Biostratigraphy of Santonian-Campanian genus *Baculites* in the Western Interior of North America: Implications for Evolutionary Timing and Migration

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Abstract

The ammonite genus *Baculites* Lamarck contains almost every zonal index species for the macrofossil biostratigraphy of the Western Interior (WI) of North America, as well as index species for biostratigraphic frameworks in other provinces. The currently accepted ammonite biostratigraphy of the WI was pioneered by Cobban (1966, 1969, 1973, 1993) and in the Campanian consists of very narrow ($\sim 0.5 - 1$ Ma) nonoverlapping zones containing a single *Baculites* index species which occurs only within its zone. This framework posits that the WI was host to but one continuously evolving, endemic lineage of *Baculites* in which each zonal index species replaces its predecessor and evolves directly into its successor. This seems to accept gradual, phyletic change as the sole model for WI *Baculites* evolution, with no gene flow into or out of the province. Presented here are occurrence range data for 10 biostratigraphically useful ammonite species recovered from 8 outcrops across South Dakota, Wyoming, and Montana. These outcrops are correlated by means of magnetostratigraphy and both Ar/Ar and U/Pb geochronology to previous biostratigraphic records both in the WI and elsewhere. We find at two outcrops that occurrences of the WI unnamed index species *Baculites* sp.(smooth) and *Baculites* sp.(weak flank ribs) overlap stratigraphically. This falsifies the traditional placement of the two species into two successive and distinct zones, and challenges gradual, phyletic change as the sole mechanism for *Baculites* evolution in the WI, at least in this case. Additionally, we find specimens of both species to be anatomically indistinguishable from the coincident Pacific Coast species Baculites *inornatus*, and recommend the adoption of *Baculites inornatus* as a new index species in the WI, replacing both *Baculites* sp.(smooth) and *Baculites* sp.(weak flank ribs). This

challenges the extreme endemism attributed to WI *Baculites*, suggesting that there was some amount of gene flow between *Baculite* species in different Cretaceous biotic provinces, possibly resulting in truly cosmopolitan species. A critical evaluation of the standard morphological features used to define and differentiate *Baculites* species (ornament, cross-section, degree of taper, and suture pattern) finds these characters are suspect and in need of review, with the exception of suture analysis.

Introduction

The genus *Baculites* Lamarck (family Baculitidae, order Ammonotida, class Cephalopoda) is distinguished from other ammonite genera by its uncoiled phragmacone, which is straight or slightly curved. Scores of species have been described around the globe ranging from the Late Albian through the Maastrichtian, although very few species are described as occurring in more than one basin, which are recognized in the late Cretaceous as distinct biogeographic provinces (Matsumoto, 1960, Cobban, 1993). The Western Interior *Baculites* of the Santonian and Campanian stages are described as entirely endemic (Cobban, 1993).

Regional biostratigraphic frameworks for Upper Cretaceous strata in the Western Interior, the Pacific Coast, South Africa, the Gulf Coast, and Japan rely heavily on the ammonite genus *Baculites*. Matsumoto (1959, 1960) recognizes fourteen species of *Baculites* in the biostratigraphic framework of Japan and nine species in his zonation of California. This compares with only three species described by Jeletzky (in Muller and Jeletzky, 1970) in his contemporaneous framework for British Columbia.

Cobban's framework in the Western Interior provides the highest-resolution biostratigraphy for the Upper Cretaceous, with typical species duration of approximately 0.5-1 Ma. This contrasts with typical species duration of approximately 2-4 Ma in other regions such as the Pacific Coast (Figure 1).

Period	Stage		WI Ammonite Zones (Gill and Cobban, 1966)	Ar/Ar dates (Hicks 1995, 1999)	Interregional Correlation?	Pacific Ammonite Zones (Matsumoto, 1960, Ward, 1978)	
		Lower	Baculites scotti	76.07			
			Baculites reduncus			Baculites rex	
			Baculites gregoryensis				
			Baculites perplexus		?	Baculites inornatus Baculites chocoense	
			Baculites sp. (smooth species)				
ړ	CAMPANIAN		Baculites aperiformis	79.50			
8			Baculites mclearni				
UPPER CRETACEOUS			Baculites obtusus	80.04			
K CK			Baculites sp. (weak flank ribs)				
PPE			Baculites sp. (smooth)	93			
			Scaphites hippocrepis III				
			Scaphites hippocrepis II	81.71			
?	Ė.		Scaphites hippocrepis I				
	SANT.		Scaphites leei III			Inoceramus schmidti	

Figure 1: Currently accepted biostratigraphy of the Western Interior with radiometric dates, compared to the contemporaneous Pacific biostratigraphy. In the absence of globally correlative markers, exact correlations of zonal boundaries are unknown.

This sharp contrast in typical species duration between the two zones could be explained in a number of ways. It could be a difference in species definition and division: biostratigraphers in the Western Interior may have oversplit the genus relative to work in other provinces. Another alternative is that the fossil record in other provinces is incomplete and contains large depositional hiatuses, leading biostratigraphers to overestimate species durations and omit species that were in fact present in those basins. This hypothesis is supported by the comparatively high rate of deposition in the Western Interior, but is not supported by the lack of continuous fossiliferous sections currently

exposed, which has made the exact range of many zones in the Western Interior difficult to determine. Conversely, the observed pattern could in fact reflect reality: for some reason the Western Interior *Baculites* may have enjoyed far faster evolutionary rates than their counterparts in other biogeographic provinces.

Species have been defined provincially based on morphological variations in whorl cross-section, shell ornamentation, suture pattern, and degree of taper. Much of this study deals with the quantification of these characters and the evaluation of their utility in defining and differentiating *Baculites* species. Since species are traditionally described as occurring only in the Western Interior with very little or no overlap between regions, the currently accepted interpretation is that these endemic *Baculites* stocks evolved independently in different regions, sharing only a distant common descent (Cobban, 1993). The fossil record of *Baculites* in each province, therefore, is interpreted as the continuous evolution of a single isolated lineage.

Modern evolutionary theory proposes two basic models for morphologic change at the species level. The first, termed phyletic gradualism, involves slow morphologic change of a lineage through time. Species in phyletically evolving stocks are arbitrarily defined points along a continuously evolving sequence of forms. The second model is punctuated equilibrium, in which species remain morphologically constant throughout their duration and speciation events occur relatively shortly and new morphological forms appear almost instantaneously in the fossil record and without transitional or intermediary forms. (Eldridge and Gould, 1977)

The literature on the Western Interior *Baculites* clearly supports phyletic gradualism in this case. Each *Baculites* species is said to have evolved gradually from the

preceding species and to have graded gradually into the succeeding species, with very few instances of two species co-existing at the same time. In fact no such case is described in the Western Interior between the zones of *Baculites* sp.(smooth) and *Baculites clinolobatus* (Lower Campanian – Maastrichtian). A major objective of this study is to evaluate that claim: did *Baculites* in the Western Interior evolve gradually, phyletically, as a single lineage, or is there overlap between biostratigraphic zones, implying that multiple species existed at the same time?

In the total absence of gene flow between regions, isolated stocks would evolve independently in each province, and a pattern of divergent evolution would be expected, reflecting expectedly different conditions in each province. However, clear trends of similar evolution have been recognized in several basins, including the Western Interior, the Pacific Coast, Japan, and Madagascar. Small, unornamented *Baculites* (such as Baculites haresi in the Western Interior) appear in the Santonian and are replaced by larger, unornamented species (*Baculites* sp.(smooth)) in the Lower Campanian. These give rise to a succession of even larger, ornamented and keeled species (Baculites grandis, etc.) in the Upper Campanian. This is an observation that has traditionally been explained as convergent evolution: separate lineages evolved similarly in response to similarly changing conditions in each province, a pattern that has been described as Candelabra evolution. Recently, however, some overlap between biogeographic provinces has been recognized: specimens from the Pacific Coast have been identified as belonging to species that have been described in the Western Interior. Another primary objective of this study is to examine the extent to which *Baculites* species co-occur in separate basins. Answering this question may require a re-evaluation of the *Baculites*

species concept: If select species were truly cosmopolitan in distribution, regional frameworks will need to be redefined. This would greatly aid the utility of Late Cretaceous macrofossil biostratigraphy in correlating the sediments of different basins at a global scale.

Geologic Setting

From the late Aptian to the Paleocene (ca. 110 - 60 Ma), the Western Interior of North American was submerged beneath a shallow epicontinental sea, extending at its maximum from the Arctic Ocean to the Gulf of Mexico (Figure 2: map of cretaceous seaway). This sea was bounded on its western margin by an active subduction zone related to the Sevier Orogeny throughout the Cretaceous, which featured an active cordillera containing a magmatic arc which sporadically inundated the Western Interior with volcanic ash (Elison, 1991). Clastic sediments were eroded from this Western cordillera and deposited in a broad, asymmetric foreland basin trending roughly North-South. In the late Santonian through the Maastrichtian, organic-rich marine shale referred to as the Pierre shale was deposited in the basin and is now exposed in Wyoming, Montana, and the Dakotas in a sub-circular belt surrounding the Black Hills uplift. The Pierre shale was deposited rapidly (50-100 m/Ma) and contains abundant calcareous and ferruginous concretions as well as sanidine, biotite, and zircon-bearing bentonite beds, which are useful for regional correlation and amenable to both Ar/Ar and U/Pb dating techniques (Gill and Cobban, 1966). Eustatic sea-level change coupled with tectonic movements caused cyclical regional regressions and transgressions, resulting in significant regional unconformities and interfingering of the Pierre shale with shallowwater marine and terrestrial facies to the west. The early Campanian saw the onset of the

Claggett transgression, during which the Mitten Black Shale member of the Pierre shale was deposited following a significant regional depositional hiatus known as the Pierre-Niobrara unconformity, exposed at outcrops near Ardmore and Oral, SD (Gill and Cobban, 1966).



Figure 2. Geography of the Western Interior Seaway in the late Cretaceous, ca. 75 Ma (Paleomap project)

Materials and Methods

Outcrop Localities

Nine outcrops of the Santonian-Campanian Pierre and Cody formations in South Dakota, Wyoming, and Montana were chosen for study (Figure 3 – outcrop map). Many of the outcrops studied are well-known collection sites for ammonite fossils, documented by Cobban (1962, 1966, 1973,) and Larson (1997), particularly those that preserved specimens of WI zonal index species of *Baculites* and *Scaphites*.

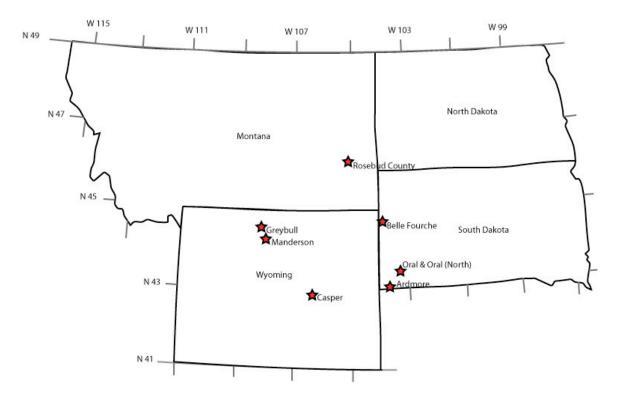


Figure 3. Map of outcrop localities

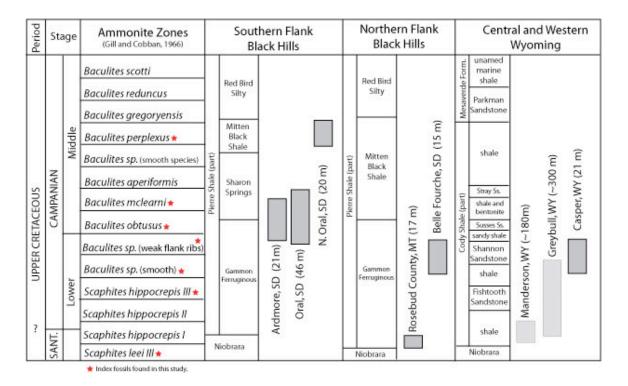


Figure 4. Stratigraphic coverage of outcrops. Light grey outcrops (Manderson & Greybull) were sampled at discrete horizons rather than measured as continuous stratigraphic sections

Outcrops were selected for broad stratigraphic coverage of the lower Pierre shale, specifically targeting the zones of *Scaphites hippocrepis I – Baculites maclearni* (Figure 4 – stratigraphic coverage of outcrops), an interval which has received little combined biostratigraphic and magnetostratigraphic study. A major criterion for outcrop selection was lithology amenable to hand-drilled paleomagnetic sampling and analysis, primarily well-lithified shale and/or abundant ferruginous and calcareous concretions. Special attention was given to outcrops containing molluscan fossils that exhibited preserved original aragonitic shell material, as this criterion is a strong indicator that the outcrop faithfully records original remnant magnetization (Filmer and Kirschvink, 1989). Another factor for outcrop selection was the presence of thick bentonite layers amenable to radiometric dating.

For each outcrop, a stratigraphic column was measured recorded using a Jacob's staff, so that all data could be recorded within a stratigraphic context. All ammonite and inoceramid fossils that preserved any of the following characteristics were collected along with a recorded stratigraphic position: original aragonitic shell material, visible septal margin suture patterns, intact phragmacone cross-section, or visible flank ribbing. Oriented paleomagnetic samples were taken with a gas-powered hand drill wherever suitable concretions or shale was present, at the highest resolution allowed by lithology. Bentonite layers, wherever present, were bulk sampled for radiometric dating.

Fossil identification and Baculites morphometric measurement techniques

Preliminary species identifications of *Scaphites* and *Baculites* fossils were made at the Black Hills Institute of Geologic Research by Neal L. Larson, an expert on the ammonites of the Pierre Shale, and myself. Additional identifications of *Scaphites* specimens were made at the American Museum of Natural History by Dr. Neil H. Landman, an expert on Santonian-Campanian *Scaphites*.

In addition, morphometric analyses of Western Interior *Baculites* specimens as well as parallel collections from the Pacific Coast province were conducted by Dr. Peter Ward and myself at the University of Washington, in an effort to quantitatively characterize the morphology of *Baculites* species as a test of existing species definitions. *Baculites* species in the Western Interior are traditionally identified by differences in suture pattern, degree of phragmacone taper, cross-section, and ornament, but no comprehensive quantitative measurement of these morphological distinctions currently

exists. Additionally, no quantitative multivariant species definitions exist for *Baculites* species.

A variety of measurements was made on a pilot set of Western Interior and Pacific Coast *Baculites*, and based on repeatability and utility in differentiating species, the following measurements were chosen and made on each specimen from the Western Interior collection that was well-preserved enough to be measured accurately:

External Phragmacone Dimensions (taken with caliper): Length of complete phragmacone, maximum and minimum height of complete phragmacone (measured from venter to dorsum), maximum and minimum width of complete phragmacone (measured perpendicular to both height and length), and position of septal margins, if visible. Rate of vertical taper was calculated by dividing the difference between maximum and minimum height over the length. Width/Height ratios of maximum and minimum cross-section were calculated (Figure 5 – external measurements taken).

External Ornament: The external flank ribbing of each specimen was described as either smooth (matching the external ornament of *Baculites* sp.(smooth), as described by Larson (1997)), weak (matching the external ornament of *Baculites* sp.(weak flank ribs), as described by Larson (1997)), or strong (matching the external ornament of B. obtusus, as described by Larson (1997)). The venter of each specimen was evaluated as either smooth or ribbed.

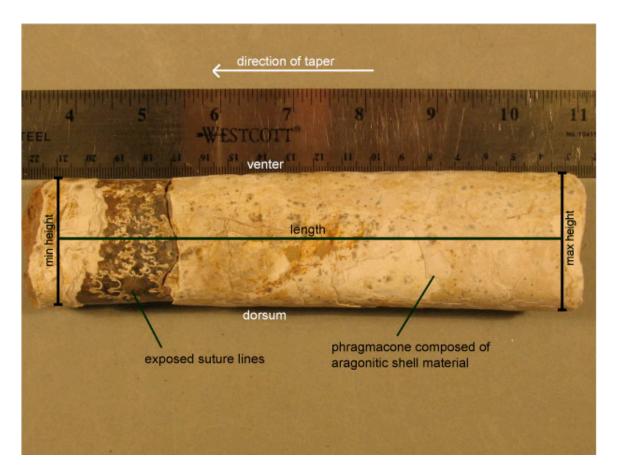


Figure 5: Basic *Baculites* anatomy with external measurements taken. Max and min width measured perpendicular to the plane of the photograph. Specimen is *Baculites* sp.(smooth) from Casper, WY.

Cross-Section: In addition to the width/height character calculated from external measurements, digital photographs of phragmacone cross-section were taken. If necessary, specimens were cut perpendicular to length in order to expose the cross-section. Digital photographs were analyzed using NIH's imageJ to calculate cross-sectional area above the midpoint (height divided by 2) and below the midpoint. This allows further description of cross-sectional shape, as many sub-elliptical shapes have similar width/height ratios (Figure 6 – Cross-section measurements taken). Using the areas of the two halves rather than just their dimensions allows egg shaped cross-sections

to be distinguished from a pear shaped cross-section or those with keeled venters.

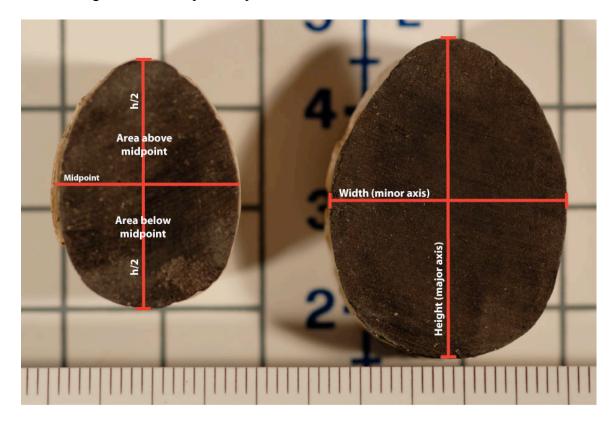


Figure 6: Measurements performed on *Baculites* cross-sections

Sutural Characters: Each specimen exhibiting visible suture patterns was photographed with a digital camera and analyzed using imageJ. If necessary, aragonitic shell material was removed to expose suture patterns. Specimens were photographed from the side (venter up) such that the Umbilical/Lateral saddle element of the suture was clearly visible (Figure 7 – standard photo layout for sutural analysis). Maximum and minimum distance across the U/L saddle were measured and expressed as a ratio (Figure 7b). The degree of roundness of the lateral lobe foliole (Figure 7a) was measured using imageJ's circularity function, which calculates the circularity of a closed element from measurements of its enclosed area and perimeter: Circularity = $4\pi \times (area / perimeter^2)$. This is derived from the equations for the area and circumference a circle: a perfect circle

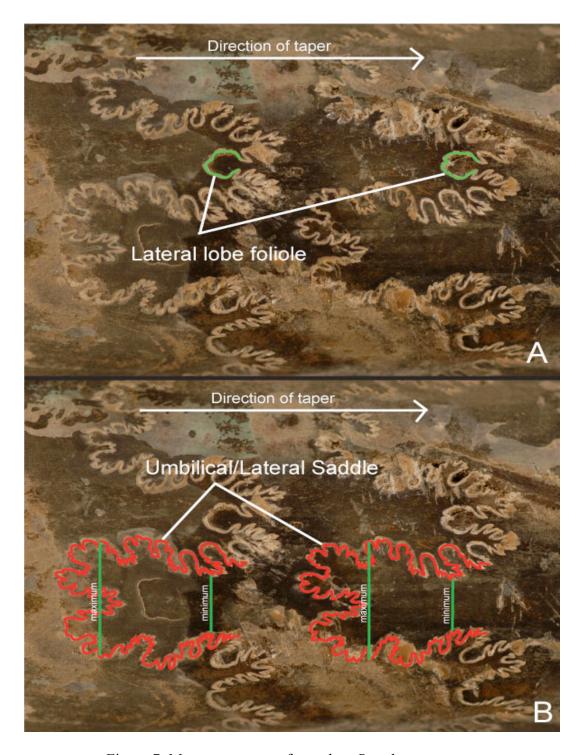


Figure 7: Measurements performed on *Baculites* sutures.

returns a value of 1.0; values approaching 0 correspond to an increasingly elongate shape. This measurement was chosen based on the observation that species of *Baculites* sp.(smooth) and *Baculites* sp.(weak flank ribs) exhibit notably rounder folioles than their adjacent zonal indices. This is equally true of *Baculites inornatus* in the Pacific Coast province.

Paleomagnetic analysis

Oriented paleomagnetic samples were analyzed by Ross Mitchell and Joseph Kirschvink at CalTech. For a detailed description of paleomagnetic methods, see Mitchell (2007).

Geochronologic analysis

Bulk samples of 8 bentonite horizons were sent to Sam Bowring at MIT for U-Pb dating of zircons. Only 3 contained a sufficient quantity of zircon to obtain a reliable date, and are cited here as unpublished data from Sam Bowring. This study also utilizes previously published dates of well-documented and correlative bentonite horizons obtained by the Ar/Ar technique from sanidine phenocrysts.

Results

Ammonite range data

Rosebud County, Montana: Rosebud County is a well-known locality among collectors of scaphitid ammonites, however it is presented here as a measured section for the first time. Cobban collected for specimens of *Scaphites leei III* and *Scaphites hippocrepis* (Cobban, 1962, Landman, 1993), although in this study only specimens of *Scaphites leei III* were recovered, from the top 5 meters of outcrop. These specimens were identified by Neil Landman. Normal polarity was detected at three distinct horizons,

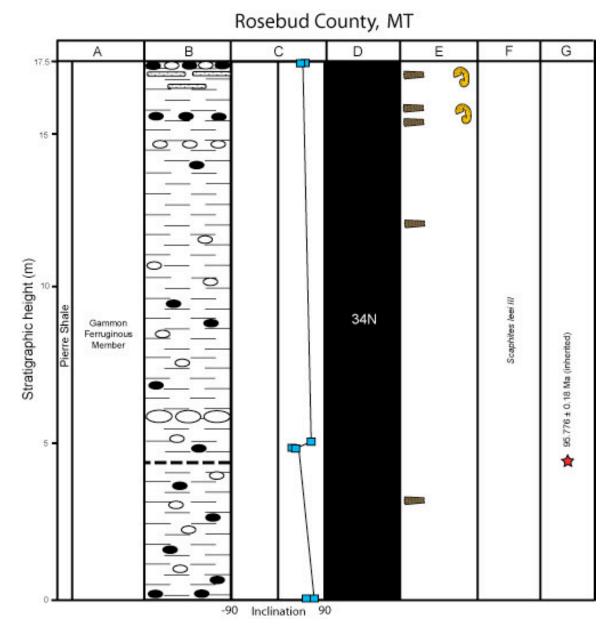


Figure 8: Composite stratigraphy of Rosebud County, MT. A: Formation and member. B: Lithology. C: Inclination of paleomagnetic samples. D: Polarity chron. E: Ammonite occurrences. Brown-colored baculitids represent specimens of *Baculites aqualaensis* and orange-colored schapitids represent specimens of *Scaphites leei III*. F: Standard Western Interior ammonite zone assigned to this section. G: Geochronologic data (Sam Bowring, personal communication). Red star represents U-Pb isotopic age obtained from zircons in bentonite layer.

placing this outcrop in Santonian 34N, the Cretaceous normal superchron (ca.118-83.5Ma). An isotopic date of 95 ± 0.18 was obtained from a zircon at 4.5m, and although

this is interpreted as detrital given the fossil assemblage, it gives an absolute upper limit to the age of the outcrop.

outcrops for Western Interior *Baculites* zonal index species sp.(smooth) and sp.(weak flank ribs), presented here stratigraphically for the first time. All paleomagnetic samples of shale preserved remnant reversed polarity magnetization, which, combined with a u-Pb date of 81.206 ± 0.16 (Sam Bowring, personal communication), places this outcrop in Campanian chron 33R (ca. 83.5-80.0 Ma). Cobban and Larson (1997) describe Belle Fourche as containing the boundary between those two zones, found roughly at the same level as the Groat Sandstone Bed, found at the top of the Belle Fourche section. Howerver, occurrence ranges of specimens recovered and identified by Neal Larson at the Black Hills Institute show no clear boundary between the two species, and in fact show a greater prevalence of *Baculites* sp.(weak flank ribs) at the bottom of the section than at the top, the opposite of the pattern described in the literature. The observed pattern at Belle Fourche is a total overlap of smooth and weakly ribbed specimens, with no clear change in the prevalence of ribbing as a function of stratigraphy.

Figure 9: Composite stratigraphy of Belle Fourche, SD. A: Formation and member. B: Lithology. C: Inclination of paleomagnetic samples. D: Polarity chron. E: Ammonite occurrences. Red-colored baculitids represent specimens of *Baculites* sp.(weak flank ribs) and green-colored baculitids represent specimens of *Baculites* sp.(smooth). F: Standard Western Interior ammonite zone assigned to this section. G: Geochronologic data. Red star represents U-Pb isotopic age obtained from zircons in bentonite layer (Sam Bowring, unpublished data).

Casper, Wyoming: To the north of Casper, WY lies a cutbank of the Platte River presented here as a previously unmeasured section. Lithology precluded high-resolution drilling for magnetostratigraphy, but all paleomagnetic samples taken from two discrete horizons record reversed polarity magnetization, interpreted as chron 33R, the same chron as the Belle Fourche section. Like Belle Fourche, the *Baculites* occurrences of the

Casper section show specimens of both *Baculites* sp.(smooth) and *Baculites* sp.(weak flank ribs), also identified by Neal Larson, but do not show a clear zonal boundary between the two species. Instead, weakly ribbed and smooth specimens overlap in the fossiliferous parts of the section with no clear trend when plotted against stratigraphy.

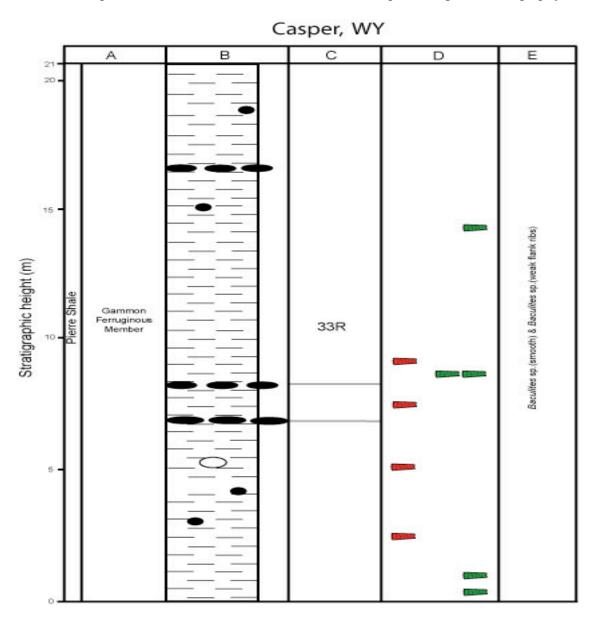


Figure 10: Composite stratigraphy of Casper, WY. A: Formation and member. B: Lithology. C: Polarity chron. Grey lines denote horizons sampled for paleomagnetic analysis. D: Ammonite occurrences. Red-colored baculitids represent specimens of *Baculites* sp.(weak flank ribs) and green-colored baculitids represent specimens of *Baculites* sp.(smooth). E: Standard Western Interior ammonite zone assigned to this section.

Ardmore and Oral, South Dakota: Ardmore, SD is the type locality for the Ardmore Bentonite, a ~1m thick bentonite horizon that has been correlated throughout the Western Interior and has been dated by the Ar/Ar method on sanidine phenocrysts at 80.04 ± 0.4 Ma (Hicks et. Al., 1999). The Oral section, a cutbank of the Cheyenne River to the northeast of Oral, SD, also contains the Ardmore bentonite, by means of which the two sections can be integrated to form the composite section presented here. Both outcrops also contain the Pierre-Niobrara unconformity, a depositional hiatus during a eustatic low before the onset of the Clagget transgression. A bentonite horizon from the upper part of the Oral section was dated by Sam Bowring at 78.527 ± 0.11 (personal communication). Polarity below the Pierre-Niobrara unconformity is entirely normal, attributed to chron 34N, the Cretaceous normal superchron. The 34N/33R boundary is contained within this unconformity, and has been dated at 83.5Ma. Above the unconformity and below the Ardmore Bentonite there is an interval of reversed polarity representing chron 33R. Coincident with the Ardmore Bentonite is a reversal back to normal polarity, representing chron 33N. The 33N/33R boundary is contained in a carbonate concretion within the Ardmore Bentonite itself.

The Ardmore section is poorly fossiliferous except for a single concretion horizon within the Ardmore bentonite which contains abundant specimens of the zonal index *Baculites obtusus*, an occurrence which has been documented by Cobban and Larson (1997). No baculitid fossils were recovered from Oral except for the top 7 meters of the section, which produced poorly-preserved specimens of *Baculites maclearni*, identified by Neal Larson. The boundary between the two zones lies somewhere between the

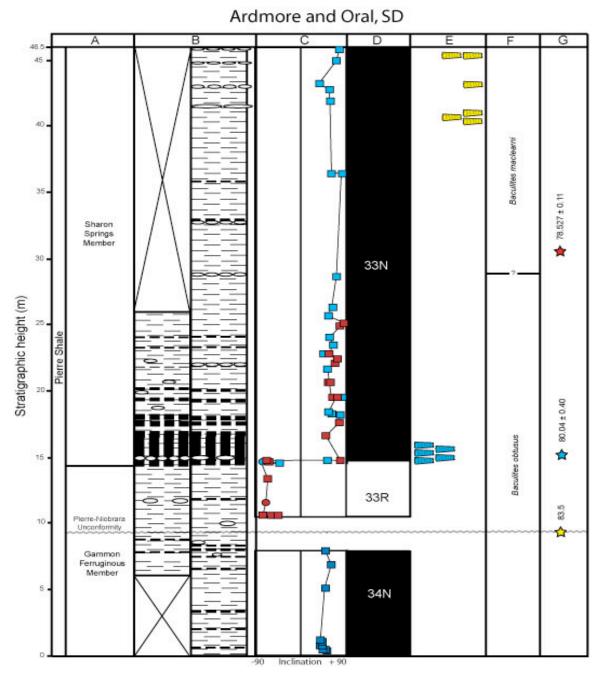


Figure 11: Integrated stratigraphy of Ardmore and Oral composite section. A: Formation and member. B: Lithology, Ardmore on the left and Oral on the right. C: Inclination of paleomagnetic samples. D: Polarity chron. E: Ammonite occurrences. Blue-colored baculitids represent specimens of *Baculites obtusus* and green-colored baculitids represent specimens of *Baculites maclearni*. F: Standard Western Interior ammonite zones. G: Geochronologic data. Red star represents U-Pb isotopic age obtained from zircons in bentonite layer (Sam Bowring, unpublished data). Blue star represents Ar-Ar isotopic age extracted from sanidine in the Ardmore bentonite, found at~14.8-16m in the composite section (Hicks et. Al., 1999). Yellow star represents age of geomagnetic polarity reversal (GPTS).

Ardmore Bentonite and the *Baculites maclearni* occurrences at Oral, but lack of fossil data precludes its exact placement in the composite section.

North Oral, South Dakota: To the north of the Oral section is another cutbank of the Cheyenne River, presented here as a measured section for the first time. The Pierre Shale dips roughly to the North in this area, so the North Oral section is stratigraphically higher than the Ardmore/Oral composite section. Lithology was not amenable to high-resolution magnetostratigraphy, although all samples from a single horizon retained normal polarity, which given the rise in stratigraphy over the Oral section are interpreted as 33N. Only four baculitid specimens recovered from the section were well-preserved enough to enable identification by Neal Larson. Five of these were identified as the zonal index *Baculites gilberti*, placing this outcrop 4 ammonite zones higher than the top of the Oral section. A single specimen was identified as *Baculites texanus*, a rare species which is previously documented to occur in the Western Interior only in the zone of *Baculites scotti*, three zones higher than the North Oral section (Kennedy & Cobban, 1999). This extends the known range of *Baculites texanus* considerably.

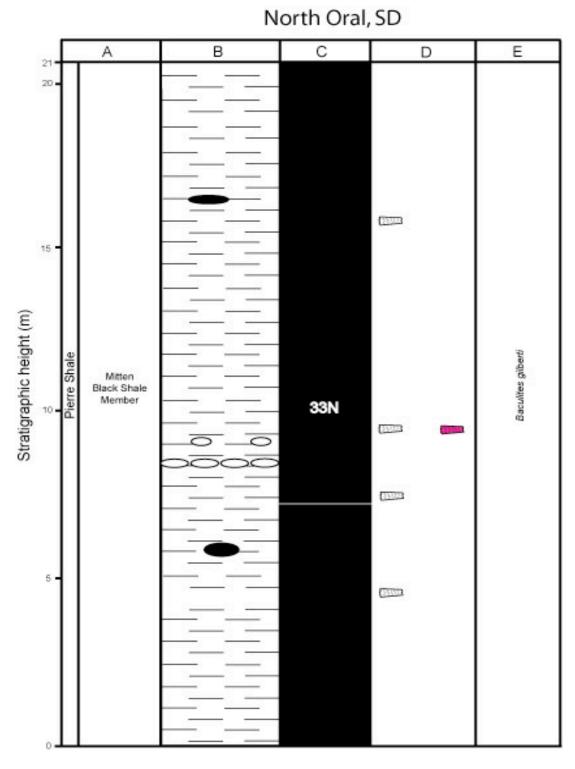


Figure 12: Composite stratigraphy of North Oral, SD. A: Formation and member. B: Lithology. C: Polarity chron. Grey lines indicate horizons sampled for paleomagnetic analysis. D: Ammonite occurrences. White-colored baculitids represent specimens of *Baculites gilberti* and green-colored baculitids represent specimens of *Baculites texanus*. E: Standard Western Interior ammonite zone.

Manderson and Greybull, Wyoming: Two well-documented outcrops of Pierre shale in Wyoming (Cobban, 1969) were collected for specimens of Scaphites hippocrepis. Exposure was poor, so that fossil data was collected at one discrete horizon at Greybull (containing specimens of Scaphites hippocrepis I, Baculites aqualaensis, and Baculites haresi) and two discrete horizons at Manderson (containing Baculites haresi and Baculites aqualaensis). Magnetostratigraphic data from these outcrops was indeterminate and there were no bentonite layers for dating, so the fossils collected were used only in development of morphology quantification techniques, with nothing inferred about their range.

Evaluation of traditional morphologic characters used in species definition

Quantitative morphologic analysis of traditional characters used in defining and differentiating species of *Baculites* suggests that many of these characters vary greatly within species, and their utility in discerning species is highly suspect and in need of further review. Rate of taper, presence and severity of ribbing, and cross-section metrics fail to separate the collections into discrete groups that could be used as a basis for species differentiation. The shortcomings of these measurements are discussed below. Suture quantification metrics show great utility in differentiating *Baculites* species of different ages and poor utility in differentiating species from different provinces. This may reflect an incorrect choice of the metrics used, or it may suggest that the traditional *Baculites* species concept of endemic lineages is in error.

Rate of taper data fails to polarize into discrete bins, nor does it show any clear trend with stratigraphy. The Lower Campanian *Baculites* all have very similar taper rates, and as such this is not a good metric for describing species. Additionally, rate of taper is

higher for small individuals, suggesting that *Baculites* get straighter as they get older.

Upper Campanian *Baculites* are described as more varied in degree of taper (Larson, 1997), and as such this may be a better metric for those species. Further collections in the Upper Campanian would be needed to test this hypothesis.

Likewise, cross-section metrics do not appear useful for describing *Baculites* species. There are two major problems with using cross-sectional analysis. Firstly, cross-section shape often changes with ontogeny, such that only mature specimens of a species reliably take similar shapes. Secondly, shell damage from presumed failed predation attempts can modify cross-section considerably, to the point that two cross-sections taken from the same individual before and after an instance of shell repair can vary more than the difference between some species (Backus, 1997).

External ornament varies wildly even at a single stratigraphic level, as shown in the Casper and Belle Fourche sections. This same observation has been made on the Pacific coast, where large populations of the typically smooth species *Baculites inornatus* demonstrate some specimens with ribbing. There are broad trends with stratigraphy, as Upper Campanian *Baculites* demonstrate a greater prevalence and severity of ribbing than do Lower Campanian species, but the variability is too great to classify external ornament as a species-specific character.

Quantified data from suture patterns shows promise in differentiating species, and more work needs to be done examining new ways to quantify differences between sutures. The two metrics used here, circularity of the lateral lobe foliole and the min/max ratio across the umbilical/lateral saddle element, show large differences between different Western Interior index species (Figure 13: Quantified suture data), with the exception of

Baculites sp. (smooth) and *Baculites* sp.(weak flank ribs), which return similar values for both measurements. An interesting observation is that *Baculites inornatus* from the Pacific returns values very similar to *Baculites* sp. (smooth) and *Baculites* sp.(weak flank ribs), although a greater sample size would be needed to make this claim with certainty.

Species (under	n	Min/Max of U/L Saddle		Circularity of LLF	
current definitions)	- 11	mean	std. dev.	mean	std. dev.
Baculites sp.(smooth)	32	0.595	0.023	0.834	0.053
Baculites sp.(wfr)	16	0.579	0.031	0.821	0.043
Baculites obtusus	9	0.717	0.042	0.895	0.072
Baculites aqualaensis	6	0.550	0.059	0.756	0.073
Baculites compressus*	2	0.345	NA	0.412	NA
Baculites scotti*	1	0.275	NA	NA	NA
Baculites inornatus (Pacific)	5	0.627	0.103	0.854	0.089
Baculites rex (Pacific)	3	0.219	0.034	NA	NA

Figure 13: Results of suture measurements. Asterix indicates specimens came from the collection of W.A. Cobban. Pacific Coast specimens from the collection of Peter Ward.

Discussion

Baculites sp.(smooth) vs. Baculites sp.(weak flank ribs)

Outcrops at Casper and Belle Fourche contain abundant smooth and weakly ribbed *Baculites*, which fit the descriptions of *Baculites* sp. (smooth) and *Baculites* sp. (weak flank ribs), two consecutive zonal indices (Larson, 1997). However, the pattern of occurrences shows no clear stratigraphic separation of the two species, in fact they seem to overlap throughout both outcrops, with no clear trend when plotted against stratigraphy (Figures 9 & 10). This study finds the placement of those two species into separate zones misleading, for at the very least we can say that the zones overlap considerably. Given the variability of external ornament within species observed among other Baculitid populations (Backus, 1997) the overlapping occurrences documented at

two outcrops here, and the similarity measured in sutural characters between the two species, this study does not find evidence to support the division of *Baculites* sp. (smooth) and *Baculites* sp.(weak flank ribs) into two separate species. Instead, the data suggest that the two species, as they are currently defined, be grouped together into a single, thicker zone.

Baculites sp.(smooth)/weak flank ribs) vs. Baculites inornatus

Roughly coincident with the occurrence of *Baculites* sp.(smooth/weak flank ribs) in the Western Interior, there exists on the Pacific Coast a smooth or weakly ornamented Baculitid of similar size named *Baculites inornatus*, a zonal index for the Pacific biostratigraphic framework. The range of *Baculites inornatus* has been documented magnetostratigraphically to begin in chron 33R and continue into chron 33N (Ward, unpub.), which overlaps with the Western Interior *Baculites* sp. (smooth/weak flank ribs) zone. In addition, measurements on sutures return almost identical data for the 3 species (Figure 13), although more specimens of *Baculites inornatus* need to be measured to give this claim any statistical significance. However, the morphological similarity of the two populations cannot be denied. Given these three observations, it is probable that *Baculites* inornatus, Baculites sp. (smooth) and Baculites sp. (weak flank ribs) all belong to the same species. Baculites inornatus has historical precedence, so this study recommends the adoption of that species as a new zonal index for the Western Interior, replacing both Baculites sp. (smooth) and Baculites sp. (weak flank ribs). Unornamented Baculites appear around the globe in the early Campanian, and it is probable that all are of the same species. This gives *Baculites inornatus* the potential to become a truly cosmopolitan biostratigraphic index species, increasing our ability to correlate between Cretaceous

sediments outside their own province. More biostratigraphic data integrated with globally correlative markers like magnetic reversals is needed from other regions to determine the first and last appearance datum of *Baculites inornatus* in each region before the exact precision of the species' correlative utility can be determined, but it seems promising as a global Lower Campanian marker.

Correlations to Pacific Coast

Based on new integration of ammonite occurrences with the globally correlative markers of magnetostratigraphic reversals, we offer an updated correlation of the Western Interior and Pacific Coast biostratigraphies for the Lower Campanian (Figure 14).

Hicks et. al. GPTS (1995, 1999)		This Study	Pacific Ammonite Zones (Matsumoto 1960, Ward 1978, Ward unpub	
Baculites perplexus		Baculites perplexus	Baculites rex	
висине в регріехиз		Baculites sp. (smooth species)		
Baculites sp. (smooth species)		Baculites aperiformis		
Baculites aperiformis	33N	Baculites mclearni		
Baculites mclearni		Baculites obtusus	Baculites inornatus	
Baculites obtusus				
Baculites sp. (weak flank ribs)		Baculites sp. (weak flank ribs)		
Baculites sp. (smooth)	33R	Baculites sp. (smooth) (=Baculites inornatus?)		
		Scaphites hippocrepis III	Baculites chicoense	
		Scaphites hippocrepis II		
		Scaphites hippocrepis I		
	34N	Scaphites leei III	Inoceramus schmidti	

Figure 14: New correlation between biozones of the Western Interior and the Pacific, with modifications to Western Interior biostratigraphy.

Major points of correlation are the two magnetic reversals surrounding chron 33R. The 33N/33R boundary, documented here at the base of the *Baculites obtusus* zone, is found on the Pacific coast in the zone of *Baculites inornatus* (Ward, unpub.). The 33R/34N boundary is constrained in the Western Interior by detection of normal polarity in the zone of *Scaphites leei III* in this study to between the zones of *Scaphites leei III* and *Scaphites hippocrepis III*. This same reversal is found on the Pacific Coast nearly coincident with the zonal boundary of *Inoceramus schmidti* and *Baculites chicoense* (Enkin, 2001). These new tie-points aid previously ambiguous correlations between the two provinces.

Implications for the Baculites species concept

The traditional interpretation of *Baculites* evolution makes the following claims about the distribution of the genus through time and space: 1) *Baculites* evolved separately in each biogeographic province as endemic stocks, with no gene flow between basins. 2) Each endemic stock of *Baculites* evolved by Phyletic gradualism: there was really only one species of *Baculites* in each basin that evolved gradually through time, and the species definitions used today are arbitrary points along that continuous evolution chosen for their biostratigraphic utility. This implies no overlap between zones; two species rarely co-existed at the same time.

The evidence presented in this study supports neither of these claims. The first claim is refuted by the worldwide distribution of baculitids matching the morphological descriptions of *Baculites inornatus* by Matsmoto (1959, 1960) in the Lowe Campanian, including the Western Interior species *Baculites* sp.(smooth) and *Baculites* sp.(weak flank ribs), which the suture measurements in this study do not differentiate from one another

or from their Pacific Coast contemporaries. The second claim becomes suspicious in light of the overlapping occurrence ranges presented here of *Baculites* sp.(smooth) and *Baculites* sp.(weak flank ribs) at two outcrops. Additionally, critical analysis of the morphological characters traditionally used to describe species finds them, with the exception of sutural analysis, too variable to reliably differentiate species, and their use may be responsible in part for the current state of confusion in *Baculites* biostratigraphy.

A critical re-evaluation of the *Baculites* species concept is sorely needed in order to create a reliable and useful worldwide biostratigraphy of Late Cretaceous *Baculites*. This will require a revision of nomenclature in the Western Interior and elsewhere, which reflects the observed degree of inter-regional distribution and gene flow. This study is in the unfortunate position of criticizing the existing species definitions without proposing a demonstrably reliable alternative. Species of *Baculites* are very difficult to define, but new occurrence data integrated with correlative markers and quantified morphological data provides the best perspective from which to examine the problem on a worldwide scale, as it has here.

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