Teiid-Like Scincomorphan Lizards from the Late Cretaceous (Campanian) of Southern Utah

RANDALL L. NYDAM1 AND GINA E. VOCI

Department of Basic Sciences, Arizona College of Osteopathic Medicine, Midwestern University, 19555 North 59th Avenue, Glendale, Arizona 85308, USA

ABSTRACT.—Teiid-like scincomorphan lizards from the Late Cretaceous (Campanian) of the Kaiparowits Formation of southern Utah include Chamops cf. Chamops segnis, cf. Leptochamops, a new species of Meniscognathus, and a new taxon with well-developed tricuspid teeth. These taxa comprise some of the only confirmed reports of these types of lizards from Late Cretaceous rocks south of Wyoming, allowing for a more comprehensive investigation of the distributional and evolutionary patterns of teiid-like scincomorphans from the Campanian. The majority of the known taxa are from the Western Interior west of the margin of the midcontinental sea that bisected North America during the Late Cretaceous. The teiid-like scincomorphans from the Campanian comprised two distinct faunas; one in the north (e.g., Montana, Western Canada) and one in the south (e.g., Utah, New Mexico). These two faunas share Chamops and potentially Leptochamops, but each region also has two to four endemic taxa representing a diversity that correlates to latitudinal differences. Teiid-like scincomorphans present in North America prior to the establishment of the midcontinental seaway are not nearly as diverse as during the Campanian, indicating that the radiation of forms followed the establishment of the seaway, although it may not have played a direct role.

Lizards are a common component of the vertebrate fossil record from the Late Cretaceous (specifically Campanian-Maastrichtian; approximately 84–75 mya) of the Western Interior of North America. However, most of these remains have been recovered from the northern United States and southern Canada (Estes, 1964, 1969, 1983; Gao and Fox, 1996; Peng et al., 2001). This Late Cretaceous lizard fauna includes dozens of species of scincomorphan and anguimorphan lizards as well as some of the earliest reports of inguanians (Estes, 1983; Gao and Fox, 1996; Gilmore, 1923; Nydam, 1999a), but the most common lizards in these faunas are the “teiids” or teiid-like scincomorphans (see particularly Estes, 1983; Gao and Fox, 1996). To date, these taxa have been placed in the family Teiidae based on the presence of a hypertrophied splenial as well as the presence of heavy deposits of cementum and subcircular replacement pits at the bases of the teeth (Estes, 1983; Gao and Fox, 1996). Some or all of the fossil taxa have been variably assigned to the teiid subfamilies Tupinambinae and Teiinae (Estes, 1969, 1983), whereas other workers have placed various taxa in equivalent families or subfamilies composed entirely of extinct taxa, such as the Macrocephalosauridae (Alifanov, 1993) and the Chamopsii-nae (Denton and O’Neill, 1995). The results of a phylogenetic analysis by Nydam and Cifelli (2002) indicated that the fossil teiids from North America (and Asia) form a monophyletic clade distinct from the modern teiids, and a more recent analysis has shown that this clade of fossil taxa falls outside of Teiioidea (Nydam et al., in press). For these reasons we have chosen to refer to the taxa described herein as “teiid-like scincomorphans” to recognize the uncertain taxonomic status of these fossil forms.

Within the Western Interior of North America, Campanian-aged (approximately equivalent to the North American Land Mammal ages Aquilian-Judithian) rocks that are known to produce vertebrate fossils are represented by exposures that extend from southwestern Canada to Baja California (Kilmer, 1963; and summary by Lehman, 1997). In the northern United States and southern Canada, investigations into the microvertebrates (small-bodied vertebrates; e.g., small mammals, lizards, amphibians) have been ongoing for more than a century. This has resulted in an extensive record of fossil lizard taxa known from Alberta and Saskatchewan (Gao and Fox, 1991, 1996; Peng, 1997) and Montana and Wyoming (see reviews by Estes, 1983; Gilmore, 1923). Similar investigations of the southern regions have only been occurring regularly for the past 10–20 years, but a moderately diverse record of lizards has been described from Texas (Rowe et al., 1992), New Mexico (Armstrong-Ziegler, 1978, 1980; Sullivan, 1981), Baja California (Nydam, 1999a), and also southern Utah. The reports on lizards from southern Utah have consisted of either new records of polyglyphano-
dontine taxa (unusual scincomorphans with complex teeth; McCord, 1998; Nydam, 1999a) or taxonomic lists (Eaton et al., 1999). Although lacking figures or referrals to voucher specimens, the report by Eaton et al. (1999) indicated that the diversity of lizards from the Kaiparowits Formation was similar to that of the better known lizard faunas of the north. In a continuing effort to investigate the evolution of lizards during the Cretaceous, one of us (RLN) has examined all of the specimens collected from the Kaiparowits Formation and initiated additional collecting of specimens. We report herein on the known teiid-like scincomorphans from the Kaiparowits Formation of southern Utah. These fossils represent both new taxa and materials referable to known fossil taxa and allow for a more detailed examination of evolutionary and distributional patterns through comparison with other teiid-like scincomorphans from the Late Cretaceous.

MATERIALS AND METHODS

The specimens described herein are housed in the collections at either the Sam Noble Oklahoma Museum of Natural History (OMNH), Norman, Oklahoma, or the Utah Museum of Natural History (UMNH), Salt Lake City, Utah. Additional locality data were obtained from the Museum of Northern Arizona (MNA), Flagstaff. Specimens were recovered through bulk sampling and underwater screenwashing following the techniques outlined by Cifelli et al. (1996) and examined using a stereo microscope. Photographs of magnesium oxide coated specimens were taken using a digital camera mounted on a stereomicroscope, and scanning electron micrographs (SEM) were produced using an ETEC Autoscan scanning electron microscope.

GEOLOGICAL SETTING

The Kaiparowits Formation is a series of fine-grained mudstones, sandstones, and friable sandy mudstones exposed primarily in the Kaiparowits Plateau (Eaton, 1991) within the Grand Staircase-Escalante National Monument in Kane and Garfield Counties of southern Utah (Fig. 1). It is underlain by the Wahweap Formation (early Campanian) and overlain unconformably by the Canaan Peak Formation. The depositional environment of the Kaiparowits Formation is interpreted as a series of floodplains associated with a meandering river system west of the midcontinental seaway (Eaton, 1991; Eaton et al., 1987). During the mid- to late Campanian, the western shoreline of the midcontinental seaway was in the vicinity of the current Utah-Colorado border (Lehman, 1997). In a series of badland exposures named

"The Blues" along Utah Highway 12 north of Henrieville (localities 1–3 in Fig. 1), the Kaiparowits Formation has been measured at 840–850 m thick (Eaton, 1991). The age of the Kaiparowits Formation was estimated to be equivalent to the marine invertebrate age of late Campanian (approximately 77–71 mya) as determined primarily through correlations with palynomorphs and terrestrial vertebrate (mammal) fossils (see summary review by Eaton, 1991). 40Ar/39Ar analyses of volcanic ashes from the Kaiparowits Formation have resulted in an age of between 76.1 and 74.0 mya for the
place within the late Campanian (approximating the Judithian North American Land Mammal Age).

The fossils reported herein were recovered from friable mudstones or sandy siltstones associated with overbank flood deposits. Localities OMNH V6, OMNH V9, OMNH V61, and MNA 108 are in the lower-middle Kaiparowits Formation, and OMNH locality V5 is in the upper Kaiparowits Formation. Although the unit is extremely thick, analysis of the mammals and other vertebrates found few differences in faunal components between the lower and upper portions of the unit (Cifelli, 1990a; Eaton and Cifelli, 1988; Eaton et al., 1999). This is likely caused by the apparently rapid sedimentation rates in the Kaiparowits Basin from the erosion of the mountains of the Sevier Orogenic Belt to the west (Eaton and Nations, 1991).

**SYSTEMATIC PALEONTOLOGY**

*Squamata*, Opell 1811  
*Scincomorpha*, Camp 1923  
*Tripennaculus* New Genus

**Type species.**—*Tripennaculus eatoni*, see below.  
**Etymology.**—Latin *Tri*, three; *pinnaculum*, peak or pinnacle. Generic name is in reference to the prominent tricuspid shape of the tooth crowns.  
**Horizon.**—Kaiparowits Formation, Kane County, Utah, Upper Cretaceous (Campanian/Judithian).  
**Diagnosis.**—Differs from all known Cretaceous teiid-like scincomorphans in having strongly tricuspid tooth crowns with mesial and distal accessory cusps nearly as tall as central cusp, mesial and distal accessory cusps curving toward central cusp, mesial and distal accessory cusps separated from central cusp by deep, well-defined sulci on labial and lingual surfaces of tooth crown, central cusp with very strong labial and lingual vertical crenulations. Further differs from *Chamops* in having teeth less widely spaced, lacking barrel-shaped bases.  
**Remarks.**—These differences in tooth crown morphology of *Tripennaculus* and other relevant taxa are of a similar grade to tooth characteristics that have been used (in whole or in part) to distinguish generic-level taxa among teiid-like scincomorphans from the Cretaceous (Estes, 1983; Gao and Fox, 1996) as well as Recent Teiidae (Presch, 1974).

*Tripennaculus eatoni*  
New Genus and Species  
**Figure 2**

**Etymology.**—Species name is in honor of Jeffery G. Eaton who discovered the type locality and has contributed significantly to the study, interpretation, and understanding of the biostratigraphy and paleontology of the Kaiparowits Plateau.

**Holotype.**—OMNH 23146 broken left dentary with six teeth.  
**Referred material.**—OMNH 63128 (paratype), broken left dentary with two teeth.  
**Type locality and horizon.**—OMNH V6, Kaiparowits Formation, Kane County, Utah, Upper Cretaceous (Campanian/Judithian).  
**Diagnosis.**—Same as for genus.  
**Description.**—The holotype, OMNH 23146 (Fig. 2) is a partial left dentary containing six teeth. Tooth attachment is subpleurodont with heavy cementum around the tooth bases. A short subdental shelf (Fig. 2A) extends for the length of the specimen narrowing toward the sixth tooth and then widening again. The subdental shelf borders a wide, shallow subdental gutter (sulcus dentalis). The teeth are relatively closely spaced (closer than in *Chamops*, wider than in *Mensicognathus*). The teeth are weakly recurved and have columnar shafts that are weakly swollen but not barrel-shaped. The tooth crowns are strongly tricuspid with the shorter mesial and distal cusps gently curving toward the central cusp. On the lingual surfaces of the tooth crowns, the mesial and distal cusps have sharp, well-developed, blade-like ridges descending toward the midline of the tooth (Fig. 2B). The ridge of the mesial cusp descends approximately one-third of the crown, and that of the distal cusp descends to less than one-third of the crown. On the labial surface of the tooth crowns, the accessory cusps are separated from the central cusp by short, deep sulci, and the central cusp is less prominent than as on the lingual surface (Fig. 2C). Well-developed vertical crenulations are present on both the labial and lingual surfaces of the tooth crowns and are restricted primarily to the...
central cusp. On the labial surface of the element, there is a large nutrient foramen inferior to the second tooth.

OMNH 63128 is a broken left dentary fragment with two complete and three broken teeth. The sulcus dentalis is narrow and shallow and bordered medially by a tall subdental shelf that narrows posteriorly. The ventral surface of the subdental shelf is grooved for the articulation with the splenial. The meckelian fossa is widely open to the symphysis, indicating a hypertrophied splenial. The labial surface of the dentary is convex and forms a thick ridge paralleling the tooth row and is pierced by two nutrient foramina anteriorly. The teeth are very small, subpleurodont, and have heavy cementum at the bases. The relatively diminutive size of the specimen likely indicates that it is a juvenile.

*Meniscognathus* Estes 1964  
*Meniscognathus molybrochoros*  
New Species

**Figure 3A**

*Etymology.*—Greek: *molybros*, blue (lead colored); *choros*, place. The specific name is in reference to “The Blues,” a region of badland exposures of the Kaiparowits Formation where the type and only known specimen was found.

*Type and only known specimen.*—OMNH 23743, broken right dentary preserving six teeth.

*Type locality and horizon.*—OMNH locality V61, Kaiparowits Formation, Upper Cretaceous (Campanian/Judithian), Garfield County, Utah.

**Diagnosis.**—Differs from *Meniscognathus altmani* in having teeth that are strongly recurved.

**Description.**—OMNH 23743 (Fig. 3A) is an anterior portion of a right dentary preserving eight tooth spaces with six pleurodont teeth. The anterior two tooth spaces are empty. The third tooth space contains the base of a tooth missing the crown. The tooth in the fourth tooth space is weakly recurved, unicuspid, and has a mesiodistally expanded tooth crown with two prominent lingual striae that descend from the apex of the tooth. The tooth in the fifth tooth space is also missing its crown. The teeth in the sixth, seventh, and eighth tooth spaces are complete and become increasingly larger posteriorly, are recurved, and have tricuspid crowns with weak lingual striae. At the base of the tooth row is a shallow subdental gutter bordered medially by a tall subdental shelf. The Meckelian fossa is open along the entire length of the specimen, is wide anteriorly, and narrows appreciably just inferior to the preserved unicuspid tooth (Fig. 3A arrow), which indicates the anterior extent of a hypertrophied splenial.

*Chamops* sp., cf. *Chamops segnis* Marsh 1892

**Figures 3B–F**

*Referred material.*—OMNH 23605, broken right maxilla; OMNH 33852 jaw fragment with two teeth; OMNH 23201, jaw fragment; UMNH VP 18062, broken left dentary.

*Locality and horizon.*—OMNH localities V6 (OMNH 23605) and V9 (OMNH 33852), Kaiparowits Formation, Kane County, Utah, Upper
Cretaceous (Campanian); MNA locality 108, Kaiparowits Formation, Kane County, Utah, Upper Cretaceous (Campanian).

Description.—Although the material on hand is fragmentary, all of the specimens preserve teeth that are characteristic for Chamops (as per the revised diagnosis of Gao and Fox, 1996); subpleurodont, well-spaced, becoming tricuspid posteriorly, bases swollen and barrel-shaped. OMNH 23605 (Fig. 3B) is the anterior portion of a right maxilla preserving a narial boss that encloses the posterior opening of the anterior superior alveolar foramen (just superior to the small posterior tooth). The supradental shelf is mediolaterally wide but not tall, and the facial process has a steep anterior angle suggesting that the naris was not greatly retracted. There are four tooth spaces preserved but only two complete teeth. The anteriormost tooth space retains the base of a broken tooth. The anteriormost preserved tooth (next tooth space posterior) is large (slightly recurved) and has a base of similar dimensions to the broken base just anterior. The posteriormost preserved tooth occupies the space just posterior to the other complete tooth. This tooth is less than half the size of its neighbor and is firmly ankylosed to the lateral parapet. The next tooth space is empty but was occupied by a tooth larger than the small preserved tooth but not as big as the large preserved tooth. OMNH 33852 has two subpleurodont teeth with barrel-shaped bases and crowns with mesial and distal accessory structures that form cusps in larger teeth.

Cf. Leptoclamops Estes 1964

Figures 3G–I

Referred material.—OMNH 23863, isolated tooth; OMNH 64151, maxilla fragment; and OMNH 64152, jaw fragment; OMNH 64152, jaw fragment.

Locality and horizon.—OMNH locality V5, Kaiparowits Formation, Kane County, Utah, Upper Cretaceous (Campanian), OMNH locality V61, Kaiparowits Formation, Garfield County, Utah, Upper Cretaceous (Campanian).

Description.—Both OMNH 64151 and OMNH 64152 are partial jaw fragments each preserving two subpleurodont teeth. In OMNH 64151 (Fig. 3G) the teeth are tricuspid with well-developed mesial and distal accessory cusps. The teeth are straight (no recurve) and have heavy deposits of basal cementum. OMNH 64151 also preserves a portion of a narrow supradental shelf. OMNH 64152 (Fig. 3H) is a jaw fragment that also preserves two straight, tricuspid teeth that are similar in structure to those of OMNH 64151. OMNH 23863 (Fig. 3I) is an isolated tricuspid tooth identical in morphology, albeit substantially larger in size, to the teeth of OMNH 64151 and OMNH 64152.

Tentative referral of these specimens to Leptoclamops is based on the presence of unrecurved, subpleurodont teeth lacking swollen bases but with well-developed tricuspid crowns. However, more complete material is required to confirm this assignment.

Discussion

In their list of microvertebrate taxa recognized from the Kaiparowits Formation, Eaton et al. (1999a) included the teiid-like scincomorphans C. segnis Marsh 1892, Leptoclamops denticulatus Estes 1964, and M. altmani Estes 1964; all taxa that were previously only known from the Maastrichtian of the northern regions of the Western Interior (Estes, 1964, 1983; Estes et al., 1969; Gao and Fox, 1996). Our examination of the specimens recovered from the Kaiparowits Formation supports the recognition of Chamops sp. cf. C. segnis and cf. Leptoclamops, but we are not able to support conclusive species-level identifications for these taxa. The retention of the “cf.” in our species referral for Chamops is because of our uncertainty of the taxonomic importance of the well-developed “step” (marked difference in crown height of two adjacent teeth) in the maxillary tooth row seen in OMNH 23605 (Fig. 3B). This step is more exaggerated than in other described and figured maxillae of C. segnis, but, as noted by Gao and Fox (1996), this a variable feature (absent-moderate step) in Chamops and requires more extensive study. We agree with Eaton et al. (1999a) on the presence of Meniscognathus, but OMNH 23743 is morphologically distinct from M. altmani and represents a new species, M. molybrochoros. In addition to these taxa, we also recognize the new taxon Tripennaculus eatoni.

Chamops segnis and L. denticulatus have both been reported to occur in the Campanian of New Mexico (Armstrong-Ziegler, 1978, 1980; Sullivan, 1981), but in their comprehensive review of the records and occurrences of these taxa, Gao and Fox (1996) found that the Chamops specimens from New Mexico were too fragmentary to be identified beyond Chamops sp. In addition, Gao and Fox (1996) were unable to support species level identifications for any of the Chamops specimens from the Campanian of western Canada, but they did note that Campanian-aged specimens appeared to be more primitive than C. segnis; a hypothesis they based on the assumption that the taller teeth with less swollen bases of the Campanian-aged material represents a less derived condition. Although no less fragmentary than the specimens from New Mexico, we refer the specimens from the
Kaiparowits Formation to *Chamos* sp. cf. *C. segnis* based on the shared diagnostic features in dental morphology (i.e., lower-crowned with the swelling of the tooth bases giving them a barrel-shaped appearance; sensu Gao and Fox, 1996) between the Utah specimens and those described from the Maastrichtian localities from the north (Estes, 1969, 1983; Gao and Fox, 1996).

Gao and Fox (1996) find the identification of *Leptochamops* in the Campanian of New Mexico (Armstrong-Ziegler, 1978, 1980) doubtful because many of the specimens are misidentified amphibians, and none of the lizard material is well enough preserved to assess characters. Although the specimens we identify as cf. *Leptochamops* from the Kaiparowits Formation are also too fragmentary for positive identification, the teeth are well preserved and are more similar to the teeth of known *Leptochamops* jaws than to other taxa. Regardless, the specimens we describe herein indicate that *Leptochamops* was almost certainly present at least in Utah during the Campanian. The record of *Leptochamops* from the northern part of the Western Interior includes *Leptochamops thrinax* Gao and Fox, 1991 and *Leptochamops* sp. cf. *L. denticulatus* from the Campanian and *L. denticulatas* from the Lancian.

*Meniscognathus* has previously been known only by the taxon *M. altmani* from the Maastrichtian of the northern part of the Western Interior (Estes, 1964, 1983; Gao and Fox, 1996). The presence of *M. molybrochoros* sp. nov. in the Campanian of Utah represents not only the oldest record of *Meniscognathus* but is the first documented occurrence of *Meniscognathus* south of Wyoming.

The new taxon, *T. eatoni*, is currently known only from the Kaiparowits Formation. This taxon likely represents regional endemism for teiid-like scincomorphans, which was also noted for some of the mammals described from the Kaiparowits Formation (Cifelli, 1990a,b). Based on our additions to the fossil record, it now appears that *Chamos* and quite possibly *Leptochamops* ranged within the Western Interior from Utah/New Mexico north to southern Alberta during the Campanian (Fig. 4). Furthermore, the presence of *M. molybrochoros* in the Campanian of Utah, preceding the known occurrence of *M. altmani* in more northern latitudes during the Maastrichtian, opens the possibility that *Meniscognathus* evolved in more southerly regions and dispersed north by the Maastrichtian. Similarly, the presence of specimens of *Chamos* referable to *C. segnis* in the Campanian of Utah indicate that at least the morphotype, if not the taxon, was present earlier than previously thought and that the potentially “more primitive” material of *Chamos* sp. from the Aquilan-Judithian of western Canada (sensu Gao and Fox, 1996) may just as likely be a regional variation or unique species.

In his review of the mammals from the Kaiparowits Formation, Cifelli (1990a) found that the composition of the mammal fauna (particularly the scarcity of marsupial taxa) was similar to that of paracontemporaneous mammal faunas from other southerly units (e.g., New Mexico, Texas) but distinct from those of the north. He attributed this difference, at least in part, to possible latitudinal differences in the North American mammal faunas during the Campanian. Similar latitude-based differences have been noted by Lehman (1997) for other vertebrate groups such as dinosaurs, crocodilians, and lizards. Of the 10 recognized taxa of “teiids” from the Campanian of the Western Interior, there are now four recognized taxa (*Chamos*, cf. *Leptochamops*, *Meniscognathus*, *Tripeucnactus*) for Utah/New Mexico and six taxa (*Chamos*, *Leptochamops*, *Soocognathus*, *Sphenosia*, *Gepgonias*, *Grontoseps*) confirmed by Gao and Fox (1991, 1996) for the Montana/Wyoming/Alberta/Saskatchewan region with only *Chamos*, and potentially *Leptochamops*, occurring in both the northern and southern latitudes. This difference in diversity between the north and south is likely caused by latitudinal variation, with *Chamos* and *Leptochamops* being more “cosmopolitan” within the Western Interior, but sampling bias or small scale differences in relative ages (not all localities are exactly the same age) may also influence the diversity. The only known teiid-like scincomorphans from the Campanian of North America outside of the Western Interior is *Prototeius stageri* from the Marshalltown Formation of New Jersey (Denton and O’Neill, 1995). Phylogenetic analysis has supported the relationships of this taxon to other teiid-like scincomorphans (Denton and O’Neill, 1995; Nydam and Cifelli, 2002), but it is clearly distinct from other known teiid-like scincomorphans from the Cretaceous of North America in that it appears to have reduced tooth cuspation during ontogenetic development (Denton and O’Neill, 1995; Gao and Fox, 1996). It is likely that the teiid-like scincomorphans from the Western Interior represent a radiation event that was contained within the west by the midcontinental seaway that bisected North America during the Late Cretaceous.

Teiid-like scincomorphans were also present in the Early Cretaceous of North America. Relatively primitive “teiids” have been reported from the Aptian-Albian (approximately 115–110 mya) of Texas (Winkler et al., 1990) and Oklahoma (Nydam, 1999b) and a more derived form, the *Chamos*-like taxon *Harmodontosaurus*...
Fig. 4. Map of the distribution of lizard producing localities from the Campanian of North America with approximate shape of landmasses in white and oceans in gray. (A) Oldman Formation; Dinosaur Provincial Park; (B) Oldman Formation, Irvine; (C) Milk River Formation; (D) Judith River Formation; Blackbird Ridge; (E) Kaiparowits Formation, Grandstaircase Escalante National Monument; (F) Fruitland Formation; San Juan Basin; (G) Marshalltown Formation, Ellisdale; (H) Aguja Formation; Big Bend; (I) El Gallo Formation; El Rosario. A–G have produced teiid-like scincomorphans; H and I lack “chamopsiine” teiid-like scincomorphans but have produced polyglyphanodontines. (C) is from early to mid-Campanian; (A, B, D–I) are from mid- to late Campanian. (A–D) from Gao and Fox (1996); (E) from this study; (F) from Lehman (1997); (G) from Denton and O’Neil (1995); (H) from Rowe et al. (1992); and (I) from Lilligraven (1972).
emergensis, is known from the Alban-Cenomanian boundary (98.5 mya, Cifelli et al., 1997) of central Utah (Nydam, 2002). These records all predate the transgression of the midcontinental seaway (mid- to late Cenomanian) and indicate that a potential source of teiid-like scincomorphan lizards existed in North America prior to the separation of the western and eastern portions of North America.

With the inclusion of the records of teiid-like scincomorphan lizards from southern Utah, the fossil record for the Campanian west of the midcontinental seaway demonstrates a relatively uniform level of moderate diversity of these lizards along the Western Interior. In addition, there is also clearly some localized endemism, which is reflective of, if not a function of, latitudinal differences. There is no evidence that any of the teiid-like scincomorphan taxa from North America survived the K/T extinction event that marked the loss of the dinosaurs at the close of the Cretaceous.

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