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OSTEOLOGY OF A COMPLETE SKELETON OF *DIPOIDES STIRTONI* (RODENTIA, CASTORIDAE) FROM THE LATE MIOCENE OF NORTHERN OREGON

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ABSTRACT

The most complete skeleton of the small castorid, *Dipoides stirtoni*, was collected from late Miocene (early Hemphillian North American Land Mammal Age) deposits in northern Oregon. The specimen is spectacularly preserved, even including sesamoids; missing only the distal portion of the tail, which was eroded prior to discovery. The individual was found in a crouched position and appears to have been preserved in a burrow. The articulated skeleton exhibits incisors with rounded enamel faces, parastriae/parastriids on P^4/P_4, and elongate hind limbs, particularly the rear feet. The transverse processes of the caudal vertebrae are expanded laterally, but not so much as those of extant *Castor canadensis*. The proportions of the forelimbs are unlike those of *C. canadensis*, and could be interpreted as indicating that the Miocene beaver had a greater capability for burrowing. Overall, *D. stirtoni* appears to have been adapted for a swimming lifestyle, although perhaps not quite to the degree as that of *C. canadensis.*

INTRODUCTION

The castorid skeleton, University of Washington, Burke Museum (UWBM) 59242, was collected in 1978 by the first author from south of the town of Arlington in Gilliam County, northern Oregon (Figure 1). The site of discovery was designated as the Big Cut Locality, and at the time of discovery of the skeleton, was a deep set of intersecting trenches (Figure 2) dug for geological analyses for a proposed nuclear power plant. Martin was admitted into the site where he found and extracted, among other specimens, UWBM 59242, which was found from near the top of the trenches in late Miocene riparian sediments. Soon after, the proposed nuclear power was abandoned, the Big Cut was backfilled, and the locality is now inaccessible.

Vertebrate fossils were recovered from various stratigraphic units with the trenches, including an articulated skeleton of a small horse that exhibits dental pathology and retains fossilized costal cartilages, as well as a large saber-toothed cat skull, among others. The beaver was found high in the section at the Big Cut and later taken to the Burke Museum at the University of Washington, Seattle, where it was expertly prepared by Ms. Beverly Witte and found to be a nearly complete skeleton, even the sesamoids were preserved. The dentition exhibits the typical occlusal S-pattern characteristic of *Dipoides* (Shotwell, 1955) and is slightly worn, representing that of a young adult. Both the upper and lower fourth premolars exhibit parastriae/ids. This character coupled with moderate overall size led to the assignment of the skeleton to *Dipoides stirtoni*. The posterior end of the skeleton was found eroding from a brown siltstone that resembles floodplain deposits. When the articulated nature of the specimen was discovered, the specimen was removed in a large block of matrix. Upon preparation, the beaver was found in a crouched position with its forelimbs folded beneath and hugged to the chest. The rear legs were folded parallel to the body. Overall, the configuration indicates the skeleton was preserved in life position, most likely crouched in a burrow. In order to maintain the articulation of this unique specimen, not all osteological elements could completely exposed during preparation. As a consequence, measurements (in mm) of every element were not possible (Table 1).

One of the principal goals of the study was to interpret the functional morphology of the fossil beaver. Therefore, the skeletal morphology of the castorid was compared to that of the muskrat, *Ondatra*, a rodent adapted for swimming, and to that of the gopher, *Thomomys*, a fossorial rodent. In addition, the skeleton of the fossil beaver was compared to that of *Castor*, its closest living relative.

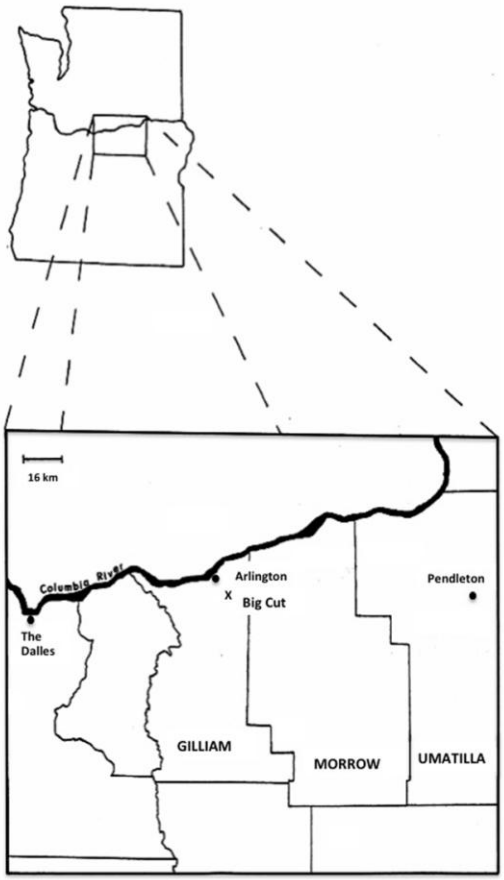

FIGURE 1. Location in northern Oregon of the discovery of the skeleton of *Dipoides stirtoni* (UWBM 59242).

GEOLOGICAL SETTING

In addition to the Big Cut, other trenches were open in 1978 that were also part of the power plant investigation. These trenches, coupled with the intersecting trenches of the Big Cut, and naturally occurring exposures, provided the basis for assembling the overall local geological section; in this area south of Arlington, the late Miocene section is relatively complete. In the Big Cut area, the Pomona Basalt was identified during investigations for the power plant (Dames & Moore, 1985) and appears to underlie the section in the Big Cut area. For comparison, in central Washington, the Rattlesnake Ridge Member of the Ellensburg Formation overlies the Pomona Basalt and has produced fossils characteristic of the late Clarendonian North American Land Mammal Age (Martin and Pugnac, 2009). At the base of the lithostratigraphic section in the Big Cut area, late Clarendonian fossils have been described (Fry, 1973) from tuffaceous fluvial deposits. The beaver skeleton came from a level (uppermost unit of Figure 3) normally covered with vegetation but was well exposed in the intersecting trenches of the Big Cut. This interval within the Big Cut contained tuffaceous sediments, including basalt conglomerates, as well as blue-gray sandstones with high pumice content, claystone, and siltstone. From this succession (Figure 3), early Hemphillian fossils were derived, including the beaver skeleton, a machairodont skull, and small hipparionine skeleton. The assemblage and overall lithology here greatly resembles that of the Wilbur Locality in central Washington (Martin and Mallory, 2011). This depositional succession illustrated in Figure 3 is capped by a widespread caliche that formed after the top of the interval had been scoured.

The units above unconformity delineated by the thick caliche vary from riparian deposits to slackwater deposits of the Missoula Flood. The riparian sediments are composed of ferruginous basalt gravel interbedded with reddish claystones and tan siltstone and fine-grained sandstone. This uppermost riparian interval in the Big Cut area was named the Shutler Formation, in part (Hodge, 1938), and more recently, the Alkali Canyon Formation (Farooqui et al., 1981). Late Hemphillian vertebrates have been described from this interval above the unconformity in the Arlington area (Martin, 1984, 1998, 2008).

Therefore, three vertebrate fossil-producing intervals occur in the area of the Big Cut: late Clarendonian (Fry, 1973), early Hemphillian (this contribution), and late Hemphillian assemblages (Martin, 1984, 1998, 2008). These levels have all been considered part of the Alkali Canyon Formation of the Dalles Group (Farooqui et al., 1981), although further analysis that lies beyond the scope of this contribution may result in stratigraphic revision.

The castorid skeleton was found in a brown tuffaceous siltstone that occurs near the top of the early Hemphillian section exposed in the trenches at the Big Cut. Figure 3 represents the section that was exposed in the deep, intersecting trenches, and because this section is no longer exposed, diagrams and photos are included of these trenches (Figures 2 and 3). The location of the castorid skeleton is indicated on Figures 2 and 3.

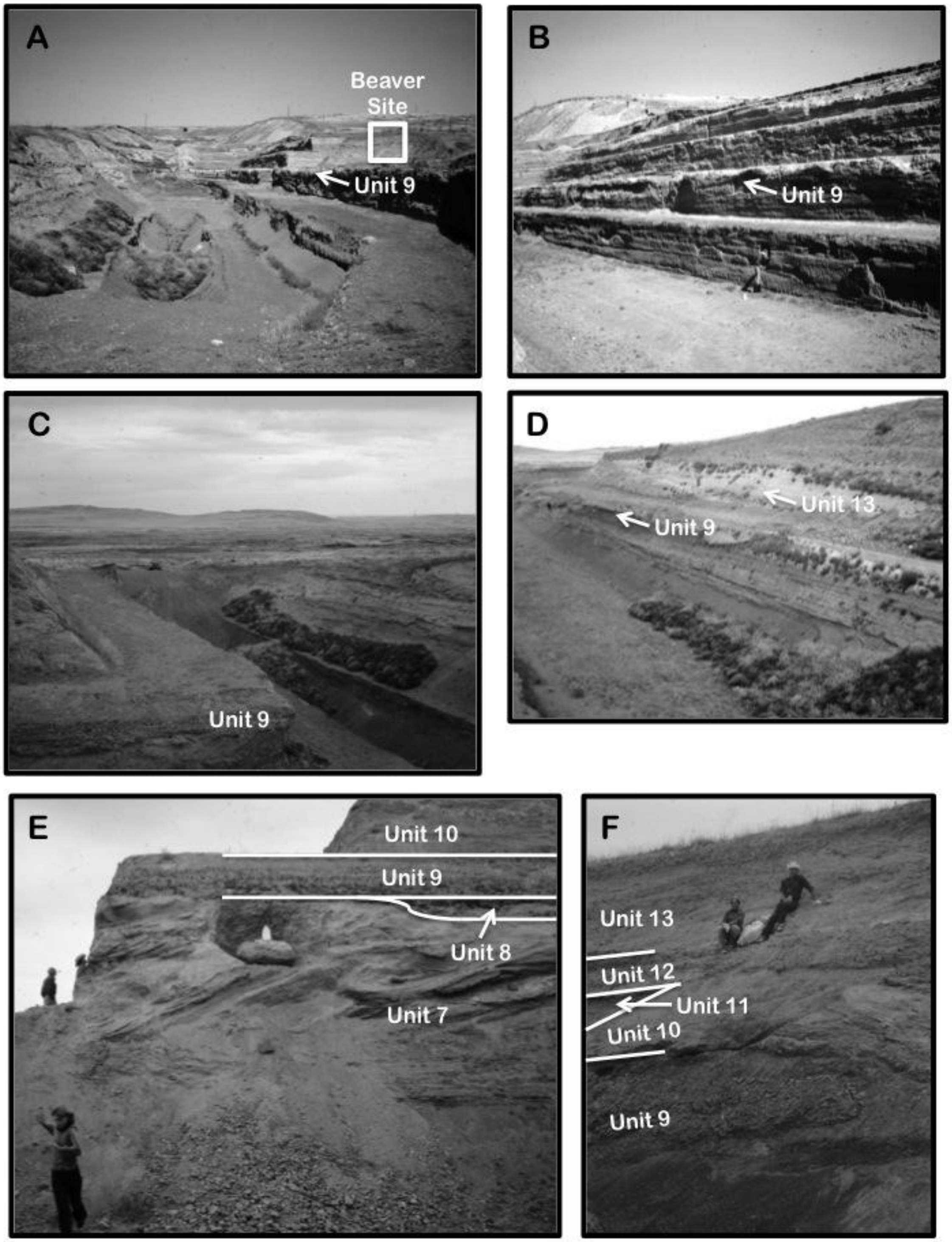

FIGURE 2. Photographs of the Big Cut Locality, intersecting trenches excavated for geological studies for a proposed nuclear power plant, 1978. A=view to the north; box indicates site of UWBM 59242, B=view to the north of east side of trench, C=view to the south, D=view to the south of the west side of trench, E=view to the west of the northwestern corner of trench intersection, the occurrence of a small horse skeleton, F=site of discovery of UWBM 59242. Stratigraphic units are described on Figure 3.

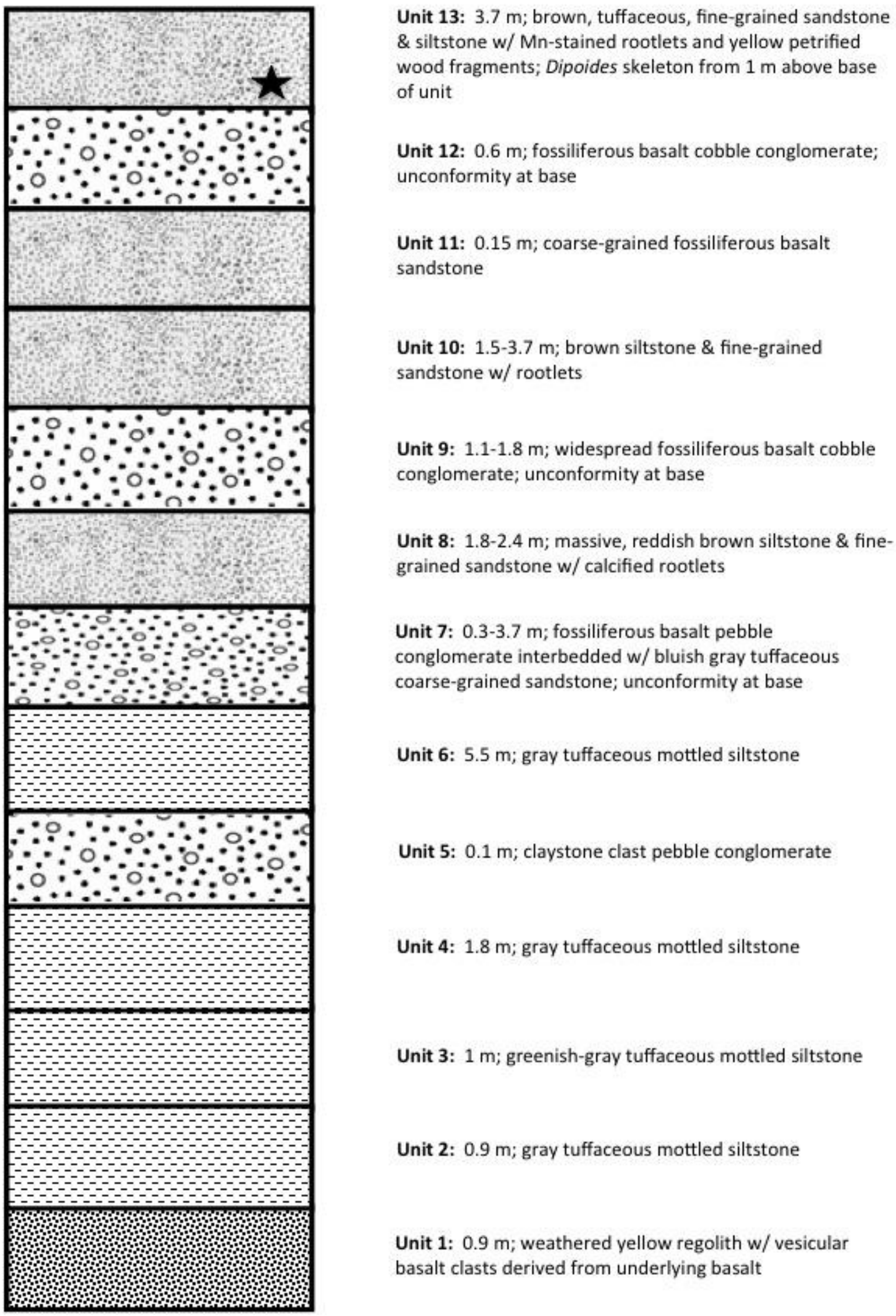

FIGURE 3. Geological section of the intersecting trenches in the Big Cut area. Star indicates position of UWBM 59242.

SYSTEMATIC PALEONTOLOGY
Class Mammalia Linnaeus, 1758
Order Rodentia Bowditch, 1821
Family Castoridae Gray, 1821
Dipoides stritoni Wilson, 1934

Dipoides was originally described in Europe (Jaeger, 1835) and several species are known from North America, including *D. tanneri* from the late Clarendonian NALMA, *D. stirtoni* and *D. williamsi* from the early Hemphillian NALMA, *D. wilsoni*, *D. smithi*, and *D. vallicula* from the late Hemphillian NALMA, *D. intermedius* and *D. rexroadensis* are very large species retaining plesiomorphic characters from the Blancan NALMA, and *D. stovalli* from the Irvingtonian NALMA (See Martin, 2008, for additional information). *D. wilsoni* was recorded from the highest levels in the Arlington/Big Cut vicinity (Martin, 2008). *D. wilsoni*, *D. williamsi*, and *D. vallicula* are small species, whereas *D. stirtoni* and *D. smithi* are larger, of the same relative size as the specimen described herein. *D. stirtoni* is distinguished from *D. smithi* by the more common possession of a parastria/id on P^4/P_4 (Shotwell, 1955), which is exhibited by UWBM 59242.

Referred Specimen—UWBM 59242, skeleton (Figure 4) from the Big Cut Locality, south of Arlington in Gilliam County, Oregon.

DESCRIPTION

The beaver skeleton is complete with the exception of the distal end of the tail (Figure 4). The preservation is exquisite, uncrushed except the cranium, and preserves details of all bones and teeth. The individual appears to represent a sub-adult, because epiphyseal ends of many bones are not fused; the dentition exhibits permanent fourth premolars, and the teeth exhibit mild occlusal wear.

Cranium—Dorsally, the cranium (Figure 5A) is broad and flat (Table 1) with a relatively short, wide, rectangular rostrum. The nasals flare anteriorly from a convex suture with the frontals. The premaxillae possess an anterior projection, but are otherwise small and rhomboid. They share a sutures with the nasals dorsally and the maxillae posteriorly. The zygomatic process of the maxilla is triangular and projects laterally. From the dorsal perspective, the zygomatic arch thins and flares distally until it turns back medially to join the squamosal perpendicularly. The frontals are flat and triangular. Dorsally, they are expanded anterolaterally where they have a flat suture against the maxillae, thin distally almost to a point, and suture against the parietals. The result is that the frontals appear to invade the parietal table. The parietals are large, rounded in the braincase area, and expand distally where they abut against the supraorbitals. The external auditory meatus is a long projection oriented anterodorsally.

Ventrally, little of the cranium is visible (Figure 5B,C). The entire skull is slightly distorted obliquely to the right side, and the medial palatine suture is displaced about 0.5 mm to the right, causing slight compression and upheaval, whereas the left side is relatively undeformed. From the ventral aspect, the premaxillae are long, wider anteriorly, and exhibit a midline ridge. On either side of the ridge are deep concavities that become flattened laterally. The anterior portion of the premaxillae are expanded laterally at the incisors and taper slightly medially where they join the maxillae. Little of the maxillae are visible ventrally, but are slightly expanded posteriorly to accommodate the tooth row. The process for the masseter superficialis is triangular and robust. Palatine exposure ventrally is limited to slightly anterior to the last molar to in line with the posterior of the tooth row.

Dentary—The long right dentary (Table 1, Figure 6A,B) was removed from articulation in order to observe the dental anatomy and facilitated description of the dentary. Overall, the dentary is angulate but not to the degree of that of extant *Castor canadensis.* The dentary below the diastema is long and robust, sweeping upward to house the long, protruding incisor. A long symphysis lies along the medial aspect that extends beyond the ramus ventrally, resulting in the angulate structure of the jaw. The ramus is horizontal but thins below the tooth row posteriorly and flares laterally and ventrally in a large angular process. The coronoid process of the ascending ramus is short and wide, with the anterior edge angled less steeply at 65 degrees than the posterior margin at 80 degrees, resulting in a process that is slanted posteriorly and 80 degrees labially before the process tapers to a point. A deep fossa occurs lingual to the coronoid process. The broken articular process appears robust with a large condylar surface. A large, triangular masseteric scar extends along the lateral side of the dentary. Most foramina of the dentary, like those of the cranium, are obscured.

Dentition—The upper incisors are rounded labially with worn/broken tips. The occlusal surfaces of the upper incisors are notched, owing to occlusion with the lower incisors. Relatively smooth, thin enamel covers the anterolabial third of the tooth; the posterior two-thirds is comprised of dentine. The long upper tooth row (Table 1, Figure 5C)) flares posteriorly. The lower tooth row (Table 1, Figure 6B) appears oriented at three degrees away from the midline of the symphysis and tilted labially five degrees from vertical.

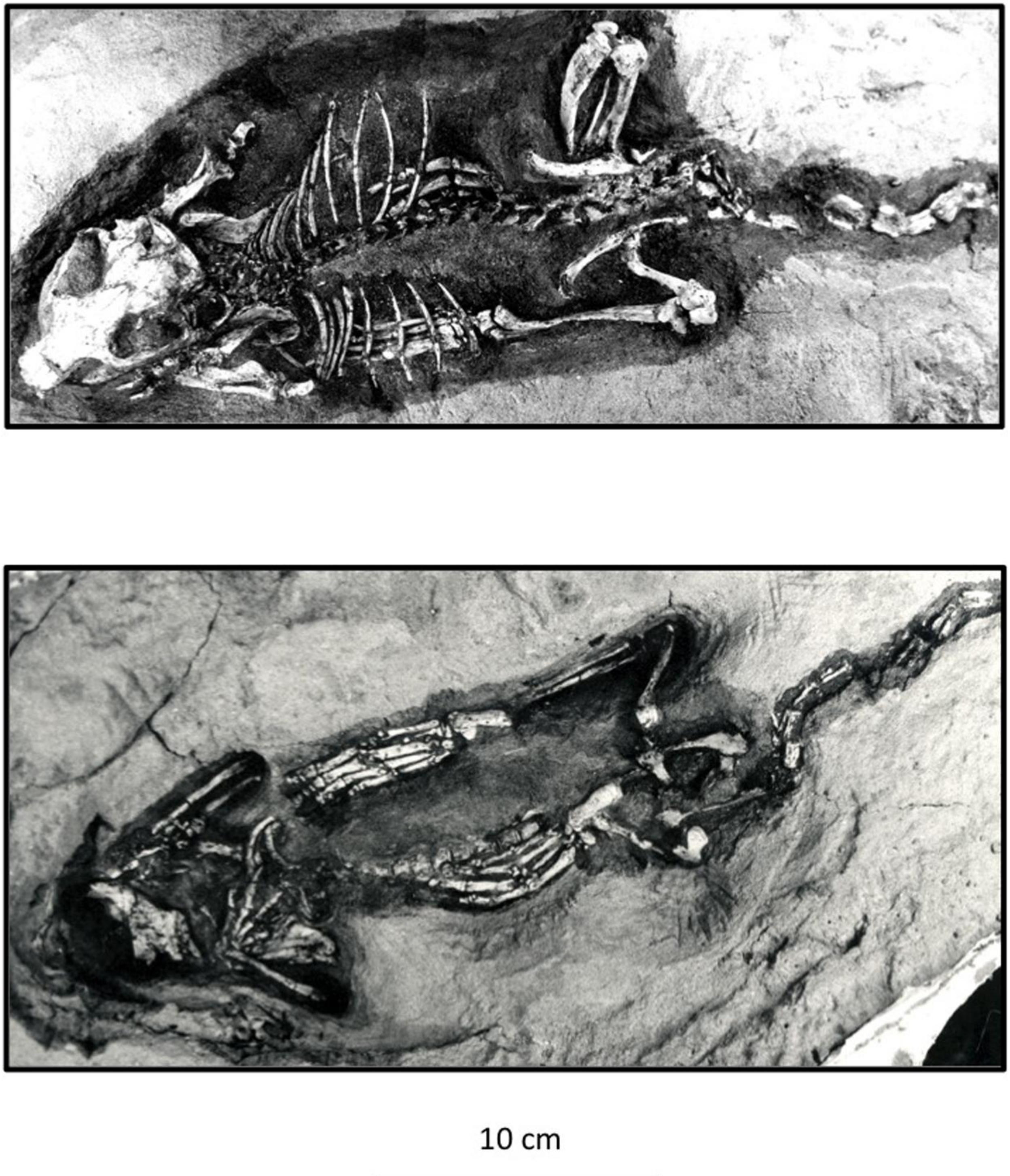

FIGURE 4. UWBM 59242, *Dipoides stirtoni* dorsal and ventral views.

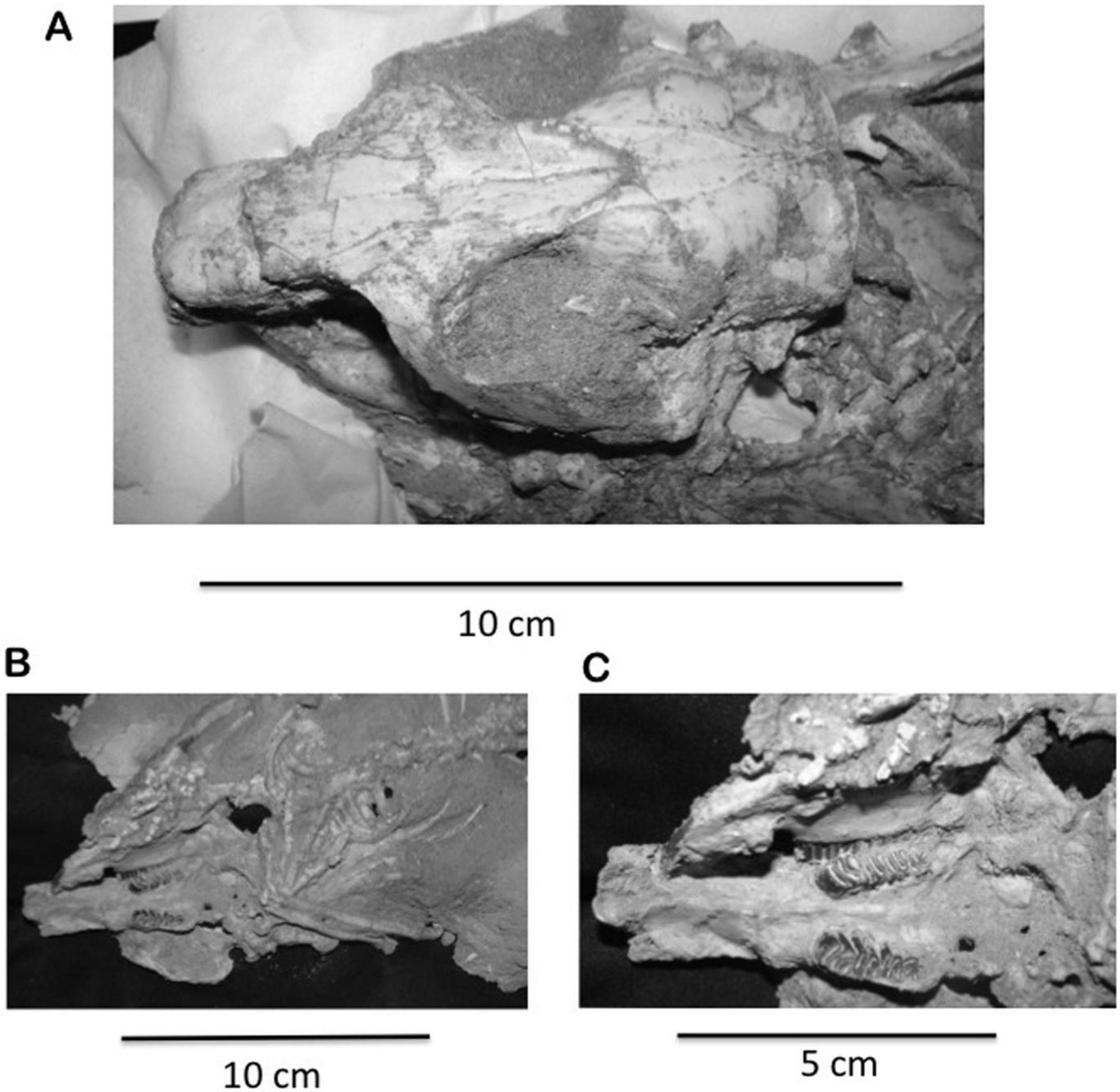

FIGURE 5. Close-up photographs of the skull of UWBM 59242, *Dipoides stirtoni*; anterior is to the left on all photographs. A= dorsal view of cranium, B= ventral view of anterior portion of skeleton, C=ventral view of skull.

The large P^4 (Table 1) is molariform and exhibits an overall "S" occlusal pattern. The anterior loph is uniformly wide from the rounded lingual end to the crescentic labial end. An isthmus divides the paraflexus from the mesostria and prevents the anterior and medial lophs from fusing. The paraflexus is closed labially, crescentic, and uniformly wide until it flares on the lingual side. The parastria extends down the entire exposed length of the tooth crown. The mesostria on the labial margin is shallow but also extends the exposed length of the tooth. The hypoflexus is uniformly wide, curves posteriorly across the occlusal surface, and ends in a squared extremity. The hypostria is long and extends down the exposed tooth crown. The resultant lophs separated by cementum form the S-shape occlusal pattern with an extra labial projection resulting from division of the medial loph by invasion of the mesostria. The medial loph parallels the anterior loph for much of its length until curving sharply posteriorly on the lingual side.

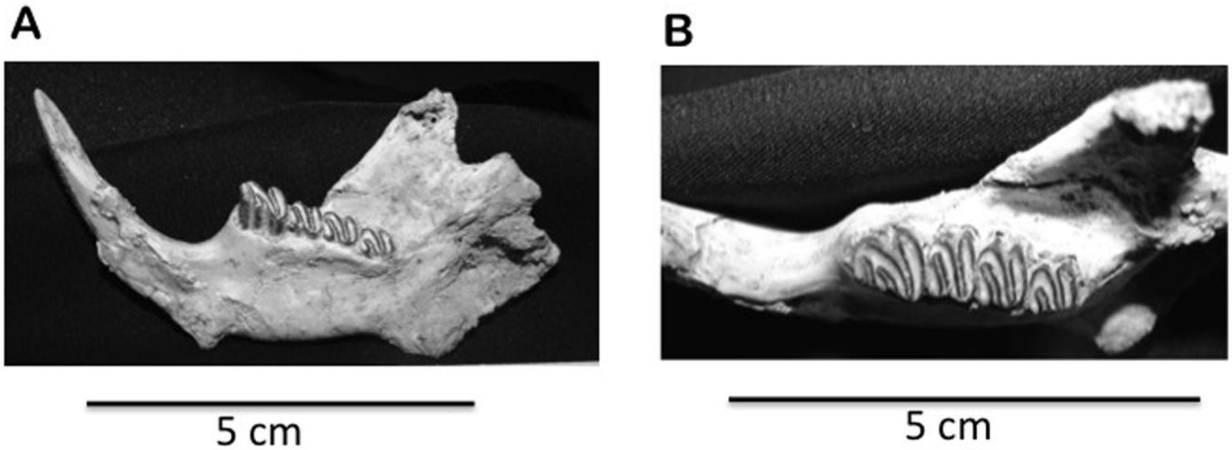

FIGURE 6. Close-up photographs of the dentary of UWBM 59242, *Dipoides stirtoni*; anterior is to the left on both photographs. A=medial view of right dentary, B=dorsal view of right dentary.

The posterior loph is bulbous to tear-shaped in outline and rounded off labially.

The upper molars have the distinctive S-shaped occlusal pattern of *Dipoides*, and become smaller distally. The anterior loph is tear-shaped and rounded off lingually. The medial loph is obliquely oriented, whereas the posterior loph is bulbous, wider labially, tapers sharply lingually, and lies perpendicular to the anteroposterior axis of the tooth row. The rounded paraflexus is slightly curved and slightly wider at its closed labial extremity. The hypoflexus is closed lingually and relatively uniform in width along its entire length. Both the parastria and hypostria extend the length of the exposed tooth crown.

The large P_4 (Table 1, Figure 6B) is somewhat molariform, but not to the extent of the P^4. The overall occlusal shape appears as an elongate “S” with an extra anterior lophid. Therefore, four lophids occur: the anterior three are obliquely oriented, whereas the posterior lophid is aligned more perpendicular to the anteroposterior axis of the tooth row. The paraflexid is narrow, curves anteriorly from 45 to 70 degrees from the tooth midline, extends nearly to the opposite margin of the premolar, terminates with a squared end, and essentially isolates the anterior lophid. Importantly, the parastriid extends down the entire exposed crown length as do the mesostriid and hypostriid. The second lophid is similar in shape to the first, but not well isolated. The mesoflexid is long, of uniform width, has a rounded distal end, and is oriented anterolabially at 75 degrees from the anteroposterior tooth row axis. The hypoflexid is the longest of the flexids, widely open at its origin, and slanting posteriorly to a rounded end. Very small fossettids attesting to the relative youth of the individual were observed at the lingual end of the anterior lophid, just below the paraflexid in the middle of the second lophid, and at the lingual end of the medial lophid.

The lower molars are smaller than the premolar (Table 1, Figure 6B) and exhibit the classic occlusal S-shape. The anterior lophids are tear-shaped and rounded off at their lingual ends. The medial lophid is long, expanded labially, and tapers at the lingual end. This lophid is straighter on M_1 but becomes more crescentic on successive molars. The posterior lophid is uniformly wide and very straight on M_1, becoming successively more curved and wider on distal molars. The paraflexids are narrow, relatively uniformly wide, and rounded at their distal ends; however, they curve anteriorly and cross less of the occlusal surface distally; that of M_3 is very short and more rounded. The hypoflexid is also uniformly wide, crescentic, and rounded distally. Both the parastriid and hypostriid extend down the entire exposed tooth crown, and the hypostriids cross nearly the entire occlusal surface. The parastriids curve anteriorly and cross less of the occlusal surface distally; that of M_3 crosses only half of the occlusal width.

Cervical Vertebrae—The cervical vertebrae are not visible from the ventral aspect, and only partially exposed dorsally (Figure 7A-D). The atlas is barely visible but appears to be the largest cervical and is very much like that of *Castor*. The first cervical is large, robust, lacks a neural spine, and exhibits short massive transverse processes unlike the long posterodorsally sweeping processes of *Castor*.

The axis of UWBM 59242 is more similar to that of *Castor* and much different than that of the muskrat, *Ondatra*. The robust axis of UWBM 59242 has a rectangular neural spine that projects vertically from the centrum but angles posteriorly at approximately 45 degrees, similar to that of *Castor*. The transverse

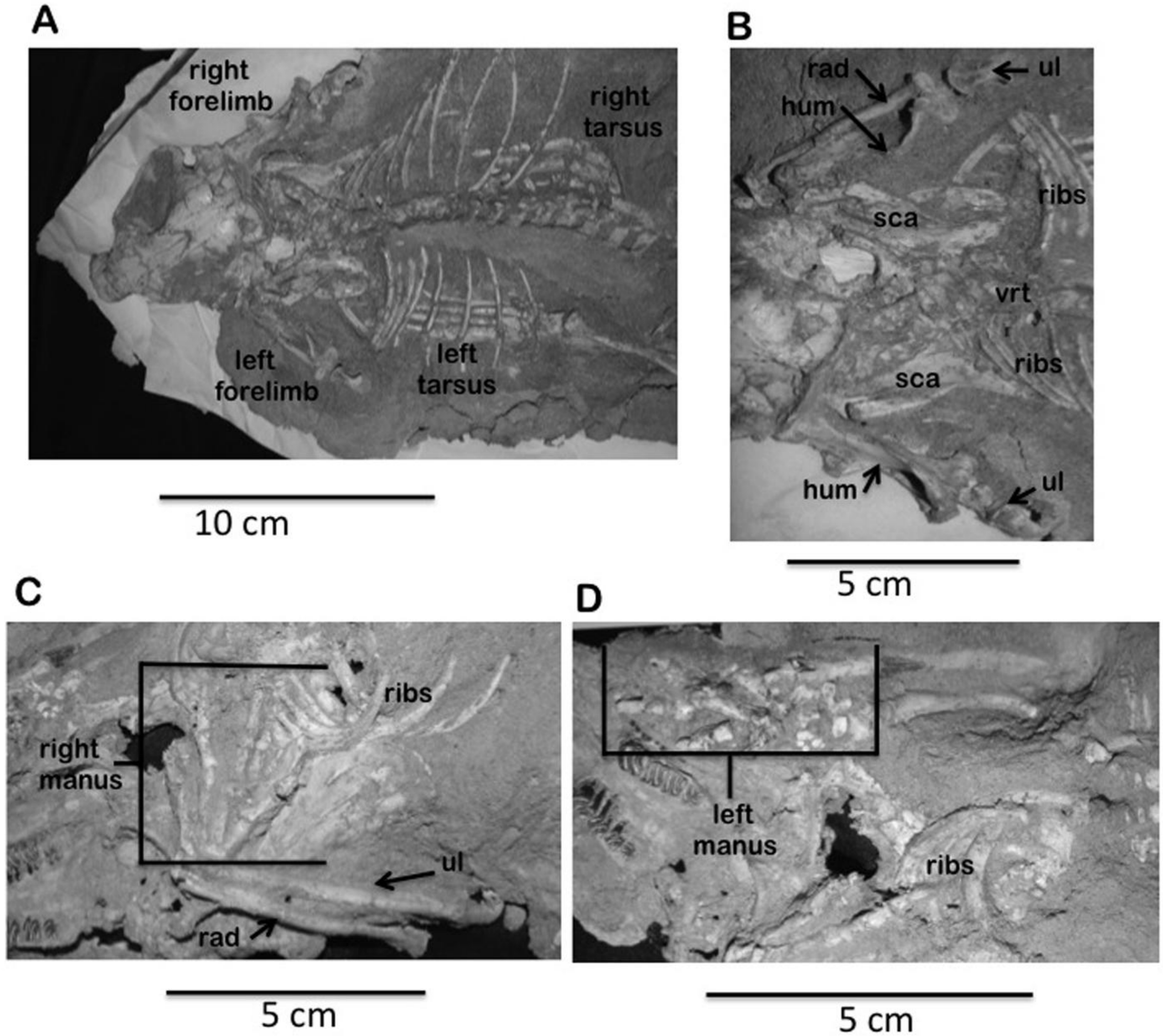

FIGURE 7. Close-up photographs of UWBM 59242, *Dipoides stirtoni*; anterior is to the left on all photographs. A=dorsal view of anterior portion of skeleton, B=dorsal view of cervical area of skeleton, C=ventral view illustrating right forelimb, D=ventral view illustrating left forefoot. Abbreviations for Figures 7-12: cal=calcaneum, fem=femur, hum=humerus, in=innominate, rad=radius, sca=scapula, tfib=tibiofibula, ul=ulna, vrt=vertebrae.

processes are short, robust, narrow, and squared at their extremities, unlike the large, wing-shaped anterodorsally directed processes of *Castor*. The axis differs significantly from that of *Ondatra*, which possesses no neural spine and abbreviated transverse processes.

The posterior cervical vertebrae of UWBM 59242 have relict neural spines, a small protuberance at the dorsal midline of each vertebra, more similar to those of the geomyid, *Thomomys*, a fossorial rodent and unlike those of *Castor* or *Ondatra*, whose vertebrae lack neural spines. The superior articular process of UWBM 59242 is short, rectangular, and oriented slightly posterodorsally. The transverse processes are not visible.

Thoracic Vertebrae—The thoracic vertebrae of UWBM 59242 appear relatively uniform in size and shape posteriorly along the vertebral column (Table 1, Figure 8A,B). However, the large but short, heavily built, rectangular, neural spines are oriented slightly anteriorly and become more robust posteriorly. The transverse processes of thoracic vertebrae of UWBM 59242 are large, rectangular, and sweep posteriorly. Comparatively, the thoracic vertebrae of *Castor* have long, slender, pointed neural spines that are oriented posteriorly, similar to those of *Thomomys*, which are slightly shorter. *Ondatra* possesses no neural spines on its thoracic vertebrae. The transverse processes of *Castor* are long, robust and perpendicular to the centrum, unlike the abbreviated processes of *Ondatra*. Overall, the thoracic vertebrae of UWBM 59242 most closely resemble those of *Thomomys*, and are more dissimilar with those of *Castor* and *Ondatra.*

TABLE 1. Measurements in mm of skeleton of *Dipoides stirtoni* (UWBM 59242).

Element	Length	Width	Proximal Width	Distal Width
Cranium	10.2	6.2		
Right Dentary	6.5			
Upper Tooth Row	22.0			
Lower Tooth Row	23.0			
P^4	7.4	6.2		
P_4	7.8	6.3		
M_1	5.5	5.8		
M_2	5.4	5.6		
M_3	5.1	4.5		
Thoracic Series	57.9			
Lumbar Series	47.4			
First Caudal Vertebra	17.1	15.7		
Last Preserved Caudal	17.2	12.0		
Scapula	51.5		21.4	14.95
Humerus	38.0			
Radius	54.0			
Metacarpal III	15.7			
Proximal Phalanx, Digit III	8.2			
Medial Phalanx, Digit III	5.9			
Innominate	83.0			
Ilium	45.5	14.7		
Femur	55.8		17.3	15.9
Tibiofibula	81.0		19.9	6.4
Calcaneum	27.6		8.8	8.5
Astragalus	12.7	9.0		
Metatarsal III	27.3			
Proximal Phalanx, Digit III	18.8			

Lumbar Vertebrae—The lumbar vertebrae of UWBM 59242 are similar in size and shape along the vertebral column (Table 1, Figure 8A, B), although many features are obscured by matrix. The neural spines are tall, very robust, wide, rectangular, and oriented slightly anteriorly; the transverse processes are short. The lumbar vertebrae of *Castor* possess neural spines that are slightly shorter than those of UWBM 59242, that are robust and square, but not as wide as those of UWBM 59242. The neural spines of *Ondatra* are very short, as are those of *Thomomys*, particularly compared to those of UWBM 59242. The transverse processes of *Ondatra* are very short, shorter than those of UWBM 59242, whereas those of *Thomomys* and *Castor* are long.

Caudal Vertebrae—The tail vertebrae of UWBM 59242 (Figure 9A-C) exhibit dorsoventrally flattened hexagonal centra that taper distally and distinct epiphyseal sutures. Two pronounced ridges extend the length of the ventral portion of the vertebrae, becoming more pronounced distally. The transverse processes range from large, wing-like projections with rounded extremities on the anterior vertebrae to shorter, robust processes that extend the length of distal vertebrae (Table 1). Interspersed among the caudal vertebrae are rectangular sesamoids.

Comparatively, the caudal vertebrae of *Ondatra* and *Thomomys* are rounded, unlike the dorsoventrally flattened caudal vertebrae of *Castor* and UWBM 59242. The caudal vertebrae of *Castor* are dosoventrally compressed and exhibit very large, wing-like transverse processes. Those caudal vertebrae of UWBM 59242 are also flattened but have shorter transverse processes, resulting in a flattened tail that is half as broad as that of extant *Castor*, and decidedly unlike that of the rounded tails of *Ondatra* or *Thomomys.*

Scapula—On UWBM 59242, the scapula is barely visible from the ventral aspect, but well exposed dorsally (Figure 7A,B, 10A). The blade is overall ovate (Table 1) similar to the shape of *Castor*, and unlike the triangular scapulae of *Ondatra* and *Thomomys*. The scapular spine of UWBM 59242 is very long, but not as straight as those of *Ondatra* and *Thomomys*, and the acromion process is large, robust, and rectangular unlike the shorter acromion process of *Ondatra* and *Thomomys* that are almost equal in length to the coracoid processes; both processes fold over slightly laterally in UWBM 59242. The coracoid process of UWBM 59242 and *Castor* is large (unlike the shorter coracoid process of *Ondatra*), rectangular, and slightly cupped. The proximal articulation of UWBM 59242 is on the lateral edge but faces medially. Overall, the rounded scapulae of UWBM 59242 resemble those of *Castor*, much more closely than the triangular scapulae of *Ondatra* and *Thomomys*. The rounded scapula indicates the ability for a "reaching" movement (Hildebrand, 1995), suggesting that *Castor* and UWBM 59242 utilized their front limbs for grasping and reaching for manipulation, indicating similar lifestyle and locomotion.

Humerus—The relatively short, robust humerus (Table 1, Figure 7A,B, 10A) of UWBM 59242 is poorly exposed from the ventral aspect. Dorsally, the humerus possesses a large, rounded head similar to that of *Castor*. The deltoid process is large and triangular (length=9.7mm; width=5.2 mm) on UWBM 59242, *Castor*, and *Thomomys*, unlike the more rounded process of *Ondatra*. A large, expanded, supinator crest (length=21.4 mm; width=8 mm) lies at the distal end

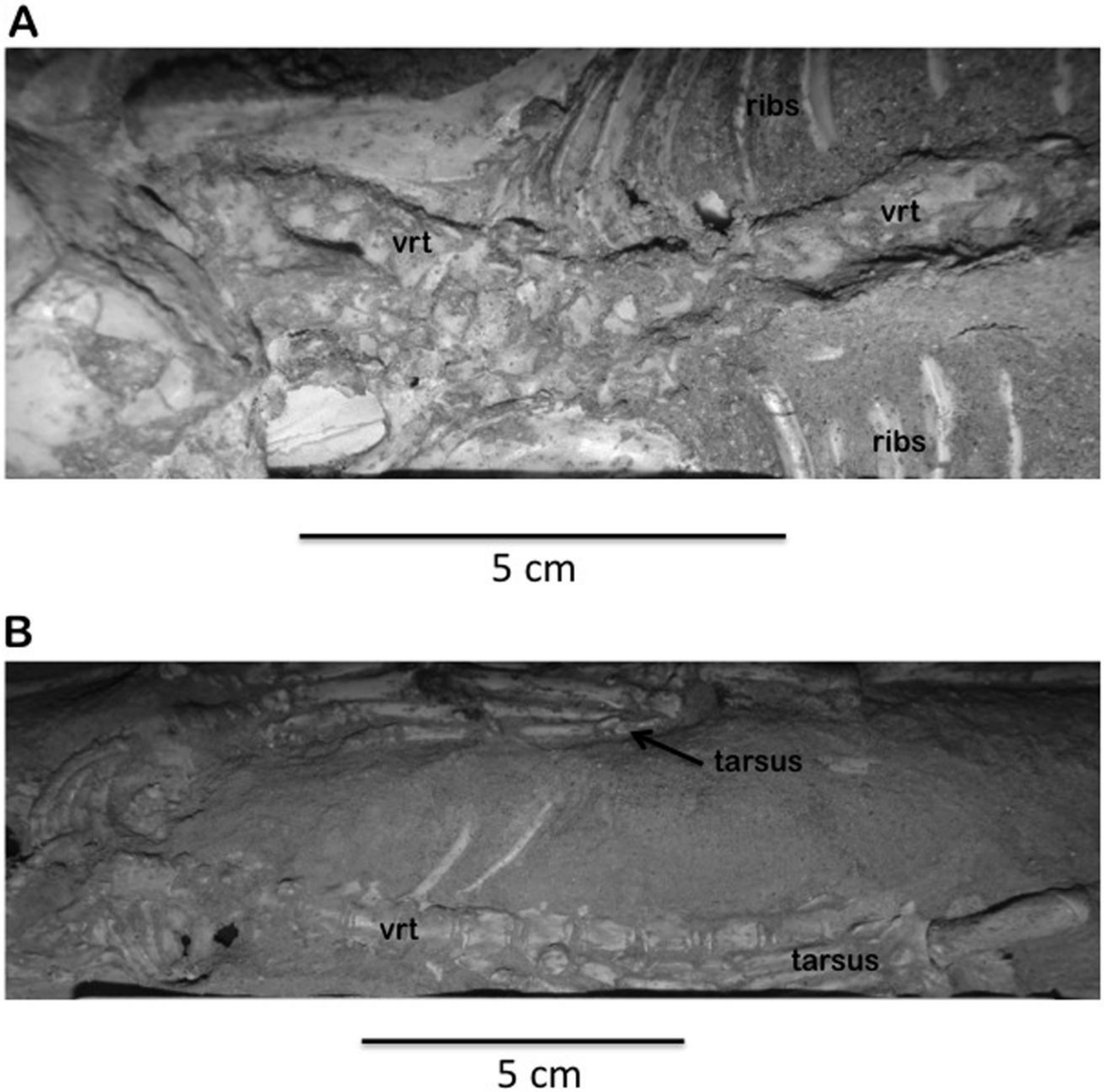

FIGURE 8. Close-up photographs of the vertebral column of UWBM 59242, *Dipoides stirtoni*; anterior is to the left on both photographs. A=dorsal view of thoracic region of skeleton, B=dorsal view of lumbar region of skeleton. See Figure 7 for abbreviations.

like the humeri of *Castor* and *Thomomys* and unlike the more abbreviated crest of *Ondatra*. The olecranon fossa is shallow and ovate on UWBM 59242, *Castor*, and *Thomomys*; that of *Ondatra* is deep. The distal articulation of UWBM 59242 is laterally expanded and medially truncated. Lateral edges of the articular surface are slanted diagonally outward, so the front limbs would have been held close to the body. Overall, the morphology of the humerus of UWBM 59242 most closely resembles that of *Castor* except in its smaller size. Both exhibit large supinator crests and shallow olecranon fossae that suggest extensive supination and pronation, indicating extensive movement for great manipulation of objects.

Radius—The radius of UWBM 59242 is short and robust (Table 1, Figure 7A, B, 10A), closely appressed to the ulna, and forms the lower portion of the semilunar notch. The proximal head is ovate (length =5 mm; width=7 mm), broad, flat, and slightly concave similar to that of *Thomomys*. The distal styloid processes of UWBM 59242 and *Thomomys* are large and rounded. *Castor* and *Ondatra* have a styloid

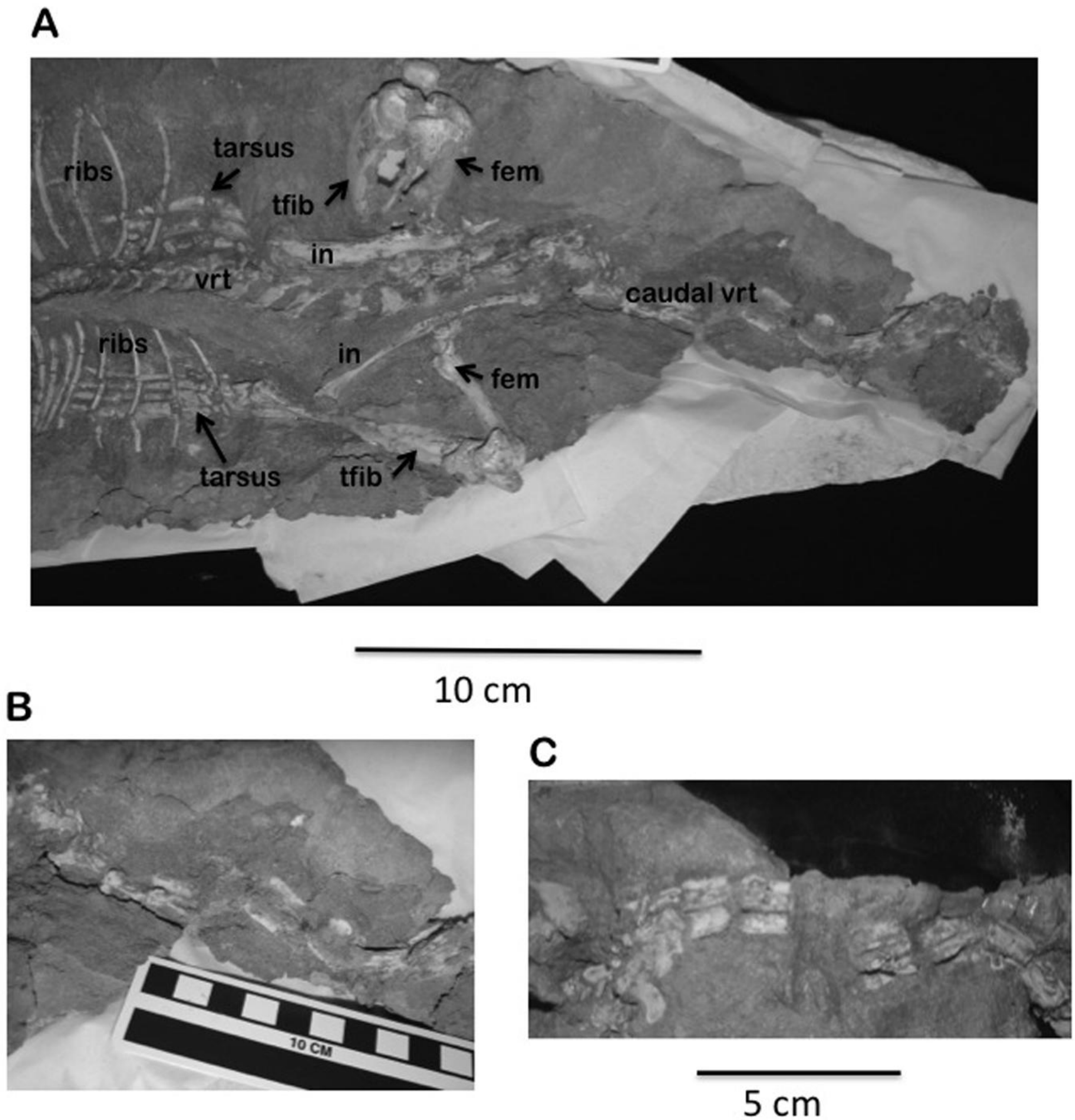

FIGURE 9. Close-up photographs of the caudal vertebrae of UWBM 59242, *Dipoides stirtoni*; anterior is to the left on all photographs. A=dorsal view of posterior skeleton, B=dorsal view of caudal vertebrae, C=ventral view of caudal vertebrae. See Figure 7 for abbreviations.

process that is rounded ventrally with a higher extended projection dorsally; *Ondatra* has a longer projection than *Castor*. Therefore, the radius of UWBM 59242 most closely resembles that of *Thomomys*.

Ulna—The ulna of UWBM 59242 is a robust, relatively straight bone (Figure 7C). Proximally, the olecranon processes of UWBM 59242 (length=9.7 mm; width=6.8 mm) and *Thomomys* are greatly expanded with the end of the process forming a shelf that extends medially. *Castor* and *Ondatra* both have an olecranon process that is expanded but only curves slightly medially. The ulna of UWBM 59242 appears to be missing an articular facet on the lateral bottom surface of the semilunar notch or is greatly reduced and flattened as in *Thomomys*. *Ondatra* and *Castor* have similar articular facets, but are not as reduced as that of UWBM 59242. The shape of the semilunar notch of

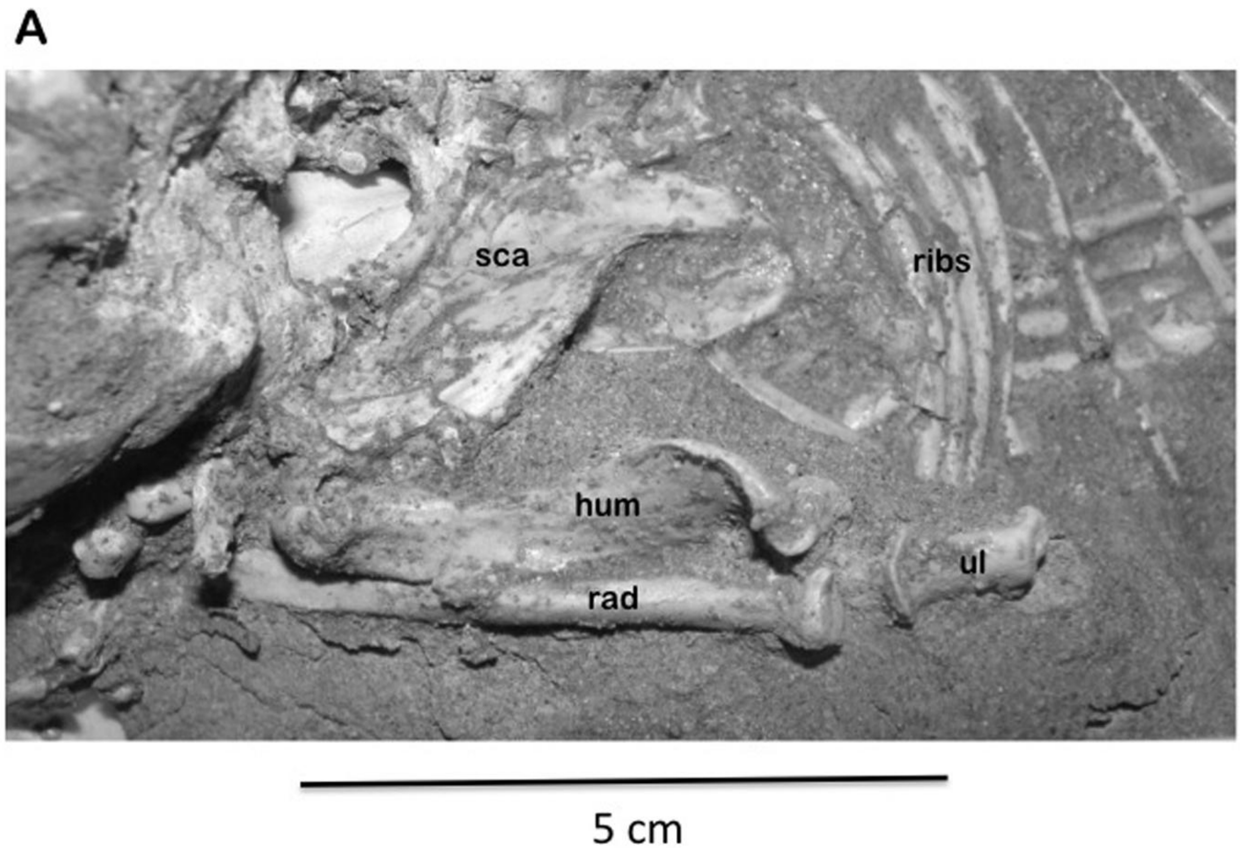

FIGURE 10. Close-up photographs of the forelimb area of UWBM 59242, *Dipoides stirtoni*; anterior is to the left on photograph. A=dorsal view of forelimb area. See Figure 7 for abbreviations.

UWBM 59242 (width 7.9 mm; height= 8.4 mm) and *Thomomys* is semicircular and deep. In *Castor* and *Ondatra*, the fossa is more shallow and a more crescentic. UWBM 59242 and *Thomomys* have a relatively straight ulnar shaft with just slight dorsal curvature. Both *Castor* and *Ondatra* have a curved shaft that hooks dorsally. The ulnar groove of UWBM 59242 is obscured by matrix. Overall, the ulna and radius of UWBM 59242 most closely resembles that of *Thomomys*, perhaps suggesting some burrowing movement of the forelimbs.

Carpals—Some carpals of UWBM 59242 are only visible from the ventral aspect (Figure 7C). The scaphoid is somewhat kidney-shaped and flat with a slight convexity on the ventral surface. The scaphoid may be one-third the size of the distal radius. The lunar appears to be the largest carpal of UWBM 59242, although this is probably owing to greater exposure of this carpal. The scaphoid and lunar are not fused, and the lunar has an "L" shape with both extremities somewhat expanded and bulbous. The cuneiform is somewhat triangular, very robust, and has a slightly concave proximal articulation. The unciform is somewhat saddle shaped, with a deeply concave distal articulation. The remainder of the carpals are obscured by matrix.

Distal Manus—The metacarpals of UWBM 59242 are long (Table 1, Figure 7C), slender, and more expanded proximally than distally. The proximal ends are compressed laterally to create a wedge ventrally. The dorsal sides are flattened, expanded, and somewhat bulbous. The ventral side exhibits laterally expanded sides and a raised medial ridge. The dorsal metacarpal is acutely angled and flattened distally. The phalanges of UWBM 59242 become progressively shorter distally (Table 1). Their proximal ends are expanded both laterally and dorsoventrally, triangular to rhombic with a concave articulation. The distal end is expanded and somewhat bulbous with two lateral ridges. Two circular concave depressions occur on the lateral sides of the phalanges. The proximal ends of the unguals are identical to those of the phalanges; the distal end would support a claw. The distal end is comprised of ventral and dorsal triangular projections forming a long, flattened claw with a rounded extremity. The claws of the manus appear to comprise two-thirds of the length

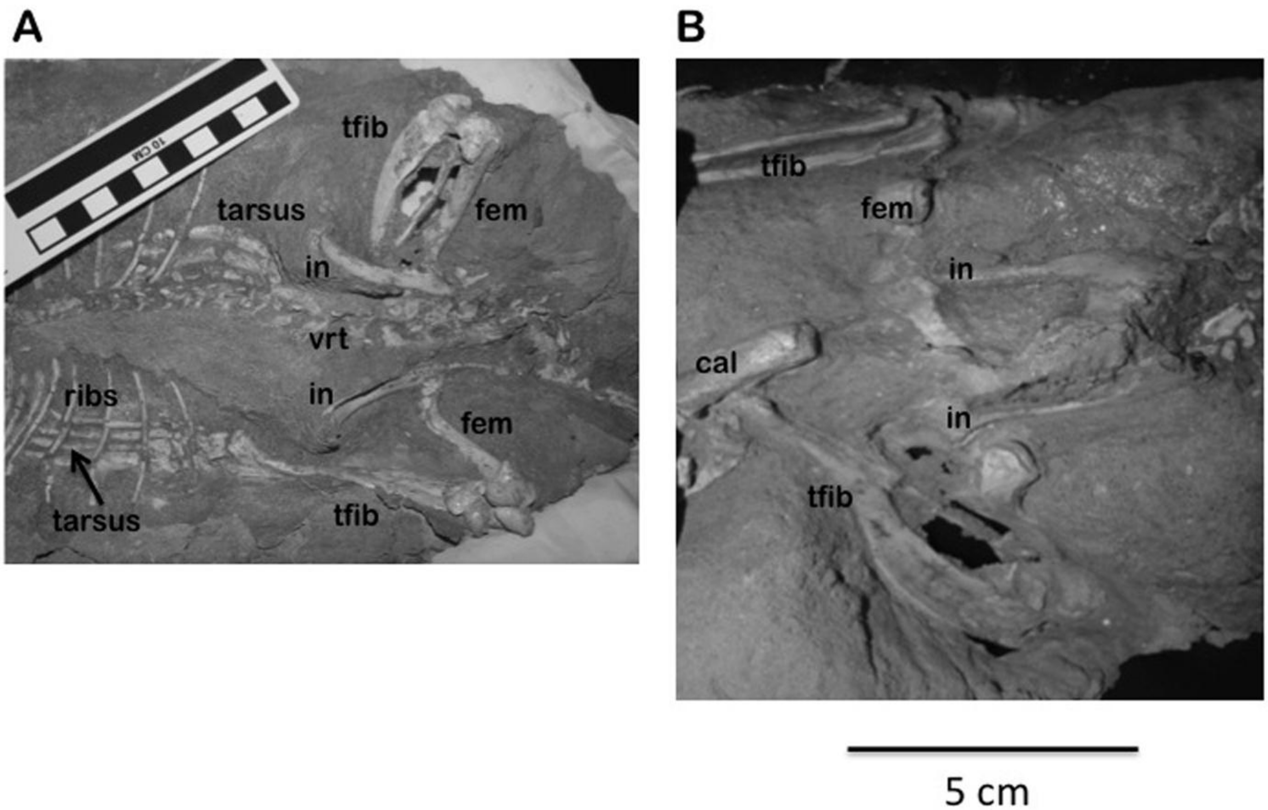

FIGURE 11. Close-up photographs of the pelvic area of UWBM 59242, *Dipoides stirtoni*; anterior is to the left on both photographs. A=dorsal view of pelvic area, B=ventral view of pelvic area. See Figure 7 for abbreviations.

of the unguals, which are proportionally longer than the claws of the pes. The manus of *Castor*, *Ondatra*, and UWBM 59242 has long metacarpals and phalanges with sharp unguals. The manus of *Thomomys* is very small with short phalanges. Overall, the manus most closely resembles that of *Castor*, with heavy, thick, blunt claws; the unguals of *Ondatra* are much more laterally compressed.

Pelvis—The ventral pubis of UWBM 59242 (Figure 11A,B) is broken, distorted, and displaced. The obturator foramen is almond-shaped unlike the large, ovate foramen of *Castor* and *Ondatra*. The ilium is long (Table 1), rectangular, robust, and hooked slightly laterally. The pubis and ischium are not clearly visible, but the pubic symphysis is long in UWBM 59242, *Castor*, and *Ondatra*, unlike the short narrow symphysis of *Thomomys*. The pelvis of UWBM 59242 most closely resembles that of *Castor* in having a long, robust ilium, a triangular ischium, a ventrolaterally directed acetabulum, and a long pubic symphysis. The pelvis of *Ondatra* is much less robust, the ischium is more crescentic, and the ilium is narrow. The pelvis of *Thomomys* is very lightly built with the acetabulum directed more laterally.

Femur—The femur of UWBM 59242 (Figure 11A) is a large, robust, straight element (Table 1). The head is round, has a long neck (much longer than that of *Thomomys*), and exhibits a very large, expanded greater trochanter that gently tapers at the extremities and extends higher than the femoral head. This trochanter appears even higher than that of *Castor*, which it most closely resembles, and is higher than that of *Ondatra*, which is lower than the femoral head, and that of *Thomomys*, which is only slightly higher than the femoral head. The lesser trochanter of UWBM 59242 is very pronounced, wedge-shaped, and extends dorsally nearly 90 degrees, returning ventrally to the shaft from 75 to 80 degrees. The lesser trochanter exhibits a very pronounced muscle scar. The gluteal tuberosity is large (but no so much as that of *Castor*), rounded, and triangular and extends from the base of the greater trochanteric neck to near the middle of the shaft. The distal end of the femur of UWBM 59242 is greatly expanded and very robust like those of *Castor* and *Ondatra*, but unlike the narrow distal femur of *Thomomys*. The epicondyles of UWBM 59242 are expanded slightly more than the condyles, particularly the medial epicondyle that is even larger and more

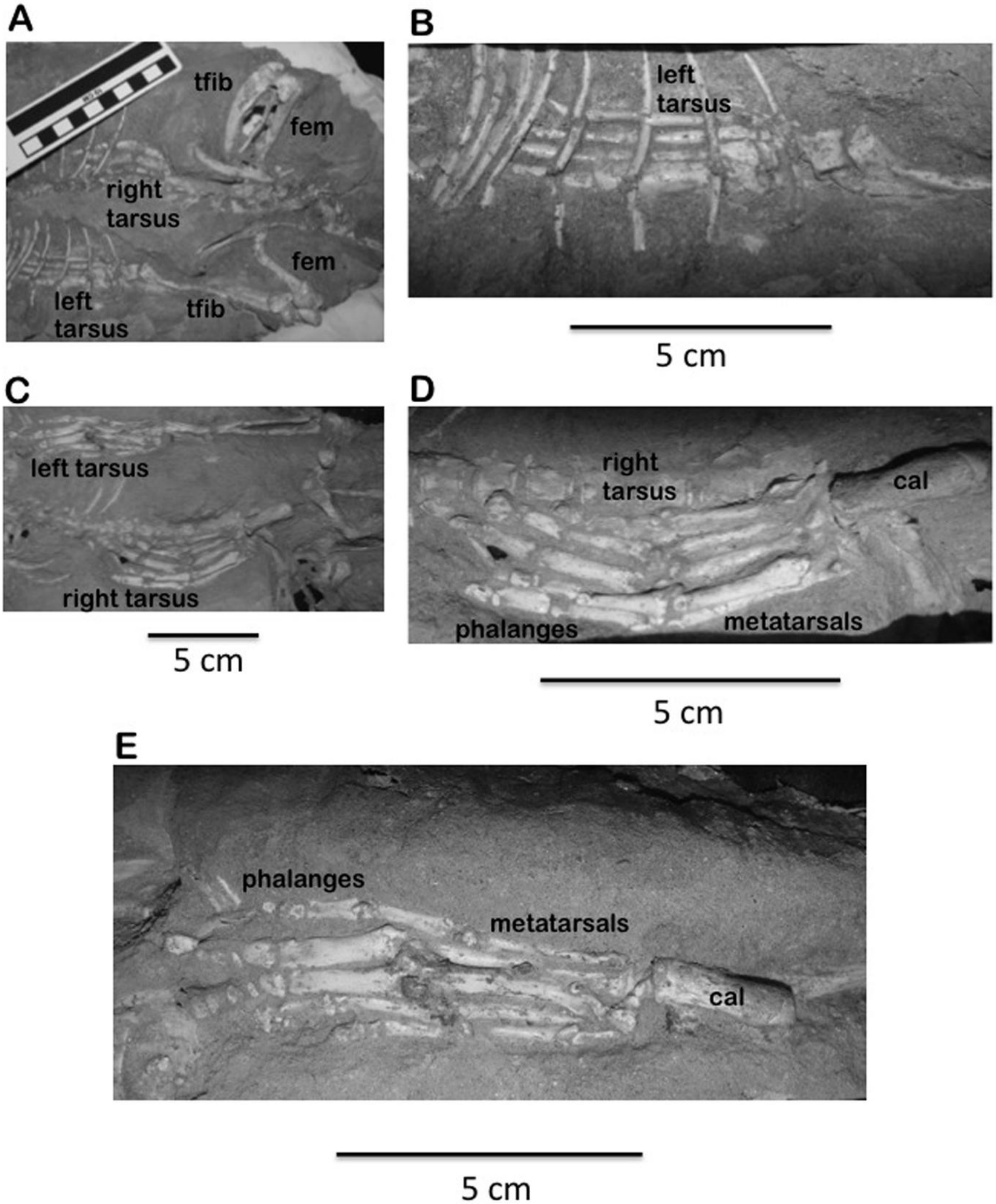

FIGURE 12. Close-up photographs of the rear limbs and feet of UWBM 59242, *Dipoides stirtoni*; anterior is to the left on all photographs. A=dorsal view of hind limbs, B=dorsal view of left rear foot, C=ventral view of hind limbs, D=ventral view of right rear foot, E=ventral view of left rear foot. See Figure 7 for abbreviations.

expanded than that of *Castor*. The patellar groove of UWBM 59242 is large, wide, and shallow. The medial side of the distal end is greatly expanded. Overall, the femur of UWBM 59242 most closely resembles that of *Castor*, particularly the long femoral neck, height of the greater trochanter (height=10.3 mm), and proportions of the epicondyles.

Tibiofibula—The tibiofibula of UWBM 59242 (Figure 11A,B) is 1.5 times longer (Table 1) than the femur. These bones are fused (34.5 mm) along the distal half of the element, like those of *Ondatra* and *Thomomys*, but unlike the condition of *Castor* whose tibia and fibula remain unfused. The anterior portion of the tibia of UWBM 59242 is greatly expanded and exhibits a shallow recess across the anterior face of the element. This excavation originates on the lateral side just below the tibial head and extends the length of the unfused portion of tibia and terminates where fusion with the fibula occurs at midshaft. The fibular portion is much less robust than the tibial. The fibular head is expanded and forms a distally curved hook similar but less hooked than that of *Castor*. The head ascends into a rounded point and descends into a greatly rounded, flattened hook on the interior side of the fibula. Overall, with the obvious exception of the distal fusion, the tibiofibula of UWBM 59242 resembles that of *Castor* more than that of *Ondatra* and *Thomomys.*

Tarsals—Only the ventral side of the calcaneum of UWBM 59242 is exposed, but the element is very long (Table 1), narrow medially, robust, and rectangular with a slightly rounded and rectangular distal end (Figure 12D,E). The proximal articulation surface is angled at 35 degrees. The internal side possesses a rounded lip that extends posteriorly as part of the proximal articulation surface. Overall, the proportions of the calcaneum of UWBM 59242 resemble most closely those of *Castor*, although its proximal neck is slightly shorter. The proportions are dissimilar compared to those of *Ondatra* and *Thomomys* whose astragalar articulation is more distally positioned.

The astragalus (Figure 12B) and navicular of UWBM 59242 resembles that of *Castor*, although smaller (Table 1). The proximal trochlear articulation of the astragalus is expanded at both ends, truncated medially, and concave. Between the equal-sized trochlea is a deep fossa for ligamental attachment, which is absent in *Ondatra* and *Thomomys.* The latter genus is also unlike UWBM 59242 because of its unequal-sized trochlea.

The large, robust cuboid of UWBM 59242 exhibits a deep peroneal groove, extending diagonally from the distal medial corner to the proximal lateral corner. The groove is wider on the lateral face. The proximal articular surface is partially obscured, but its surface appears bilobate and flattened.

The ectocuneiform is triangular with rounded corners; the proximal end is more expanded than and tapers slightly to the distal end. Other tarsals are obscured by matrix.

Distal Tarsus—The metatarsals and phalanges (Figure 12A-E) are very long, slender, and twice the length of those of the carpus (Table 1). The extremely long distal tarsus is striking and indicates the importance of the rear foot in locomotion. The distal ends of the metatarsals appear rhomboidal to rectangular with oval depressions on the lateral sides of the head. The dorsal articulation of the distal extremity of the metatarsals appears somewhat flattened. The phalanges are twice as wide proximally as distally. The distal extremity is characterized by circular depressions on either side, and the distal articular surface is saddle-shaped. The unguals of the pes are similar to those of the manus but are more robust, dorsoventrally flattened, relatively shorter, and rectangular. The proximal articular ungual surface is rounded to rhombic and concave with two teardrop-shaped foramina at the lateral edges dorsal to the midline. Overall, the pes of UWBM 59242 most closely resembles that of *Castor* and also resembles that of *Ondatra* in having long, slender metatarsals; those of *Thomomys* are short. However, the unguals of *Ondatra* are laterally compressed, unlike those of *Castor* and UWBM 59242, which are robust and flattened dorsoventrally.

DISCUSSION

UWBM 59242 possesses the size and molar structure of *Dipoides*, and the occurrence of a parastria(id) on the premolars suggests assignment to *Dipoides stirtoni*. This skeleton of *D. stirtoni* represents the most complete skeleton thus far known of *Dipoides*, and reveals important structures that indicate the habits of this beaver. For example, the rounded incisors are unlike those of the flat, chisel-shaped incisors of fossorial rodents. Overall, the *Dipoides* skeleton most closely resembles that of extant *Castor canadensis*, adapted to a semi-aquatic lifestyle; however, important differences occur. In addition to differences in the dentitions, the fused tibiofibula of UWBM 59242 and other specimens of *Dipoides* is in distinct contrast to the unfused tibia and fibula of *C. canadensis.* Even so, the overall morphology of UWBM 59242 most closely resembles that of the aquatically adapted living beaver particularly in the cranium, elongate rear foot, and somewhat flattened tail and exhibits significant differences between the semi-aquatic muskrat (*Ondatra*) and the fossorial gopher (*Thomomys*).

Although many postcranial elements of UWBM 59242 are obscured by matrix remaining to support the articulation of the skeleton, exposed features of the postcranial skeleton reveal important structures indicative of habit. The vertebral series is similar to that of *Castor*, but the atlas-axis does not possess the long posteriorly sweeping transverse processes of the extant beaver. The posterior cervical vertebrae retain rudimentary neural spines unlike *Castor.* The thoracic series has more robust neural spines that are oriented somewhat anteriorly, unlike the long, slender, posteriorly directed neural spines of *Castor*. The lumbar series is long, and the neural spines of the lumbar vertebrae are longer on UWBM 59242 than *Castor*. The sacral vertebrae are obscured, but the caudal vertebrae are dorsoventally flattened like those of *Castor* but have shorter transverse processes. The result is a flattened tail that is half as broad as that of extant *Castor*, and decidedly unlike that of the rounded tails of *Ondatra* or *Thomomys.*

The front limb of UWBM 59242 exemplifies important characteristics indicative of lifestyle. The scapula of UWBM 59242 is rounded like that of *Castor* and unlike the triangular scapulae of *Thomomys* and *Ondatra.* The rounded scapular outline indicates a "reaching"ability. The humerus of UWBM 59242 is similar but smaller than that of *Castor*. Both humeri exhibit large deltoid and supinator crests and shallow olecranon fossae that suggest extensive supination and pronation. As a result, dexterity for manipulation is indicated, in distinct difference to either *Ondatra* or *Thomomys.* The radius and ulna of UWBM 59242 resemble those of *Thomomys* more than those of *Ondatra* or *Castor.* The shape of the semilunar notch of UWBM 59242 and *Thomomys* is semicircular and deep unlike the shallow, crescentic notch of *Castor* and *Ondatra*. The ulnar shaft of UWBM 59242 and *Thomomys* is relatively straight, unlike the dorsally curved shaft of *Castor* and *Ondatra.* Therefore, *Dipoides stirtoni* may have also had some fossorial ability, and the occurrence of UWBM 59242 in a burrow supports this contention. However, the manus most closely resembles that of *Castor*, with heavy, thick, blunt unguals unlike the laterally compressed unguals of *Ondatra* and *Thomomys.*

The pelvis and rear limb of UWBM 59242 are also most similar to those of *Castor*. Both pelves have a long, robust ilium, a triangular ischium, a ventrolaterally directed acetabulum, and a long pubic symphysis; that of *Ondatra* is overall more delicate with a more crescentic ischium and narrow ilium. The pelvis of *Thomomys* is even more delicately constructed with the acetabulum directed more laterally. The femura of UWBM 59242 and *Castor* share a long femoral neck, high greater trochanter, and very wide distal articulation. This articulation in *Thomomys* is particularly narrow. Except for the obvious distally fused tibiofibula, the overall structure of the lower leg is similar between UWBM 59242 and *Castor.* The tarsus of UWBM 59242 is also similar to that of *Castor*, especially the very long dorsal calcaneal process, elongate metatarsals and phalanges, and flattened unguals.

Overall, the morphology of *Dipoides stirtoni* as exemplified by UWBM 59242 indicates that *Dipoides* was adapted for semi-aquatic habitat, similar to that of the extant beaver. The postcranial skeleton of UWBM 59242 exhibits characters that indicate a well-developed ability for swimming. Only the less widely flattened tail is a significant difference between the two beavers in their semi-aquatic mode of existence. Certainly, the well-adapted morphology begs the question as to the extinction of this North American castorid lineage.

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LITERATURE CITED

Dames & Moore, Inc., unpublished report. 1985. Geology of the Arlington Nuclear Power Facility. Number 7722-035 (November 15).

Farooqui, S. M., J. D. Beaulieu, R. C., Bunker, D. E., Stensland, and R. E., Thoms. 1981. Dalles Group; Neogene formations overlying the Columbia River Basalt Group in north-central Oregon. Oregon Geology 43(10):131-140.

Fry, W. F. 1973. Fossil giant tortoise of the genus *Geochelone* from the late Miocene-early Pliocene of north-central Oregon. Northwest Science 47(4):239:249.

Hildebrand, M. 1995. Analysis of Vertebrate Structure. John Wiley Publications, New York.

Hodge, E. T. 1938. Geology of the lower Columbia River. Geological Society of America, Bulletin 49:831-930.

Jaeger, G. F. 1835. Uber die Fossilen Säugethiere, welche in Wurhemberg geunden worden sinc. 1^c Abth., p. 17-18.

Martin, J. E. 1984. A Survey of Tertiary Species of *Perognathus*, and a description of a new genus of Heteromyinae. Papers in Vertebrate Paleontology Honoring Robert Warren Wilson. Carnegie Museum Natural History, Special Publication 9:90-121.

Martin, J. E. 1998. A new species of chipmunk, *Eutamias malloryi*, and a new genus (*Parapaenemarmota*) of Ground Squirrel from Hemphillian deposits in northern Oregon. In J. E. Martin, (ed.), Stratigraphy and Paleontology of the West Coast. In Honor of V. Standish Mallory. Thomas Burke Washington State Museum, University of Washington, Research Report 6:31-42.

Martin, J. E. 2008. Hemphillian rodents from northern Oregon and their biostratigraphic implications. Paludicola 6(4):155-190.

Martin, J. E. and D. C. Pagnac. 2009. A Vertebrate Assemblage from the Miocene Rattlesnake Ridge Member of the Ellensburg Formation of Central Washington. Museum Northern Arizona, Bulletin 65:197-216.

Martin, J. E. and V. S. Mallory. 2011. Vertebrate Paleontology of the Late Miocene (Hemphillian) Wilbur Locality of Central Washington. Paludicola 8(3):155-185.

Shotwell, J. A. 1955. Review of the Pliocene Beaver *Dipoides*. Journal of Paleontology 29:129-144.