# The first occurrence of *Ptychodus latissimus* from the Codell Sandstone Member of the Carlile Shale in Kansas

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Three teeth of the late Cretaceous shark *Ptychodus latissimus* (Agassiz) are described from the upper Middle Turonian Codell Sandstone Member of the Carlile Shale. These teeth are significant because they are the first documented occurrence of the species in Kansas, extending the paleobiogeographic range of species and adding a new paleoecological component to the Codell Sandstone fauna. Its association with various ammonite species living in different trophic levels with other ptychodontid sharks may be indicative of niche partitioning.

*Keywords: Late Cretaceous, Middle Turonian, niche portioning, paleogeographic range, paleoecology, sharks, trophic levels.*

## INTRODUCTION

*Ptychodus latissimus* is a late Cretaceous shark species occurring within marine deposits in North America, Europe and Japan. It is known from a limited stratigraphic and temporal range, with the greatest numbers of specimens collected from the Late Turonian-Early Coniacian (Zone of *Terebratulina lata*) of the English Chalk (Dibley 1911; Woodward 1911). Other occurrences include the Late Turonian of France (Vullo and Arnaud 2009), the Blackcoloured Formation in northwestern Germany (Diedrich, 2013), the Strehlen Formation in eastern Germany (Fischer et al. 2017); the Itombe Formation of Angola (Antunes and Cappetta 2002), the Phosphatic Horizons IVb and V from the Mangyshlak Mountains of western Kazakhstan (Radwański and Marcinowski 1996); the Opole trough in Poland (Niedźwiedzki and Kalina 2003); and the Early Coniacian of Japan (Tan 1949).

In the Western Interior Seaway *Ptychodus latissimus* is known only by isolated teeth and has its first and only occurrence during the middle Late Turonian to the Early Coniacian. To date, only 31 teeth have been reported, primarily from the basal Atco Formation of the Austin Chalk in Texas (Welton and Farish 1993; Hamm 2004, 2005, 2008; Hamm and Cicimurri 2011) and a single tooth from the Sage Breaks Member of the Carlile Shale in South Dakota (Cicimurri 2004).

This paper describes previously unreported, and isolated *P. latissimus* teeth which are housed in the Sternberg Museum of Natural History at Fort Hays State University (FHSM), Hays, Kansas.

## MATERIALS EXAMINED

FHSM VP-19632 three isolated teeth recovered from the Codell Sandstone in Jewell County, Kansas (Fig. 1). Detailed locality information is on file at FHSM. Additional comparative material in this study include specimens from the Natural History Museum in London (NHMUK) and Southern Methodist University (SMU) Dallas, Texas.

## GEOLOGICAL OCCURRENCE

The Codell Sandstone (Fig. 2) is a Middle Turonian (~90.5 mya) marine deposit that conformably overlies the Blue Hill Shale Member of the Carlile Formation and unconformably the Fort Hays Limestone Member of the Niobrara Chalk Formation

(Hattin 1962). Deposition of the Codell
Sandstone was slow and was followed by
a long period of non-deposition until the
Niobrara cyclothem (Hattin et al. 1987). The
Codell Sandstone represents the final stage in
the regression of the Greenhorn Seaway and a
depositional hiatus prior to the transgression of
the Niobrara Seaway.

The paleoenvironment of the Codell Sandstone
is interpreted as a shallow, nearshore
marine deposit with water level depths
interpreted to be no more than 30-60 meters
(Kauffman 1967). Biostratigraphically the
Codell Sandstone lies within the ammonite
*Prionocyclus wyomingensis* zone (Hattin
et al. 1987; Molenaar et al. 2002; Cobban
et al. 2006). Ammonite diversity within the
Codell Sandstone is low, consisting only of
*Baculites* sp., *Prionocyclus wyomingensis*, and
*Scaphites* sp. Other invertebrate fossils from
the deposit include annelid worm burrows like
*Ophiomorpha* and *Thalassinoides,* and the
bivalves *Inoceramus* cf. *I. dimidus*, *Inoceramus*
cf. *I. flaccidus*, and *Inoceramus* sp. Fecal
pellets, spores, and foraminiferans are common
occurrences (Hattin 1962). These taxa indicate
that the sediment was rich in organic detritus,
further supporting a lower energy setting in
which organic material could settle out of the
water column (Meyers 2014).

**SYSTEMATIC PALEONTOLOGY**

Class CHONDRICTHYES Huxley, 1880
  Subclass ELASMOBRANCHII Bonaparte,
                                      1838
    Cohort EUSELACHII Hay, 1902
      Sub cohort NEOSELACHII Compagno,
                                      1977
      Order PTYCHODONTIFORMES
                          Hamm 2019
        Family PTYCHODONTIDAE
                          Jaekel, 1898
          Genus *Ptychodus* Agassiz, 1835
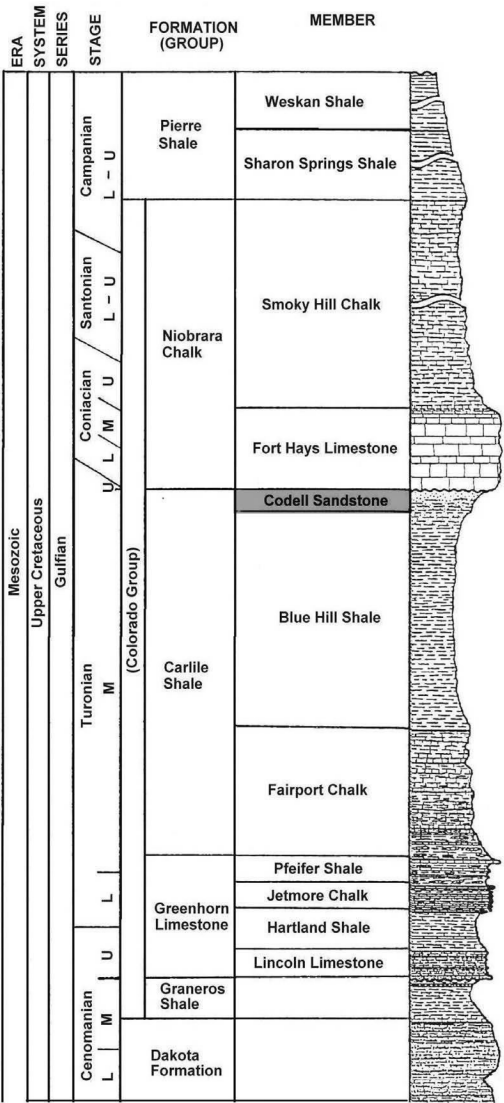
*PTYCHODUS LATISSIMUS* Agassiz, 1835



Figure 1. Stratigraphic occurrence of *Ptychodus
latissimus* FHSM VP-19632 in the Codell
Sanstone Member of the Carlile Formation.
Stratigraphic column adapted from Shimada
1996, fig. 2

**DESCRIPTION**

The genus *Ptychodus* is represented by species
that possess either a high-cusped crown as
demonstrated by *P. whipplei* and *P. rugosus*
or low-cusped crown as in *P. martini* and *P.
polygyrus*. *Ptychodus latissimus* falls within
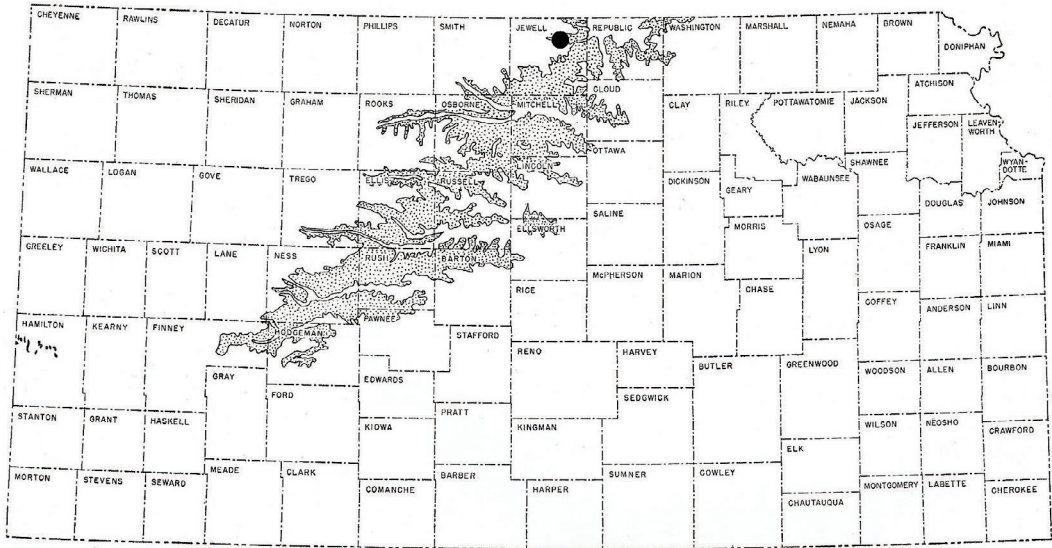the low-crowned group as defined by crown

Figure 2. Geographic location (black circle) of *Ptychodus latissimus* FHSM VP-19632 and generalized outcrops of the Carlile Formation. Adapted from Hattin 1962, fig. 1.

height to tooth height ratios (see Hamm 2008 for additional data). The tooth morphology of the type specimen of *Ptychodus latissimus* is very distinctive compared to other members of the genus (Fig. 3). The tooth crowns are low and wide with a gently raised cusp. The lower symphyseal file tooth is a massive tooth with very thick and widely spaced transverse ridges that are restricted to the apex of the crown. The ridges are thick at their base and thin upward toward their apex, forming a sharp cutting edge. The ridges are restricted to the central portion of the tooth crown, then become narrow and thin at the crown edge, curving at the tooth margin.
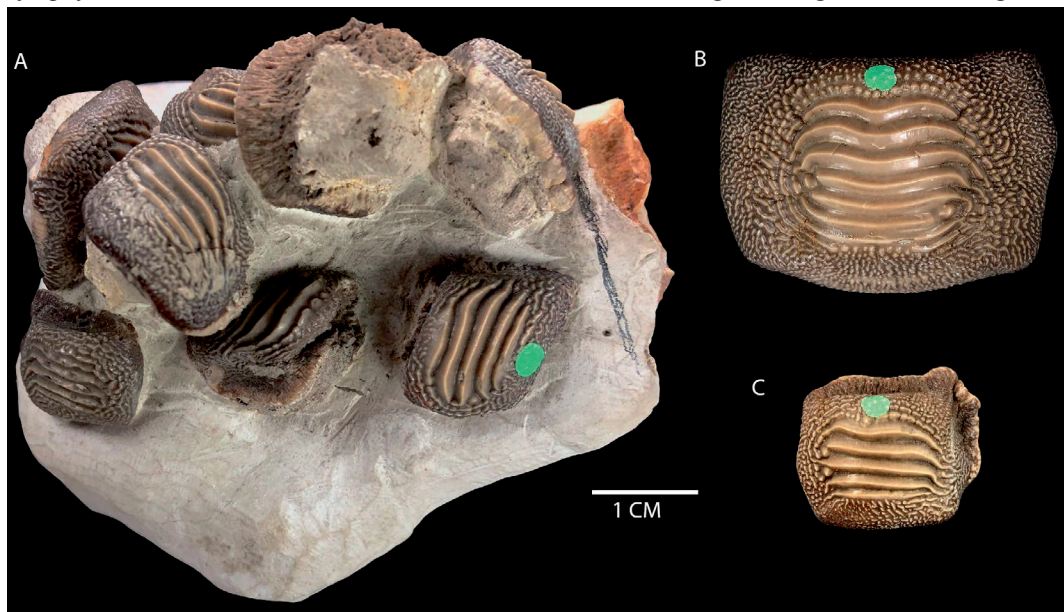


Figure 3. NHMUK OR 4355, *Ptychodus latissimus* syntypes. A, associated lateral tooth files; B. lower medial file; C, left paramedial file.
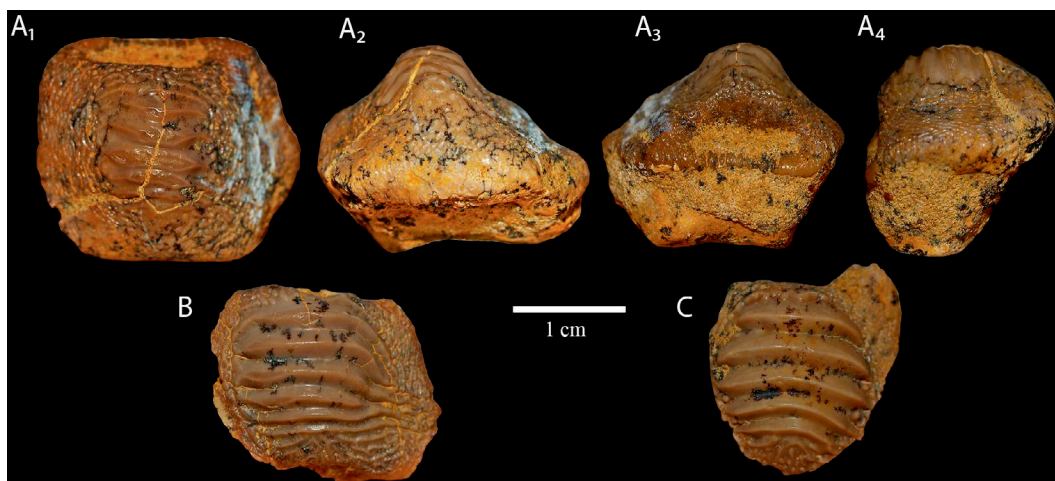
Figure 4. FHSM VP-19632, *Ptychodus latissimus*. A, right paramedial in 1 apical, 2 anterior, 3 posterior and 4 lateral views; B, right anterolateral apical view; C, partial crown apical view.

These ridges do not bifurcate, loop or connect with any other ridges as seen in other low-crowned species. The marginal area is wide and has a very thick, rugose or granular texture. The labial tooth margin exhibits a dendritic pattern of fine longitudinal ridges, whereas the lingual edge bears the typical granular pattern as in other ptychodontids. The tooth root is weakly bilobed, and there is a deep lingual crown sulcus.

The teeth in FHSM VP-19632 include a right paramedial tooth (Fig. 4a), which is19 mm wide, 16 mm long with a 16 mm tooth height. It has an elevated and offset crown that is 6 mm high crossed by five thick transverse ridges that terminate sharply at the marginal area. The tooth margin is narrow (5 mm wide), coarsely granulated and concentric with the crown. The anterior margin is wide and extended, which would attach to the lingual sulcus of the preceding tooth with the tooth file. The mesial and distal crown edges are multi-angled to fit within teeth from the next lateral tooth file to make a strong and flexible battery of teeth within the dentition.

Figure 4b shows a partially preserved crown of a right lateral tooth that is 16 mm wide, 12 mm long, and 5 mm in crown height. The crown apex is crossed by six slightly wavy,

thick transverse ridges. It does not preserve the tooth root or marginal areas, but the offset crown allows diagnosis to the right side of the dentition. Figure 4c a partial tooth crown that is 14 mm wide, 15.8 mm long, and 6 mm in tooth height as preserved. Five anteriorly curved ridges are evident. It is uncertain as to the side of the dentition this tooth belongs to, not enough of the tooth is preserved to make a determination.

### Discussion

The tooth morphology of *P. latissimus* was very specialized, with a reduced number of ridges that are thicker at the base and thin at the apex, creating a series of thick wedge-like ridges. This specific tooth morphology had a limited stratigraphic range worldwide. It has been suggested that the teeth of *Ptychodus* were specifically derived to feed on hard-shelled, widely distributed inoceramids (Kauffman 1972, 1977; Kirkland 1983; Stewart 1988). Species of *Ptychodus* can be placed into low, medium and high crown morphologies with *P. latissimus* being a low-crowned variety (Hamm 2008; 2020). Each of these crown morphologies evolved to process specific prey items in specific marine conditions (i.e. nearshore versus off shore). The differences in tooth design would seem to also indicate

differences in jaw morphologies that could functionally produce the appropriate amount of force to overcome and crack varying shell morphologies.

Studies of the feeding mechanisms between modern durophagous sharks, rays, batiods and chimaeras has focused primarily on cranial musculature and the kinematics of prey acquisition and feeding (Wilga et al. 2000; Summers et al. 2004, Dean et al. 2005; Kolmann et al. 2015). Each study demonstrated the relationships between jaw morphologies, its mode of attachment to the skull, tooth morphologies and how these variables relate to crushing strength. They have radically different skeletal and jaw morphologies, highly divergent tooth morphologies, and differing feeding strategies and all of them specialize on a variety of hard prey (Dean et al. 2005). Kolmann et al. (2015) showed that modern durophagous vertebrates are morphologically variable even among closely related taxa. This necessitates the need for an alternative food acquisition strategy in a highly competitive environment.

With numerous variations in tooth crown morphologies, there must have been species-specific durophagous dietary preferences for each species of *Ptychodus* (Cappetta 1987; Williamson et al. 1993). It is unlikely that each species was dependent on a diet of only inoceramids as a major food source, but could feed on a variety of hard-shelled prey including squids, shrimp and other decapods and ammonites, which were widely dispersed throughout the Western Interior Seaway. Prey processing abilities in elasmobranchs may be indicative of underlying environmental pressures, and that prey availability may have driven the evolution of the durophagous feeding mechanism (Dean et al. 2005). This was most likely the scenario throughout the stratigraphic range of *Ptychodus* as multiple species consisting of low and high-crowned species are coeval within the same deposits, as exemplified by *P. mortoni*, *P. whipplei* and *P. latissimus* in the Codell Sandstone.

Ammonites are an ecologically diverse group of marine organisms with varied shell morphologies that inhabited various environments based on depth, water temperature and salinity. Because of their abundance, they may have been a good nutrient source for marine predators, just as modern cephalopods are important prey for large marine animals such as sharks, teleosts and sperm whales (Clarke 1980; Takeda et al. 2015). Ammonite taxa from the Codell Sandstone include *Baculites, Prionocyclus,* and *Scaphites* (Hattin 1962), taxa that lived in waters of less than 100 m in depth (Batt 1989; Sessa et al. 2015) which is within the 30-60 meter depth estimation of Kauffman (1969). Each species of ammonite lived within different levels in the water column, and the variations in shell morphology suggest different modes of locomotion (Sessa et al. 2015). Having a straight shell, *Baculites* floated vertically and inhabited the upper part of the water column and were capable of rapid vertical movement including into the benthos (Westermann 1996; 2013), whereas *Scaphites* was primarily benthic, heavily bodied and open hooked shell shape that made it sluggish (Batt 1989; Tsujita and Westermann, 1998). This made scaphitid ammonites an important food source for durophagous predators in the Western Interior Seaway (Takeda et al. 2015). The shells of *Prionocyclus* are involute and compressed, and ornamented with ribs and tubercules (Kennedy et al. 2001). It was more widely distributed throughout the water column as juveniles lived in pelagic waters, developing more coarse ribs through ontogeny, and eventually developing horns and becoming more benthic as adults (Batt 1989).

Although the skeletal and cranial musculature is unknown in *Ptychodus*, it is probable that the high crowned species such as *P. mortoni* and *P. whipplei* could have fed on thinner shelled ammonites that lived higher in the water column such as *Baculites* and juvenile *Prionocyclus*, bony fishes, and squids rather than skimming the ocean floor specifically for

inoceramids. Conversely, the low crowned species *P. latissimus*, *P. marginalis*, *P. martini* and *P. polygyrus* could have been primarily benthic predators (Hamm and Harrell, Jr. 2013). Their thicker tooth crowns with raised, sharp and deep transverse ridges have a greater mechanical advantage towards thicker-shelled prey, including gastropods, bivalves, decapods and heavily ridged and spiny ammonites like *Scaphites* and adult forms of *Prionocyclus*.

The disparity in the number of *Ptychodus latissimus* specimens from the Western Interior Seaway is intriguing. The majority of specimens recovered from North America are from a residual lag deposit that sits on top of a disconformity at the Austin-Eagle Ford Group contact zone in north central Texas (Hamm 2008, 2009, 2020; Hamm and Cicimurri 2011). The lag deposit consists of glauconite, phosphate nodules and is abundant in marine vertebrate fossils including *P. latissimus*. The lag formed as a result of a sharp eustatic lowering of sea level, in a shallow shore face environment (Hancock and Walaszczyk 2004). Condensed phosphatic intervals in the Eagle Ford Group are interpreted to be formed by slow sedimentation during maximum flooding or maximum transgression events (Loutit et al. 1988; Dawson 2000). Hancock and Walaszczyk (2004) stated that the disconformity at the base of the Austin Group represents sea level low stand and is uppermost Turonian and represents a significant rise in sea level at the beginning of Austin Group sedimentation. Lithologically, this zone represents a deep regressive trough that cuts through the upper Arcadia Park Formation of the Eagle Ford Group (Hancock and Walaszczyk 2004). The upper part of the Arcadia Park Formation shale unit contains the bivalves *Mytiloides incertus* and *M. scupini* which correlate to the *Prionocyclus hyatti* Zone to the *Prionocyclus wyomingensis* Zone. The Codell Sandstone in Kanas and the Sage Breaks Member of the Carlile Shale in South Dakota also represent shallow, nearshore marine environments and both units contain these biostratigraphic

markers. Each deposit represents a similar facies and depositional environment and preserve a wide variety and high abundance of marine vertebrates (Cicimurri 1998, 2004; Bice 2015). By comparison, European occurrences of *P. latissimus* within the Middle to Late Turonian Zone of *Terebratulina lata* (formerly *T. gracilis*) of the English Chalk (Dibley 1911; Woodward 1911) has yielded a large and diverse shark fauna (Guinot et al. 2013). The environmental conditions and food sources changed radically from the latest Turonian to earliest Coniacian due to a major rise of sea level during the Niobrara Cyclothem (Kauffman and Caldwell 1993). There was a major incursion of cool boreal water from the north through the Western Interior Seaway into Texas, and warm Tethyan waters from the south producing a caballing effect that stirred current circulation and improved benthic oxygenation (Hay et al. 1993). Evidence for this in Kansas is recorded in the basal Codell Sandstone which was deposited in a lower distal shoreface environment (Meyers 2014). In Texas there was a change from the siliciclastic shales of the Arcadia Park Formation to the coccolith-rich pelagic chalk of the Austin Chalk (Hancock and Walaszczyk 2004). A major component of the Austin Chalk is diverse dinocyst assemblage that is indicative of an open marine environment with well-oxygenated and oligotrophic marine conditions (Eldrett et al. 2017).

Several factors lead to the disappearance of *P. latissimus* and other ptychodontids in the Western Interior Seaway at the end of the Turonian. Changes in salinity, water temperature, and oceanic circulation patterns may have caused the disappearance in the number of and differing shell morphotypes of ammonite species that were a major food source. Kennedy (1988) reported 18 genera and 28 species of ammonite from the upper Eagle Ford group. By the early Coniacian sea level rise had slowed and the input from boreal and tethyan waters stopped benthic circulation, which lead to dysoxic bottom

conditions (Lowery 2015). Ammonite diversity was much lower with only two genera and species being present; *Forresteria hobsoni* and *Scaphites preventicosus* (Kennedy and Cobban 1991). *Ptychodus latissimus* disappears from the English Chalk during the early Coniacian. The abundance of specimens from European deposits can best be explained by deeper water environments with less turbulent waters and slower depositional rates, which allowed for higher potential for preserving dentitions whole.

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