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Early Evolution, Stratigraphy and Taxonomy of *Eiffellithus eximius* and Closely-Related Species

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With 1 Figure, 1 Table and 2 Plates

Evolution Calcareous nannofossils Mid Cretaceous

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Zusammenfassung

Eiffellithus eximius entwickelte sich vor dem ersten Auftreten von *E. turriseiffelii* im späten Alb und nicht im mittleren oder späten Turon wie in der Literatur oft zitiert. Diese Beobachtung basiert auf Untersuchungen an Ober-Alb- und Unter-Cenoman-Proben von N-Texas und S-Oklahoma. Merkwürdigerweise sind aus dem mittleren und oberen Cenoman keine Funde von *E. eximius* bekannt geworden. *E. eximius* wurde bereits öfters an der Cenoman/Turon-Grenze gefunden. Auch wir haben auf diesem Niveau in zwei Profilen des "Western Interior" der USA, im italienischen Cismon-Profil sowie am DSDP-Standort 551 (Nord-Atlantik) einige wenige Exemplare von *E. eximius* gefunden.

Wir glauben, daß die Angaben über das Erstauftreten von *E. eximius* nach dem Alb in Wirklichkeit Häufigkeitsmaxima sind und daß das wirkliche erste Auftreten oft wegen der Seltenheit von *E. eximius* im untersten Teil seiner stratigraphischen Verbreitung, wo er möglicherweise auch paläobiogeographisch beschränkt war, nicht gefunden wurde.

Die hohe morphologische Variabilität der Eiffellithiden während des mittleren Albs und frühen Cenomans erschwert die taxonomische Zuordnung vieler Formen. Folgende leicht betimmbare "end members" treten in unserem Material auf: *E. eximius, E. turriseiffelii* und *Vagalapilla matalosa*. Die zahlreichen Zwischenformen, die ebenfalls gefunden wurden, sind schwierig zu klassifizieren.

Wir mahnen zur Vorsicht beim stratigraphischen Gebrauch des ersten Auftretens von *E. eximius*. Dies basiert auf Problemen, die sich aus dem seltenen und diskontinuierlichen Auftreten dieser Art in ihrem untersten Verteilungsbereich und auf taxonomische Schwierigkeiten, die sich aus hoher morphologischer Variabilität und Unterschieden in der Erhaltung ergeben.

Abstract

Eiffellithus eximius envolved prior to the late Albian first appearance datum of *E. turriseiffellii*, not in the middle to late Tu-

ronian time as is often reported in the literature. This observation is based on well-preserved samples from the upper Albian and lower Cenomanian of northern Texas and southern Oklahoma. Curiously, no middle to late Cenomanian occurrences of *E. eximius* have been reported. *Eiffellithus eximius* has been observed previously at the Cenomanian/Turonian boundary, and we confirm rare occurrences at this level from two sections from the Western Interior of the United States, the Cismon section of Italy and DSDP Site 551 (North Atlantic Ocean).

We believe that the post Álbian "first appearance datums" of *Eiffellithus eximius* reported in the literature are actually abundance acmes, and that the true first appearance datum is commonly not found because of low abundance, spotty occurrence and paleogeographic restriction within the lower stratigraphic range of this species.

High morphological variability within middle Albian to early Cenomanian eiffellithids makes taxonomic assignment of many forms difficult. Easily-identified end-member species in the samples studied include *Eiffellithus eximius*, *E. turriseiffelii* and *Vagalapilla matalosa*. Numerous, difficult-to-classify, morphologicallyintermediate forms were also observed.

We urge caution when using the first appearance datum of *Eiffellithus eximius* stratigraphically because of problems associated with rare and inconsistent occurrences within its lower range and taxonomic difficulties resulting from high morphologic variability and differences in preservation.

1. Introduction

Eiffellithus turriseiffelii and *E. eximius* are commonly used as biostratigraphic markers in nannofossil studies (e.g. THIERSTEIN, 1976; MANIVIT et al., 1977). Whereas the upper Albian FAD (first appearance datum) of the former is well established, the FAD of the latter is problematic.

Difficulties in determining the FAD of *E. eximius* result partly from the paucity of continuously-exposed, fossiliferous upper Albian through Cenomanian sections, and from taxonomic inconsistencies attributable to the

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gradation between *Eiffellithus eximius* and other eiffellithid species.

To reduce the stratigraphic and taxonomic confusion within the *Eiffellithus eximius/E. turriseiffelii* group, we

- chart the stratigraphic ranges of various eiffellithid species in this and previous studies;
- review the taxonomy of key eiffellithid end-member species and several intermediate forms, and illustrate a wide range of morphologic variability; and
- 3) suggest that extreme caution be exercised if using the first appearance of *E. eximius* stratigraphically since its occurrence is spotty and its abundance extremely variable throughout its range.

2. Stratigraphic Ranges of Eiffellithid Species

Variations in interpreted ranges for a given species can result from many factors, including:

1) lack of independent time control;

- 2) preservational bias;
- 3) varying paleobiogeographic distributions;
- 4) differing taxonomic concept.

All these possibilities have contributed to the variation in ranges cited for *Eiffellithus eximius* in the literature.

Table 1 and Figure 1 illustrate the stratigraphic distribution of our samples and the ranges of various eiffellithid species in this and in previous studies.

E. eximius and forms transitional with *E. turriseiffelii* occur in the Albian Duck Creek Formation of Texas prior to the first occurrence of *E. turriseiffelii*, which does not occur in the Duck Creek Formation. *E. eximius, E. turriseiffelii* and forms transitional between them occur in the overlying Fort Worth Limestone, Denton Marl, Weno Formation and Pawpaw Shale. These formations are considered late Albian/early Cenomanian in age based on macrofossils (PERKINS, 1960; CLARK, 1965; YOUNG, 1966).

Based on his morphometric data, VERBEEK (1977) recorded specimens we would classify as *E. eximius* from the Albian El Burrueco section in Spain (Fig. 1).

Although STOVER (1966) indicated that *E. eximius* originated in the basal Turonian, we found this species in his Sample 18, a lower Cenomanian marl (Table 1; Fig. 1).

E. eximius has an apparent FAD at the Cenomanian/ Turonian boundary in two Western Interior sections with good macrofossil control (Blue Point, Black Mesa, Arizona; Rock Canyon, Colorado). In both cases, transitional forms between *E. eximius* and *E. turriseiffelii* occur well below the boundary. *E. eximius* occurs in the Turonian directly above the Cenomanian/Turonian boundary black shale horizon at DSDP Site 551 and in the Cismon section of Italy. In all cases *E. eximius* is very rare in basal Turonian samples. We advocate that this occurrence and the apparent FAD of *E. eximius* within the middle to late Turonian in several biostratigraphic studies (e. g. THIERSTEIN, 1976; MANIVIT et al., 1977) actually represent an increase in relative abundance.

Neither we nor previous authors have observed *E. eximius* in middle or upper Cenomanian samples. Consequently, an apparent gap in the range of this species exists (Fig. 1). Since neo-Darwinian evolutionary theory holds that an individual species cannot have a gap in its range, previous authors have

- assigned the pre-Turonian form another name (e. g. STOVER, 1966; PERCH-NIELSEN, 1977; PRINS, personal communication, 1985);
- lumped *E. eximius* with another species (e.g. VER-BEEK, 1977);
- 3) ignored the problem (ROTH, personal communication, 1985).

Although we agree with the concept that gaps in the true range of a species cannot exist, we believe that it is artificial to erect a new species on the basis of a discontinuous range when it is impossible to differentiate the new "species" on morphological characteristics. The relatively short middle to upper Cenomanian gap in the range of *E. eximius* may be apparent rather than real; resulting from incomplete sampling or very low abundance.

Ranges of transitional forms between *E. turriseiffelii* and *E. eximius* are generally consistent among this study, VERBEEK (1977) and PERCH-NIELSEN (1979). In all three studies, these transitional forms occur throughout the Cenomanian to Coniacian interval.

Early in this study, we attributed high eiffellithid diversity in the Duck Creek Formation (several "end members" plus several "transitional" forms) to excellent preservation and speculated that previous authors had not described *E. eximius* from Albian and Cenomanian samples because they lacked material as well preserved as ours. We now believe, however, that *E. eximius* is so similar in construction to *E. turriseiffelii* that neither would be preferentially dissolved or overgrown. We speculate, that *E. eximius* is much more restricted paleobiogeographically than *E. turriseiffelii*, and that "FADs" recorded for *E. eximius* from the Turonian are actually acmes and that the true first appearance is commonly not recog-

Table 1. Camples studied and	Table 1: Samples studied and sample of earliest age in which Eiffellithus eximius occurs.				
Locations*)	Samples**)	Age of earliest occurrence	Reference		
France	4, 14, 18, 19, 25	early Cenomanian (18)	STOVER (1966)		
Winnett, Montana	1 sample	Santonian (Loc. 11)	OBRADOVICH & COBBAN (1975		
Texas and Oklahoma	HTL6238-6310	late Albian (HTL6300)	HILL (1976)		
Rock Canyon Section, Colorado	0, 2, 7, 22, 32, 46, 60, 63, 76, 78, 82, 85, 92, 111	Cenomanian-Turonian boundary (78)	KAUFFMAN (1977)		
Cismon Section, Italy	14 samples	Cenomanian-Turonian boundary (790.8 m)	CHANNELL et al. (1979)		
Blue Point Section, Black Mesa, Arizona	17 samples	Cenomanian-Turonian boundary (38B)	PRATT & THRELKELD (1984)		
DSDP Site 551	3 samples	Čenomanian-Turonian boundary (5−2, 18 cm)	BRALOWER (in preparation)		

*) For specific locations and maps, see original reference.

**) Samples studied are listed in numerical order. See original reference for the stratigraphic order.

STAGE	AGE RANGE OF SAMPLES EXAMINED THIS STUDY	VAGALAPILLA ANGUSTAª	ANGUSTA/ EXIMIUS	EXIMIUS	EXIMIUS/ TURRISEIFFELI	TURRISEIFFELI
		1 2 3 4*	3 4	1234	1 3 4	1 2 3 4
CONIACIAN	Ť					
TURONIAN	- 1111				I	
CENOMANIAN	E (STOVER. 1966) TEXAS & OKLAHOMA (HILL, 1976) COLORADO (KAUFFMAN, 1977) COLORADO (KAUFFMAN, 1977) COLORADO (KAUFFMAN, 1977) COLORADO (KAUFFMAN, 1977) COSMON SECTION ITALY (CHANNELL, et al., 1979) ARIZONA (PRATT & THRELKELD, 1984) DSDP SITE 551 (BRALOWER, in prep.)		Т			
ALBIAN			Image: Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image of the system Image o			
FRANCE (STOVER, 1966) T TEXAS & OKL			a. WE CONSIDER THIS SPECIES TO BE A SYNONYM OF <i>E. eximius.</i> b. LOWER RANGE CONSISTS OF <i>E.</i> sp. 1 AND <i>E.</i> sp. 3. c. LOWER RANGE DETERMINED THIS STUDY. d. LOWER RANGE INTERPRETED FROM VERBEEK'S MORPHOMETRIC DATA. e. RANGE IS FOR <i>E.</i> sp. 2.			

nized because of low abundance and spotty occurrence within its lower stratigraphic range.

3. Taxonomy

Our concept of *Eiffellithus eximius* is discussed in detail in the **Systematic Paleontology** section below. Previous authors have observed specimens similar to those we consider to be Albian *E. eximius* (i. e. VERBEEK, 1977; PERCH-NIELSEN, 1979; PRINS, personal communication, 1985) but did not record them as such because of the slight differences in taxonomic concepts and the lack of continuity with Turonian occurrences.

HILL (1976, pl. 6, figs. 19-33) first recorded *E. eximius* from the same Albian and lower Cenomanian samples studied here. One of the specimens figured as *E. eximius* is virtually identical to *Zygolithus angustus* STOVER (1966, pl. 3, fig. 14) (herein considered a synonym of *E. eximius*), another is a transitional form, and another is virtually identical to the figured *E. eximius* holotype of STOVER (1966, pl. 2, fig. 15); (see **Systematic Paleon-tology**, below).

VERBEEK (1977) apparently recorded species in the Albian-Cenomanian El Burrueco section (southern Spain) that are identical to those we have observed. He systematically recorded bar angle with respect to the major axis and openness of the central area. Virtually every combination of central area, from fully open to fully closed, was documented with bar angles ranging from 0 to 60 degrees. VERBEEK assigned names only to the most common "end member" species, and we suspect that since *E. eximius* was rare, he did not identify it.

PERCH-NIELSEN (1979, fig. 12) published sketches and stratigraphic ranges of 12 *Eiffellithus* species and related forms. Two of her middle to late Albian species (*E.* sp. 1 and *E.* sp. 3) fit our concept of *E. eximius*. These species were originally drawn by PRINS (unpublished) who differentiated them from *E. eximius* on the basis of a higher number of central area elements (PRINS, personal communication, 1985). We have been unable to document these differences with either the light microscope or SEM.

Preservation markedly affects the openness of the central area in *Eiffellithus* species and has thereby influenced taxonomic concepts. STOVER (1966) originally described *E. eximius* from a Santonian chalk sample in which all nannofossils are secondarily overgrown with calcite. The illustrated holotype (STOVER, 1966, pl. 2, figs. 15a-c) is a typical overgrown specimen, having a thick rim and central area which appear bright white, yellow and blue in crossed nicols. We found no specimens with open or half-open central areas in STOVER's sample and so do not know whether "transitional" forms existed prior to the secondary precipitation of calcite.

An "evolutionary" trend toward an increasingly-closed central area (which may be related to preservation) was described in the EI Burrueco section by VERBEEK (1977, p. 18). Regarding the preservation in his samples, VER-BEEK stated:

"The preservation of the fossils is generally rather poor, because of overgrowth with secondary calcite, especially in the upper part of the section, which consists of limestones".

Central areas in *E. eximius* ranged from fully open to fully closed in our samples from Texas and Oklahoma.

However, forms with open central areas were much more common, exceeding those with closed central areas by about two orders of magnitude. Specimens with closed central areas always appeared to be more secondarily overgrown than those with open central areas. This observation leads us to conclude that preservational factors greatly affect central area size; therefore, the taxonomy of eiffellithids should not be based on central area openings.

4. Systematic Paleontology

Division HAPTOPHYTA Class COCCOLITHOPHYCEAE Order EIFFELLITHALES Family EIFFELLITHACEAE

Genus Eiffellithus REINHARDT 1965

Eiffellithus eximius (STOVER) PERCH-NIELSEN

(Pl. 1, figs. 2-8; Pl. 2, figs. 1-4)

- 1966 Clinorhabdus eximius STOVER, p. 138, pl. 2, figs. 15-16; pl. 8, fig. 15.
- 1966 Zygolithus angustus STOVER, p. 147, pl. 3, figs. 14-15; pl. 3, fig. 22.
- 1968 Eiffellithus eximius (STOVER) PERCH-NIELSEN, p. 30, pl. 3, figs. 8-10.
- 1969 *Eiffellithus angustus* ВUKRY, p. 51, pl. 28, figs. 10-12; pl. 29, fig. 1.
- 1971 Eiffellithus dennisoni WORSLEY, p. 1307, pl. 1, figs. 11–13. 1976 Eiffellithus eximius (STOVER) PERCH-NIELSEN. HILL, p. 139;
- pl. 6, figs. 24–29; non figs. 19–23, 30–34. 1976 Eiffellithus dennisoni? WORSLEY. WISE & WIND, pl. 55, figs.
- 1-3. 1977 Vekshinella angusta (STOVEB) VERBEEK p. 96 pl. 6
- 1977 Vekshinella angusta (STOVER) VERBEEK, p. 96, pl. 6, figs. 11-12.
- 1979 Eiffellithus sp. 1 PERCH-NIELSEN, p. 243.
- 1979 Eiffellithus sp. 3 PERCH-NIELSEN, p. 243.
- Comments: *Eiffellithus eximius* is very similar in construction to *E. turriseiffelii* but differs by having the crossbars oriented more nearly with, rather than 45 degrees from the principal axes. VERBEEK (1977) used two criteria to differentiate these species:
 - the angle of the longest crossbar relative to the principal axis of the rim: when 0 to 20 degrees = *E. eximius*, when greater than 20 degrees = *E. turriseiffelii*; and
 - 2) the presence of slightly forked crossbar tips in *E. eximius*.

Our species concepts are in accord with this description and the illustrations of other authors (i.e. THIERSTEIN, 1976, pl. V, figs. 28, 29).

Our original intent was to recognize *Zygolithus angustus* STOVER as an end-member in the morphocline ranging from this "species" to *E. eximius*. The main distinction between these forms is the openness of the central area; that of the former being open and that of the latter being closed. However, preservation greatly affects the openness of the central area and makes taxonomic differentiation based on this characteristics very difficult. Since we were unable to recognize other characteristics upon which to base a differential diagnosis, we lumped *Z. angustus* in *E. eximius*. VERBEEK (1977, p. 124) also found it difficult to distinguish *E. eximius* from *Vekshinella angusta*: "Differentiation of (*E. eximius* from *V. angusta*) may be based on our observations that the former is accompanied by *E. turriseiffeli*, the latter is not".

We do not follow VERBEEK on these points because:

- we observe V. angusta of VERBEEK (=E. eximius) and E. turriseiffellii in the same samples; and
- species differentiation should be based on morphologic differences, not differences in assemblage composition.

Other authors (i. e. PERCH-NIELSEN, 1979; PRINS, personal communication, 1985; VAN HECK, personal communication, 1985) split Albian/early Cenomanian *E. eximius* (*E.* sp. 1 and sp. 3 of PERCH-NIELSEN) from Turonian *E. eximius* on the basis of more numerous central-area plates in the former. However, no published photographs have verified this difference and we were unable to do so in this study.

Eiffellithus turriseiffelii (DEFLANDRE in DEFLANDRE & FERT) REINHARDT

(Pl. 1, fig. 10)

- 1954 Zygolithus turriseiffeli DEFLANDRE in DEFLANDRE & FERT, p. 149, pl. 13, figs. 15-16, textfig. 65.
- 1965 Eiffellithus turriseiffeli (DEFLANDRE in DEFLANDRE & FERT) REINHARDT, p. 32.
- 1966 Clinorhabdus turriseiffeli (DEFLANDRE in DEFLANDRE & FERT) STOVER, p. 138, pl. 3, figs. 7-9.
- Comments: See comments above under *Eiffellithus* eximius.

Genus Vagalapilla BUKRY 1969

Vagalapilla matalosa (STOVER) THIERSTEIN (Pl. 1, fig. 1)

- 1966 Coccolithus matalosus STOVER, p. 139, pl. 2, figs. 1-2; pl. 8, fig. 10
- 1969 Staurolithites matalosus (STOVER) CEPEK & HAY, p. 325, fig. 2, no. 4 (invalid, ICBN Art. 33, par. 4).
- 1973 Vagalapilla matalosa (STOVER) THIERSTEIN, p. 37, pl. 3, figs. (?)15-(?)18.
- Comments: Based on the original light micrographs and an examination of his material, we believe that STOVER (1966, pl. 2, figs. 1 & 2) figured two different species as V. matalosa. The rim of the holotype (Fig. 1, from the lower Cenomanian) differs from that of the paratype (fig. 2, from the Albian) by being larger, scalloped, and lacking a very narrow outermost cycle. The paratype rim is distinctly *Eiffellithus*-like, whereas that of the holotype is different. Central structures also differ by being more complex in the holotype (most easily seen in crossed nicols). Forms resembling the paratype of V. matalosa grade into *Eiffellithus* eximius in our samples.

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Figs.	1a–c Vagalapilla matalosa (Stover) Thierstein
	Fort Worth Ls., sample HTL6242.
	This specimen is similar to the paratype but differs from the holotype (STOVER, 1966; compare Pl. 2, Fig. 1 to Pl. 2, Fig. 2). The rim structure of this form is virtually identical to that of the eiffellithids and the orientation of the central cross makes it difficult to differentiate from <i>E. eximius</i> . However, in crossed nicols, the arms of the cross lack the medial extinction line typical of <i>E. eximius</i> .
Figs.	2a-c, 3a-c, 4a-c
	Eiffellithus eximius (= Zygolithus angustus STOVER) Figs. 2a-c and 3a-c are from the Forth Worth Ls., samples HTL6242 and HTL6240. Figs. 4a-c are from the Duck Creek
	Fm., sample HTL6302. This form differs from typical <i>E. eximius</i> by having an open central area. This morphotype is about two orders of magnitude more common than those with closed central areas in Albian and Cenomanian samples studied.
Fias	5a-c. 6a-c
1 190.	Effellithus eximius
	Both specimen are from the Fort Worth Ls., sample HTL6240. This form has a partially-filled central area.
Figs.	7a-c, 8a-c
	Eiffellithus eximius Figs. 7a-c are from the Telegraph Creek Formation, sample HT84-258, Winnett, Montana. Figs. 8a-c are from the Blue
	Point Section, sample 38, Black Mesa, Arizona.
	Both specimen illustrate "typical" E. eximius with a filled central area.
Figs.	
	<i>Eiffellithus eximius/E. turriseiffelii</i> transition form The specimen is from the Blue Point Section, Black Mesa, Arizona.
	Note that the angle of the central cross is intermediate between that of E. eximius and E. turriseitfeli.
Figs.	10a-c
	Eiffellithus turriseiffelii
	The specimen is from the Fort Worth Ls., sample HTL6240.
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Plate 1



Plate 2

Figs. 1-4: *Eiffellithus eximius* All specimens are from the Duck Creek Formation, sample HTL6302. Figs. 1 and 2 are the same specimen. The apparent difference in eccentricity is is due to the different tilt angle of the specimen in the SEM.



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