Cenomanian (Late Cretaceous) reptiles from northwestern Russell County, Kansas

GREGORY A. LIGGETT^{1, 5}, KENSHU SHIMADA^{2, 5}, S. CHRISTOPHER BENNETT^{3, 5}, and BRUCE A. SCHUMACHER ^{4, 5}

¹Northern California Natural History Museum, College of Natural Sciences, California State University, Chico, CA 95929-0555; gliggett@csuchico.edu. ²Environmental Science Program and Department of Biological Sciences, DePaul University, 2325 North Clifton Avenue, Chicago, IL 60614. ³Department of Biological Sciences, Fort Hays State University, Hays, KS 67601. ⁴USDA Forest Service, Comanche National Grassland, La Junta, CO 81050. ⁵Sternberg Museum of Natural History, Fort Hays State University, Hays, KS 67601

Several Late Cretaceous reptilian fossils were found at and immediately above the contact between the Graneros Shale and the Lincoln Limestone Member of the Greenhorn Limestone in northwestern Russell County, Kansas. The taxa recovered include: (1) an indeterminate plesiosaur taxon; (2) the rare pliosaurid plesiosaur *Brachauchenius lucasi*; (3) a pteranodontoid pterosaur, which constitutes the earliest occurrence of a flying reptile in Kansas; and (4) the rare aquatic lizard *Coniasaurus*. Several morphologic characters of *B. lucasi* are clarified: an apomorphy in the paddle of *B. lucasi* where both the fourth and fifth metapodials intrude on the mesopodial row is noted for the first time; and striations of tooth enamel vary from the tooth crown to the root and from the front to the back of the tooth. Additionally, the stratigraphic occurrence of *B. lucasi* suggests that the minimal stratigraphic range for that species is from the late Cenomanian through middle Turonian. This diverse reptile fauna occurs with a variety of fossil fishes consisting of at least twelve chondrichthyan and four osteichthyan taxa. The age of the fauna is middle Cenomanian based upon the site's stratigraphic occurrence and a radiometric date of 95.53 ± 0.159 Ma obtained one meter below the excavation. Whereas reptilian faunas of this age from the eastern margin of the Cretaceous Interior Seaway are relatively rare, this faunal assemblage adds significant paleoecological information about Western Interior Basin biogeography.

INTRODUCTION

Sedimentary rocks from the Cretaceous Interior Seaway have yielded thousands of vertebrate fossils spread over a wide geographic extent of the central plains states of the United States and Canada (Russell 1988). Many specimens have been collected from highly fossiliferous units such as the Smoky Hill Chalk Member of the Niobrara Chalk of Kansas. Fewer remains have been documented from older Late Cretaceous rocks of Kansas (Russell 1988). Here we report on a diverse reptilian fauna from a locality in northwestern Russell County, Kansas, that adds new data on vertebrates in the Seaway during the middle Cenomanian.

In 1996, Randy and Paula Staab of Hays, Kansas, found bone fragments at a site in northwestern Russell County. Staff from the Sternberg Museum of Natural History (FHSM), also in Hays, visited the site and excavated a plesiosaur paddle. The paddle was located at the Upper Cretaceous contact between the Graneros Shale and Greenhorn Limestone. While excavating this fossil from an area of approximately one square meter, many isolated fish teeth were found in the basal Greenhorn Limestone overlying the paddle and a bulk rock sample was collected for further study. The sample was gently mechanically disaggregated to collect small vertebrate remains. A few specimens also were collected from the surface at the same stratigraphic horizon approximately 10 m south of the main excavation. All fossils are curated in the Vertebrate Paleontology collection (VP) of FHSM. Additional material referred to is housed in the United States National Museum (USNM), Washington D.C.

GEOLOGY

The Graneros Shale is a gray, silty shale that is disconformably overlain by the Lincoln Limestone Member of the Greenhorn Limestone. The Lincoln Limestone consists primarily of shaly chalk with scattered interbeds of well-cemented skeletal limestone, coarse-grained calcarenite, bentonite seams, and chalky limestone (Hattin 1975). The Graneros Shale represents the early phase of the transgression in the Greenhorn cyclothem (Hattin et al. 1987). Coarse-grained calcarenite and skeletal limestone at the base of the Lincoln Limestone Member indicate deposition in turbulent waters slightly over 30 m in depth (Hattin 1975).

At the excavation site, six distinct layers of rocks are exposed: in ascending order, (1) a 28 cm-thick bed of orangeto-gray bentonite, the "X" bentonite discussed in Hattin (1965 and 1975); (2) 37 cm of gray-black fissile shale; (3) 60 cm of thinly bedded, yellowish-brown sandstone alternating with fissile gray-black shale; (4) 5-8 cm of fossiliferous, moderately sorted sand containing numerous bone fragments and bony fish and shark teeth; (5) 15-20 cm of calcareous, slightly crossbedded, limey sandstone that is petroliferous; and (6) 130 cm of indurated, crystalline, shaly limestone with several bentonite seams. The plesiosaur paddle (FHSM VP-13997) was lying at the unconformable contact between the third (uppermost Graneros Shale) and the fourth (lowermost Lincoln Limestone) units described here. Although the presence of a hiatus between the deposition of the plesiosaur paddle and the remainder of the fauna is possible, its exact duration cannot be determined because the contact between the two stratigraphic units is diachronous across Kansas (Hattin 1965).

Argon/argon analysis of an "X" bentonite sample taken one meter below the fossil excavation yielded a date of 95.53 ± 0.159 Ma (Miggins 2004; Shimada et al. in press).

SYSTEMATIC PALEONTOLOGY

Order: PLESIOSAURIA de Blainville 1835 Family: PLIOSAURIDAE Seeley 1874 Genus: *Brachauchenius* Williston 1903 *Brachauchenius lucasi* Williston 1903

Referred material—FHSM VP-13997, partial paddle; FHSM VP-14782, two teeth

Description—FHSM VP-13997 consists of 16 articulated epipodial, mesopodial, and phalangeal elements. Articulated dimensions of all elements measure 60 cm in proximodistal dimension and 35 cm in anteroposterior dimension. Both teeth (FHSM VP-14782) are conical and show prominent striations that extend all or part way from base towards tip.(Figs. 1, 2).

Remarks—The paddle collected from the site is exceptionally large and displays unusual morphology (Fig. 3). Fused distal mesopodials 2 and 3 form a massive element (here identified as distal carpal 2-3 for discussion) that is markedly wider than long and is larger in overall size than the overlying intermedium. In most plesiosaurs, the distal carpal 2-3 is not nearly as large compared to the other elements and is generally equidimensional (see Figs. 3-5). Most striking in this specimen is the configuration of the fourth and presumably the fifth metapodial elements. Owen (1865) was the first to note that the fifth metapodial is shifted proximally into the distal mesopodial row in all pleiosaurs, a character noted by many subsequent workers (Welles 1943; Brown 1981;

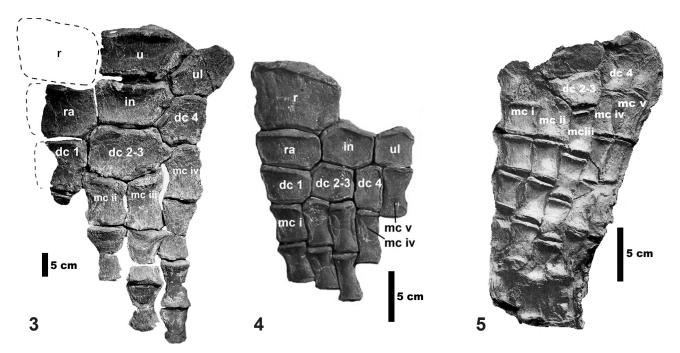


Figs. 1-2. Broken teeth of the pliosaur *Brachauchenius lucasi* (both curated as FHSM VP-14782). Bar scale is 1 cm.

O'Keefe 2001). However, FHSM VP-13997 reveals that the fourth metapodial, and therefore the entire fourth digit, is also shifted proximally into the mesopodial row. Although the fifth metapodial and its successive phalangeal row are not preserved, it is also likely that they were shifted proximally in the manner of all plesiosaurs. This unique configuration of the mesopodial row provides a contact of distal carpal 2-3 with seven other elements, including the proximal-anterior edge of metacarpal 4. This configuration is quite unlike that observed in other plesiosaurs, where metacarpal 4 is isolated from distal carpal 2-3 by the metacarpal 3 and distal carpal 4. This condition is also seen in the Texas specimen of Brachauchenius lucasi (USNM 2361). Although only a portion of the mesopodial row is preserved in the Texas specimen, the proximal shift of the fourth and fifth metapodials is clearly visible in the articulated specimen (Fig. 5). Based upon this, FHSM VP-13997 is referred to B. lucasi, and this taxon's podial apomorphy is noted here for the first time.

In his review of short-necked plesiosaurs, Carpenter (1996) discussed tooth striation for Brachauchenius lucasi, noting that the striations branch towards the root. Teeth of the large skull of B. lucasi (FHSM VP-321) display significantly more striae (i.e., raised ridges of enamel) around the base than near the crown. Spacing of the striae near the tooth tip is not even, there being more valley space of smooth enamel between striae on the anteriolateral side (approximately 3-4 striae in 10 mm of tooth circumference) than on the rest of the tooth crown (approximately 4-6 striae in 10 mm of tooth circumference), particularly 5-10 mm from the tooth tip. Some of the striae branch as they extend from the crown towards the root, but more commonly new striae arise without contacting neighboring striae and they continue toward the root so that the density of striae around the base of the crown is even (approximately 10-12 striae in 10 mm of crown circumference). The striation patterns on FHSM VP-14782 are consistent with those of B. lucasi. Similar patterns are seen on Kronosaurus (Colin McHenry, personal communication).

The type specimen of B. lucasi (USNM 4989) was found near Delphos, Ottawa County, Kansas, in rocks Williston (1903) called "Benton," a term used at that time for the rocks above the Dakota Formation and below the Niobrara Chalk (Hattin et al. 1987). The "Benton" in Colorado was divided into three formations by Gilbert (1896)—Graneros Shale, Greenhorn Limestone, and Carlile Shale-and those units were recognized in Kansas by Logan (1899) with the names applied in Kansas by Darton (1904; Hattin et al. 1987). Rocks exposed in Ottawa County near Delphos include all three formations formerly included in the "Benton." Carpenter (personal communication) stated that the specimen came from the Greenhorn Limestone based on his examination of the matrix. However, the age of the Greenhorn Limestone ranges from late Cenomanian through early middle Turonian, and without further evidence the exact age of the type cannot be determined more precisely (see also Schumacher and Everhart 2005 for discussion).



Figs. 3-5. Plesiosaur paddles showing morphologic variation in the epipodial, mesopodial, and metapodial regions. Elements labeled as as forelimbs for reference. Figures at various scales. 3. *Brachauchenius lucasi* (FHSM VP-13997) from the Russell County fauna. 4. *Trinacromerum bentonianum* (FHSM VP-12059). 5. Texas specimen of *Brachauchenius lucasi* (USNM 2361) reproduced from Williston (1907), transposed for comparison. Abbreviations: dc, distal carpal; in, intermedium; mc, metacarpal; r, radius; ra, radiale; u, ulna; ul, ulnare.

A possibly younger occurrence of *B. lucasi* is a specimen (USNM 2361) from exposures of the Eagle Ford Group along a Bouldin Creek tributary near Austin, Texas (Williston 1907; Carpenter 1996). At that locality, the Eagle Ford Group consists of the late Cenomanian Lake Waco Formation unconformably overlain by the the late Turonian South Bosque Formation (Pessagno, 1969), but these units were not differentiated when the specimen was recorded.

Russell (1988) noted a *B. lucasi* in the Fairport Chalk Member of the Carlile Shale that was undoubtedly the large skull of *B. lucasi* from Russell County, Kansas (FHSM VP-321). Carpenter (1996) stated that this specimen came from the Greenhorn Limestone. However, our field observations and discussions by BAS and GAL with one of the participants in the excavation of FHSM VP-321 leads us to conclude that the skull is from the middle of the Fairport Chalk Member of the Carlile Shale, approximately 12 m above the Fencepost Limestone Bed of the Greenhorn Limestone (Schumacher and Everhart 2005). Thus, the age of that specimen is early middle Turonian.

The Kansas specimens of *B. lucasi*, which have the best stratigraphic data, suggest a minimal stratigraphic range of late Cenomanian through the middle Turonian.

Family, Genus, and Species Indeterminate

Referred material—FHSM VP-14811, one tooth.

Description—FHSM VP-14811 is a broken tooth crown with smooth enamel measuring 4 mm in height.

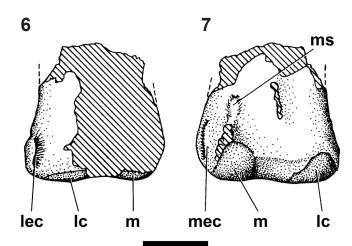
Remarks—This specimen is not complete enough to confidently assign to a more specific taxon.

Order: PTEROSAURIA Kaup 1834 Family, genus, and species indeterminate

Referred material—FHSM VP-13998, distal end of right femur.

Description—Specimen (Figs. 6, 7) measures 21 mm for both its maximum length and width, and consists of distal end of right femur, slightly deformed in an oblique posteriolateral plane. Much of thin cortical bone of anterior surface has been lost, revealing sediment-filled medulla. Large medial and lateral condyles form much of distal surface and extend onto posterior surface, and are separated by a shallow intercondylar sulcus. There is a large rugose medial epicondyle, and an even larger rugose lateral epicondyle. A ridge extends a short distance proximally from posterolateral corner of lateral condyle, and just proximal to it is a small rugose ridge that is probably a muscle attachment scar. Most of ridge apex is broken, revealing coarse cancellous bone within epiphysis.

Remarks—The morphology of the large condyles and epicondyles indicate that the specimen is a pterosaur, and the thin cortical bone and large medullary cavity reveal that it is a pterodactyloid. Although the specimen is indistinguishable from *Pteranodon* from the Niobrara Chalk (Coniacian-early Campanian), it does not exhibit any characters that would enable assignment to a known pterodactyloid taxon. Com-



Figs. 6-7. Distal right femur of a pterodactyloid pterosaur (FHSM VP-13998). Hatched areas are where the thin cortical bone has flaked off or is broken through. Bar scale is 1 cm. 6. Anterior view. 7. Posterior view. Abbreviations: lc, lateral condyle; lec, lateral epicondyle; m, medial condyle; mc, metacarpal; mec, medial epicondyle; ms, muscle scar.

parisons with complete femora of *Pteranodon* indicate that the overall length of the femur was approximately 150 mm. If the proportions of this animal were similar to those of *Pteranodon* reported by Bennett (1992), this specimen would have an estimated wingspan of 3.5 m.

FHSM VP-13998 represents the earliest pterosaur record from Kansas. It also adds to the sparse record of large

pterodactyloids, including dsungaripteroids, azhdarchids, and pteranodontoids in the Cretaceous Western Interior Seaway of North America, which currently consists of ten occurrences, itemized in Table 1.

Family: DOLICHOSAURIDAE Gervais 1852 Genus: Coniasaurus Owen 1850 Coniasaurus cf. C. crassidens Owen 1850

Referred material—FHSM VP-13999, a partial left maxilla; FHSM VP-14000, two shed teeth; FHSM VP-14001, two vertebrae (one dorsal, one caudal); FHSM VP-14002, one dorsal vertebra (found approximately 10 m south of the main excavation site); FHSM VP-14778, two shed teeth.

Description—Partial maxilla (FHSM VP-13999) contains nine bulbous, posteriorly curved teeth within the 10 mm section of preserved bone, showing at least four maxillary foramina along labial side (Figs. 8, 9). Dentition is slightly heterodont, with posterior teeth slightly more robust and bulbous than anterior teeth. Several of those teeth show a shallow anterior sulcus along labial aspect. Four shed teeth (FHSM VP-14000 and VP-14778) show similar morphology. All vertebrae are procoelous, and their cotyles are slightly deformed dorsoventrally.

FHSM VP-14002 (Figs. 10-14) is the best preserved vertebra from this site. Although fragmentary, cotyle is 5.0 mm wide and 3.4 mm dorsoventrally, and anterioposterior length of centrum is 10.0 mm. Maximum width across the prezygapophyses as preserved is 9.4 mm, and across postzygapophyses is 8.1 mm. Dorsal portion of specimen

Table 1. Annotated list of large pterodactyloid records from the Cretaceous Western Interior Seaway of North America.

- Partial humerus of pteranodontid and indeterminate materials, Eagle Ford Fm. (late Cenomanian-late Turonian), central Texas (Gilmore 1935; Bennett 1989)
- Indeterminate materials, Antlers Fm. (Neocomian-middle Albian), northern Texas (Zangerl and Denison 1950; Langston 1974; Winkler et al. 1990; Murry et al. 1991)
- 3 Indeterminate first wing phalanx, Buda Formation (Cenomanian), central Texas (Langston 1974)
- 4 Numerous fragments of limb bone shafts, including one referable to an azhdarchid from the late Campanian "Mesaverde" Fm. of Wyoming (Bennett unpublished data). (For comments on the "Mesaverde" see Lillegraven and McKenna 1986.)
- 5 Humeri of pteranodontoids, Mowry Shale (Albian), eastern Montana (Bennett 1989)
- 6 Humerus of dsungaripteroid or azhdarchid, Glen Rose Fm. (late Aptian-early Albian), Texas (Murry et al. 1991)
- Partial skull of pteranodontid *Coloborhynchus wadleighi*, Paw Paw Fm. (late Albian), northern Texas (Lee 1994)
- 8 Pteranodon and Nyctosaurus, Niobrara Chalk (Coniacian-early Campanian), Kansas and South Dakota (Bennett 1994)
- 9 Pteranodon, Pierre Shale (middle-late Campanian), Kansas, South Dakota, and Wyoming (Bennett 1994)
- 10 Metacarpal IV, Greenhorn Limestone (late Cenomanian), South Dakota (VonLoh and Bell 1998)





Figs. 8-9. Partial left maxilla (FHSM VP-13999) of *Coniasaurus* cf. *C. crassidens*. Bar scale is 1 cm. 8. Labial view. 9. Lingual view.

is not well preserved, with most of neural arch broken off, but maximum dorsoventral height is 7.9 mm. Dorsal lip of cotyle, if complete, would slightly overhang ventral margin. Condyle is narrower than margins of centrum in posterior view. Ventral surface of centrum is smooth and broad. Only condyle preserved among three vertebrae is part of caudal vertebra (FHSM VP-14001) that can be differentiated from centrum by a slight constriction.

Remarks-Coniasaurus crassidens is a slender marine lizard that reached approximately 1 m in total length (Caldwell and Cooper 1999), and the specimens reported here constitute the geologically oldest Coniasaurus material from Kansas (see Shimada and Bell in press for additional material). Owen (1850) described C. crassidens from chalk beds in Sussex, England, and named a junior synonym the next year (Liggett 2004). The material was redescribed by Caldwell and Cooper (1999). Coniasaurus crassidens also has been described from late Cenomanian deposits of Germany (Diedrich 1997); two late Cenomanian-Turonian localities in North America—the Eagle Ford Group of Texas (Bell et al. 1982) and the Greenhorn Formation of South Dakota (VonLoh and Bell 1998); a middle Cenomanian deposit from southeastern Colorado (Shimada et al. in press); and the Santonian portion of the Niobrara Chalk (Shimada and Bell in press). The Texas and South Dakota material includes sections of maxilla showing a tooth-to-length ratio of about five teeth for every centimeter of jaw length (Bell et al. 1982, fig. 1; VonLoh and Bell 1998, fig. 7B), and this is consistent with the type specimen of C. crassidens based on figures in Caldwell and Cooper (1999, fig. 5A). In contrast to those other North American specimens, FHSM VP-13999 has twice the tooth-to-length ratio, the teeth overall being much smaller than those of specimens previously referred to C. crassidens. Caldwell (1999) also described Coniasaurus gracilodens, whose specimens are diminutive compared to those of C. crassidens and show a tooth-to-length ratio similar to the Kansas specimen. However, the teeth of *C. gracilodens* are thick and conical, not bulbous as in *C. crassidens* (Caldwell 1999). Thus, the tooth morphology of *C. gracilodens* does not match the Kansas specimen. Morphologically, the Kansas specimen is more similar to *C. crassidens* in having bulbous expansions of the tooth crown. It may be a juvenile *C. crassidens* or a new taxon.

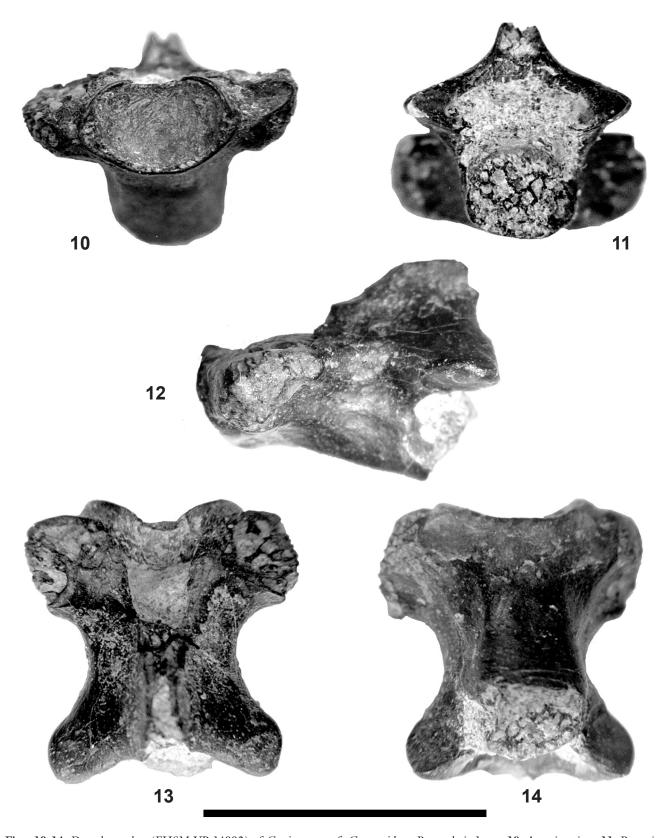
The assignment of the vertebrae (FHSM VP-14001 and VP-14002) to *Coniasaurus* is tentative. Known Late Cretaceous marine squamates include the Aigialosauridae (Carroll and Debraga 1992), *Coniasaurus* (Caldwell and Cooper 1999; Caldwell 1999), and *Dolichosaurus* (Caldwell 2000). Vertebrae of aigialosaurids are all much larger than the Kansas specimens, but because of their morphological similarity, assignment to this group cannot be ruled out. Because *Dolichosaurus* is known only from postcranial material, there is the distinct possibility that *Dolichosaurus* is a junior synonym of *Coniasaurus* (Caldwell 2000). Until more material from these taxa is recovered, we tentatively assign FHSM VP-14001 and VP-14002 to *Coniasaurus* cf. *C. crassidens*.

DISCUSSION

Table 2 lists non-reptilian taxa identified from our site. The site is assigned a middle Cenomanian age based upon the radiometric date of the "X" bentonite just below the site $(95.53 \pm 0.159 \text{ Ma})$ and the locality's stratigraphic occurrence. Kauffman et al. (1993) revised the Cretaceous molluscan biostratigraphic zones for the Western Interior Basin of North America, and the radiometric date and stratigraphic occurrence is consistent with a middle Cenomanian age assignment for the locality. Likewise, the chondrichthyan component of the fauna is also consistent with this assignment, based on the association of Ptychodus cf. P. anonymus Williston 1900, P. decurrens Agassiz 1843, P. occidentalis Leidy 1868, Carcharias amonensis (Cappetta and Case 1975), C. tenuiplicatus (Cappetta and Case 1975), C. saskatchewanensis (Case et al. 1990), Squalicorax curvatus (Williston 1900), and S. falcatus (Agassiz 1843).

Late Cretaceous reptiles from Kansas strata older than the Smoky Hill Chalk Member (late Coniacian-early Campanian) of the Niobrara Chalk are poorly known. Russell (1988, p. 25-26) listed over 110 vertebrate species from the Smoky Hill Chalk, nearly half of which are tetrapods. In contrast, Russell (1988, p. 22) listed only 10 vertebrate taxa from the Greenhorn Limestone of Kansas, four of which are tetrapods. Most of the few vertebrate species reported from the Greenhorn Limestone have very poor stratigraphic data.

There are a few recent reports of Cenomanian-aged reptiles from other parts of the Western Interior Seaway. From the western margin of the Cretaceous Interior Seaway Basin are faunas from the Greenhorn in South Dakota (VonLoh and Bell 1998) and Colorado (Shimada et al. 2003; Shimada et al. in press). The only other reptilian fauna described from the eastern margin of the basin comes from various



Figs. 10-14. Dorsal vertebra (FHSM VP-14002) of *Coniasaurus* cf. *C. crassidens*. Bar scale is 1 cm. 10. Anterior view. 11. Posterior view. 12. Left lateral view. 13. Dorsal view. 14. Ventral view.

Table 2. Non-reptilian vertebrate fossils from a Cenomanian locality in northwestern Russell County, Kansas.

Taxon	Referred Specimen	Description
Vertebrata indet.	FHSM VP-14783	Numerous indet. bones
Indet. coprolites	FHSM VP-14784	66 phosphatic pebbles
Elasmobranchii indet.	FHSM VP-14774	vertebra
Ptychodus decurrens	FHSM VP-14764	43 teeth
Ptychodus occidentalis	FHSM VP-14801	5 teeth
Ptychodus cf. P. anonymus	FHSM VP-14802	2 teeth
Lamniformes indet.	FHSM VP-14772	3 teeth
Teleost indet.	FHSM VP-14773	tooth
Carcharias amonensis	FHSM VP-14765	tooth
Carcharias tenuiplicatus	FHSM VP-14803	39 teeth
Carcharias saskatchewanensis	FHSM VP-14766	55 teeth
Cretolamna appendiculata	FHSM VP-14767	4 teeth
Cretoxyrhina mantelli	FHSM VP-14768	19 teeth
Squalicorax curvatus	FHSM VP-14804	19 teeth
Squalicorax falcatus	FHSM VP-14769	193 teeth
Teleost indet.	FHSM VP-14805	tooth
Squalicorax volgensis	FHSM VP-14770	6 teeth
Rhinobatos sp.	FHSM VP-14771	2 teeth
Teleost indet. (2 species)	FHSM VP-14775	2 bones
Teleost indet. (multiple species)	FHSM VP-14806	15 teeth
Teleost indet. (multiple species)	FHSM VP-14807	60 teeth
Teleost indet. (multiple species)	FHSM VP-14808	77 teeth
Teleost indet.	FHSM VP-14809	tooth
Teleost indet.	FHSM VP-14810	tooth
Teleost indet. (multiple species)	FHSM VP-14780	approx. 50 vertebrae
Teleost indet. (multiple species)	FHSM VP-14781	3 jaw fragments with teeth
Teleost indet. (multiple species)	FHSM VP-14813	2 quadrates
Pachyrhizodus minimus	FHSM VP-14812	set of fused hypurals
Enchodus sp.	FHSM VP-14776	100+ teeth/palatines
Xiphactinus audax	FHSM VP-14777	4 teeth
Protosphyraena sp. (or Saurodon sp.)	FHSM VP-14779	5 teeth

lithostratigraphic units in Saskatchewan, Canada (Cumbaa and Tokaryk 1999; Schroder-Adams et al. 2001). Therefore, this current report adds significant information about basin biogeography from that age. In addition, this fauna is significant for its taxonomic diversity and range extensions, both stratigraphically (i.e., *Brachauchenius lucasi* and a large pterodactyloid pterosaur) and geographically (i.e., *Coniasaurus* cf. *C. crassidens*).

ACKNOWLEDGMENTS

We thank Randy and Paula Staab and their children for bringing the site to our attention and helping with fieldwork. The Eulert family and Robert Jennrich are gratefully acknowledged for their contributions to this project. Jim Huenergarde helped with fieldwork and laboratory preparation of the material. Steve Wallace found the coniasaur vertebrae away from the main excavation site. Mike Caldwell, Gorden Bell, Jr., and Mike Polcyn all provided helpful early discussions on the coniasaur material. Mike Everhart provided valuable discussions on plesiosaur paddles and stratigraphic occurrences. Colin McHenry provided information on *Kronosaurus* and *Brachauchenius*. Funding for the radiometric date was provided by the United States Department of Agriculture Forest Service as part of a larger study. Cameron Liggett, Hannan LaGarry, Brian Witzke, and Ken Carpenter provided valuable comments on the manuscript. Both Richard Zakrzewski (FHSM) and Mark Florence (USNM) generously allowed access to collections in their care.

LITERATURE CITED

- Agassiz, L. 1833-1843 [1833, 1835, 1843]. Recherches sur les poisons fossils [5 volumes]. Imprimerie de Patitpierre, Neuchatel. 1420 pp.
- Bell, B.A., P.A. Murry, and L.W. Osten. 1982. Coniasaurus Owen, 1850 from North America. Journal of Paleontology 56:520-524.
- Bennett, S.C. 1989. A pteranodontid pterosaur from the Early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. *Journal of Paleontology* 63:669–677.
- Bennett, S.C. 1992. Sexual dimorphism of *Pteranodon* and other pterosaurs, with comments on cranial crests. *Journal of Vertebrate Paleontology* 12:422–434.
- Bennett, S.C. 1994. Taxonomy and systematics of the Late Cretaceous pterosaur *Pteranodon* (Pterosauria, Pterodactyloidea). Occasional Papers of the Museum of Natural History, University of Kansas 169:1–70.
- Brown, D.S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum of Natural History* (geol.) 35(4):253–347.
- Caldwell, M.W. 1999. Description and phylogenetic relationships of a new species of *Coniasaurus* Owen, 1850 (Squamata). *Journal* of *Vertebrate Paleontology* 19:438–455.
- Caldwell, M.W. 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in squamates. *Journal of Vertebrate Paleontology* 20:720–735.
- Caldwell, M.W., and J. Cooper. 1999. Redescription, palaebiogeography, and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the English Chalk (Cretaceous; Cenomanian). Zoological Journal of the Linnean Society 127:423–452.
- Cappetta, H., and G.R. Case. 1975. Sélacians nouveaux du Crétacé du Texas. Géobios 8:303–307.
- Carpenter, K. 1996. A Review of short-necked plesiosaurs from the Cretaceous of the western interior, North America. *Neues Jahrbuch fur Geologie und Palaeontologie*, Abhandlungen 201: 259–287.
- Carroll, R.L., and M. Debraga. 1992. Aigialosaurs: Mid-Cretaceous varanoid lizards. *Journal of Vertebrate Paleontology* 12:66–86.
- Case, G.R., T.T. Tokaryk, and D. Baird. 1990. Selachians from the Niobrara Formation of the Upper Cretaceous (Coniacian) of Carrot River, Saskatchewan, Canada. *Canadian Journal of Earth Sciences* 27:1084–1094.

- Cumbaa, S.L., and T.T. Tokaryk. 1999. Recent discoveries of Cretaceous marine vertebrates on the eastern margins of the Western Interior Seaway. Saskatchewan Geological Survey Summary of Investigations 1:57–63.
- Darton, N.H. 1904. Comparison of the stratigraphy of the Black Hills, Bighorn Mountains, and Rocky Mountain Front Range. *Geological Society of America Bulletin* 15:379–448.
- de Blainville, M.H. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'erpétologie et d'amphibiologie. *Nouvelles Annales du Muséum* (*National*) d'Histoire Naturelle, Paris 4:233–296.
- Diedrich, C. 1997. Ein Dentale von *Coniosaurus crassidens* Owen (Varanoidea) aus dem Ober-Cenoman von Halle/Westf. (NW-Deutschland). *Geologie und Paläontologie in Westfalen* 47: 43-51.
- Gervais, P. 1852. Zoologie et Paleontologie Francaises (Animaux Vertebres) (first edition). Paris, 271 pp.
- Gilbert, G.K. 1896. The underground water of the Arkansas Valley in eastern Colorado. 17th Annual Report of the U.S. Geological Survey. Part 2:551-601.
- Gilmore, C.W. 1935. A new occurrence of the flying reptile, Pteranodon. Science 82:77–102.
- Hattin, D.E. 1965. Stratigraphy of the Graneros Shale (Upper Cretaceous) in central Kansas. Kansas Geological Survey Bulletin 178:1-83.
- Hattin, D.E. 1975. Stratigraphy and depositional environment of Greenhorn Limestone (Upper Cretaceous) of Kansas. Kansas Geological Survey Bulletin 209:1–128.
- Hattin, D.E., C.T. Siemers, and G.F. Stewart. 1987. Upper Cretaceous stratigraphy and depositional environments of western Kansas. Kansas Geological Survey Guidebook Series 3:1-55.
- Miggins, D. 2004. ⁴⁰Ar/³⁹Ar results for Cretaceous bentonite beds of Colorado and Kansas. Report provided to USDA Forest Service under intra-agency agreement 04-IA-1102. 11 pp.
- Kauffman, E.G., B.B. Sageman, J.I. Kirkland, W.P. Elder, P.J. Harries, and T. Villamil. 1993. Molluscan biostratigraphy of the Cretaceous Western Interior Basin, North America. Pp. 397–434 in W.G.E. Caldwell and E.G. Kauffman (eds.). Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.
- Kaup, J. 1834. Versuch einer Einteilung der Säugetiere. *Isis von Oken*, Jena, p. 315.
- Langston, W., Jr. 1974. Nonmammalian Comanchean tetrapods. Geoscience and Man 8:77-102.
- Lee, Y. 1994. The Early Cretaceous pterodactyloid pterosaur *Coloborhynchus* from North America. *Palaeontology* 37:755–763.
- Leidy, J. 1868. Notice of American species of *Ptychodus*. *Proceedings* of the Academy of Natural Science of Philadelphia 20:205–208.
- Liggett, G. 2004. Discovery of a junior synonym for the Late Cretaceous genus *Coniasaurus* (Reptilia, Squamata). *Journal of Vertebrate Paleontology* 24(1):251–252.
- Lillegraven, J.A., and M.C. McKenna. 1986. Fossil mammals from the "Mesaverde" Formation (Late Cretaceous, Judithian) of the Bighorn and Wind River basins, Wyoming, with definitions of Late Cretaceous North American Land Mammal "Ages." American

- Museum Novitates 2840:1-68.
- Logan, W.N. 1899. A discussion and correlation of certain subdivisions of the Colorado formation. *Journal of Geology* 7:83–91.
- Murry, P.A., D.A. Winkler, and L.L. Jacobs. 1991. An azhdarchid pterosaur humerus from the Lower Cretaceous Glen Rose Formation of Texas. *Journal of Paleontology* 65:167–170.
- O'Keefe, R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). Acta Zoologica Fennica 213:1-63.
- Owen, R. 1850. Description of the fossil reptiles of the chalk formation. Pp. 378–404 *in* F. Dixon (ed.). The Geology and Fossils of the Tertiary and Cretaceous Formations of Sussex. Longman, Brown, Green and Longman, London. 422 pp.
- Owen, R. 1865. A monograph on the fossil Reptilia of the Liassic formation. Part 3. *Plesiosaurus*, *Dimorphodon*, and *Icthyosaurus*. Palaeontological Society of London, London. pp. 1-40.
- Pessagno, E.A. 1969. Upper Cretaceous stratigraphy of the western Gulf Coast area of Mexico, Texas, and Arkansas. *Geological Society of America Memoir* 111:1–139.
- Russell, D.A. 1988. A check list of North American marine Cretaceous vertebrates including fresh water fishes. *Royal Tyrrell Museum of Palaeontology Occasional Paper* 4:1–58.
- Schroder-Adams, C.J., S.L. Cumbaa, J. Bloch, D.A. Leckie, J. Craig, S.A.S. El-Dein, D.J.H.A.E. Simons, and F. Kenig. 2001. Late Cretaceous (Cenomanian to Campanian) paleoenvironmental history of the eastern Canadian margin of the Western Interior Seaway: bonebeds and anoxic events. *Palaeogreography, Palaeoclimatology*, *Palaeoecology* 170:261–289.
- Schumacher, B.A., and M.J. Everhart. 2005. A stratigraphic and taxonomic review of plesiosaurs from the old "Fort Benton Group" of central Kansas: a new assessment of old records. *Paludicola* 5(2):33–54.

- Seeley, H.G. 1874. On Muranosaurus leedsii, a plesiosaurian from the Oxford Clay. Part 1. Quaternary Journal of Geological Society of London 30:197-208.
- Shimada, K., and G.L. Bell, Jr. In press. *Coniasaurus* Owen, 1850 (Reptilia: Squamata), from the Upper Cretaceous Niobrara Chalk of western Kansas. *Journal of Paleontology*.
- Shimada, K., J.A. Parkin, J.M. Palermo, and B.A. Schumacher. 2003. Late Cretaceous marine vertebrates from the basal Greenhorn Limestone in southeastern Colorado. *Journal of Vertebrate Pale-ontology* 23(supplement to 3):96A.
- Shimada, K., B.A. Schumacher, J.A. Parkin, and J.M. Palermo. In press. Fossil marine vertebrates from the lowermost Greenhorn Limestone (Upper Cretaceous: middle Cenomanian) in southeastern Colorado. *Journal of Paleontology Memoir*.
- Von Loh, J.P., and G.L. Bell, Jr. 1998. Fossil reptiles from the Late Cretaceous Greenhorn Formation (late Cenomanian-middle Turonian) of the Black Hills region, South Dakota. *Dakoterra* 5:29–38.
- Welles, S.P., 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Memoirs of the University of California 13:125–254.
- Williston, S.W. 1900. Some fish teeth from the Kansas Cretaceous. Kansas University Quarterly 9:27-42.
- Williston, S.W. 1903. North American plesiosaurs: Part I. Fieldiana Geology 2:1–77.
- Williston, S.W. 1907. The skull of *Brachauchenius*, with observations on the relationships of the plesiosaurs. *Proceedings of the United States National Museum* 32(1540):477-489.
- Winkler, D.A., P.A. Murry, and L.L. Jacobs. 1990. Early Cretaceous (Comanchean) vertebrates of central Texas. *Journal of Vertebrate Paleontology* 10:95–116.
- Zangerl, R., and R.H. Denison. 1950. Discovery of Early Cretaceous mammals and frogs in Texas. *Science* 112:61.