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Halligan, William Keith

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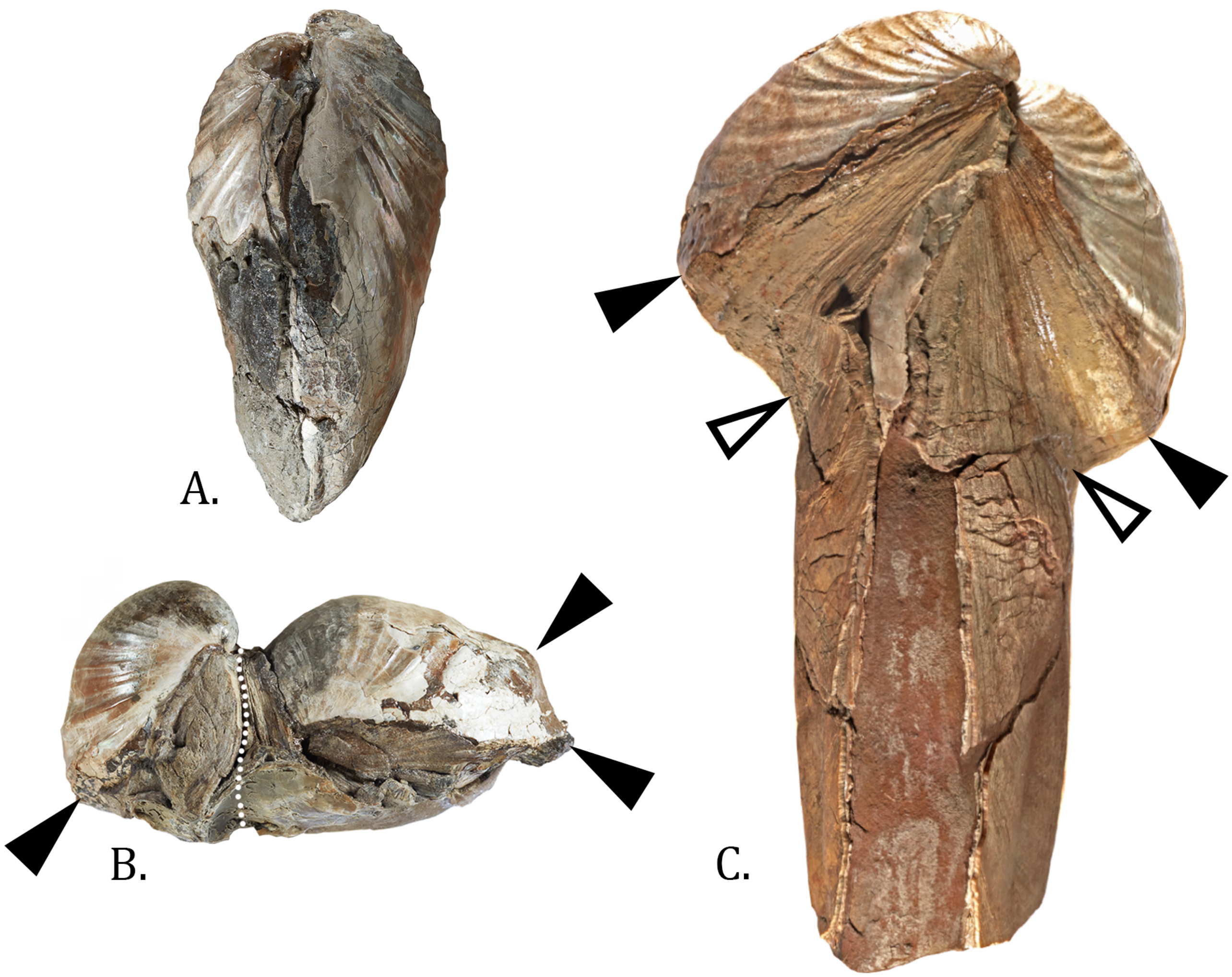

William K. HALLIGAN (2025). Multiple geniculated types in a single inoceramid (Bivalvia) species: "*Inoceramus*" *nebrascensis*

Cover: Three of the five morphotypes of "*Inoceramus*" *nebrascensis*: A. Type I. B. Type III. C. Type IV.

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Multiple geniculated types in a single inoceramid (Bivalvia) species: "*Inoceramus*" *nebrascensis*

Willam K. Halligan
Burke Museum of Natural History and Culture
University of Washington, Seattle, Washington 98105, USA
bhalligan@wavecable.com

Inoceramids have been studied extensively over the last 200 years and, along with ammonites, have become an important tool for Late Cretaceous biostratigraphy. Geniculation, the abrupt change in convexity/inflation of the valve disc, occurs in many inoceramids and has been recognized for decades. But despite extensive inoceramid research, it remains a relatively under-documented phenomenon. To understand the phylogenetic relationships within this cosmopolitan bivalve family, it is necessary to recognize the range of intraspecies variation. "*Inoceramus*" *nebrascensis* is known to geniculate, but its morphological variability has not been effectively documented. This study identifies five morphotypes of *"I." nebrascensis* from a single locality of the Late Campanian Pierre Shale in South Dakota. The most common form is non-geniculated (Type I). The four geniculated forms are: Type II–a positive geniculation along the ventral, anterior, and posterior margins with subsequent negative geniculations anteriorly and posteriorly; Type III–an extreme positive geniculation along the ventral and posterior margins; Type IV–a positive geniculation followed by a negative geniculation along the ventral and anterior margins generating a conspicuous neck; Type V–a positive and negative geniculation in rapid succession along the ventral margin generating an inconspicuous neck, followed by a positive geniculation along the anterior and posterior margins of the adult shell. This study also argues for a three-stage shell development for this species (juvenile, intermediate, and adult) rather than the two stages described in previous studies..

Keywords: Late Cretaceous, Late Campanian, Pierre Shale, South Dakota, *Didymoceras cheyennense* zone.

INTRODUCTION

The first inoceramids (Bivalvia, Myalinida [Carter et al. 2011]) were described from the Permian, but major expansion of the family occurred during the mid- to Late Cretaceous (Crampton 1996, Harries et al. 1996). Their ubiquity, cosmopolitan range, and rapid evolution have established inoceramids as important Late Cretaceous zonal index fossils (Cobban et al. 2006). Although they were first recognized as a new bivalve genus over 200 years ago by Sowerby (1814) and have been studied extensively world-wide with many inoceramid genera and species described (e.g., Woods 1911, 1912; Heinz 1932; Dobrov and Pavlova 1959; Sornay 1966; Tröger 1967; Kauffman and Powell 1977; Keller 1982; Rasemann 1986; Aliev et al. 1988), the phylogenetic relationships between these taxa are poorly understood (Crampton 1998; Walaszczyk et al. 2001; Crampton and Gale 2009). Inoceramid classification schemes have undergone multiple revisions and are still badly in need of clarification (Crampton 1998). A consequence of this uncertainty is that many inoceramids with morphologies that differ significantly from *Inoceramus sensu stricto* Sowerby, 1814 have been assigned to *"Inoceramus" sensu lato* (Walaszczyk et al. 2001). The subject of this article, *"Inoceramus" nebrascensis* Owen, 1852, is one of those inoceramids

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										Series
	LATE CRETACEOUS (Part)									Series
	Campanian (Part)									Stage
	Late									Western Interior Substage
	D. nebrascense	*D. stevensoni*	*E. jenneyi*	*D. cheyennense*	*B. compressus*	*B. cuneatus*	*B. reesidei*	*B. jenseni*	*B. eliasi*	Ammonite zones
	"I." tenuilineatus	*S. pertenuiformis*		*"I." altus*			*"I." oblongus*		*"I." redbirdensis*	Inoceramid zones
"I." whitfieldi		—	—							Inoceramids from the *D. cheyennense* zone
"I." nebrascensis			—	—	—					
"I." sagensis			—	—	—					
"I." altus				—	—	—				
"I." altusiformis					—					

Figure 1. Biostratigraphy of the three inoceramids found in the *Didymoceras cheyennense* zone of the U. S. Western Interior. *B.* = *Baculites. D.* = *Didymoceras.. E.* = *Exiteloceras. "I."* = "*Inoceramus*". *S.* = *Sphaeroceramus.* (From Walaszczyk et al. 2001).

that needs taxonomic clarification.

"*Inoceramus*" *sagensis* Owen, 1852 and "*I.*" *nebrascensis* were originally described from the Pierre Shale at Sage Creek, South Dakota. In 1876 F. B. Meek argued that the two were conspecific with the latter being a variation of "*I.*" *sagensis*. Walaszczyk et al. (2001), however, observed that the specimen presented by Meek was "*I.*" *sagensis*, not "*I.*" *nebrascensis*, and closer examination of Owen's holotypes demonstrated that he was correct to designate them as separate species.

Geniculation is defined as an abrupt change in the convexity/inflation of the valve disc; it can be "positive" (increase in convexity) or "negative" (decrease in convexity) (Crampton 1998). This has been well-illustrated by Walaszczyk (1997). Although geniculation has been recognized in many inoceramid species (e.g., Seitz 1967, Walaszczyk 1992, Crampton 1998), it has not been a focus in species descriptions (e.g., Elder and Box 1992, Walaszczyk et al. 2001; Walaszczyk 2004). Moreover, photographs are often suboptimal in documenting the morphology of geniculated forms. Owen's original 1852 description of "*I.*" *nebrascensis* makes no mention of geniculation and more recent descriptions of the species only vaguely mention it. The most detailed description of geniculation for "*I.*" *nebrascensis* reads: "Often the geniculation step (with closely spaced positive and negative geniculation following) is observed at approximately the juvenile/adult stage junction" (Walaszczyk and Dhondt 2005). In addition to the predominate non-geniculated form, four geniculated forms of "*I.*" *nebrascensis* will be documented and described in this study.

GEOLOGIC SETTING

The Western Interior Basin is a retro-arc foreland basin formed by the complex interplay of multiple forces including fold and thrust belt deformation created by the Sevier Orogeny to the west ("static load" forces) and "dynamic load" subsidence (Miall et al. 2008; Slattery 2011). From the Middle Jurassic to the early Paleocene this basin underwent multiple marine transgression-regression cycles (Blakey 2014). The marine Pierre Shale was deposited within the basin from the Early Campanian to the Early Maastrichtian (≈ 81.86–69.59 Ma) with sediments originating from the western highlands of the Sevier Orogeny (Slattery 2011). The study site sediments were deposited during the Late Campanian *Didymoceras*

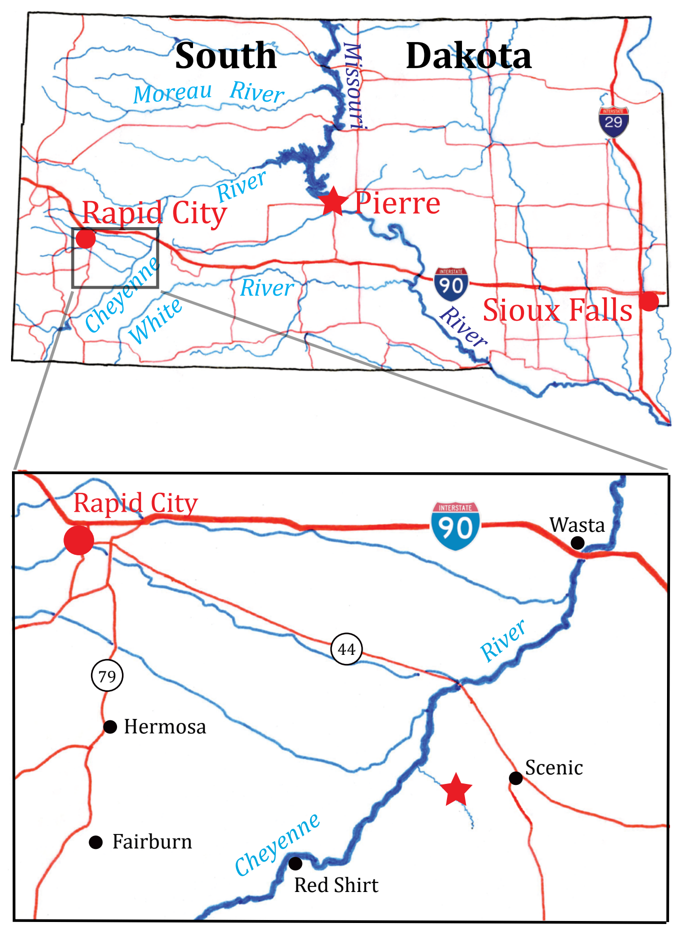

Figure 2. Map showing approximate location of the collection site (star on lower, inserted map).

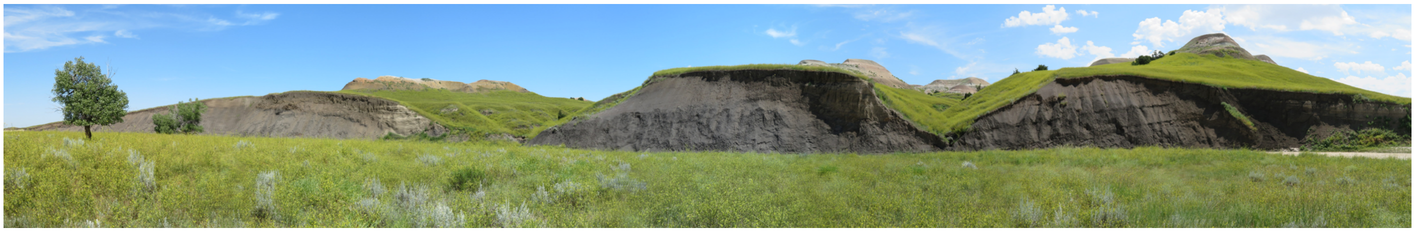

Figure 3. Photo of collection site. Black/dark gray shale banks cut into three exposures by two gullies.

cheyennense zone (≈ 74.5 Ma) as the Western Interior Seaway was nearing the maximum extent of its last major transgression, the Bearpaw Transgression (T9) (He et al. 2005, Li and Aschoff 2022). During its deposition the study site was never closer than 150 km from its nearest (western) shore (Blakey 2014). The depth of the seaway at the study site during its formation is not well-established. The only inoceramids known from the *D. cheyennense* zone of the U.S. Western Interior are *"I." sagensis*, *nebrascensis*, and *altus* Meek, 1871 (Fig. 1) (Walaszczyk et al 2001); they are readily distinguishable from each other.

The study site (AMNH loc. #3489/UWBM loc. B9578) is a steep shale bank on the east side of Indian Creek located 9.2 km WSW of Scenic, SD (Fig. 2). The sediments consist of thin layers of dark gray to black shale. The bank is divided into three exposures by two gullies (Fig. 3). The maximum heights of the exposures vary from 13 to 15 meters. In the shale there are scattered fossiliferous concretions that erode out and accumulate at the base of the exposures. The dominant fossil is "*I.*" *nebrascensis*. The presence of dark shales and an inoceramid dominant fauna implies a dysoxic marine environment (Slattery 2011). Although "*I.*" *nebrascensis* is the dominant organism of the site, other fossils found at the site include: *Didymoceras cheyennense* (Meek and Hayden, 1856), *Placenticeras meeki* Böhm, 1898, *Hoploscaphites brevis* (Meek, 1876), *Baculites corrugatus* Elias, 1933, "*I.*" *sagensis*, and *Nymphalucina occidentalis* (Morton, 1842). There are bentonite layers in each exposure and a fossil methane seep site approximately 110 meters NE of the middle shale bank.

MATERIALS AND METHODS

The fossils studied were extracted from concretions or found free in the shale. Specimens with concretionary material still attached were more fully exposed with pneumatic micro-percussion PaleoTools ME-9100 and Micro Jack 4 instruments. Specimens with loose shell were stabilized with a thin coating of cyanoacrylate to preserve morphologic detail. Inoceramid shells are prismatonacreous consisting of inner aragonitic and outer calcitic layers (Crampton 1996). The ornamental details of the nacreous shell (the interface surface of Crampton 2004), when obscured by the outer prismatic shell, were exposed by carefully removing some of the overlying prismatic shell.

ABBREVIATIONS AND DEFINITIONS

Institutional abbreviations: AMNH-American Museum of Natural History, New York, New York; **UWBM**-University of Washington Burke Museum, Seattle, Washington; **USNM**-United States National Museum (Smithsonian National Museum of Natural History), Washington, District of Columbia.

Morphologic terms (Fig. 4)

RV: right valve

LV: left valve.

L: length. The distance between two lines perpendicular to the hinge axis and touching the anterior and posterior extremities of the shell.

H: height. The distance between two lines parallel to the hinge axis and touching the dorsal and ventral extremities of the shell.

W: width of valve. The distance of a line drawn perpendicularly from the commissure plane to the point of maximal shell inflation.

Folds (also called rugae): a broad sculptural element in the external surface of the shell that affects the full thickness of the shell and is expressed on the internal mold.

Costae: sculptural elements of the shell that are not expressed on the internal mold (Crampton 1996).

Lines: very narrow sculptural elements of the shell that have no noticeable relief (Carter et al 2012).

Threads: shell sculptural elements that are narrower than costae but wider than lines.

Disc: the main body of the valve; does not include the wings.

Geniculation: an abrupt change in convexity/inflation

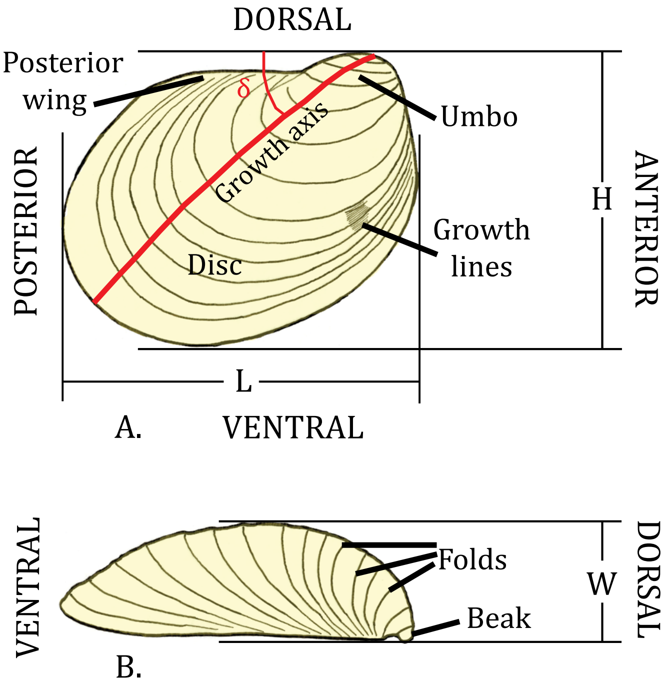

Figure 4A, B. Morphologic terms in the juvenile shell. **A.** Lateral view, RV. **B.** Anterior view, RV. Because the juvenile shell of *"I." nebrascensis* is the only shell stage of the mature valve with a consistent shape and ornamentation, its morphometrics along with the tripartite shell development should be used as the bases for identification of the species. L = Length, H = Height, W = Width

of the valve disc (Crampton 1996). For this study only obvious abrupt changes will be considered a geniculation. Minor or subtle changes (< 25°) will not be considered a geniculation (Fig. 5).

Positive geniculation: an abrupt increase in convexity of a valve disc (Crampton 1996). Indicated in this study's photos by: ►

Negative geniculation: an abrupt decrease in convexity of a valve disc (Crampton 1996). Indicated in this study's photos by: ▻

Juvenile shell: the initial shell. Its ornament is the most prominent of the mature valve. Its ornamentation and valve shape are relatively constant regardless of the geniculation type that may ultimately develop. Geniculation never occurs during juvenile shell formation.

Intermediate shell: the portion of shell that forms between the juvenile and adult stages. Its ornamental folds are farther apart, less prominent, and more irregular than the juvenile.

Adult shell: the final phase of shell formation. It is nearly featureless and smooth.

Junction between the juvenile and intermediate shell indicated in photos by: →

Junction between the intermediate and adult shell indicated in photos by: ⇒

Neck: the portion of shell between a positive and negative geniculation.

Shell sizes: Small: L < 50 mm. Medium: L = 50-99 mm. Large: L = 100-149 mm. Very Large: L ≥ 150 mm.

RESULTS

In 2016, 2019, and 2023 nine specimens demonstrating the various forms of "*Inoceramus*" *nebrascensis* were collected from the study site. These specimens retain most of their nacreous shell and four have some prismatic shell coverage. Although the overall shapes of the specimens vary significantly because of geniculation, the sequence and appearance of basic shell ornamental patterns are the same in all specimens. While Walaszczyk et al. (2001) describes the shell development of *"I." nebrascensis* in two stages, juvenile and adult, the nacreous shell of the specimens in this study consistently presents in three stages; they are designated juvenile, intermediate, and adult (Fig. 6A-D). In the diagrams they

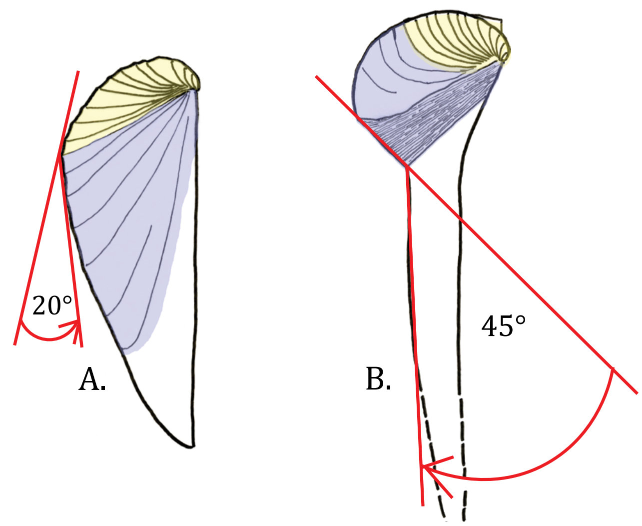

Figure 5A, B. Geniculation angles. **A.** Type I, RV, anterior view. The diagram indicates an abrupt positive angulation of the shell (increasing the convexity of the shell), but because it is less than 25°, it is not considered a geniculation in this study. **B.** Type IV, RV, anterior view. Indicated in this diagram is an abrupt negative angulation of the shell (decreasing the convexity of the shell). It is greater than 25° so it is considered a negative geniculation in this study.

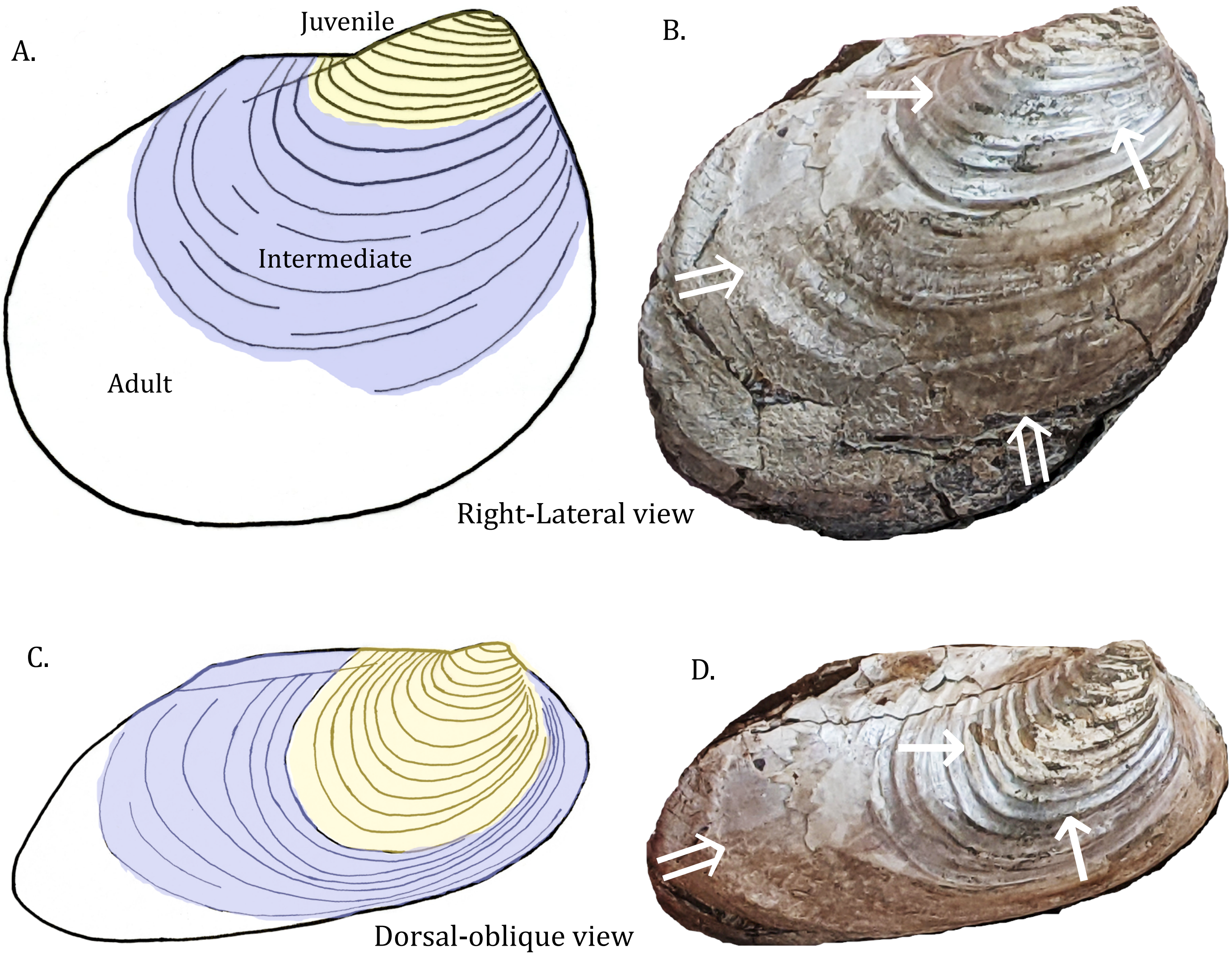

Figure 6A-D. The three shell stages illustrated in the RV of a non-geniculated (Type I) valve. **A.** Diagram, right lateral view. **B.** Corresponding photo of specimen. **C.** Diagram, dorsal-oblique view. **D.** Corresponding photo of specimen. Juvenile (yellow), intermediate (blue), and adult (white). These shell stages are consistent in *"I." nebrascensis* regardless of the presence or absence of geniculation. (See text for detailed description.)

are color-coded yellow, blue, and white respectively. (For a more detailed description see the Systematic Paleontology section.)

The small to medium sized juvenile shell has a consistent shape and ornament regardless of the ultimate morphological type that develops later. The shape and ornament of the juvenile shells in this study are consistent with previous descriptions of the early ontologic shell development of *"I." nebrascensis* (Owen 1852, Walaszczyk et al. 2001, Walaszczyk 2004, Walaszczyk and Dhondt 2005). Geniculation never occurs during this stage.

The medium to large sized intermediate shell stage follows the juvenile. Although the shell shape of this stage depends on the presence or absence of geniculation, the appearance of the shell ornament is as has been described in prior studies: the commarginal ornamental folds are farther apart, less prominent, and more irregular than in the juvenile.

The final shell stage is the adult; it is medium to very large sized, nearly featureless, and is flatter and thinner than the first two stages.

The ultimate shape of the mature valve depends on the presence or absence of geniculation and, when present, the type of geniculation. For clarity, sketches of the five types presented in this study are shown in Fig. 7A-M. (For a more detailed description see the Systematic

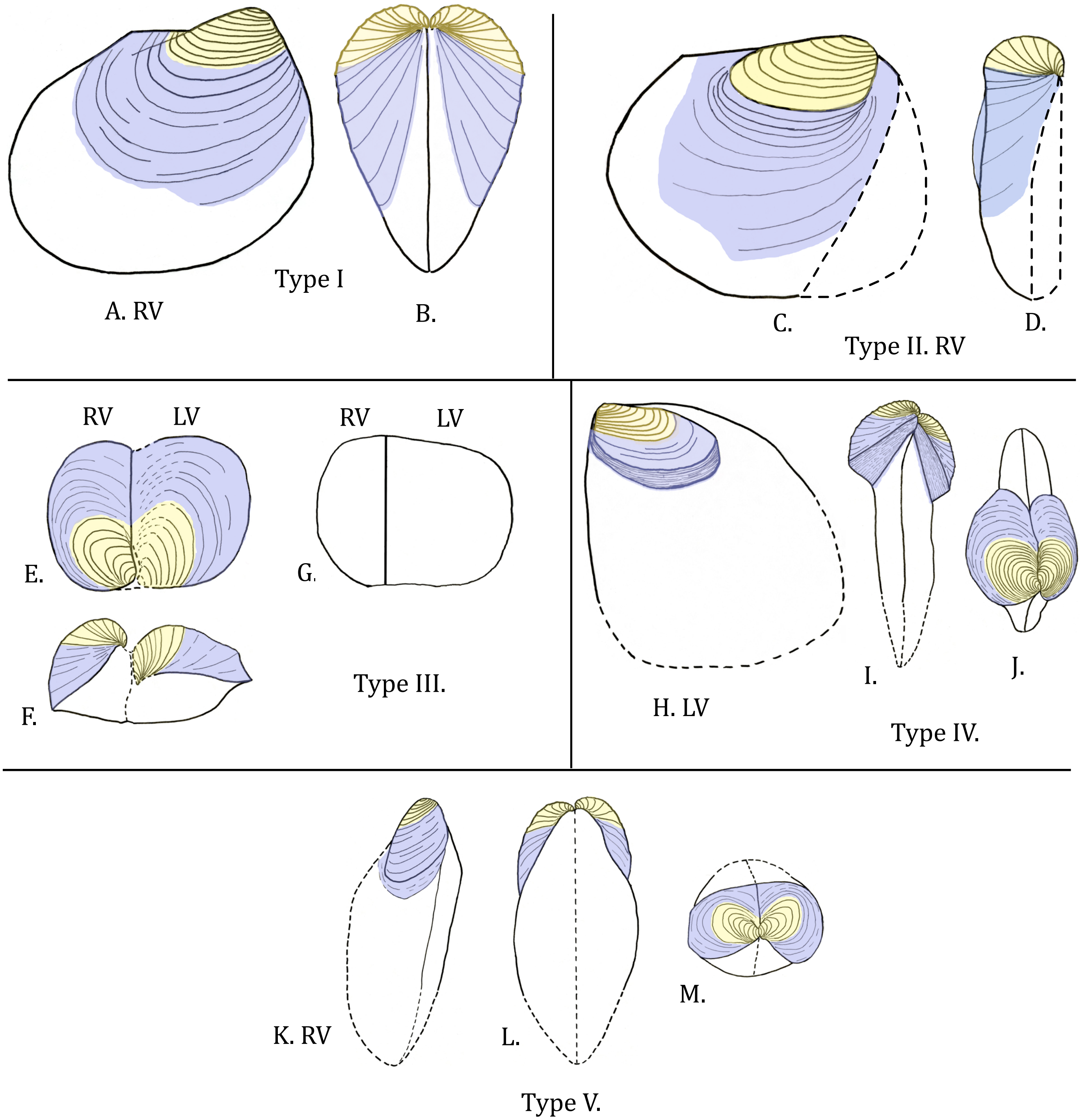

Figure 7A-M. Morphologic types in *"I." nebrascensis*. **A, B.** Type I: **A.** Lateral view, RV. **B.** Anterior view. **C, D.** Type II, RV: **C**. Oblique lateral view. **D**. Anterior view. **E-G.** Type III: **E.** Dorsal view. **F.** Anterior view. **G.** Ventral view. **H-J.** Type IV: **H.** Oblique lateral view, LV. **I.** Anterior view. **J.** Dorsal view angled to show the anterior and posterior contours. **K-M.** Type V: **K.** Lateral view, RV. **L.** Anterior view. **M.** Dorsal view angled to show the convex anterior contour and the wedge-shaped posterior margin. Dotted lines indicate estimated missing parts of shell and/or commissure. Yellow = juvenile, blue = intermediate, white = adult shell.

Paleontology section.)

Type I: No geniculation. This type is the most common "*I.*" *nebrascensis* form found and documented in the literature (Walaszczyk et al. 2001, Walaszczyk 2004, Walaszczyk and Dhondt 2005). In the literature it has been considered a non-geniculated form. Although this type does have positive changes in shell convexity, none is greater than 25°. Therefore, in this study this type is also considered non-geniculated.

Type II: A marked positive geniculation forms on the ventral, anterior, and posterior margins near the juvenile/intermediate shell junction. Following this geniculation, there may be negative geniculations on the posterior and anterior margins of the intermediate shell which can extend the valve outward in these directions. The mature valve has the appearance of an ornamented juvenile perched at a right angle on top of the relatively unornamented intermediate and adult shells, similar to the shape of *Sphaeroceramus pertenuiformis* Walaszczyk, Cobban, and Harries, 2001 (Walaszczyk 2004). This form can produce very large specimens.

Type III: After forming a juvenile and intermediate shell as in Type I, an extreme positive geniculation (90+°) along the ventral and posterior margins initiates the adult shell formation. The subsequent adult shell growth causes the juvenile and intermediate shells to rotate about the dorsal margin in a hinge-like fashion. The adult shell eventually creates a nearly flat platform on the ventral surface creating a form similar to *"Inoceramus" incurvus* Meek and Hayden, 1856 (Walaszczyk et al. 2001).

Type IV: The juvenile and some of the intermediate shell form as in Type I. A positive geniculation followed by a negative geniculation along the ventral and anterior margins generate a conspicuous neck. The adult shell begins forming soon thereafter. This is the only geniculated form described in prior literature for this species (Walaszczyk and Dhondt 2005).

Type V: The juvenile and early intermediate shells develop as in Type I. A positive geniculation along the ventral margin followed promptly by a negative geniculation creates an inconspicuous neck. At this point, this form could be considered a Type IV variant. However, as the adult shell is developing, it undergoes a positive geniculation along its anterior and posterior margins. This increases the inflation of the valves, creating a fusiform shape that distinguishes it from Type IV.

It should be apparent from these findings that the only morphologically consistent characteristics of *"I" nebrascensis* are the tripartite shell development and the shape and ornamentation of the juvenile shell. It is recommended, therefore, that these criteria be the bases for the identification of this species and that detailed descriptions of the geniculated types be included as morphological variants.

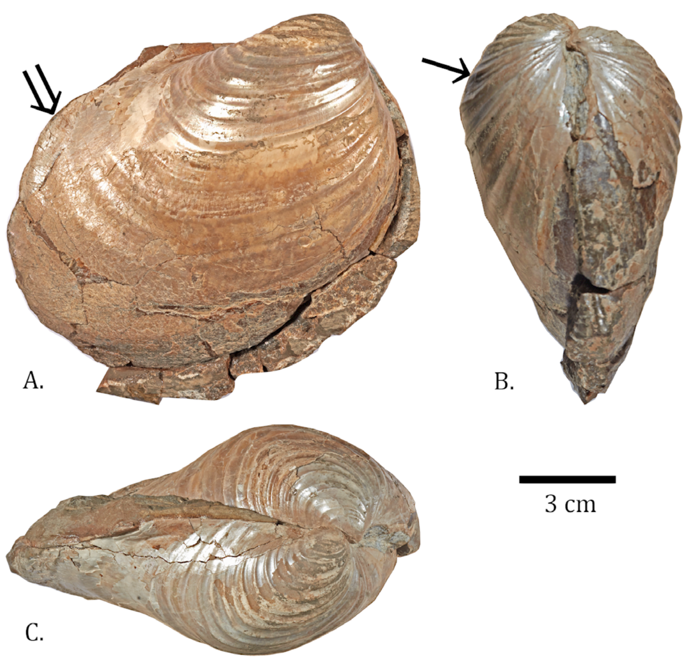

Figure 8A-C. *"Inoceramus" nebrascensis* Type I, articulated. UWBM IP 117991. **A.** Right lateral view. **B.** Anterior view. **C.** Dorsal view. This is the form most commonly described in the literature.

SYSTEMATIC PALEONTOLOGY

PTERIOMORPHIA BEURLEN, 1944
OSTREOMORPHI FÉRUSSAC, 1822
MYALINIDA PAUL, 1939
INOCERAMOIDEA GIEBEL, 1852
INOCERAMIDAE GIEBEL, 1852
"INOCERAMUS"
"*INOCERAMUS*" *NEBRASCENSIS* OWEN, 1852
Figs. 8A-C, 9A-C, 10A-C, 11A-B, 12A-C, 13A-D, 14A-D, 15A-C, 16A-D

Inoceramus Nebrascensis (N. S.) Owen 1852; p. 582, Table 8A, fig 1.

[non] *Inoceramus Sagensis* var. *Nebrascensis* Owen; Meek 1876; p. 52, Plt. 13, fig. 2. (The specimen illustrated as *I. sagensis* var. nebrascensis is conspecific with *"I." sagensis*. Walaszczyk et al. 2001).

[non] *Inoceramus nebrascensis* Owen; Tsagareli 1963; p. 98, plt. 4, fig. 4 (= *"I." sagensis*). (See Walaszczyk et al.

2001 for explanation.)
[?part] *Inoceramus pteroides pyrenaicus* Sornay 1978, in Sornay and Bilotte 1978; p. 32, plt. 4, fig. 1 (non plt. 2, fig. 1). (See Walaszczyk et al. 2001 for explanation.)
[non] *Inoceramus* aff. *pteroides pyrenaicus* Sornay 1982; p. 10, plt. 3, fig. 4. (See Walaszczyk et al. 2001 for explanation.)
"*Inoceramus*" *nebrascensis* Owen; Walaszczyk, Cobban, and Harries 2001; p. 208, plt. 15, fig. 1; plt. 16, fig.2; plt. 20, fig. 1; plt. 38, fig. 4.

Holotype—USNM PAL 20247. Smithsonian National Museum of Natural History, Washington, D.C.

Material—All specimens are "*Inoceramus*" *nebrascensis* from UWBM loc. B9578 (AMNH loc. #3489) (*Didymoceras cheyennense* zone). UWBM IP 117991: slightly displaced, articulated Type I (Fig. 8A-C). UWBM IP 117999: minimally displaced, articulated Type I (Fig. 9A-C). UWBM IP 117992: RV of Type II (Fig. 10A-C). UWBM IP 117993: LV of Type II (Fig. 11A, B). UWBM IP 118000: LV of Type II (Fig. 12A-C). UWBM IP 117996: articulated Type III (Fig. 13A-D). UWBM IP 118001: articulated Type III (Fig. 14A-D). UWBM IP 117995: articulated Type IV (Fig. 15A-C). UWBM IP 117994: articulated Type V (Fig. 16A-D).

Occurrence—Upper Campanian, Western Interior United States, *Exiteloceras jenneyi* zone through the *Baculites compressus* zone (Walaszczyk et al. 2001). Upper Campanian Europe: Central Poland (upper *Didymoceras donezianum* zone) (Walaszczyk 2004); NE Belgium (middle Upper Campanian) (Walaszczyk and Dhondt 2005).

Description—

Tripartite shell formation (Fig. 1A-D)

Juvenile shell. Small to medium sized, moderately gibbous, inflated (W/H = 0.43), longer than high (H/L = 0.73 – 0.83), nearly equivalve, strongly inequilateral (umbo anterior, nearly terminal), moderately prosocline, subtrapezoidal; umbo prominent, prosogyrate, projecting above hingeline; beak pointed. Posterior wing small with straight dorsal margin; weakly separated from disc. Anterior margin relatively short, slightly convex, nearly straight, curving gently into the broadly convex ventral margin which increases in convexity posteriorly. The elongated posterior margin is convex and intersects the dorsal margin at ~ 55°. Growth axis (δ) increases from ~ 30° in early ontogeny to ~ 37° in later growth. Shell ornamented with regular to subregular, conspicuous, commarginal, rounded folds that attenuate dorsally and anteriorly. Faint radial threads course into the intermediate shell.

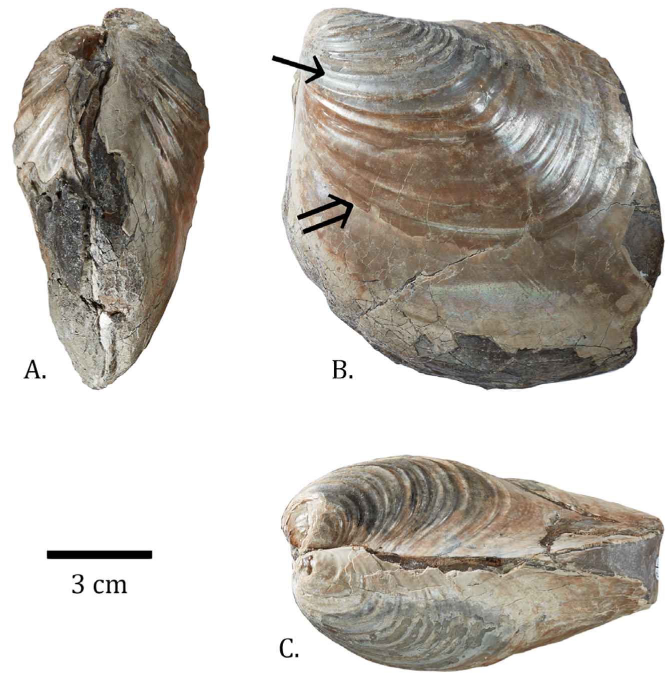

Figure 9A-C . *"Inoceramus" nebrascensis* Type I, articulated. Missing posterior margin. UWBM IP 117999. **A.** Anterior view. **B.** Left lateral view. **C.** Dorsal view.

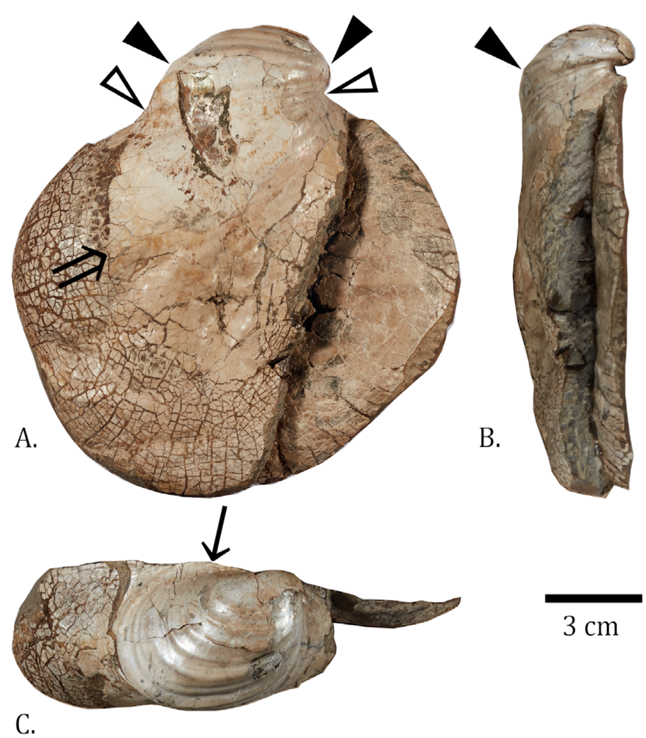

Figure 10A-C. *"Inoceramus" nebrascensis* Type II, RV with fractured and displaced anterior section. UWBM IP 117992. **A.** Lateral view. **B.** Anterior view. **C.** Dorsal view.

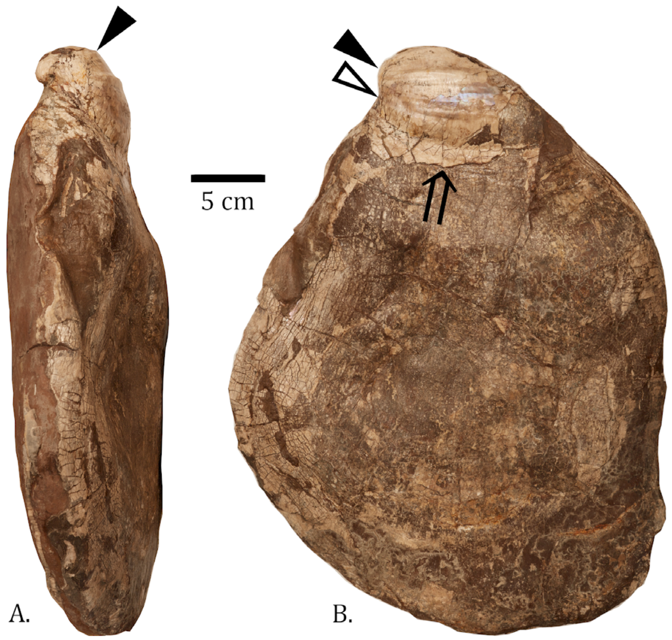

Figure 11A, B. *"Inoceramus" nebrascensis* Type II, LV. UWBM IP 117993. **A.** Lateral view. **B.** Anterior view. This specimen demonstrates the very large size this type can attain.

Very fine, closely spaced growth lines are visible with magnification on well-preserved nacreous shell.

Intermediate shell. Positioned between the juvenile and adult. Medium to large sized. Ornamental folds are more widely-spaced and irregular than the juvenile, becoming nearly smooth near the junction with the adult shell. The shell surface is flatter and less gibbous than the juvenile. Geniculation, if present, most commonly occurs during this stage. Until geniculation occurs, however, the intermediate shell retains the general subtrapezoidal outline shape of the juvenile.

Adult shell. Medium to very large sized. Shell is thin, nearly flat, and devoid of ornament. The nacreous shell surface usually has a reticulated pattern of fractures. If geniculation has not occurred (Type I), the general subtrapezoidal outline of the valve persists to maturity.

Geniculated forms

Type I (Fig. 8A-C, 9A-C). Non-geniculated. The three shell stages develop and merge smoothly with no obvious abrupt changes in disc convexity. Shell sizes: juvenile (small-medium); intermediate (medium-large); adult (large). The shell gradually flattens as it becomes less gibbous and loses its ornamental folds while maintaining the same general subtrapezoidal outline shape throughout ontogeny. The growth axis (δ) increases gradually from 30° to 40°. This is the most common type found.

Type II (Fig. 10A-C, 11A, B, 12 A-C). Juvenile shell is small and ornamented as in Type I. At approximately the juvenile-intermediate shell junction, an abrupt, ~ 40° to 50° positive geniculation occurs along the ventral, anterior, and posterior margins. Following this geniculation, there may be weaker negative geniculations anteriorly and posteriorly which can extend the valve outward in these directions. As the intermediate shell develops into a medium-sized valve, it progressively loses ornament and merges smoothly into the large to very large, flat, unornamented adult shell. This gives the mature valve

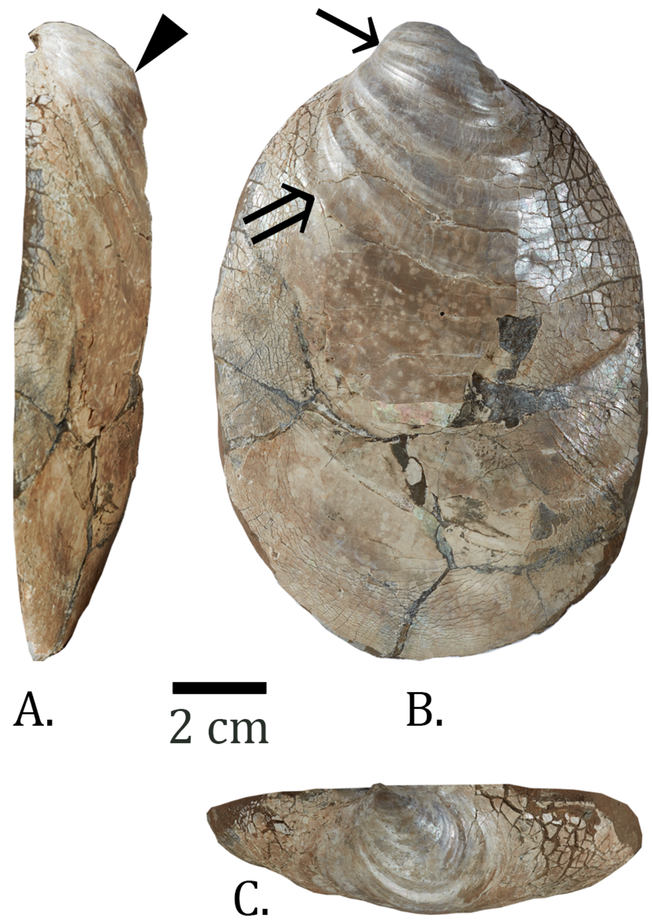

Figure 12A-C. *"Inoceramus" nebrascensis* Type II, LV. UWBM IP 118000. **A.** Anterior view. **B.** Left lateral view. **C.** Dorsal view. The positive geniculation in this specimen is not as profound as in figures 10 and 11. Although this specimen meets the criteria for Type II, it could be considered an intermediary between Type I and Type II the appearance of a small, ornamented juvenile perched perpendicularly on top of the relatively unornamented intermediate and adult shells. This type can become very large.

Type III (Fig. 13A-D. 14A-D). After formation of a small to medium juvenile shell and a medium to large intermediate shell as in Type I, an acute to rounded 90+° geniculation along its ventral and posterior margins initiates the adult shell deposition. The subsequent growth of the adult shell slowly rotates the previously formed juvenile/intermediate shells about the dorsal margin in a hinge-like fashion. The adult shell growth ultimately forms a nearly flat platform on the ventral surface.

Type IV (Fig. 15A-C). The medium sized juvenile and early intermediate shells develop as in Type I. Then, along the anterior and ventral margins, the valve undergoes an abrupt 45° to 60° positive geniculation followed by a 50° to 60° negative geniculation forming a conspicuous neck. Soon thereafter a very large, flat, unornamented, subtriangular adult shell begins to form.

Type V (Fig. 16A-D). A medium-sized juvenile and large intermediate shell develops as in Type I. Near the end of the intermediate stage and along its anterior, ventral, and posterior margins, a 30° to 35° positive geniculation forms followed promptly by a 40° to 60° negative geniculation generating an inconspicuous neck. At this point the bivalve appears to be a Type IV variant with weak geniculations and neck. However, the subsequent growth of the adult shell undergoes positive geniculations along its anterior and posterior margins, transforming the bivalve into a very large, inflated, fusiform shape with a posterior elongation. The anterior profile becomes broadly convex, while the posterior is wedge-shaped.

Discussion—It is unusual, if not unprecedented, for so many geniculated forms to be formally assigned to a single inoceramid species. While the geniculated types documented in this study are representative of the major forms encountered at the study site, the type system used in this study is a simplification of the complex geniculation process. There are in fact gradations and hybrids of the major types presented. And as the reader may have noted in the figured specimens, opposing valves can develop different geniculation patterns and shell growth rates that ultimately produce conspicuously inequivalve shells. Nonetheless, as more specimens are found for this and other species, the geniculation type approach used in this study may be useful to compare and differentiate the morphologic variability of other species in this important bivalve family.

This study adds information to the inoceramid database, but leaves many questions unanswered and raises even more: Are there other species capable of producing varied geniculated forms? Why do some inoceramids species geniculate while others do not? Why

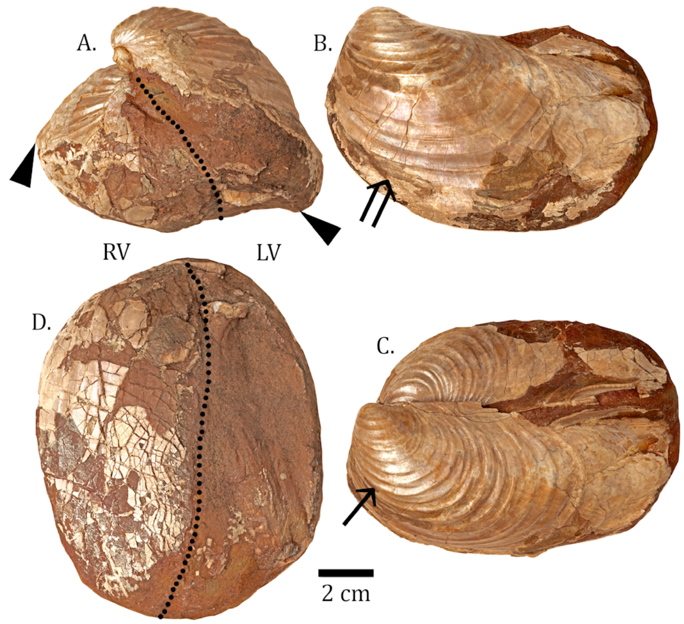

Figure 13A-D. *"Inoceramus" nebrascensis* Type III, articulated. UWBM IP 117996. **A.** Anterior view. **B.** Left lateral view. **C.** Dorsal view. **D.** Ventral view. Dotted line indicates commissure.

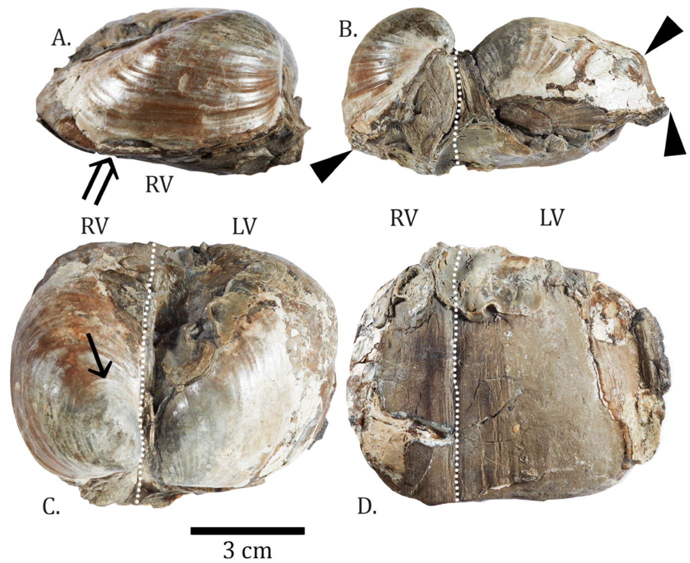

Figure 14A-D. *"Inoceramus" nebrascensis* Type III, articulated. UWBM IP 118001. **A.** Right lateral view. **B.** Anterior view. **C.** Dorsal view. **D.** Ventral view.

does a single inoceramid species generate a particular geniculation type over another? And finally, with all these morphologic shell possibilities, how did "*I.*" *nebrascensis* modify and adapt its internal organs to accommodate these various valve shapes? It is hoped that some of these questions will be addressed in a follow-up paper after more specimens are collected from this remarkable site.

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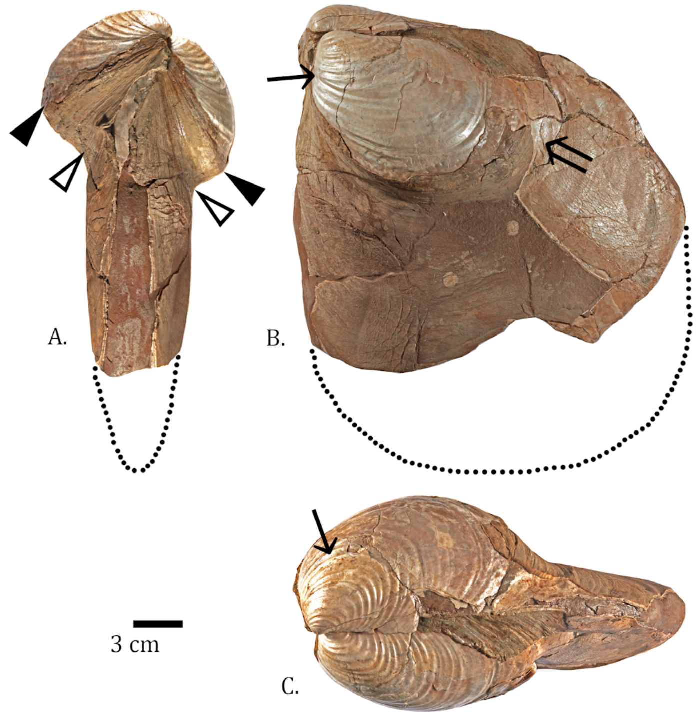

Figure 15A-C. *"Inoceramus" nebrascensis* Type IV, articulated. UWBM IP 117995. **A.** Anterior view. **B.** Left lateral view. **C.** Dorsal view.

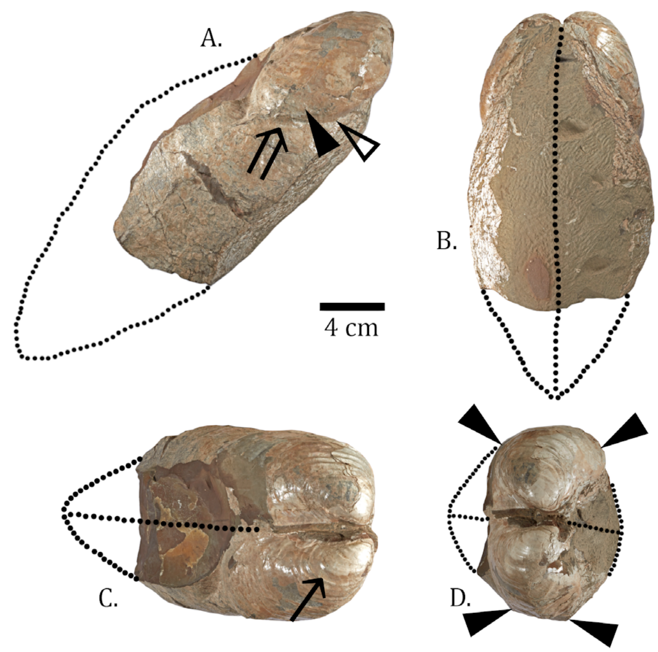

Figure 16A-C. *"Inoceramus" nebrascensis* Type V, articulated. UWBM IP 117994. **A.** Right lateral view showing the positive geniculation followed promptly by a negative geniculation. **B.** Angled anterior view. **C.** Posterodorsal view **D.** Dorsal view. Note the positive geniculations on the anterior and posterior surfaces of the adult shell.

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