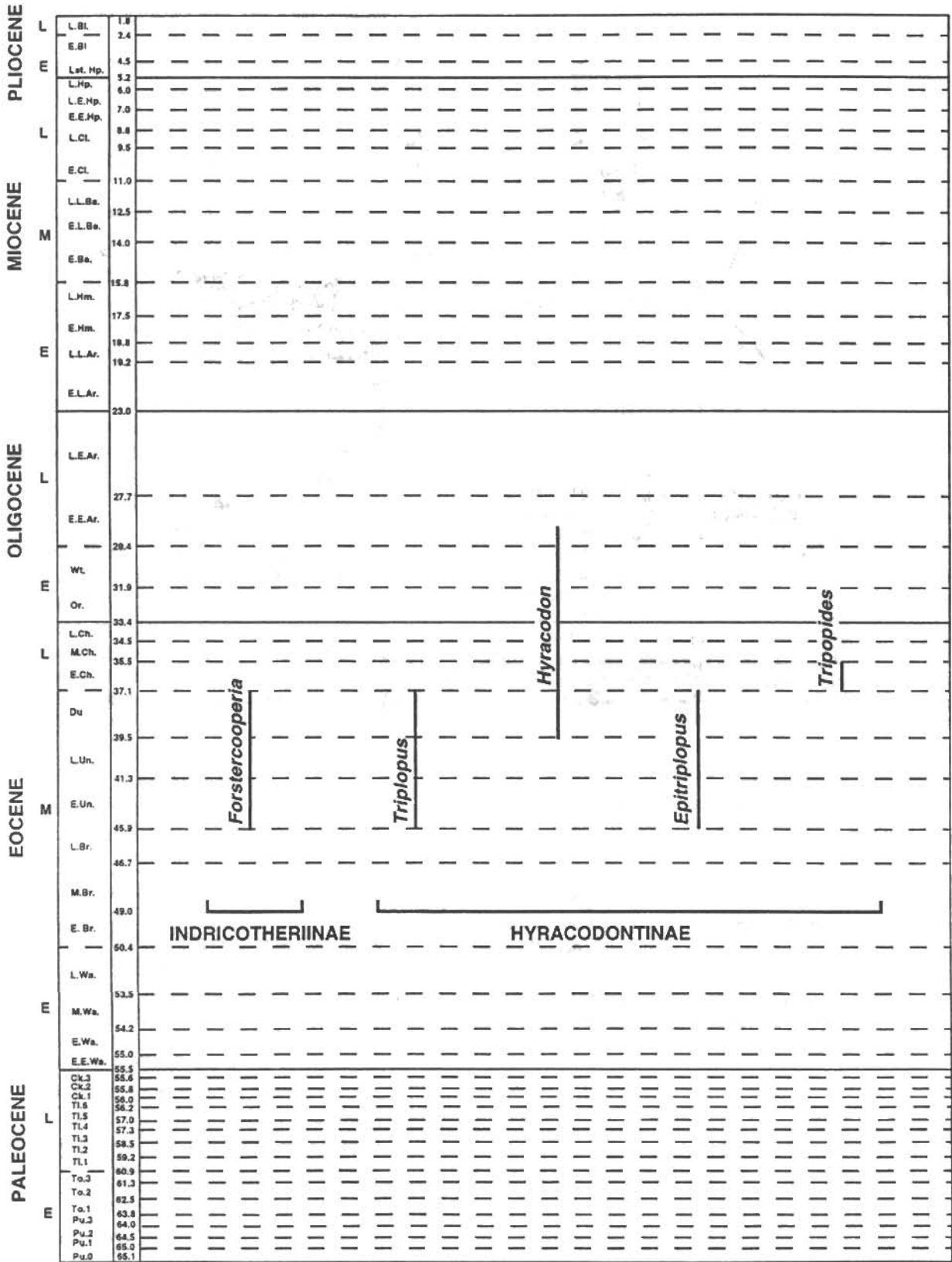
Comments: *Hyracodon* (see Figures 41.1, 41.2) is the most common and best known of the hyracodontid rhinoceroses because many skulls and skeletons have been found in the White River beds of the High Plains. It is the largest of the hyracodontine hyracodonts and also the most cursorial. It is known from the Duchesnean to the latest Whitneyan (about 40–30 Ma), so its 10-million-year range is among the longest in the mammals. The genus was greatly oversplit based on subtle variations in the upper premolars, leading Radinsky to lump them all into one species. Many authors (e.g., Wilson and Schiebout, 1984) considered this lumping to be excessive, and I recognize only five easily distinguished species (Prothero, 1996).

#### *Epiptriplopus* Wood, 1927

Type species: *Epiptriplopus uintensis* (Peterson, 1919).

Type specimen: CMNH 3007a.

Characteristics: *Epiptriplopus* is a small, relatively hypsodont (crown height index = 0.78) hyracodontid from the late Uintan and Duchesnean. It is recognized by its upper molars, which have curved cross crests and paracones projecting labial to the parastyles. M1–M2 are relatively long and



Bl.=Blancan, Hp. = Hemphillian, Cl.= Clarendonian, Ba.= Barstovian, Hm.= Hemingfordian, Ar. = Arikareean, Wt. =Whitneyan, Or.= Orellan, Ch. = Chadronian, Du.= Duchesnean, Un. = Uintan, Br. = Bridgerian, Wa. = Wasatchian, Ck. = Clarkforkian, Tl. = Tiffanian, To. = Torrejonian, Pu. = Puercan.

Figure 41.4. Temporal ranges of North American hyracodontid genera.

narrow, with a pronounced antecrochet. The M3 metacone is completely lost.

Average length of M2: 11.3 mm.

Included species: *E. uintensis* only (known from localities CP6B, CP7A, CP7C, CP29C, [CP36]).

#### *Triplopides* Radinsky, 1967

Type species: *Triplopides rieli* Radinsky, 1967.

Type specimen: CMNH 9370.

Characteristics: *Triplopides* is a small hyracodontid from the early Chadronian McCarty's Mountain locality in Montana. It is known from the type skull, which is badly crushed and missing the dorsal portion, and a mandible. The incisors are very spatulate, and the canine is small and slender. The premolars are greatly shortened relative to the molars, and both upper and lower first premolars are lost. As in *Epitriplopus*, the cross crests are obliquely deflected and the M1–M2 are very long and narrow. The paracones on these teeth project labially, and the protocones are not constricted. M3 has no trace of a metacone.

Average length of M2: 25.0 mm.

Included species: *T. rieli* only, known from locality NP25C only.

#### INDETERMINATE HYRACODONTIDS

Fragmentary remains ascribed to hyracodontids have also been reported from localities CC7B, CP46, NP9, NP22, NP29C, CP86A.

#### BIOLOGY AND EVOLUTIONARY PATTERNS

As many authors have noted, the elongate limbs and feet of hyracodonts clearly indicate that they were among the most cursorial ungulates in the late Eocene and Oligocene of North America. Their limb proportions are comparable with the horses of their time. Their teeth are among the most hypsodont of any mammal of the time, so they may have been able to browse on tougher vegetation. The total sample size of hyracodonts has always been small, so it is difficult to make many inferences about their ecology. It is possible they may have roamed in herds, although no mass death assemblages have been found to my knowledge. There is no obvious sexual dimorphism or other indications of unusual social structure. Clark, Beerbower, and Kietzke (1967) were not able to find any particular ecological association for *Hyracodon*. It was rare but present in near-stream, open plains, and swampy plains facies.

*Hyracodon* split into two species in the Whitneyan, the normalized *H. nebraskensis* and the much larger *H. leidyanus* (Prothero, 1996). It then disappears at the end of the Whitneyan, after a 10-million-year history. Its disappearance is probably related to the increase in aridity that marked the late Whitneyan and affected many other persistent White River taxa.

Hyracodontids had a rather peculiar geographic distribution (Figure 35.3). They were apparently very successful in migrating

between North America and Asia during the late Eocene because several genera occur in both regions at the time. Yet within North America, they were very restricted. *Triplopus* occurs in great abundance in the Washakie Basin of Wyoming and in the Uinta Basin of Utah, but was completely absent from the late Eocene of California (Golz and Lillegraven, 1977) and the Clarno Formation of Oregon (which had the oldest North American rhinocerotid, and an amynodont). It was one of many organisms that showed the endemism typical of the Uintan (Lillegraven, 1979). Throughout the Chadronian, Orellan, and Whitneyan, *Hyracodon* remained a rare but ubiquitous member of the fauna. When it vanished, the group also disappeared from North America. In Eurasia, however, the gigantic indricotheres persisted into the early Miocene.

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