Journal of Vertebrate Paleontology 31(3):712–716, May 2011

SHORT COMMUNICATION

FIRST OCCURRENCE OF THE LONG-SNOUTED CROCODYLIFORM *TERMINONARIS* (PHOLIDOSAURIDAE) FROM THE WOODBINE FORMATION (CENOMANIAN) OF TEXAS

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INTRODUCTION

Here we report the occurrence of *Terminonaris* represented by three specimens recovered from the early middle Cenomanian (96 Ma) Woodbine Formation of Lewisville Lake, Denton County, Texas. Crocodyliform fossils are relatively common throughout the Woodbine Formation of north-central Texas, typically represented by isolated teeth, vertebrae, and osteoderms (Lee, 1997a, 1997b; Jacobs and Winkler, 1998; Tykoski and Fiorillo, 2010). As yet, the only named species of crocodyliform from the Cenomanian of Texas is *Woodbinesuchus byersmauricei* Lee, 1997a, found in the lowermost Woodbine Formation (Lee 1997a; Jacobs and Winkler, 1998).

The first specimens of the longirostrine crocodyliform *Terminonaris* Osborn, 1904 (= *Teleorhinus*), were collected from the Late Cretaceous (early Turonian) of southeastern Montana in 1903 (Mook, 1934; Wu et al., 2001). Osborn (1904) described one of the two original skeletons recovered as *Teleorhinus browni* and Mook (1934) described the second as *Teleorhinus robusta*. Due to the preoccupation of the name *Teleorhinus*, Wu et al. (2001) replaced the genus name with *Terminonaris*, which had originally been provided by Osborn (1904). Wu et al. (2001) also placed *Teleorhinus mesabiensis*, described by Erickson (1969), into synonymy with *Terminonaris robusta* Mook, 1934. *Terminonaris robusta* differs from the type species *T. browni* in having overall broader rostral and cranial widths and in the presence of a small external mandibular fenestra (Wu et al., 2001; Shimada and Parris, 2007). In addition to the two Montana specimens, *Terminonaris* is known from an upper jaw fragment from the late Cenomanian of Bavaria, Germany (*Terminonaris* cf. *T. browni*; Buffetaut and Wellnhofer, 1980; Wu et al., 2001), an anterior portion of rostrum from the early Turonian of Minnesota (*T. robusta*; Erickson, 1969), a nearly complete skeleton from Saskatchewan (*T. robusta*; Wu et al., 2001), and partial nasals and maxillae from the middle Turonian of Kansas (*Terminonaris* cf. *T. browni*; Shimada and Parris, 2007).

Institutional Abbreviations—**AMNH**, The American Museum of Natural History, New York, New York, U.S.A.; **FHSM**, Fort Hays State University, Sternberg Museum of Natural History, Hays, Kansas, U.S.A.; **SMM**, Vertebrate Paleontology Section of the Science Museum, Minnesota, Saint Paul, Minnesota, U.S.A.; **SMNH**, Royal Saskatchewan Museum (formerly the Saskatchewan Museum of Natural History), Regina, Saskatchewan, Canada; **SMU**, Southern Methodist University Shuler Museum of Paleontology, Dallas, Texas, U.S.A.

AGE AND GEOLOGIC SETTING

The Upper Cretaceous Woodbine Formation of north-central Texas unconformably overlies the Grayson Marl, the uppermost formation of the Washita Group, and is unconformably overlain by the Eagle Ford Group (Fig. 1; Dodge, 1969; Lee, 1997a, 1997b; Jacobs and Winkler, 1998). In outcrop, it extends from the Red River and thins to the south (Dodge, 1969; Jacobs and Winkler, 1998). Dodge (1969) designated four lithologic units within the formation near Dallas and Fort Worth, in ascending order: the Rush Creek, Dexter, Lewisville, and Arlington members. The Texas *Terminonaris* fossils were collected along the northern shore of Lewisville Lake at low lake level in the Arlington Member in the uppermost part Woodbine Formation (SMU Loc. Nos. 142 and 495; Fig. 2). The ammonite *Conlinoceras tarrantense*, a zonal marker for the base of the middle Cenomanian, were found within the Lewisville Member and in the Tarrant Formation (lowermost Eagle Ford Group), indicating an age no younger than early middle Cenomanian (approximately 96 Ma; Kennedy and Cobban, 1990; Emerson et al., 1994; Lee, 1997a; Jacobs and Winkler, 1998; Gradstein et al., 2004).

The matrix encasing specimen SMU 76590 is very fine- to fine-grained sandstone with ferruginous cement and iron concretions. SMU 71698 occurred in fine-grained glauconitic, trough cross-bedded sandstone, whereas SMU 71699 comes from ripple cross-bedded sandstone with planar laminations. The upper Woodbine sediments represent a lowstand sequence within an early transgressive system tract of the Greenhorn Cycle of Kauffman and Caldwell (1993). The uppermost Woodbine represents a terrigenous coastal depositional system with fluvio-deltaic influences (Powell, 1968; Dodge, 1969; Lee, 1997a, 1997b; Jacobs and Winkler, 1998).

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Hay, 1930
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
NEOSUCHIA Benton and Clark, 1988
PHOLIDOSAURIDAE Zittel and Eastman, 1902
TERMINONARIS Osborn, 1904, sensu Wu, Russell, and Cumbaa, 2001
TERMINONARIS cf. *T. ROBUSTA* Mook, 1934
(Figs. 3–4)

Referred Materials—SMU 76590: nearly complete rostrum consisting of partial premaxillae, maxillae, nasals, dentaries, and partial splenials; fragment of left posterior mandible; posterior dorsal vertebra. SMU 71698: fragment of left maxilla. SMU 71699: partial osteoderm.

Locality and Horizon—Arlington Member, uppermost Woodbine Formation, Upper Cretaceous (lower middle Cenomanian). SMU 76590 is from the Lakewood Village Locality (SMU Loc. No. 495), Lewisville Lake, Denton County, Texas. SMU 71698 and 71699 are from the Easy Street Locality (SMU Loc. No. 142), Lewisville Lake, Denton County, Texas.

DESCRIPTION

General Description—The rostrum (SMU 76590), broken anterior to the orbits at the 22nd maxillary alveoli, is well preserved

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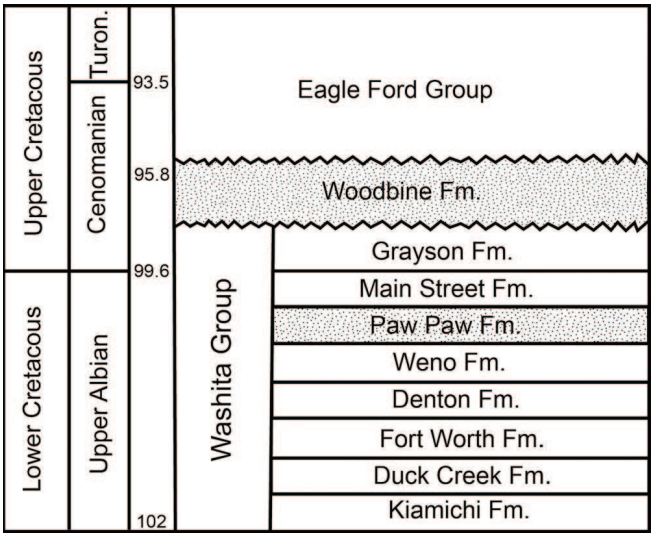

FIGURE 1. Stratigraphic column for the Cretaceous of north-central Texas showing the position of the Woodbine Formation. Stippled intervals represent terrestrial deposits. Time scale based on Gradstein et al. (2009). Modified from Jacobs and Winkler (1998). The basal age for the *Conlinoceras tarrantense–Conlinoceras gilberti* Zone (upper Woodbine and lower Eagle Ford formations) is 96.01 in Gradstein et al. (2004).

and strongly resembles that of the type specimen (AMNH 5850) and SMNH P2411.1 of *T. robusta* (Mook, 1934; Wu et al., 2001). Two transverse fractures separate the rostrum into thirds. The anterior one-third has maxillae and dentaries articulated in tight occlusion, whereas the remaining two-thirds are separated into upper and lower elements. The maximum length along the midline is 620 mm. At the posterior end, the rostrum has a maximum width 135 mm. It gradually narrows anteriorly to a minimum width of 55 mm and then broadens at the most anterior end to 74 mm. The dorsal and ventral surfaces are ornamented with elongated pits and ridges, similar to SMNH P2411.1 described by Wu et al. (2001).

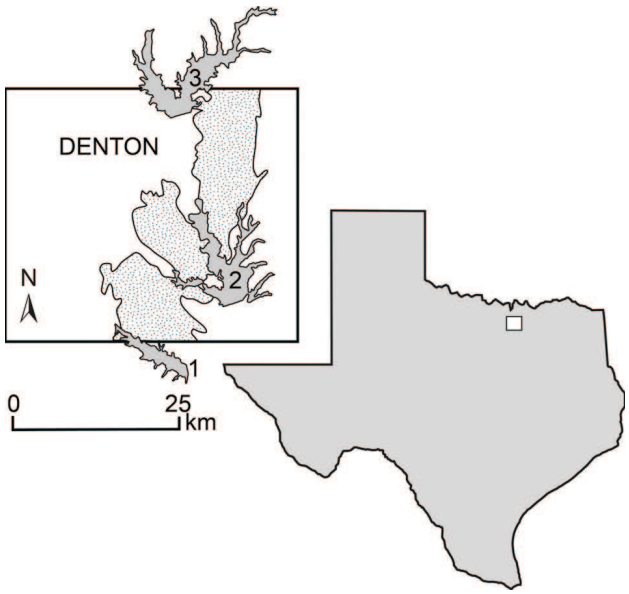

FIGURE 2. Map of Texas, U.S.A., highlighting the Woodbine Formation outcrop belt relative to lakes in Denton County: Grapevine Lake, 1; Lewisville Lake, 2 (*Terminonaris* localities); Ray Roberts Lake, 3.

Cranial Elements—The premaxillae are incomplete and do not include the anterior terminus. The preserved portion is elongate and narrows posteriorly to extend between the maxillae to the level of the ninth maxillary alveoli. The dorsal aspect of the anterior palate is exposed, and shows that the ventral premaxillae are separated by the anterior process of the maxillae just anterior to the first maxillary tooth.

The maxillae are separated dorsomedially by the premaxillae anteriorly and by the nasals posteriorly. The posterior termination of the maxillae is not preserved. There are 22 alveoli preserved in the right maxilla and 19 on the left. The maxillary alveoli are subequal in size with an average alveolar diameter of 14 mm. The interaveolar spacing ranges from 9 to 16 mm anteriorly and reduces to less than 5 mm at the posterior end. The alveolar edges are prominent, giving the rostrum an undulating appearance. As seen in *T. robusta* AMNH 5850, SMNH P2411.1, and SMM P68.56.1 (Mook, 1934; Erickson, 1969; Wu et al., 2001), a distinct longitudinal groove extends along the entire length of the lateral surface, dorsal to the dental margin. Wu et al. (2001) observed a similar groove, although weakly developed, in *Terminonaris browni* (AMNH 5851). The majority of the ventral palate of the maxillae is not visible, due to either occlusion with the mandible or a lack of preservation. SMU 71698 is a fragment of the left posterior maxilla. There are nine alveoli preserved with an average diameter of 10 mm (Fig. 4A and B).

The nasals are long and slender. At the 20th maxillary alveoli, the nasals are 25 mm wide. They gradually narrow anteriorly to the level of the eighth alveoli, forming a wedge between the premaxillae. On their ventral surface, the nasals are smooth and concave and create a longitudinal ridge running along the midline, similar to *T. robusta* FHSM VP-4387 (Shimada and Parris, 2007). Only the most anterior portion of the left lacrimal can be discerned lateral to the posterior margin of the nasal. Although the frontals are not preserved, their position can be discerned at the posterior margin of the nasals, indicating that they extended anteriorly to the same level as the lacrimal.

The dentaries have a longitudinal groove ventral to the dental margin, running along the lateral extent of the rostrum. The presence of a ventral groove was described in the type (AMNH 5850), and in SMNH P2411.1 and SMM P68.56.1 of *T. robusta*, but is absent in *T. browni* (AMNH 5851; Mook, 1934; Erickson, 1969; Wu et al., 2001). There are 23 alveoli preserved on the left dentary and 22 on the right. The anterior portion of the splenials extends between the dentaries to the level of the 14th alveoli, and comprises 50% of the symphyseal length in ventral view. The rami diverge at the 21st alveoli. The fragment of the left posterior ramus of the mandible (SMU 76590) consists of posterior dentary, splenial, and anterior angular (Fig. 4C).

The 2nd maxillary tooth is present in SMU 76590 and the remaining alveoli are occupied by either broken or replacement teeth. The teeth are homodont, conical, and recurved, projecting slightly anterior and labial. A carina is present along both the concave lingual and convex labial surfaces. The enamel is generally smooth, although there are fine striations on the surface of several broken teeth.

Postcranial Skeleton—An isolated dorsal vertebra (SMU 76590) was recovered from the Lakewood Village Locality (Fig. 4D and E; SMU Loc. No. 495). It is amphicoelous and preserves the base of the neural arch. A partial dorsal osteoderm (SMU 71699) was found at the Easy Street Locality (Fig. 4F; SMU Loc. No. 142). It is 104 mm wide and is characterized by irregular pits, with no indication of a keel. The anterolateral portion of the osteoderm is not preserved, so the presence of a spur cannot be determined.

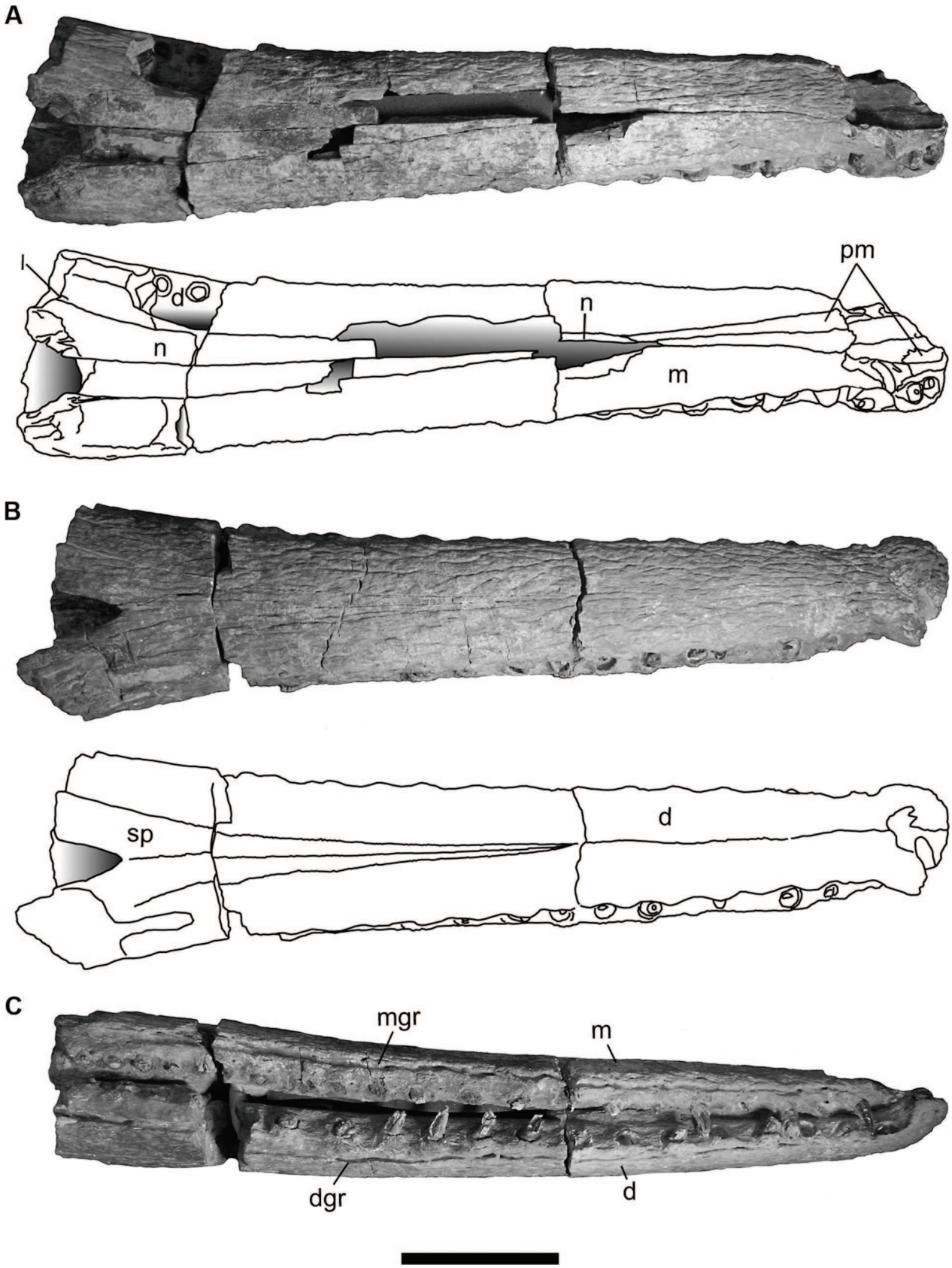

FIGURE 3. Partial rostrum of *Terminonaris* cf. *T. robusta* SMU 76590 in dorsal (**A**), ventral (**B**), and lateral (**C**) views. **Abbreviations**: **d**, dentary; **dgr**, groove along dentary; **l**, lacrimal; **m**, maxilla; **mgr**, groove along maxillary; **n**, nasal; **pm**, premaxilla; **sp**, splenial. Scale bar equals 10 cm.

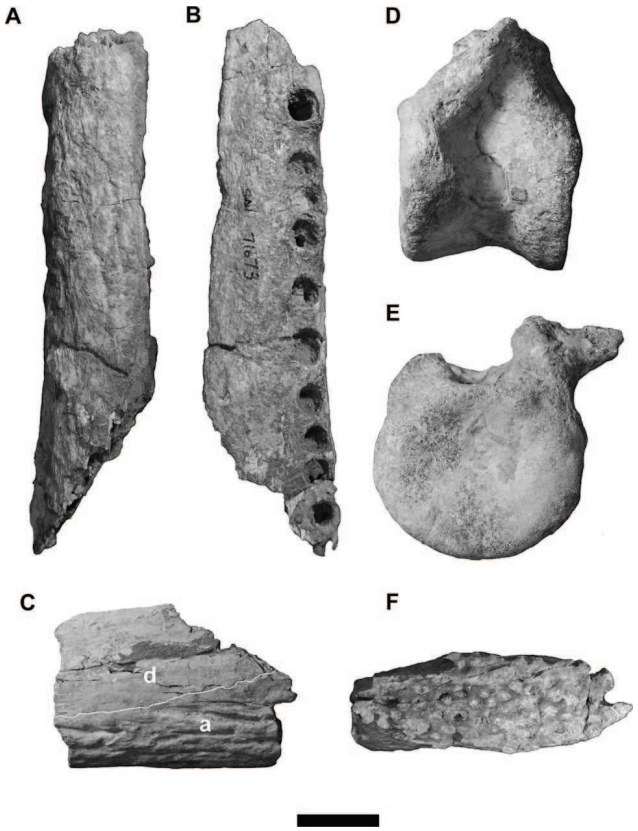

FIGURE 4. Additional elements of *Terminonaris* cf. *T. robusta*. SMU 71698, fragment of left maxilla in **A**, dorsal and **B**, ventral views; **C**, fragment of left posterior mandible (SMU 76590) in lateral view; SMU 71698, posterior dorsal vertebra in **D**, lateral and **E**, anterior views; **F**, partial osteoderm (SMU 71699) in dorsal view. **Abbreviations**: see Figure 3; **a**, angular. Scale bar equals 3 cm.

FIGURE 5. Middle Cretaceous (Cenomanian-Turonian, 96–90 Ma) paleogeographic map showing the distribution of *Terminonaris*. Star, middle Cenomanian; square, late Cenomanian; circles, early Turonian; diamond, middle Turonian. Base map from PALEOMAP Software: PLATE TRACKER.

DISCUSSION

Phylogeny—The exclusion of the nasals from the external nares by premaxillary contact is synapomorphic of Pholidosauridae according to Sereno and Larsson (2009, character 8). The posterodorsal premaxillary process extension beyond the third maxillary alveolus and the absence of sculpturing along the alveolar margin on lateral surface of maxilla, present in SMU 76590, noted as apomorphic of the clade with *Dyrosaurus*, *Terminonaris*, *Pholidosaurus*, and *Sarcosuchus* (Sereno and Larsson, 2009), allow a confident inclusion of SMU 76590 within Pholidosauridae.

Diagnostic characters for the genus *Terminonaris* include (1) the anterior terminus of the premaxillae transversely broad and strongly reflected ventrally; (2) the posterolateral process of squamosal bearing a pronounced ventral process enclosing the dorsal half of lateral end of paroccipital process; (3) the lateral termination of the paroccipital process is greatly broadened dorsoventrally; (4) the exoccipital has a small but clear tuberosity dorsolateral to foramen magnum on its occipital surface (sensu Wu et al., 2001), which are not preserved in SMU 76590. However, the nasal contact with the premaxilla at the level of the ninth maxillary alveoli and the longitudinal groove running along the lateral expanse of the maxillae and dentaries justify identification as *Terminonaris* with a stronger affinity to *T. robusta* than that of *T. browni*. Because the posterior portion of the skull is missing, the Lewisville Lake specimen is referred to as *Terminonaris* cf. *T. robusta*.

Occurrences—The Lewisville Lake specimens are significant for being the first record of *Terminonaris* in Texas, as well as the earliest and the southern-most occurrence of this crocodyliform globally. *Terminonaris* is found in marginal marine and offshore deposits, and because of that, its distribution is known to include warm-temperate waters along the margins of seaways (Wu et al., 2001; Shimada and Parris, 2007). They have been considered either marine (Hua and Buffetaut, 1997) or as a "sea-going 'terrestrial' vertebrate" as noted by Wu et al. (2001:507). Hua and Buffetaut (1997) proposed a life habit for *Terminonaris* similar to that of *Crocodylus porosus*, the extant salt-water crocodile.

Up until now, known occurrences in North America were restricted to the early and middle Turonian deposits of the Western Interior Sea (Fig. 5). The earliest known occurrence was from the late Cenomanian of Europe (Buffetaut and Wellnhofer, 1980; Wu et al., 2001; Shimada and Parris, 2007). Shimada and Parris (2007) proposed that dispersal of *Terminonaris* from Europe into North America took place by latest Cenomanian or earliest Turonian, crossing the narrow Atlantic Ocean from Europe, possibly on Tethys currents. The multiple occurrences of *Terminonaris* in North America and the age of the Lewisville Lake specimens require a reevaluation of previous hypothesis of dispersal.

ACKNOWLEDGMENTS

We thank B. Condon for the donation of SMU 76590 to Southern Methodist University Shuler Museum of Paleontology. Thanks to K. Shimada for sharing comments on this taxa. X.-C. Wu and D. Schwarz-Wings provided thoughtful comments that greatly improved an earlier version of the manuscript.

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Submitted October 18, 2010; accepted February 26, 2011.
Handling editor: Randy Nydam.