

Lower Jaw of *Spathites*
(Ammonoidea: Acanthoceratoidea)
from the Upper Cretaceous (Turonian)
of New Mexico

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ABSTRACT

A lower jaw was recently discovered in a limestone concretion in association with the Late Cretaceous (Turonian) ammonite *Spathites puercoensis* (Herrick and Johnson, 1900) from the Carlile Member of the Mancos Shale in Sandoval County, New Mexico. It is nearly complete and comprises the aptychus with a hinge along the midline. The better-preserved plate, the left (according to its position in life), is roughly triangular in shape with a broadly rounded lateral margin, a narrowly rounded posterior margin, and a weakly concave anterior margin. It is 26.2 mm wide and 33.0 mm long. Together, the left and right plates form an escutcheonlike shape that projects slightly forward at the apex. The ratio of jaw width to length (26.2 mm \times 2 / 33.0 mm) equals 1.59. The aptychus consists of yellow-orange calcite and is covered with comarginal ribs that parallel the lateral and posterior margins and become more prominent toward the posterior end. It is likely that this jaw belongs to the associated ammonite and would have comfortably fit inside the body chamber, based on a comparison of the length of the jaw and the whorl height, suggesting that it functioned as a jaw, rather than as an operculum. It is the first report of an ammonite jaw in the genus *Spathites* and the first reported occurrence of an ammonite jaw from New Mexico.

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INTRODUCTION

Jaws are among the few features that are preserved in ammonites in addition to their shells. They occur in Devonian to Cretaceous deposits and have been used in taxonomic and paleoecological studies. Based on variation in their shape and structure, they have been classified into several morphotypes, of which the aptychus type is the most enigmatic in terms of function (Engeser and Keupp, 2002; Tanabe et al., 2015). The aptychus-type jaw occurs in Jurassic and Cretaceous Ammonitina and Ancyloceratina and is characterized by two calcareous plates that cover the ventral surface of the lower jaw. Because of the thickness and ornamentation of the calcareous plates, they have also been interpreted as opercula rather than jaws (Trauth, 1927–1936). Seilacher (1993) argued for a dual function—both as a jaw and as an operculum and detailed the evolutionary steps culminating in this innovation (for further discussion about this interpretation, see Lehmann and Kulicki, 1990; Parent et al., 2014). The discovery of another aptychus-type jaw, as reported here, adds to our knowledge of the taxonomic and stratigraphic distribution of these structures.

The discovery of jaws also furnishes clues into the taphonomy and the environment of deposition of the ammonites with which they are preserved. Investigations of jaw preservation in modern *Nautilus* indicate that jaws are rapidly lost after the death of the animal (Wani, 2007; Wani et al., 2005). Laboratory experiments with coleoid jaws in aquaria further suggest that these structures begin to disintegrate after a few months on the sea bottom (Kear et al., 1995). Thus, the presence of jaws at a site indicates that the deposits are autochthonous and were buried rapidly. Landman and Klofak (2012) used these arguments to infer the rate of formation of fossiliferous, calcareous concretions containing ammonite jaws in the Campanian Pierre Shale of South Dakota. According to their estimates, such concretions formed in less than 10 years.

STRATIGRAPHY

The specimens of *Spathites puercoensis* (Herrick and Johnson, 1900) and the aptychus described here were collected by one of us (M.P.F.) in July 2017 in the Carlile Member of the Mancos Shale in the southeastern San Juan Basin of northwestern New Mexico (fig. 1). The Carlile Member of the Mancos Shale in this area is a shale-dominated unit 60–120 m thick that is exposed over a 65 km long, nearly southwest-northeast-oriented outcrop belt that extends from east of Mesa Prieta on the south to east of the village of Cuba on the north (Molenaar, 1983; Sealey and Lucas, 2019).

The Carlile Shale in the southeastern San Juan Basin is a three-part unit—lower shale interval, Semilla Sandstone, and upper shale interval. It overlies the Greenhorn Limestone Member of the Mancos Shale. Gray or black shale with layers of limestone nodules (many septarian) characterize the shale-dominated intervals of the Carlile. The Semilla Sandstone consists of very fine to medium-grained sandstone that generally coarsens upward and is a laterally discontinuous sandstone unit, the base of which is approximately 61 m above the Greenhorn Limestone. It represents discrete, offshore, shallow marine bars that formed 50–80 km northeast of the shoreline at that time, which is referred to as the Atarque Shoreline (La

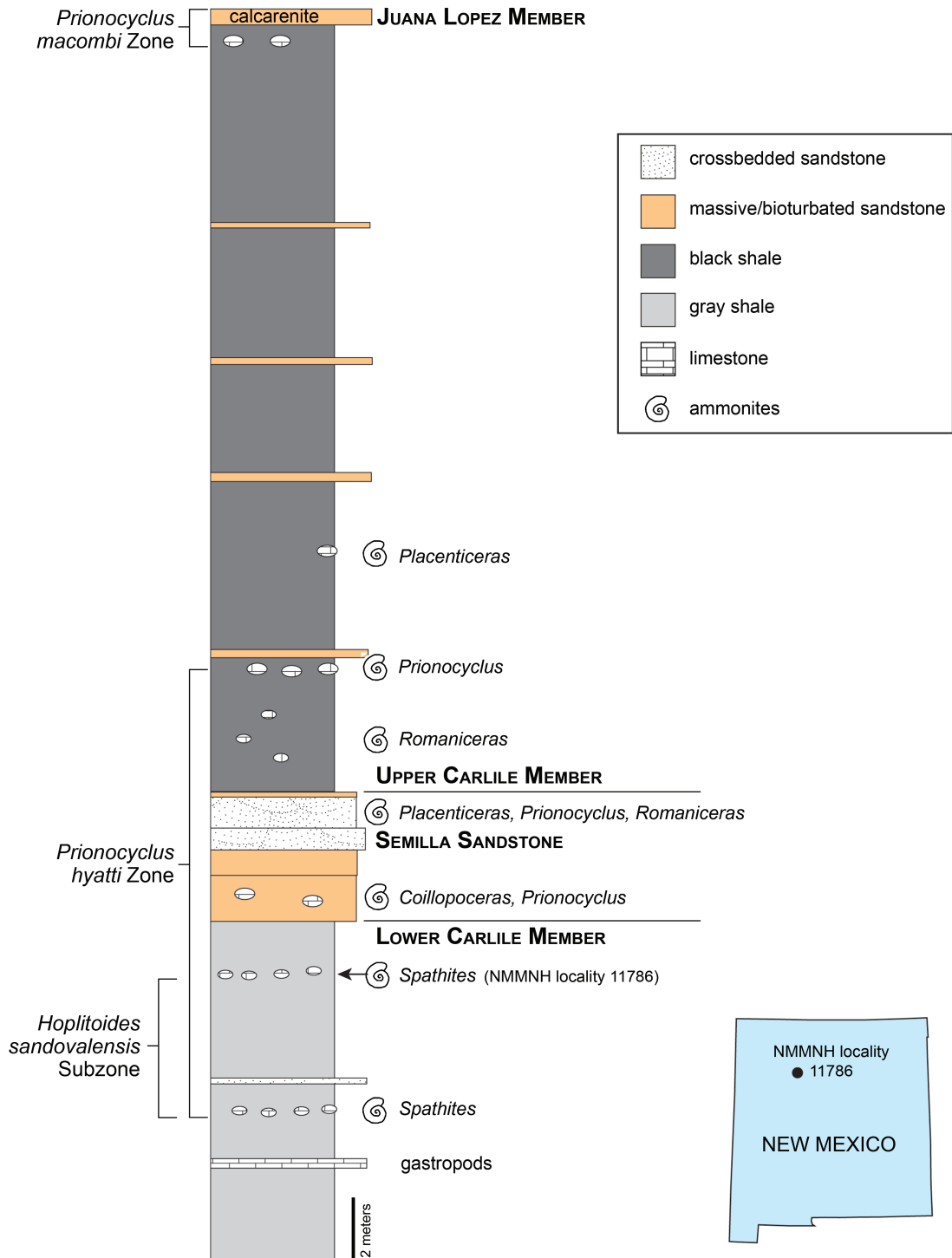


FIGURE 1. Map and stratigraphic section showing the locality of *Spathites puercoensis* (Herrick and Johnson, 1900) and its aptychus.

Fon, 1981). The Juana Lopez Member of the Mancos Shale overlies the Carlile Member and forms one of the most distinctive and laterally persistent lithostratigraphic units in the Upper Cretaceous section of New Mexico (e.g., Dane et al., 1966; Hook and Cobban, 1980; Sealey et al., 2006). The Carlile and Juana Lopez members of the Mancos Shale in the southeastern San Juan Basin are Turonian in age (Sealey and Lucas, 2019). Almost all of the Carlile Member is dated as middle Turonian based on the occurrence of the lower middle Turonian *Collignonicerias woollgari regulare* Subzone in the lower part of the member and the upper middle Turonian *Prionocyclus hyatti* Zone in the upper part of the member. In addition, the lowermost upper Turonian *Prionocyclus macombi* Zone occurs in the upper part of the member in the study area (Sealey and Lucas, 2019).

The specimens of *Spathites puercoensis* and the aptychus are repositated at the New Mexico Museum of Natural History, Albuquerque, New Mexico (NMMNH) and are cataloged as P-79962. They were collected at NMMNH fossil locality 11786 in T. 15 N., R. 1W., south of Marquez Wash in a 0.2 m thick interval of small limestone nodules that is 1.7 m below the base of the Semilla Sandstone (fig. 1). (Detailed locality data in the NMMNH database are available to qualified researchers.) Thus, the specimens are from the upper part of the lower shale interval of the Carlile Member and at the top of the interval that contains *S. puercoensis*. They are in the *Hoplitoides sandovalensis* Subzone of the upper middle Turonian *Prionocyclus hyatti* Zone, based on the occurrence of *S. puercoensis* (see Cobban and Hook, 1980: 11; Cobban and Hook, 1983: table 1; Cobban, 1984: 86).

TERMINOLOGY

Our use of terms to describe the lower jaws of ammonites follows that of Kanie (1982), Tanabe (1983), and Tanabe and Fukuda (1987), as recently summarized by Tanabe et al. (2015). The terms anterior, posterior, ventral, dorsal, left, and right refer to the jaw as it was oriented in life. The apical end of the jaw is called the apex. The most recently formed portion of the jaw is at the posterior end. An aptychus-type lower jaw is defined as a lower jaw that exhibits a hinge line (symphysis = commissure) with a calcareous plate on either side, comprising the aptychus. The two symmetrical halves of the lower jaw are called the wings. We measured the width and length of each wing, irrespective of their curvature. The width of the jaw equals twice the width of each wing. The ratio of jaw width to length affords an approximation of jaw shape.

MATERIAL

The lower jaw is embedded in a chunk of sandy calcareous concretion from the Carlile Member of the Mancos Shale in Sandoval County, New Mexico. The concretion is approximately 110 mm in maximum diameter (fig. 2A). When it was broken open, it revealed the jaw. In addition to the jaw (see description below), the concretion contains parts of two ammonites (fig. 2), the more complete one of which can be confidently assigned to *Spathites puercoensis*. It is 75 mm in diameter, but much of it is still embedded in the concretion. It consists of the

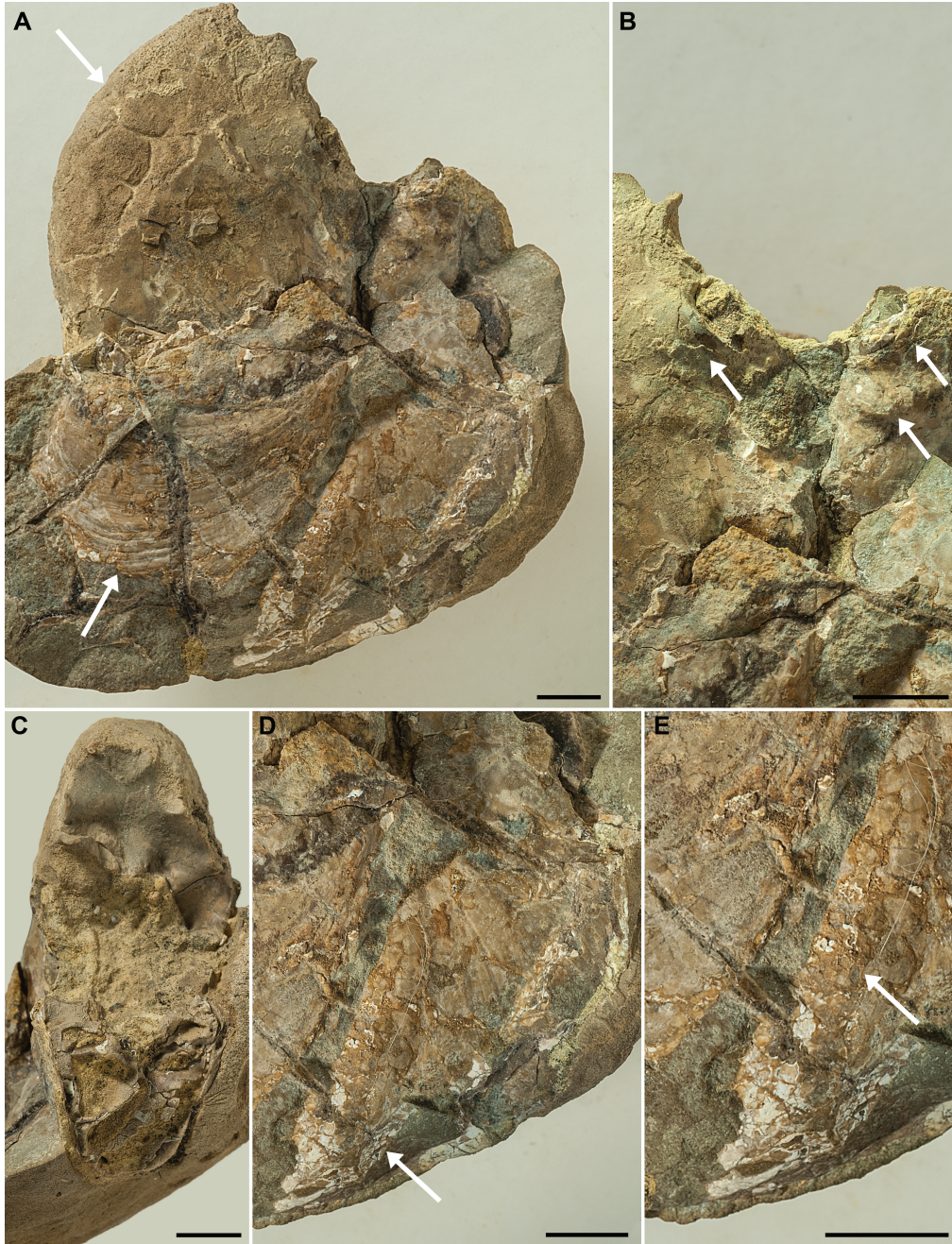


FIGURE 2. **A.** Overview of New Mexico Museum of Natural History P-79962 showing the specimen of *Spathites puercoensis* (upper arrow) and the associated jaw (lower arrow). **B.** Close-up of the umbilical nodes (arrows) surrounding the umbilicus, which is a characteristic of this species. **C.** Whorl cross section at the base of the body chamber with the last septum of the phragmocone on top. **D.** Fragment of the apertural margin (arrow) of another specimen of *S. puercoensis* next to the aptychus. **E.** Close-up of the inflated apertural margin (arrow) and part of the shell covered with growth lines. Scale bar = 1 cm.

phragmocone, most of which is missing, and one-quarter whorl of the body chamber (the rest is embedded in the concretion). The cross section of the whorl at the base of the body chamber is compressed subquadrate (whorl width/whorl height = 0.79) with maximum whorl width at one-quarter whorl height. The umbilicus is narrow (7.5 mm wide) and deep, and the umbilical shoulder is sharply rounded. The flanks are broadly rounded and converge toward the ventrolateral shoulder. The venter is broad and nearly flat. The umbilical margin bears strong umbilical nodes (fig. 2B), which are characteristic features of this species.

The concretion also contains a fragment of the apertural margin of another specimen, presumably belonging to the same species (fig. 2D). It is possible that it even belongs to the same specimen described above, but it is pointing in the opposite direction. The whorl height is 43.1 mm, and the aperture is weakly sinuous and slightly flared (fig. 2D, E). The rest of this shell fragment (0.125 whorl) is covered with weak ribs that cross the flanks with a broad concavity. Cobban (1988: 19) also noted a specimen of *Spathites puercoensis* with a similarly flared apertural margin, but did not illustrate it nor provide any locality data for it.

DESCRIPTION OF THE JAW

The lower jaw is plastered on top of the body chamber of the more complete ammonite specimen (fig. 3A), although that part of the body chamber is still below the surface of the concretion. The jaw is just in front of the fragment of the apertural margin. It bears three cracks, the middle one of which coincides with the symphysal margin (fig. 3B). The jaw is butterflyed out, although the right wing preserves some of its original convexity.

The ventral surface of the jaw is exposed and is covered with two plates comprising the aptychus sensu stricto. The left plate is better preserved than the right plate. It is roughly triangular in shape with a weakly concave anterior margin (fig. 3C), a broadly rounded lateral margin, and a narrowly rounded posterior margin (fig. 3D). The left plate is 26.2 mm wide and 33.0 mm long. Together, the two plates form an escutcheonlike shape that projects slightly forward at the apex (fig. 3A). The ratio of jaw width to length ($26.2 \text{ mm} \times 2 / 33.0 \text{ mm}$) equals 1.59.

The aptychus is yellow-orange in color. The ventral surface is covered with comarginal ribs that parallel the lateral and posterior margins. The ribs are fine and closely spaced near the anterior end but become coarser and more widely spaced toward the posterior end (fig. 3D). The crest of each rib is broadly rounded to nearly flat. In profile, some of the ribs are asymmetric in shape, with gently sloping anterior sides and more steeply sloping posterior sides.

A fragment of the aptychus was removed from the left plate close to the anterior margin to examine it under a scanning electron microscope. The aptychus is 0.19 mm thick and consists of a thin outer (ventral) layer, 7.7 μm thick, and a thicker inner (dorsal) layer comprising the rest of the aptychus (fig. 4). The microstructure of both the outer and inner layer is massive, although the inner layer exhibits some oblique laminations on the ventral side, each of which is approximately 3 μm thick (fig. 4B).

Another piece of the aptychus was analyzed by Micro X-ray diffraction (Texray Laboratory Services, Argyle, Texas) to determine its mineralogy. This analysis was performed using a



FIGURE 3. **A.** Ventral view of the lower jaw (arrows) comprising two calcareous plates (= the aptychus). **B.** Close-up of the median hinge (arrow) between the two calcareous plates. **C.** Close-up of the broadly concave anterior margin (arrow) of the left plate. **D.** Close-up of the posterior margin (arrow) of the left plate near the median hinge showing the comarginal ribs. Scale bar = 1 cm.

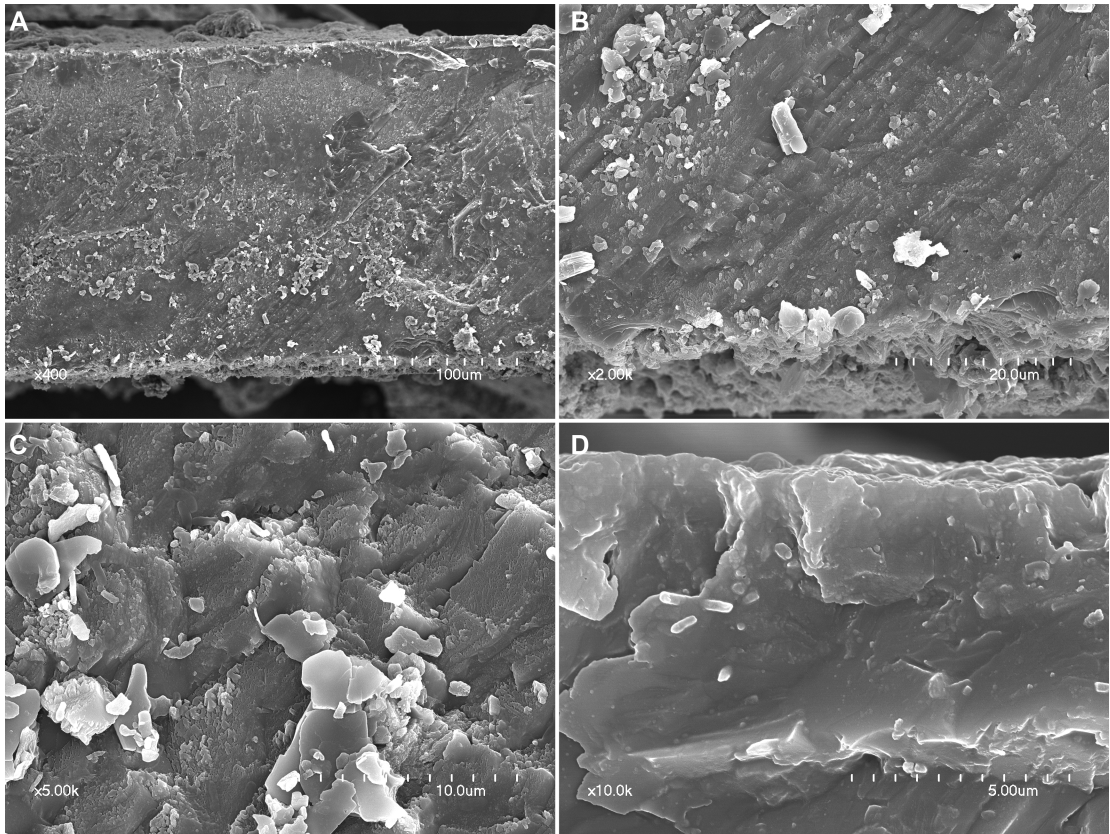


FIGURE 4. Cross section of a piece of the aptychus from the anterior edge of the left plate, with the outer (ventral) surface on top. **A.** The aptychus is 0.19 mm thick and consists of a very thin outer layer 7.7 μm thick and a thicker inner (dorsal) layer—the rest of the aptychus. **B.** Close-up of the bottom of the inner layer showing oblique laminations. **C.** Close-up of the middle of the inner layer showing massive microstructure. **D.** Close-up of the outer layer showing massive microstructure.

Bruker D5000 X-ray diffractometer with $\text{CuK}\alpha$ radiation source ($\lambda = 1.5405\text{\AA}$) and silicon drift detector. The X-ray source was operated at 40 kV and 40 mA. The XRD scan range was 5° – 70° 2θ at a step size of 0.02° . Phase identification was performed on the sample using Search/Match application in MDI Jade 2010 and ICDDs PDF database of standard XRD patterns. The results indicate that the aptychus is mainly composed of calcite. However, an amorphous phase is also present, which may represent the remnant of the organic layer on the dorsal side.

DISCUSSION

Although the jaw is not inside the body chamber, it is adjacent to the shell fragment of the apertural margin and, based on its association, size, and morphology, it can reasonably be attributed to *Spathites puercoensis*. As such, this is the first report of a lower jaw from the genus *Spathites* and the first reported occurrence of an ammonite jaw from New Mexico. Similar lower jaws have previously been reported from the Turonian in four other genera of the super-

family Acanthoceratoidea, to which *Spathites* belongs (Tanabe et al., 2015: table 10.1). Tanabe and Fukuda (1987) reported upper and lower jaws inside the body chamber of the collignoniceratid ammonite *Subprionocyclus* from the Turonian of Hokkaido, Japan (it was originally referred to as *Reesidites* by them but later attributed to *Subprionocyclus* by Tanabe et al., 2015). As in *Spathites*, the lower jaw is composed of two calcareous plates covered with comarginal ribs. A cross section of the apex reveals a series of serrated ridges and grooves along the anterior margin, each approximately 12 μm wide (Tanabe and Fukuda, 1987: figs. 1A, B, 3, 4D). Ifrim (2013: fig. 3) also reported a lower jaw in the ammonite *Pseudaspidoceras* from the lower Turonian of Mexico. The jaw is smooth without any ribs, but the specimen does not appear to be well preserved.

Two other lower jaws have been reported in the Acanthoceratoidea from both older and younger deposits. Tanabe et al. (2015: table 10.1, fig. 10.7c) reported a lower jaw of *Prohystero-ceras* from the Albian of Hokkaido. It is an aptychus-type jaw and is covered with comarginal ribs. Kennedy and Klinger (1972) reported an aptychus-type jaw in close association with a specimen of *Texanites* from the Santonian of Zululand, South Africa. The jaw occurs in the ventral part of the body chamber close to the aperture. However, the calcareous plates are covered with spiny protuberances and bear no resemblance to the aptychus in *Spathites*. It resembles instead the form-genus *Spinaptychus* based on its shape and kind of ornamentation. Similar specimens of *Spinaptychus* occur in the Santonian Smoky Hill Chalk of Kansas and are also attributed to *Texanites* (see Everhart, 2005).

The function of the aptychus-type jaw has been endlessly debated (Landman et al., 2007; Tanabe et al., 2015). One of the clues to its function is the relationship between the size of the jaw and the shape of the ammonite whorl section. In the *Spathites* specimen described here, the ratio of jaw width/length (1.59) is much higher than the ratio of whorl width/whorl height, as measured at the base of the body chamber (0.79). However, the jaw would not have been butterflyed out in life and would instead have formed a U-shaped structure. Indeed, the right wing captures some of this original curvature, as shown in a hypothetical reconstruction (fig. 5). For this reason, the length of the jaw is a much more reliable indicator of the fit of the jaw inside the body chamber. Based on a comparison between the length of the jaw (33.0 mm long) and the whorl height of the apertural fragment (43.1 mm high), the jaw would have comfortably been accommodated inside the body chamber of *Spathites puercoensis*.

However, the presence of the two calcareous plates poses a conundrum in terms of explaining the function of the jaw—is it a feeding apparatus or an operculum? We favor a compromise solution. As mentioned above, the jaw in *Spathites puercoensis* would have easily fit inside the body chamber, which is consistent with a feeding function. However, if the jaw occasionally protruded outside of the aperture to facilitate food capture, it would have been vulnerable to predation. The calcareous plates would have served to protect the soft tissues, even if the jaw were only exposed for short periods of time.

One of the issues in interpreting deposits containing ammonites is whether the ammonites floated into the area after death. For example, if a predator destroyed the body chamber of an ammonite, the shell could have theoretically floated for a long time afterward

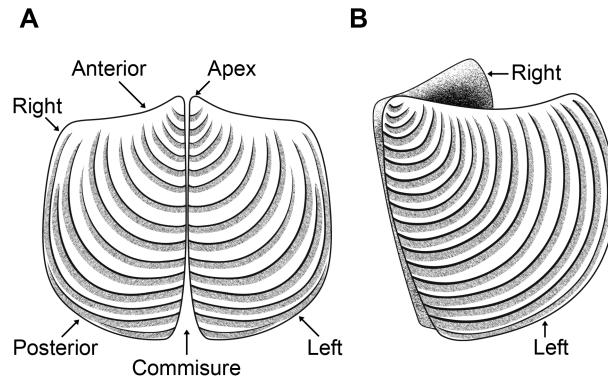


FIGURE 5. Three-dimensional reconstruction of the lower jaw of *Spathites puercoensis* (NMMNH P-79962) showing **A**, ventral and **B**, lateral views.

because of its buoyant phragmocone. This interpretation was predicated on observations that dead shells of *Nautilus* are broadly distributed in the Indo-Pacific far from their original habitats (for a recent reinterpretation, see Yacobucci, 2018). However, Chamberlain et al. (1981) investigated this hypothesis using a mathematical approach and determined that the probability of postmortem drift depended on the size of the shell and the depth at which it died. Tanabe (1979) further emphasized that the presence of jaws associated with ammonites is an important clue that the ammonites did not drift into the area after death. Thus, the presence of the jaw in association with *Spathites puercoensis* documented here suggests that these ammonites similarly did not drift into the site but rather died there and were rapidly buried.

CONCLUSIONS

The discovery of a jaw in close association with *Spathites puercoensis* contributes to our understanding of the taxonomic and stratigraphic distribution of these features. The structure conforms to the aptychus-type jaw, which is restricted to the Jurassic and Cretaceous Ammonitina and Ancyloceratina. Based on the relationship between the size of the jaw and the whorl section of the ammonite, the jaw would have comfortably fit inside the body chamber and presumably would have fulfilled a feeding function. It is the first report of an ammonite jaw in the genus *Spathites* and the first from the Upper Cretaceous of New Mexico, and suggests that the horizon in which it occurs represents an autochthonous deposit.

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