A NEW SPECIES OF THE LUNGFISH *CERATODUS* (DIPNOI) FROM THE EARLY CRETACEOUS OF THE EASTERN U.S.A.

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Lungfish species of the genus *Ceratodus* are widespread but infrequently encountered elements within post-Triassic terrestrial and marginal marine faunas of North America (Schultze, 1981; Kirkland, 1987). These species normally are known by sparse yet diagnosable fossils consisting of either the pterygoptalatine (upper) or prearticular (lower) dental plates. Because of the general rarity of associated skeletal material, previous work has treated *Ceratodus* as a form genus to include most post-Triassic North American species (e.g., Kirkland, 1987, 1998; Milner and Kirkland, 2006; Shimada and Kirkland, 2011; Main et al., 2014; Parris et al., 2014). A notable exception is *Potamoceratodus guentheri* (Marsh, 1878), known by a skull roof and partial palate (Pardo et al., 2010). Systematic interpretation based on tooth plates must be approached cautiously because of intraspecific and ontogenetic variability, which can hinder both quantitative and qualitative analyses (Kemp, 1996, 1997). This problem may be exacerbated by a limited sample size and the fragmentary nature of some specimens. Nevertheless, broad differences in tooth plate morphology are generally recognized as sufficient basis for species recognition (Kirkland, 1987, 1998; Kemp, 1993, 1997; Shimada and Kirkland, 2011).

Paradoxically, North America is relatively rich in fossil-bearing rocks of Cretaceous age, but lungfish diversity from this period is still poorly understood (Kirkland, 1987; Peters and Heim, 2010; Main et al., 2014). In Lower Cretaceous formations, lungfishes tend to be uncommon and irregular finds (Kirkland, 1987). When present, most of the identifiable taxa from these deposits appear nearly indistinguishable from species that first occur in the Late Jurassic (e.g., *Ceratodus frazieri*, Ostrom, 1970; Kirkland, 1987, 1998; Oreska et al., 2013), an exception being *Ceratodus texanus*, recently described from the Trinity Group of Texas (Parris et al., 2014). These Early Cretaceous ceratodontids are largely found in areas near or associated with the Western Interior Seaway (e.g., Schultze, 1981), restricting our knowledge of the diversity and evolution of these organisms to those in west-central part of the continent. The record from Upper Cretaceous units is similar: unique, well-documented occurrences are limited to *C. gustasoni*, from the Naturita Formation of Utah (Kirkland, 1987; Carpenter, 2014), and *C. carteri*, from the Woodbine Formation of Texas (Main et al., 2014). The geologically youngest lungfish from North America is represented by a single specimen attributed to *Ceratodus aff. C. frazieri*, from the Campanian of New Jersey. Until now, this specimen has been the only record of a lungfish from the Cretaceous of eastern North America (Parris et al., 2004).

Herein we add to the known diversity of Cretaceous lungfishes by describing a new species from the Arundel Clay facies of the Potomac Formation (Lower Cretaceous) of Maryland, USA (Fig. 1). Although known by a single, incomplete (yet diagnostic) tooth plate, *Ceratodus kranzi* sp. nov. represents the only known lungfish taxon from the eastern coast of North America during the Early Cretaceous. As such, it provides new data regarding lungfish diversity and biogeography during this time.

For lungfish tooth plates and dentin, we have adopted terminology from various sources (Schultze, 1981; Kirkland, 1987; Kemp, 1992, 1998, 2001b). Previous studies have relied on metrics (e.g., angles defined by borders and major ridges of tooth plates; Kirkland, 1987; Main et al., 2014; Parris et al., 2014). For comparative purposes and to maintain uniformity in treatment, we provide these data as far as possible; abbreviations for tooth plate ridges and other features are shown in Fig. 2. However, given the above-mentioned issues related to variability, small samples, and fossil incompleteness, our systematic treatment and comparisons rely heavily on qualitative characters.

**Institutional Abbreviations—KUVP**, Kansas University Vertebrate Paleontology Lab, Kansas Museum of Natural History, Lawrence, Kansas; **NJSM**, New Jersey State Museum, Trenton, New Jersey; **USNM**, National Museum of Natural History (formerly United States National Museum), Washington, D.C.; **YPM**, Yale Peabody Museum, New Haven, Connecticut.

**AGE AND GEOLOGIC SETTING**

The Arundel Clay lies within the terrigenous Cretaceous System deposited on the coastal plain of the mid-Atlantic region. The unit, originally defined as a formation within the Potomac Group (Clark and Bibbins, 1897), is sometimes regarded as a unique facies within the middle of the Potomac (e.g., Glaser, 1969; Lipka et al., 2006; Jud and Hickey, 2013), intermittently exposed in Washington, D.C., and Maryland. The Potomac is well known for its palynological record (Brenner, 1963; Doyle and Robbins, 1977; Hochuli et al., 2006; Doyle, 2012), which indicates a late Aptian to early Albian age for the Arundel Clay facies. The specimen described herein was recovered from USNM locality 41614, in what is now Dinosaur Park in Prince George’s County, Maryland (Fig. 1A).

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The Potomac is interpreted as representing a large, meandering, eastward-flowing fluvial system. Lithologically, the Arundel Clay facies consists mainly of lignite-rich bluish-gray claystones, reaching a maximum thickness of just under 40 m (Clark and Bibbins, 1897). The Arundel Clay facies, developed as a series of lenticular to elongate, localized deposits at or near the upper surface of the Patuxent member, is believed to represent floodplain or paludal depositional environments (Hansen, 1969; Kranz, 1998; Lipka et al., 2006).

**SYSTEMATIC PALEONTOLOGY**

SARCOPTERYGII Romer, 1955  
DIPNOI Müller, 1846  
CERATODONTIDAE Gill, 1872  
*CERATODUS* Agassiz, 1838  
*CERATODUSKRANZI*, sp. nov.  
(Fig. 2A, C, D; Supplementary Data)

**Holotype**—USNM 508543, incomplete left pterygopalatine plate.

**Type Locality and Age**—USNM locality 41614, Dinosaur Park, Muirkirk, Prince George’s County, Maryland, USA; Arundel Clay facies, Potomac Formation, Lower Cretaceous (Aptian–Albian).

**Etymology**—The species is named for Peter Kranz, in recognition of his tireless efforts to study, publicize, and preserve vertebrate fossils from the Arundel Clay of Maryland (Kranz, 1989, 1998).

**Diagnosis**—A large species of *Ceratodus* with an originally five-crested pterygopalatine tooth plate characterized by a highly obtuse inner angle (<ABC), with the last two ridge crests well defined and subequal in length; a large mass present on the mesiobuccal side of the occlusal surface; and a posterior margin that is sublinear and suborthogonal to the lingual margin. The pterygopalatine tooth plate of *C. kranzi* can be distinguished from those of all other comparable species of *Ceratodus* based on a combination of its large size, square posterior margin, and the sizable mass present on the occlusal surface of the inner angle.

**Description**—The holotype and only known specimen of *C. kranzi* (USNM 508543) is an incomplete pterygopalatine tooth plate that is missing the rostral-most third. Ridge crest C1 is not preserved as such, but its base can be distinguished as separate from a swelling that represents C2 on the broken rostral edge of the tooth plate. The pterygopalatine is heavily worn, with multiple islands of circumdenteonal dentine within an interdenteonal mass. These islands give the occlusal surface a cratered appearance (occlusal pits of Kemp, 2001a); however, it does not differ texturally from other large ceratodontids with robust tooth plates (“ceratodontid morphology” of Parris et al., 2014:280). The occlusal surface is generally flat, with a prominent convexity present on the mesiobuccal side (see Supplementary Data). The pterygopalatine is present but is broken 10 mm caudal to the margin of the tooth plate. On the dorsal surface, there is a massive ascending pterygopalatine process medial to the space between the C3 and C4 ridge crests. The preserved portion of the pterygopalatine is morphologically indistinguishable from that seen in other *Ceratodus* species from North America.
the occlusal surface; however, this mass is much larger and broader in *C. kranzi*. Similarly, both species have sublinear, suborthogonal posterior and lingual margins, and are relatively large for ceratodontids. *Ceratodus kranzi* can be differentiated from *C. robustus* based on its longer *C*$_3$ ridge crest, a less developed notch between the last two ridge crests, and lingual and posterior borders that meet at an angle closer to 90", in contrast to the more rounded intersection in *C. robustus* (which creates a more obtuse angle). Finally, and most definitively, *C. robustus* is unique among North American ceratodontids in that it only has four ridge crests on the pterygopalatine plate. Although incomplete, the type specimen of *C. kranzi* has three complete ridge crests and the base of a fourth ridge crest preserved. As noted, the base of this crest (*C*$_3$) is distinct from a more mesial area, where we interpret *C*$_1$ to have originated, giving a total count of five crests.

Other ceratodontids from the Cretaceous of North America include *Ceratodus texanus* Parris et al., 2014 from the Trinity Group (Aptian–Albian) of Texas, *C. carteri* Main et al., 2014 from the Cenomanian Woodbine Formation of Texas, and *C. gustasoni* Kirkland, 1987 from the Cenomanian Naturita Formation of Utah (see Carpenter, 2014). Both species from Texas, *C. texanus* and *C. carteri*, have small, high-crested tooth plates similar to those of *Potamoceratodus guentheri* (Marsh, 1878) from the Morrison Formation (see Kirkland, 1998) and are therefore fundamentally dissimilar to *C. kranzi*. Cenomanian *C. gustasoni* is more problematic because it is known only from prearticular plates. These plates are low crowned, as in *C. kranzi*, but the available sample suggests an adult size noticeably smaller than *C. carteri*, *C. robustus* (see Kirkland, 1987), and *C. kranzi*. Furthermore, the thin ridge crests on the prearticular plates of *C. gustasoni* contrast with the broader, relatively shorter ridge crests of *C. kranzi*. Shimada and Kirkland (2011) described a giant lungfish pterygopalatine tooth plate found on the surface of Ogallala Group (Mio–Pliocene) rocks of west-central Nebraska and presumed to derive originally from Jurassic–Cretaceous-aged units of the Western Interior. This specimen is anatomically distinct from *C. kranzi* based on its substantially larger size and the presence of a *C*$_p$ ridge crest that extends more labially than any of the other ridge crests. Further, the mesiolingual edge is rounded in shape and does not possess the squared-off caudal margin (i.e., sublinear and suborthogonal to the lingual margin) seen in *C. kranzi*.

Measurements of ridge crest angles have been widely used to describe *Ceratodus* species (e.g., Kirkland, 1987; Parris et al., 2014). Although this technique has been justifiably criticized as inappropriate for small sample sizes (Kemp, 1997), these measurements remain one of the most widely used ways to diagnose species within the genus. To maintain consistency with previous studies, we present comparable data for *C. kranzi* here. Based on the relative incompleteness of this specimen, only two of the most relevant measurements can be determined. The inner angle (\(\angle ABC\)) of USNM 508543 is 169° — the highest of any North American *Ceratodus* species. The next greatest inner angle from a comparable specimen is that of KUVP 16262, a specimen of *C. texanus* from the Kiowa Shale, with an angle of 152° (Kirkland, 1987; see Fig. 2). The \(C_3-C_p\) angle in *C. kranzi* is 31°, which is comparable to values found in multiple other species of *Ceratodus* (e.g., *C. frazieri*, *C. guentheri*, and *C. fossanovum*; see Kirkland, 1987).

**FIGURE 2.** Ceratodont lungfish tooth plate terminology/basis for measurements and *Ceratodus kranzi*, sp. nov. Top (A and B), system of crest terminology and angle measurements, after Kirkland (1987), showing upper (pterygopalatine) tooth plates of *Ceratodus kranzi* (USNM 508543, holotype, left) and *C. frazieri* (KUVP 16262, right tooth plate reversed to appear as left). Crests are numbered *C*$_1$–*C*$_p$ (posteriormost crest); lines B–A and B–C approximate the mesial and lingual borders of the tooth plate respectively. Bottom (C and D), photographs of *Ceratodus kranzi*, sp. nov., USNM 508543 (left pterygopalatine plate, holotype) from USNM locality 61614, Arundel Clay facies, Potomac Formation (Aptian–Albian), Prince George’s County, Maryland. Left, occlusal view; right, dorsal view. All scale bars equal 10 mm.

*Ceratodus kranzi* is most similar to *C. frazieri* Ostrom, 1970, specifically KUVP 16262, a pterygopalatine plate described by Schultz (1981) from the Lower Cretaceous Kiowa Shale of Kansas (Fig. 2). Both specimens are relatively large and broad, with wide, low-angle ridge crests. *Ceratodus kranzi* differs from *C. frazieri* in having a conspicuous, caudolingually placed eminence on the occlusal surface and a straighter posterior margin. Additionally, the notches between the ridge crests are wider in *C. frazieri*, presumably allowing for the occlusion of wider ridges on the prearticular plate (unknown for *C. kranzi*). *Ceratodus frazieri*, originally described from the Albian Cloverly Formation of Wyoming (Ostrom, 1970), is also known from the Late Jurassic of South Dakota and, possibly, the Late Cretaceous of New Jersey (Kirkland, 1987; Parris et al., 2004). Although the range of this species might hypothetically overlap with that of *C. kranzi*, we consider them morphologically distinct, based on differences in the occlusal surface and variations in ridge crest angles.

*Ceratodus kranzi* can also be compared favorably with *C. robustus* Knight, 1898, known by broad, robust tooth plates from the Upper Jurassic Morrison Formation (Kirkland, 1987, 1998). Pterygopalatine tooth plates of both *C. robustus* and *C. kranzi* possess a convexity on the mesiolingual side of

**DISCUSSION**

**Size**

The holotype of *Ceratodus kranzi* is relatively large by comparison to other Mesozoic lungfishes of North America. Though incomplete, an estimate based on the length between
the C1–C4, ridge crests indicates that this species would have been subequal in length to *C. frazieri* (KUVP 16262; Schultz, 1981 estimated total length at approximately 60 mm) and between 77% and 120% the length of *C. robustus* (UCM 54248, see Kirkland, 1987). By using a direct comparison of tooth lengths, it is possible to approximate total body length of *C. kranzi*. Kirkland (1987) used published data for the Australian lungfish to hypothesize that large individuals of *C. frazieri* and *C. robustus* would have achieved sizes up to 1.5 m in length. Using Kirkland’s (1987) estimates, *C. kranzi* would have ranged somewhere between 1.5 and 2.0 m in total body length. Using Kemp’s (2005) regression equation for pterygopalatine tooth plates of *N. forsteri* (and again estimating the length of USNM 508543 at 60 mm) yields an estimated length of 2.2 m for *C. kranzi*. By any measure, it would appear that *Ceratodus kranzi* was one of the largest aquatic faunivores in the Arundel ecosystem.

**Biogeography**

Parris et al. (2004) reported the first unambiguous occurrence of a Cretaceous lungfish from the east coast of North America (Fig. 1B). The specimen is a prearticulare tooth plate (NJSM 18774), which the authors suggest may represent a new species and which they provisionally attributed to *Ceratodus aff. C. frazieri*. As noted, *C. frazieri* was originally described from the Clovery Formation (Albian) and has been reported from the Kimmeridgian (with all previous reports based on fossils from the Western Interior). Specimen NJSM 18774 hails from the Campanian of New Jersey, implying great temporal and geographic range extensions, if referable to *C. frazieri*. Although not directly comparable, the holotype of *C. kranzi* and NJSM 18774 share some noteworthy similarities. Both are from large lungfish with robust, flat-crested tooth plates. The ridge crests on *C. kranzi* correspond somewhat more favorably with the narrow, finger-like valleys in NJSM 18774 than with the wider valleys seen in the holotype of *C. frazieri*, YPM 5276. Parris et al. (2014) noted that small *Ceratodus* species with high-crested tooth plates, which date back to the Early Jurassic (Milner and Kirkland, 2006) and are most characteristic of the Late Jurassic (Kirkland, 1998) of North America, make their last appearance in the Cenomanian of Texas (Main et al., 2014), on the eastern side of the then newly formed Western Interior Seaway. Given the limitations of the fossil record, relationships among North American species of *Ceratodus* remain almost wholly conjectural. It is conceivable, as Parris et al. (2014) noted, that *C. aff. frazieri* from New Jersey evolved from a clade of high-crested lungfishes that were restricted to eastern North America after completion of the seaway. However, the occurrence of *C. kranzi* in the Arundel Clay of Maryland shows that large-bodied forms with robust, flat-crested tooth plates were in eastern North America by the Aptian–Albian.

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