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Journal of Paleontology, Vol. 71, No. 6. (Nov., 1997), pp. 1147-1156.

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THE ARCHOSAURIA FROM THE WOODBINE FORMATION (CENOMANIAN) IN TEXAS

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ABSTRACT—The archosaur fauna from the Woodbine Formation (Cenomanian), Tarrant County, Texas includes crocodiles, theropod, nodosaurid, and hadrosaurid dinosaurs. A new neosuchian crocodile, *Woodbinesuchus byersmauricei* new genus and species, appears to be a longirostrine goniopholid. Isolated theropod teeth include morphotypes similar to *Richardoestesia*. Nodosaurid premaxillary teeth are unique among early nodosaurids in having no marginal cusps. Hadrosaurid remains represent the oldest hadrosaurs east of the Western Interior Seaway.

INTRODUCTION

THE WOODBINE Formation, named by Hill (1901) for a small town in east-central Cooke County, Texas, is the basal formation of the Gulf Series. It is best known for being the source of the East Texas oil field, one of the largest oil fields on the North American continent (Halbouty and Halbouty, 1982). It unconformably overlies the Grayson Marl, uppermost member of the Washita Group, and is unconformably overlain by the Eagle Ford Group. Two major members are widely recognized in the Woodbine Formation. They are the Dexter Member (lower sandstone) of Taff (1893) and the Lewisville Member (upper shale) of Hill (1901). In Tarrant County, Dodge (1968) proposed four rock units, in ascending order, the Rush Creek, Dexter, Lewisville, and Arlington members. The purpose of this paper is to document for the first time archosaurs from the Woodbine Formation in Tarrant County, Texas, and to discuss the importance of their stratigraphic occurrence.

Although many paleontological studies have been conducted (mainly on invertebrates and plants), the fossil vertebrates of the Woodbine Formation had received little attention until the first investigation was initiated by the search for mammals (McNulty and Slaughter, 1968). Through bulk washing on a large scale, two mammal teeth were collected and identified as a therian premolar and a lower incisor of a taeniolabidoid multituberculate (Krause and Baird, 1979). Among other fossils found in the search for mammals, only fishes including sharks have received brief taxonomic studies (McNulty and Slaughter, 1962; McNulty, 1964; McNulty and Slaughter, 1968; Slaughter and Steiner, 1968; Welton and Farish, 1993). No archosaur fossils were described. Recently, crocodiles and dinosaurs have been recovered from newly discovered localities (Figure 1, Table 1).

Crocodylians are not rare in the Woodbine Formation and have been recovered from some localities by surface prospecting and screening. Most specimens are isolated teeth, vertebrae, and osteoderms. A reasonably complete crocodile was found by J. Byers and J. Maurice in May, 1990. The specimen was discovered in the lowermost Woodbine Formation just above the basal contact with the Grayson Formation in Tarrant County, Texas. Dinosaur teeth are known from several localities. Recently, a complete hadrosaur tibia and fibula were recovered at SMU locality 234, where G. Eckland found a femur in 1989. In southern Denton County, the skull of hadrosaur was found, but it is not described in this paper.

Outcrops developed along Bear Creek near the south entrance to Dallas-Fort Worth International Airport (Figure 2) has produced crocodylians, theropod teeth, nodosaurid and hadrosaurid teeth with a few bones. Stratigraphic sections at SMU locality 245 mark a transition phase of the Woodbine Formation into the typical deeper marine shale facies of the Eagle Ford Group.

Here, the section consists of a lower shaly sandstone unit and an upper sandy shale unit interbedded with thin fossiliferous sandstone layers. Dark, lignitic and carbonaceous strata are also common. Thin sandstone units contain fine quartzose sand with calcareous and ferruginous cement, and are rich in chert pebbles and phosphatic nodules. A phosphatic pebble conglomerate surface marks a transgressive lag deposit. This surface contains abundant reworked vertebrate bones, primarily teeth and small fragments including fishes, frogs, turtles, crocodiles, dinosaurs, and a mammal. Terrestrial fossils are concentrated with those characteristic of brackish environments.

The upper part of the Washita Group (Grayson Marl) underlying the Woodbine and the basal unit of the Eagle Ford Group, above the Woodbine, are included in the Cenomanian (Michael, 1972; Mancini, 1979; Birkelund et al., 1984). The uppermost shale unit of locality 245 yields a *Conlinoceras tarrantense* ammonite zone fauna, which represents the lower middle Cenomanian (Kennedy and Cobban, 1990). Therefore, Woodbine archosaurs are not younger than the early middle Cenomanian (approximately 95 Ma). The occurrence of transgressive lags in the depositional sequence and associated discontinuous thin bodies of coarser clastic sediment in this area suggests that the uppermost Woodbine Formation (the Arlington Member) was deposited along a low-lying coastal plain (Powell, 1968). This shoreface setting was modified by a series of relatively small transgressive and regressive events before the major transgression which deposited the sediments of Eagle Ford Group.

Abbreviations.—AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; KU, University of Kansas, Museum of Natural History, Lawrence; MAFI, Magyar Allami Földtani Intezet, Budapest; MU, University of Missouri, Columbia; ROM, Royal Ontario Museum, Toronto; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas; YPM, Peabody Museum of Natural History, Yale University, New Haven.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970

CROCODYLIFORMES Clark in Benton and Clark, 1988

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

GONIOPHOLIDAE Cope, 1875

Genus WOODBINESUCHUS new genus

Type species.—*Woodbinesuchus byersmauricei* new species

Etymology.—Referring to its occurrence in the Woodbine Formation, and Greek *souchos*, crocodile.

Diagnosis.—A goniopholid with slender, remarkably elongate snout (sixteen teeth in mandibular symphysis); short contribution of splenial to symphysis (one-fifth of symphysis length); no external mandibular fenestra; straight cranial edge of scapula.

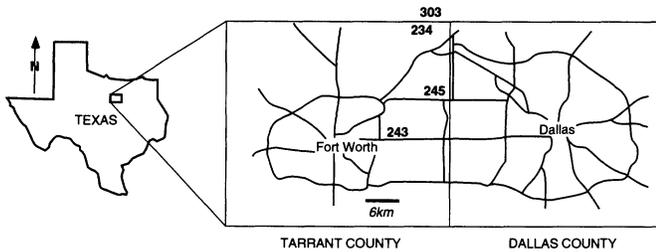


FIGURE 1—Archosaur localities marked by SMU locality numbers in Tarrant County, Texas.

WOODBINESUCHUS BYERSMAURICEI new species
Figures 3, 4

Holotype.—SMU 74626. Lower jaws, and postcranial elements.

Etymology.—The species is named in honor of Mr. J. Byers and J. Maurice, who found the specimen.

Diagnosis.—As for the genus.

Location and horizon.—Tarrant County, Texas (SMU locality 243, exact location on file at SMU). Woodbine Formation (Rush Creek Member) above basal contact with the Grayson Formation. Upper Cretaceous, Cenomanian.

Description.—Representative skeletal measurements are given in Table 2. Although distorted and covered with the pyritic concretions medially, the mandible is nearly complete (Figure 3.1–3.3). Each element of the mandible is completely fused except for the contact of the dentary with the splenial, so that most sutures are not clear. The dentary is relatively long with 26 alveoli. As in most goniopholids, the tip of the dentary is slightly expanded laterally by the third and fourth alveoli (15 mm in diameter) about twice as large as first two alveoli, forming a cranial bulge at the level of the fourth tooth. The slender mandibular symphysis is remarkably long and extends back to the sixteenth alveolus, which is longer than those of previously known goniopholids. It occupies greater than one-third the total length of each ramus. The symphysis reaches caudally the level of the seventh dentary tooth in *Goniopholis simus* (Owen, 1878, 1879), eleventh in *Vectisuchus leptognathus* (Buffetaut and Hutt, 1980), and fourteenth or fifteenth in *Sunosuchus junggarensis* (Wu et al., 1996). The width of the symphysis increases gradually from the fifth alveoli to the splenial, where the two rami diverge caudally. The angulation of the divergence is unclear due to the strong distortion of the rami. The alveoli caudal to the first four are approximately equal in size (10 mm in diameter) and are arranged at approximately equal distances to the level of the ninth tooth. Caudal to the ninth tooth socket the alveoli are closer together and smaller. All of the alveoli are directed slightly forward and outward. The medial surface of the splenial is severely broken so that its contribution to the ventral surface of the mandible is unclear. In the dorsal view, the splenial meets the dentary, comprising one-fifth of the symphysis caudally. It reaches the level of the thirteenth mandibular tooth cranially.

The splenial occupies a small portion of the symphysis in most goniopholids except for *Vectisuchus*. It extends forward to the level of the seventh tooth in *Eutretauranosuchus delfsi* having eight mandibular teeth (Mook, 1967), but occupies the half of the length of the symphysis in *Vectisuchus*. The external mandibular fenestra of *Woodbinesuchus* is closed as in derived mesoeucrocodylians such as *Goniopholis* and *Bernissartia fagesii* (Norell and Clark, 1990). The presence of the external mandibular fenestra was correlated with longirostry because all longirostrine crocodylomorphs have it (Norell and Clark, 1990), but not true in a longirostrine *Woodbinesuchus*. The dorsal edge of the surangular caudal to the tooth row is flat as in other goniopholids. It articulates with the well developed articular caudally. The articular fossa for the quadratic articulation is large, forming a rounded concavity medially. No foramen aëreum is found as in *Sunosuchus*. The retroarticular process is long and directed caudoventrally as in other goniopholids. The lateral surface of the mandible is greatly ornamented with osteodermal sculpturing.

Six isolated teeth were recovered (Figure 3.4). They are slender, blunt, and recurved distally. The teeth are finely striated longitudinally with two distinct lateral edges, which appears to be similar to that of *Goniopholis gilmorei* (Holland, 1905).

Three cervical vertebrae are preserved including the axis (Figure 4.1). The odontoid process and centrum of the axis are well united but the neural arch is missing. The odontoid process is large and moderately convex cranially. The dorsal portion of the process is prominently elevated dorsolaterally, forming large oval tubercles for articulation with the neural arch of the atlas. The area between the tubercles is broadly concave and forms the ventral floor of the neural canal. Distinct diapophysial facets are round in outline and face caudolaterally. The cranioventral margin of the centrum of the axis is slightly expanded ventrally and the caudal end of the centrum is concave.

Although the exact positions of two post-axis cervical vertebrae are not determined, they are easily distinguished from each other. The neural spines of both are low and thick caudally, but the prezygapophyses of the more cranial cervical are closer together compared to those of the more caudal cervical (Figure 4.2). The diapophyses of the cranial cervical are short and directed ventrolaterally, but they are raised in position and lengthened in the caudal cervical. The amphicoelous centra of both cervicals have strongly keeled ventral margins, of which the cranial portion is extended into a short downward process (hypapophysis), but not pronounced and strong as in eusuchians. Parapophyses on both cervicals are situated on the centra, but are closer to the ventral border in the cranial cervical.

Ten vertebrae are assigned to the dorsal series (Figure 4.3). In all the neural spine is low and its height nearly equals its length, forming a trapezoid in lateral view. The dorsal surface is flat and broader than its base. The transverse processes, which project caudolaterally in the cranial dorsals, are directed laterally in the caudal series. These processes are stout with straight caudal margins, but the cranial margins have the typical indented

TABLE 1—Archosaur fauna from the Woodbine Formation in Tarrant County, Texas. Locality numbers of this study: 243 = John T. White/820; 234 = Murrel Park; 245 = Bear Creek.

Localities	Specimens
SMU 245 (Arlington Member)	Crocodylian teeth, vertebrae, and osteoderms Theropod teeth Nodosaurid teeth, humerus, fibula, and osteoderm Hadrosaurid teeth and humerus
SMU 234 (Lewisville Member)	Hadrosaurid femur, tibia, and fibula
SMU 243 (Rush Creek Member)	<i>Woodbinesuchus byersmauricei</i> new genus and species

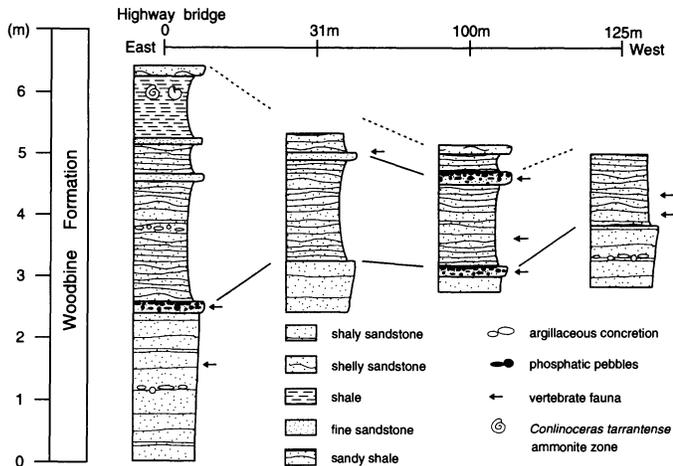


FIGURE 2—Stratigraphic sections of the Woodbine Formation exposed along Bear Creek near the south entrance to Dallas-Fort Worth International Airport (SMU locality 245).

notch for the parapophyseal facet. Both zygapophyseal surfaces are nearly on the level of the transverse processes. Prezygapophyses are directed slightly medially and dorsally, while postzygapophyses are directed slightly laterally and ventrally. The centra of all dorsals are amphicoelous. In the cranial dorsals, the ventral surfaces are slightly keeled and have a downward process like the cervicals, but centra become progressively more rounded caudally.

The caudal series is represented by three vertebrae with damaged neural arches. The zygapophyses are relatively small and close together compared with those of the dorsals. The amphicoelous centra have a deep longitudinal groove on the ventral surface.

Two cervical and twelve dorsal ribs and an ossified interclavicle (Figure 4.4) are preserved. The interclavicle is elongate and slightly convex dorsoventrally. The caudal end is pointed, compared to the moderately rounded cranial end.

The scapula and coracoid are well preserved and about equal in length. Compared with other goniopholids, the most remarkable aspect of the scapula is its nearly straight edges of the scapular blade, so symmetrical in lateral view (Figure 4.5). In *Goniopholis* (Owen, 1878, 1879; Dollo, 1883) and *Dakotasuchus kingi* (Mehl, 1941), the cranial edge is more strongly concave than the caudal edge. In lateral view, the concave proximal portion is bounded by an elevated cranial ridge and by the glenoid caudally. The glenoid region is massive and broad dorsoventrally. It is directed more laterally than ventrally. In comparison to the scapula, the coracoid is slightly longer and more massive (Figure 4.6). The glenoid is well demarcated from the base of the bone by a distinct lateral expansion. The glenoid surface of the coracoid is larger than that of the scapula. The coracoid foramen perforates the cranial portion of the glenoid, which is different from *Sunosuchus* having a coracoid foramen lying close to the scapular-coracoid suture. While the coracoid's proximal end appears rectangular, the distal end is long and greatly expanded cranioventrally into a broad flat blade. Its cranial edge is strongly curved, while the caudal edge is nearly straight. The proximal end of the radius is rounded and the distal end is broad craniocaudally (Figure 4.7).

The ilium is a heavy bone with an extended postacetabular process which are deep dorsoventrally, and tapering gradually toward the caudal end (Figure 4.8). It has two distinct articulations with the ischium and the pubis directly or indirectly. It is not certain whether its cranial articular surface meets the pubis

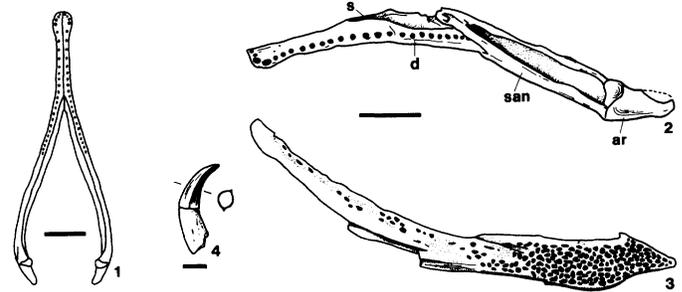


FIGURE 3—*Woodbinesuchus byersmauricei* new genus and species (SMU 74626). 1, reconstruction of mandible in dorsal view, scale bar equals 10 cm; 2-3, left mandible in dorsal and lateral views, scale bar equals 10 cm; 4, isolated tooth in lateral view and cross section, scale bar equals 1 cm. Abbreviations: ar, articular; d, dentary; s, splenial; san, surangular.

directly because the ischium is missing. Both articulations are smoothly rounded, but the caudal facet for the ischium faces ventrolaterally while the cranial facet lies at the angle of 45 degrees cranioventrally. The caudal articulation is slightly larger than the cranial. A deeply concave acetabulum is closed and situated between two articulations. The cranial margin of the ilium is smooth, not forming any prominent preacetabular process as seen in eusuchian *Leidyosuchus formidabilis* (Erickson, 1976). The ventral portion of the medial surface is rugose and irregularly shaped for the articulations with the sacral vertebrae. The expanded proximal end of the pubis forms oval in outline (Figure 4.9). Distally, the shaft becomes thinner laterally and wider craniocaudally to form a roughly triangular bone.

The right femur is sigmoidal in caudal view (Figure 4.10). The proximal end is enlarged and its head is distinctly round. The prominent fourth trochanter is located about one-fourth the length distally from the proximal end. The medial condyle is damaged. The proximal end of a tibia is massive, strong, and triangular in outline (Figure 4.11). The shaft is stout, slightly curved laterally in the proximal portion, and slender distally. The distal end is expanded in an oblique direction such that the two condyles face cranioventrally. Although a metapodial was recovered (probably a metatarsal), its exact position is not determined.

The sixty three osteoderms are preserved including 31 ventral osteoderms (Figure 4.12-4.16). The dorsal osteoderms are six from the dorsolateral region of the neck, 24 from the dorsal, three from the sacral, and three from the caudodorsal. Although these osteoderms do not represent the complete shield of this animal, it is possible to extract a general configuration from them. The six dorsolateral osteoderms of the neck are characterized by small round or teardrop-shaped osteoderms with a strong keel on the middle of the pitted surface (Figure 4.16). These are similar to those from the same region of *Sunosuchus junggarensis*. Dorsal osteoderms occur in two longitudinal rows. Right and left osteoderms meet along a straight median line, which is similar to that of *Protosuchus richardsoni* (Colbert and Mook, 1951), *Goniopholis simus* (Owen, 1879) and *S. junggarensis* (Figure 4.12-4.13). The dorsal surface of each osteoderm is irregularly pitted, but no keel as seen in *Vectisuchus leptognathus*. The osteoderms of each row are imbricated so that the caudal margins of osteoderms overlap the cranial margins of the osteoderms behind. The overlapped cranial margin of each osteoderm is smooth and unpitted. Most osteoderms have a lateral ridge with a cranially directed process. This cranioventral process underlies the cranially adjoining osteoderm so that osteoderms are longitudinally interlocked. The lateral ridge of more cranial osteoderms is bent sharply downward, producing an acute angle.

TABLE 2—Representative skeletal measurements of *Woodbinesuchus byersmauricei* new genus and species, nodosaurid, and hadrosaurid specimens (in mm).

<i>Woodbinesuchus byersmauricei</i> new genus and species	
Mandible: L	663
Mandible—Symphysis: L	218
Axis—Centrum: L × W (cranial) × W (caudal)	65 × 47 × 35
Two cervical vertebrae (positions unknown, but in anatomical order)	
—Centrum: L × W	44 × 38
" "	40 × 45
Ten dorsal vertebra (positions unknown)	
—Centrum: L × W × H (including neural spine)	49 × 43 × 74
" "	47 × 41
" "	46 × 41 × 83
" "	46 × 43 × 79
" "	45 × 40 × 74
" "	45 × 41
" "	44 × 44 × 80
" "	43 × 38 × 78
" "	41 × 42 × 90
" "	40 × 40 × 75
Three caudal vertebrae (positions unknown, but in anatomical order)	
—Centrum: L × W	46 × 31
" "	43 × 21
" "	40 × 15
Interclavicle: L × W	155 × 32
Scapula: L × W (proximal)	135 × 50
Carocoid: L × W (distal)	165 × 75
Radius: L	143
Ilium: L × H	132 × 63
Pubis: L × W (distal)	114** × 55**
Femur: L × W (mediolateral, proximal)	235 × 51
Tibia: L × W (max. proximal) × W (max. distal)	167 × 38 × 27*
Nodosaurids	
Humerus: L × W (max. proximal) × W (max. distal)	352 × 185* × 130*
Fibula: L × W (max. proximal) × W (max. distal)	296 × 72 × 60
Hadrosaurids	
Humerus: L × W (max. proximal)	245** × 105
Femur: L × W (mediolateral, proximal)	390** × 305
Tibia: L × W (craniocaudal, proximal) × W (mediolateral, distal)	920 × 360 × 280*
Fibula: L × W (craniocaudal, proximal) × W (max. distal)	860 × 194 × 138
Astragalus: W (mediolateral)	192

Abbreviations—L, length; W, width; H, height; *, estimated; **, broken length.

This angulation is wider toward the lumbar and sacral regions where dorsal osteoderms have maximum widths (158 mm). In the sacral region, osteoderms become longer than wide and lack the cranolateral process, but they have an unpitted overlapped area cranially like presacral osteoderms. Two of the three caudodorsal osteoderms do not have a cranolateral process and a cranial facet. One left caudodorsal osteoderm is more or less triangular in shape which may have been located in the middle region of the tail (Figure 4.14). It meets a cranial osteoderm and a fellow of the other side by suture without a cranial facet.

The two osteoderms are comparable to those from the dorso-lateral region of the neck in shape and size, but lack a strong keel on the pitted surface. They are almost identical in morphology to the osteoderms of the limbs of *S. junggarensis*.

Thirty one isolated ventral osteoderms are preserved in various polygonal shapes. Judging from the dermal pattern of *Teliosaurus cadomensis* (Steel, 1973, figure 12) and *S. junggarensis* (Wu et al., 1996, figure 13), twenty two dermal osteoderms with articular facets on all sides represent medial ventral osteoderms. They are generally polygonal in shape, but most of them are hexagonal in outline (Figure 4.15). Nine osteoderms are the most lateral ventral osteoderms which lack the articular facet on only one side.

OTHER CROCODYLIA

Abundant crocodylian specimens were collected from SMU locality 245 which include isolated teeth of several morphotypes,

and osteoderms. Among them, button-shaped teeth (SMU 74640, 74641, Figure 5.2–5.5) consistent with *Bernissartia*. This genus has been reported from Lower Cretaceous sediments in Europe (Dollo, 1883; Buffetaut and Ford, 1979; Buscalioni et al., 1984; Buscalioni and Sanz, 1990) and Texas (Winkler et al., 1990). Primitive amphicoelous vertebrae and dorsal osteoderms of *Woodbinesuchus*, and eusuchian prococial vertebrae and osteoderms with longitudinal keels on dorsal surfaces are found at Bear Creek (SMU 74639, Figure 5.1).

Order SAURISCHIA Seeley, 1887

Suborder THEROPODA Marsh, 1881

Two tooth morphotypes (SMU 73778, 73779) were recovered through screen-washing at SMU locality 245. One is shaped like an isosceles triangle and the other is recurved (Figure 5.6–5.7). The former resemble a tooth (AMNH 8114, Estes, 1964, figure 69) from the Lance Formation, Wyoming, which is straight and uncurved in lateral view and serrated on both sides. The recurved teeth have heavier serration in the distal edge than the mesial. Denticles are minute in size, at least four denticles per millimeter, and each denticle is rectangular in shape. These two morphotype are very similar to *Richardoestesia* from Campanian and Maastrichtian sediments (Currie et al., 1990). In *Richardoestesia*, the straight and recurved teeth represent cranial and more caudal mandibular teeth, respectively. Recently, cf. *Richardoestesia* was also recognized in the upper Cedar Moun-

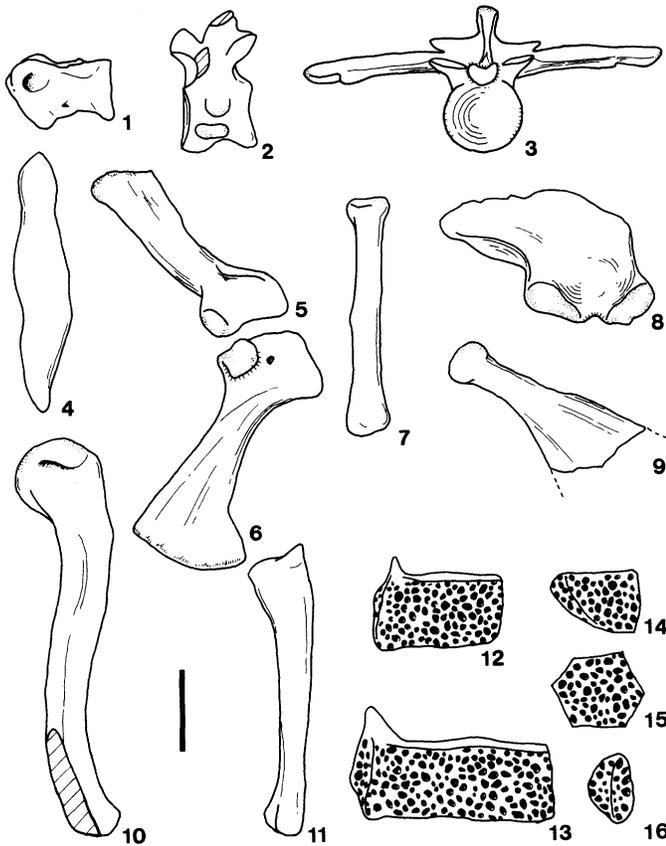


FIGURE 4—*Woodbinesuchus byersmauricei* new genus and species (SMU 74626). 1, axis in lateral view; 2, cranial cervical vertebra in left lateral view; 3, caudal dorsal vertebra in cranial view; 4, interclavicle in ventral view; 5, right scapula in lateral view; 6, right coracoid in lateral view; 7, left radius in cranial view; 8, right ilium in medial view; 9, left pubis in medial view; 10, right femur in cranial view; 11, right tibia in caudal view; 12, dorsal osteoderm from neck region in dorsal view; 13, dorsal osteoderm from middle region of trunk in dorsal view; 14, caudodorsal osteoderm from middle region of tail in dorsal view; 15, medial ventral osteoderm in ventral view; 16, osteoderm from dorso-lateral region of neck in dorsal view. Scale bar equals 5 cm.

tain Formation (lowest Cenomanian), Utah (Kirkland and Parrish, 1995).

Order ORNITHISCHIA Seeley, 1888
Suborder ANKYLOSAURIA Osborn, 1923
Family NODOSAURIDAE Marsh, 1890

Nodosaurid remains from SMU locality 245 include isolated teeth, a right humerus, a left fibula, and an osteoderm. In general, the premaxillary teeth are known to have fewer denticles than the maxillary set, for instances, two small denticles in *Pawpawsaurus campbelli* (SMU 73203, Lee, 1996). Four premaxillary teeth (SMU 74637, Figure 5.8–5.9) are distinguished from those of *Pawpawsaurus*, *Sauropelta edwardsi* (AMNH 3035), and *Silvisaurus condrayi* (KU 10296, Eaton, 1960) in that they do not have marginal denticles. The surface are well enameled and the buccal crown is slightly convex with a faint basal cingulum. The lingual crown surface, in contrast, is concave, and forms a lozenge-shaped crown with the low basal cingulum. The apex of the cusp is slightly offset from the midline toward the caudal edge relative to the crown base. The root is straight as preserved and round in cross section.

Maxillary or dentary teeth (SMU 73777, Figure 5.10–5.11)

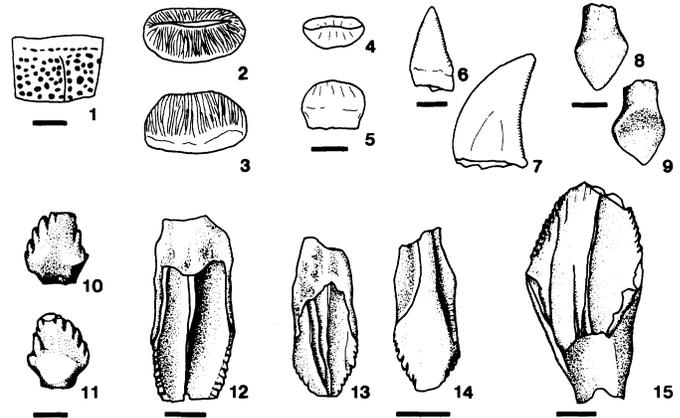


FIGURE 5—Woodbine archosaurs from SMU locality 245. 1, crocodilian dorsal osteoderm (SMU 74639) in dorsal view, scale bar equals 10 mm; 2-5, *Bernissartia?* teeth (SMU 74640, SMU 74641) in occlusal and lateral views, scale bar equals 1 mm; 6-7, theropod teeth, *Richardoestesia?* (SMU 73778, SMU 73779) in lateral views, scale bar equals 1 mm; 8-9, nodosaurid premaxillary tooth (SMU 74637) in labial and lingual views, scale bar equals 3 mm; 10-11, nodosaurid tooth (SMU 73777) in labial and lingual views, scale bar equals 3 mm; 12, hadrosaurid maxillary tooth (SMU 74638) in labial view, scale bar equals 5 mm; 13-14, hadrosaurid mesial (?) maxillary tooth (SMU 73574) in labial and lingual views, scale bar equals 5 mm; 15, hadrosaurid dentary tooth (SMU 73571) in lingual view, scale bar equals 5 mm.

have a single wear facet on the occlusal face. It is positioned in the middle of the crown base, not on the edges of the crown. The wear angulation is approximately 80 degrees from horizontal. Thus, this wear surface suggests that maxillary or dentary teeth were staggered along the vertical plane. The non-occlusal face is prominently arched with a faint basal cingulum. The apical cusp is slightly caudal to the midline of the crown. There are five mesial and three or four distal marginal cusps. The grooves separating marginal cusps do not continue down the crown face to the cingulum.

The humerus (SMU 72833, Figure 6.1) has a greatly expanded deltopectoral crest that forms a flat process. It extends smoothly from the humeral head without the demarcation seen in *Niobrarasaurus coleii* (MU 650, Carpenter et al., 1995), *Sauropelta edwardsi* (Ostrom, 1970, YPM 5191, 5312, AMNH 3035), and *Panoplosaurus mirus* (ROM 1215, Russell, 1940). The lateral edge of the deltopectoral crest is not thickened as in *Sauropelta*. In lateral view, therefore, the proximal end of the humerus is much thinner with a shallower concave flexor fossa than those of other nodosaurids. The bicapital crest is damaged. The shaft is almost straight, and not strongly twisted as is the humerus of *Pawpawsaurus*, in which the deltopectoral crest extends forward nearly perpendicular to the long axis of the distal end. On the caudolateral aspect of the shaft, there is a distinct oval depression, probably for insertion of the *M. latissimus dorsi* (Coombs, 1978). The radial capitulum is distinctly large and much closer to the ectepicondyle than the entepicondyle. The olecranon notch between the condyles is shallow, but the olecranon fossa is deep.

A left fibula (SMU 73059, Figure 6.2) is a straight bone with expanded ends. The fan-shaped proximal end is strongly compressed transversely, producing a slightly concave crescent medially. The dorsal articular surface is convex and rugose. In contrast with other ankylosaurian fibulae, the shaft is straight. There is a rugose scar approximately one-fourth the way down the shaft, a little higher than in *Sauropelta*. The distal end expands slightly cranially and forms a rugose, flattened bottom.

SMU 74081 is an incomplete small subcircular osteoderm with an asymmetrically placed keel on the heavily pitted dorsal surface. The flat ventral surface indicates that this osteoderm probably belongs to a nodosaurid (Coombs, 1971).

Suborder ORNITHOPODA Marsh, 1881
Family HADROSAURIDAE Cope, 1869

Maxillary teeth are represented by two tooth morphotypes. One is most similar to *Gilmoresaurus mongoliensis* (AMNH 6551, Gilmore, 1933) from the Iren Dabasu Formation in China (SMU 74638, Figure 5.12). The crown is tall relative to mesiodistal-width (1.7: 1), bearing a strong median carina. As in typical hadrosaurid maxillary teeth, there are no secondary ridges on the crown. The apex is bluntly rounded. The margins of the crown are well denticulated from the mid portion to the apex. The papillae are semilunate clusters (Beavan et al., 1994). The size of papillae decreases gradually from the apex to the point of maximum mesiodistal width.

The second morphotype differs from typical hadrosaurid maxillary teeth in having two secondary ridges converging from the base to the apex where they meet the primary ridge (SMU 73574, Figure 5.13–5.14). Marginal denticles are developed on the mesial and distal edges. In lingual view, the base has a longitudinal groove mesially and distally to accommodate the crowns of closely packed adjacent teeth as is characteristic of hadrosaurids. This tooth might represent a mesially positioned maxillary tooth.

A dentary tooth (SMU 73571, Figure 5.15) has a long tapering root that is thick laterally. The crown is short and broad (24 mm high and 16 mm wide). The enameled surface of the crown is divided unequally by a low but sharp median carina. It is slightly offset distally from the midline and recurved toward the apex. The distal portion of the tooth is bounded by marginal denticles and the shelf below, and is devoid of subsidiary ridges. The larger mesial portion is subdivided by a poorly defined secondary ridge. It extends parallel to the median carina from the base of the shelf to the denticles. The shelves just below the widest part of the crown produce an obliquely inclined cingulum mesially and distally as in *Iguanodon cf. atherfieldensis* (BMNH 40100, Norman, 1986). The distal cingulum is more prominent than the mesial. The marginal denticles wrap around the edges of the crown above the cingulum, reducing in size towards the apex, in contrast to the maxillary tooth. The apex is roundly pointed. All of these features suggest a primitive hadrosaurid tooth. Relatively broad dentary teeth is a primitive character in hadrosaurids such as *Claosaurus agilis* (Horner, 1990; Carpenter et al., 1995), *Gilmoresaurus mongoliensis*, *Telmatosaurus transsylvanicus* (Weishampel et al., 1993), and *Gryposaurus latidens* (Horner, 1992). The presence of supplementary ridges is retained as a plesiomorphic state in *Lophorhothon atopus* (Horner, 1992) and *Telmatosaurus transsylvanicus*. It is highly reminiscent of those of *Iguanodon* and *Ouranosaurus*. The angulation between the crown and root is low in the SMU specimens (115 degrees), which is interpreted as a primitive character in hadrosaurids (Horner, 1990).

Although the distal end is missing, a left humerus retains the sigmoidal curve in the middle portion of the shaft as in typical hadrosaurid humeri (SMU 73204, Figure 6.3, Norman, 1990). The deltopectoral crest is plesiomorphically small, projecting from the shaft (Weishampel and Horner, 1990).

A proximal left femur from SMU locality 234 is broken at the top of the fourth trochanter (SMU 73062, Figure 6.4). The hemispherical femoral head is well developed and set off from the shaft by a craniocaudally compressed short neck. The greater trochanter is convex dorsally, but not extending above the head as in most hadrosaurids (Weishampel and Horner, 1990). It lies

slightly below the level of the head as in *Telmatosaurus transsylvanicus* (MAFI v.10338, Weishampel et al., 1993, figure 5f). The lateral surface of the greater trochanter is flattened and straight as preserved. The lesser trochanter is marked by a faint groove craniolaterally, rather than by an open cleft as in most hadrosaurids.

The tibia is robust and straight, expanded at both ends (Figure 6.5–6.6). The lateral condyle is separated from the larger caudal end of the proximal tibia by a deep, wide, U-shaped groove. The distal end is expanded transversely with its long axis approximately 75 degrees to that of the proximal end. The cranial aspect of the distal end is deeply depressed and covered with a dorsal projection from the astragalus between both malleoli, while on the caudal aspect, there is a distinct ascending ridge extending proximally.

The fibula is a straight bone with a craniocaudally expanded proximal end and a small knob-like distal end (Figure 6.7–6.8). The proximal end is conspicuously projected cranially and slightly curved medially with a prominent tongue-like process. The gracile shaft twists and flattens caudomedially to conform to the tibial articulation. The long axis of the distal end is, thus, oriented at about 50 degrees from that of the proximal end.

The astragalus is tightly bound to the distal tibia. It has a thick, rounded border medially that covers almost all of medial tibial malleolus except for its cranial tip. The lateral border is much thinner than the medial, and deeply concave medially. The ascending process on the astragalus appears to be similar to the hadrosaurid astragalus-type 2 (Brett-Surman, 1975, figure 7b).

DISCUSSION

Although dinosaur footprints from the Cenomanian sediments are widespread in North America (Storer, 1975, in British Columbia; Lockley, 1985, in Colorado; Thomas and Gillette, 1985, in New Mexico; Weishampel, 1990, in Arizona), Cenomanian archosaur body fossils are extremely rare. Cenomanian terrestrial sediments are widely distributed along the Western Interior Seaway, primarily the Dakota Formation, but archosaur records from them are patchy. They include a distal end of a hadrosaurian (?) femur (Barbour, 1931; Galton and Jensen, 1979) in Nebraska, and *Dakotasuchus* (Mehl, 1941) and *Silvisaurus* (Eaton, 1960) in Kansas. Archosaur materials also have been found in some mammal localities of the Dakota Formation, Utah (Eaton, 1993), but these have not been described. Recently, theropod teeth were recognized in the upper Cedar Mountain Formation (lowest Cenomanian), Utah (Kirkland and Parrish, 1995). Therefore, the Woodbine fauna represents the first extensive Cenomanian archosaur assemblage from North America.

Although the important diagnostic characters for assigning to the family are not available due to the lack of the skull, two derived characters are recognized in *Woodbinesuchus*. They are the absence of the external mandibular fenestra and dorsal osteoderms without longitudinal keels. The former is known in *Goniopholis*, *Bernissartia*, and a primitive family, Atoposauridae including *Theriosuchus* and *Alligatorium* (Clark, 1994). The second character is, however, present only in *Goniopholis* of them as a derived one, indicating that *Woodbinesuchus* appears to be closer to genus *Goniopholis* than any other mesoeucrocodylian taxa. Therefore, *Woodbinesuchus* is tentatively referred to the Goniopholidae. The phylogenetic relationships of *Woodbinesuchus* with the Goniopholidae is not analyzed in this study because of the incompleteness of materials and the lack of the detail systematics of the Goniopholidae (Clark, 1986). Instead, *Woodbinesuchus* is compared mainly with the better-known taxa previously referred to the family.

A remarkable apomorphy of *Woodbinesuchus* is the long mental symphysis, which extends back to the level of the six-

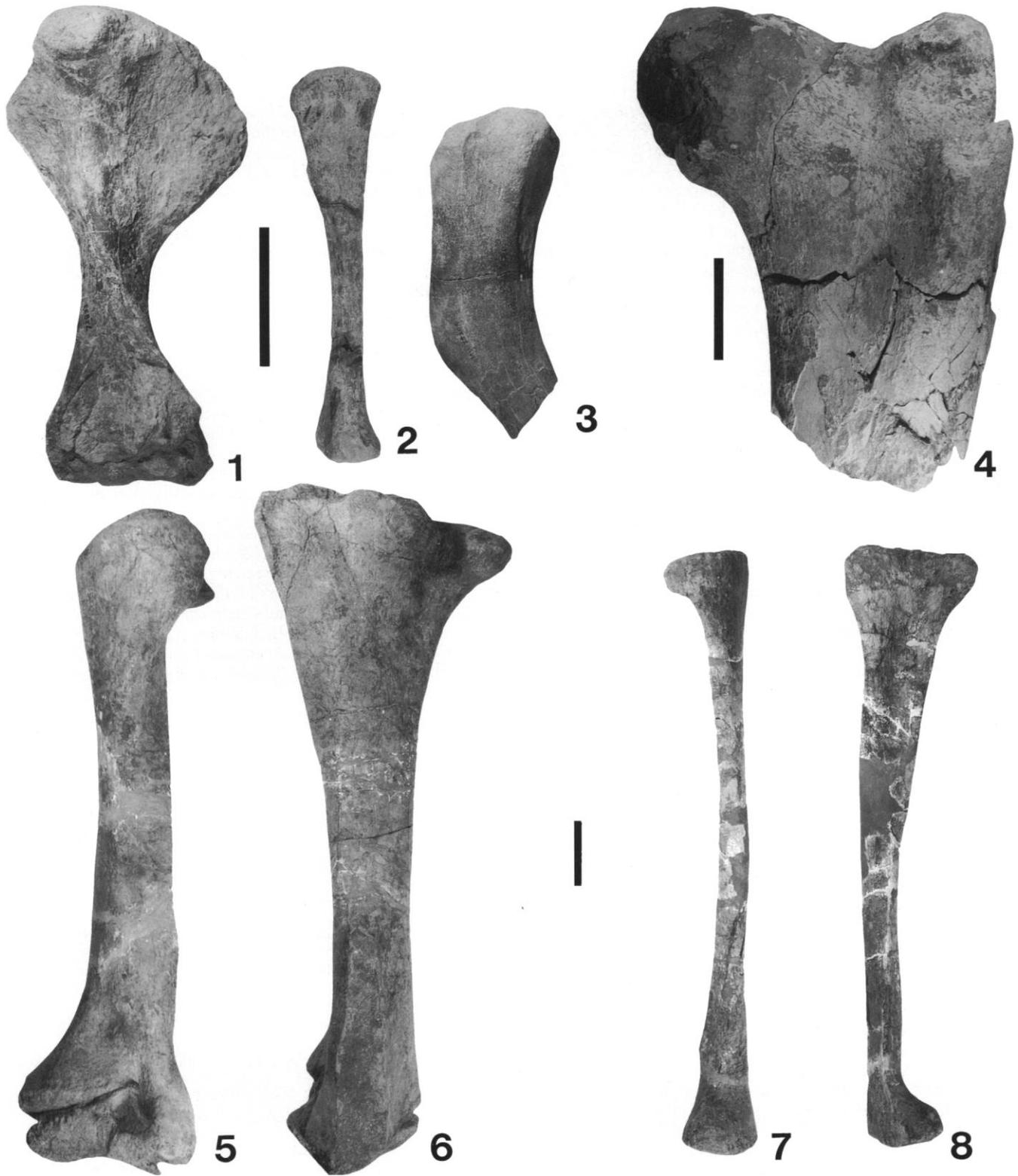


FIGURE 6—1, Nodosaurid right humerus (SMU 72833) in cranial view; 2, nodosaurid left fibula (SMU 73059) in lateral view; 3, hadrosaurid left humerus (SMU 73204) in cranial view; 4—8, hadrosaurid left femur in cranial view, tibia in caudal and lateral views, and fibula in cranial and medial views (SMU 73062). Scale bars equal 10 cm.

teeth tooth. This feature certainly distinguishes *Woodbinesuchus* from previously known goniopholid with a much shorter symphysis. *Vectisuchus*, the first supposed goniopholid with a long-snout differs from *Woodbinesuchus* in having a moderate mental symphysis in length which reaches the level of the eleventh tooth, the deeply included splenial into the symphysis, and dorsal osteoderms with two longitudinal ridges. *Woodbinesuchus* is similar to *Sunosuchus* in having a long mental symphysis, but easily distinguished from *Sunosuchus* and *Eutretauranosuchus* by the lack of the external mandibular fenestra. In addition, the proximal portion of the coracoid of *Woodbinesuchus* is more robust and massive than that of *Sunosuchus*. In *Woodbinesuchus*, the coracoid foramen is located farther below than that of *Sunosuchus* lying close to the scapular-coracoid suture. Compared with *Eutretauranosuchus*, *Goniopholis*, and *Dakotasuchus* having the cranial edge more strongly concave than the caudal edge, *Woodbinesuchus* has nearly straight cranial edge of the scapular blade.

The transition from short-snouted to long-snouted forms has been convergently evolved repeatedly within the Crocodylia (Langston, 1973). The modification shown in *Woodbinesuchus* reflects an adaptive specialization in feeding behavior. The elongation of the snout suggests a specialization for ichthyophagy in *Woodbinesuchus*, which is also indicated by the absence of undulation of the jaw margins (Iordansky, 1973). The symphysis in longirostrine crocodylians was known to incorporate the splenial to a considerable degree for strengthening the front end of the jaw (Langston, 1973), but not true in *Woodbinesuchus* and *Sunosuchus*. Compared with *Vectisuchus* having a shorter symphysis, the inclusion of the splenial into the symphysis is less extensive in *Woodbinesuchus* and *Sunosuchus*, which is unexpected in such long-snouted forms. Therefore, it does not seem that the inclusion of the splenial into the symphysis is related to the length of the symphysis.

The Woodbine nodosaurid is different from more derived nodosaurid taxa, *Edmontonia* and *Panoplosaurus* in having premaxillary teeth. The absence of premaxillary teeth is regarded as an apomorphy in nodosaurid phylogeny (Coombs and Maryanska, 1990; Lee, 1996). They are known in three primitive genera, *Pawpawsaurus*, *Sauropelta*, and *Silvisaurus*. Premaxillary teeth of the Woodbine nodosaurid are, however, distinguished from these in lacking of marginal denticles. The humerus has no demarcation between the humeral head and the deltopectoral crest, and is quite flat with little shaft twist. The fibular shaft is uniquely straight without curvature departing from typical of ankylosaurian fibulae. In all of these features, these Woodbine nodosaurid remains strongly imply a new taxon, but taxonomic conclusions based on these isolated teeth and two limb bones would be premature.

Hadrosaurids are not uncommon in Campanian and Maastriichtian terrestrial sediments of Laurasia, but earlier hadrosaurid remains are extremely rare in the world. Except for a tooth from the Cenomanian Cambridge Greensand of England (Lydekker, 1888; Unwin, 1991), the earliest well preserved hadrosaurids were described from Asia, including *Gilmoresaurus* and *Bactrosaurus* from the Iren Dabasu Formation of China (Gilmore, 1933; Brett-Surman, 1979). Meanwhile, in North America, the oldest hadrosaurids are described from the late Coniacian through late Santonian of Mississippi (Kaye and Russell, 1973; Carpenter, 1982). Therefore, the Woodbine hadrosaurids described here represent the oldest hadrosaurids east of the Western Interior Seaway. China has been suggested as the place of origin for hadrosaurids (Rozhdestvenskiy, 1966). However, along with these Woodbine hadrosaurids, the recent discovery of hadrosaurid skeletons in the Cedar Mountain Formation (?Albian), Utah, (Kirkland, 1994) and a hadrosaurid femur from Cenoma-

nian sediments in Honduras, Central America (Horne, 1994) indicates that by the Cenomanian, hadrosaurids were present in North America, but possibly not in Asia because the Iren Dabasu Formation is now regarded as early Senonian (Currie and Eberth, 1993).

In Texas, hypsilophodontids and *Tenontosaurus*, and a larger but as yet undetermined ornithomimid known in the Trinity Group (Aptian-middle early Albian) were replaced by Cenomanian hadrosaurids in the Woodbine Formation (Lee, 1995). It does appear likely that the origin of the hadrosaur family is constrained to the interval about the Albian-Cenomanian boundary—that is, in the transition from Early to Late Cretaceous. Although the oldest occurrence does not necessarily proscribe the center of hadrosaur origin, the geographic distribution of Aptian through Cenomanian large ornithomimids does not exclude a center of origin for hadrosaurids in North America.

ACKNOWLEDGMENTS

Without the cooperation of fossil enthusiasts sharing their discoveries in the Woodbine Formation in Dallas-Fort Worth metropolis, this paper would never have been completed. I thank J. Byers, G. Byrd, G. and D. Eckland, E. and N. Emborsky, J. Maurice, B. McCormick, J. Moody, C. and S. Wadleigh, and R. and S. Zack. I wish particularly to thank J. Maurice. He has long been my good collaborator in the investigation of Woodbine fossils. Thanks are also due to J. M. Clark and X.-C. Wu for kindly providing me with useful comments and their papers. I am deeply indebted to L. L. Jacobs and D. A. Winkler from the beginning of this project to reviewing the manuscript. Acknowledgment is made to the Donors of the Petroleum Research Fund, administered by the American Chemical Society, to NSF Grant EAR 9206692, to the Dinosaur Society, and to the Saurus Institute for partial support of this research. Additional support was provided by the Graduate Student Assembly, Southern Methodist University.

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