New large leptictid insectivore from the Late Paleogene of South Dakota, USA

TJ MEEHAN and LARRY D. MARTIN

From a skull and mandible, we describe a new genus and species of a primitive insectivore (Mammalia: Insectivora: Leptictida: Leptictidae). Its large body size and higher-crowned teeth indicate a different feeding ecology from other leptictid insectivores. With evidence of some heavy, flat wear on the molariform teeth, its shift in diet was likely to greater herbivory. Unlike the narrow snout of Blacktops, this new leptictid retains a broad snout, suggesting that small vertebrates were still important dietary components. The specimen was collected from the floodplain deposits of the lower or middle White River Group of South Dakota, which represent the latest Eocene to earliest Oligocene (Chadronian and Orellan North American Land Mammal "Ages").

Key words: Mammalia, Leptictidae, *Leptictis*, *Megaleptictis*, Eocene, Oligocene, White River Group, South Dakota, North America.

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Introduction

Leptictida is a primitive order of placental, insectivorous mammals convergent to extant sengis or elephant "shrews" (Order Macroscelidea; Filhol 1892; Scott and Jepsen 1936; Koenigswald et al. 1988; Rose 1999, 2001, 2006). Sengis are mainly quadrupedal bounders and runners, but some hop bipedally at high speed (Nowak 1999); leptictids apparently had a similar range of locomotory modes (Rose 2006). *Leptictis dakotensis* from North America likely was a quadrupedal cursor with possibly some bipedal hopping (intermembral index of 61), while *Leptictidium* species of Europe had shorter forelimbs (intermembral indices of 45–48), so they were likely bipedal saltators when moving rapidly (modern bipedal saltating rodents have indices below 50; Christian 1999; Frey et al. 1993; Rose 2006). The relatively short forelimbs in both genera show adaptations for digging, a common behavior in terrestrial insectivores, and *Leptictis dakotensis* has been recovered from burrow-like structures (Rose 2006; Sundell 1997).

Leptictids have been reconstructed with elongated, mobile, cartilaginous snouts similar to sengis. This is a reasonable reconstruction, since the ends of leptictid bony rostra are somewhat blunt, and for probing leaf litter, a narrow snout is functionally important. Though not as large as in sengis, leptictids do have a slight to moderate fossa for the origin of the nasal and upper lip muscles—more similar in size to moles—at the root of the maxillary zygomatic arch and dorsal to the upper molariform teeth. A fossa in this region at least suggests increased snout mobility, but no definitive anatomical argument has been made to support a highly mobile cartilaginous snout tip, as in sengis. Also, leptictids lack the first upper incisor, and some sengis have evolutionarily lost one or two upper incisors, which may correlate with flicking the tongue to lap up ants and other food particles, similar to anteaters.

Though best known from North America, the fossil record of leptictids is Holarctic and ranges from the Early Cretaceous to the Early Oligocene; the oldest North American record comes from the latest Cretaceous (Simpson 1927; Lillegraven 1976; McKenna and Bell 1997). In the North American Paleogene, virtually all described specimens belong to one subfamily, Leptictinae (McKenna and Bell 1997). In the Paleocene, leptictid diversity is represented by up to five genera, and through the remaining Paleogene, it has been thought that diversity gradually decreased to one genus, *Leptictis*, by the earliest Oligocene (Orellan North American Land Mammal "Age"; McKenna and Bell 1997). *Leptictis* was somewhat common in the Orellan, but appears to have been rare in the next mammal age (Whitneyan NALMA), being known from a few late Early Oligocene sites in the upper White River Group of South Dakota and one in Saskatchewan, Canada (Gunnell et al. 2008). Presumably leptictids went extinct in North America during the Whitneyan, but their record in lower latitudes is poorly know. This report of a new leptictid and a recent report of a new genus (*Blacktops*) with two new species (Meehan and Martin 2010) are part of a series of papers on a

latest Eocene–earliest Oligocene (Chadronian and Orellan NALMAs, approximately 31–36 million years ago) radiation from the White River Group in the northern Great Plains of North America.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, New York, USA; ANSP, Academy of Natural Sciences Paleontology, Philadelphia, Pennsylvania, USA; F:AM, Frick Collection, American Museum of Natural History, New York, USA; KUVP, Kansas University Vertebrate Paleontology, Lawrence, USA; UNSM, Division of Vertebrate Paleontology, University of Nebraska State Museum, Lincoln, USA; TMM, Texas Memorial Museum, University of Texas, Austin, USA.

Other abbreviations.—NALMA, North American Land Mammal "Age".

Material and methods

Measurements were taken with Mitutoyo (Aurora, Illinois, USA) dial calipers to the nearest tenth or hundredth of a millimeter. Tooth length and width measurements are maximal. Some photographed specimen views were lightly whitened with a coating of latent fingerprint powder, which is principally titanium dioxide, lycopodium powder, and zinc stearate. Traditional premolar nomenclature of P1–P4 is used, as opposed to P1–2, P4–5 (McKenna 1975; Novacek 1986).

Systematic paleontology

Superorder Insectivora Illiger, 1811

Order Leptictida McKenna, 1975

Family Leptictidae Gill, 1872

Subfamily Leptictinae Gill, 1872

Genus *Megaleptictis* nov.

Type species: *Megaleptictis altidens* sp. nov., see below.

Etymology: *Mega* for its large size and *leptictis* for its similarity and likely affinity to *Leptictis*.

Diagnosis.—As for the type species.

Megaleptictis altidens sp. nov.
Figs. 1–5; Tables 1, 2.

Etymology: Though the teeth are not hypsodont, this species was named *altidens*, or tall tooth, for its much higher-crowned premolars and molars compared to other leptictids.

Holotype: KUVP 2568; a nearly complete skull and mandibles with right P3–M3, left P3–M3, right p3–m2, and left i2–m3. There are no other recognized specimens.

Type locality: South Dakota Locality 2 of Kansas University (KU-SD-002), Custer County.

Type horizon: This specimen was collected from the tan siltstone floodplain deposits of the White River Group in an 1894 Kansas University expedition. Based on other material collected with it, KUVP 2568 is

Table 1. Tooth measurements (in mm) of KUVP 2568, holotype of *Megaleptictis altidens* from the latest Eocene or Early Oligocene White River Group of South Dakota, USA. Abbreviations: H, height; L, length; W, width; ( ), estimate from little distorted or missing bone; [ ], cusps moderately worn; [[ ]], cusps heavily worn.

Left Upper Teeth		Left Lower Teeth	
L upper tooth row	(38)	L lower tooth row	(36.5)
L P4–M3	13.5	L p4–m3	16.7
L M1–M3	10.2	L m1–m3	11.5
I1 lost in leptictids		L × W i1	–
L × W I2	–	L × W i2	1.25 × 1.15
L × W I3	–	L × W i3	1.13 × 1.00
L × W C	3.21 × 2.04	L × W c	2.27 × 1.70
L × W P1	(3.4 × 2.1)	L × W p1	2.60 × 1.44
L × W P2	(5.0 × 2.6)	L × W p2	3.71 × 2.03
L × W P3	4.69 × 3.48	L × W p3	4.51 × 2.17
L × W P4	4.19 × 4.95	L × W p4	4.84 × 3.46
L × W M1	3.81 × 6.15	L × W m1	3.71 × 3.74
L × W M2	3.67 × 6.05	L × W m2	3.43 × 3.68
L × W M3	2.76 × 3.66	L × W m3	3.83 × 2.00
H lingual P2	–	H lingual p2	5.5
H lingual P3	5.3	H lingual p3	–
H lingual P4	[3.5]	H lingual p4	[[3.7]]
H lingual M1	[3.3]	H lingual m1	[[2.9]]
H lingual M2	[3.2]	H lingual m2	[[2.5]]
H lingual M3	[2.8]	H lingual m3	–

most likely latest Eocene (Chadronian NALMA), but may be earliest Oligocene (Orellan NALMA).

Diagnosis.—A leptictid that differs from *Leptictis* in being larger-bodied, having higher-crowned teeth, and parasagittal crests with a long postorbital constriction. The skull is over 10% longer than in *Leptictis haydeni* Leidy, 1868 and *Leptictis dakotensis* Leidy, 1868. The nasofrontal sutures form a W-shape, as opposed to a broad U-shape as in contemporaneous *Leptictis* and *Blacktops* species. The anterior squamosal sinus foramen is large, and the suprameatal foramen is small, while *L. dakotensis* has the opposite morphology. Unlike in other Late Paleogene leptictids, the P3 is very tall, lacks cingula and cuspules, and has a vestigial metacone. In the upper molariform teeth (P4–M3), relative crown height on the lingual side is approximately 1/3 taller than in *L. dakotensis*. These upper teeth are incipiently unilaterally hypsodont. Compared to *L. dakotensis*, the lower premolars and molars are much higher-crowned as well, p1–p3 lack cuspules, and p4–m2 are more anteroposteriorly compressed, as in the upper molariform series.

Measurements.—See Tables 1 and 2.

Description and comparisons.—The skull of KUVP 2568 is undistorted, but is missing its zygomatic arches, left postglenoid process, auditory bullae, right occipital condyle, portion of the supraoccipital, small portions of the nasals, maxillae, and lateral braincase, anteriormost portion of the rostrum, and the teeth anterior to P3 (Fig. 1A). Since I1 is lost evolutionarily in leptictids, the upper teeth missing in this
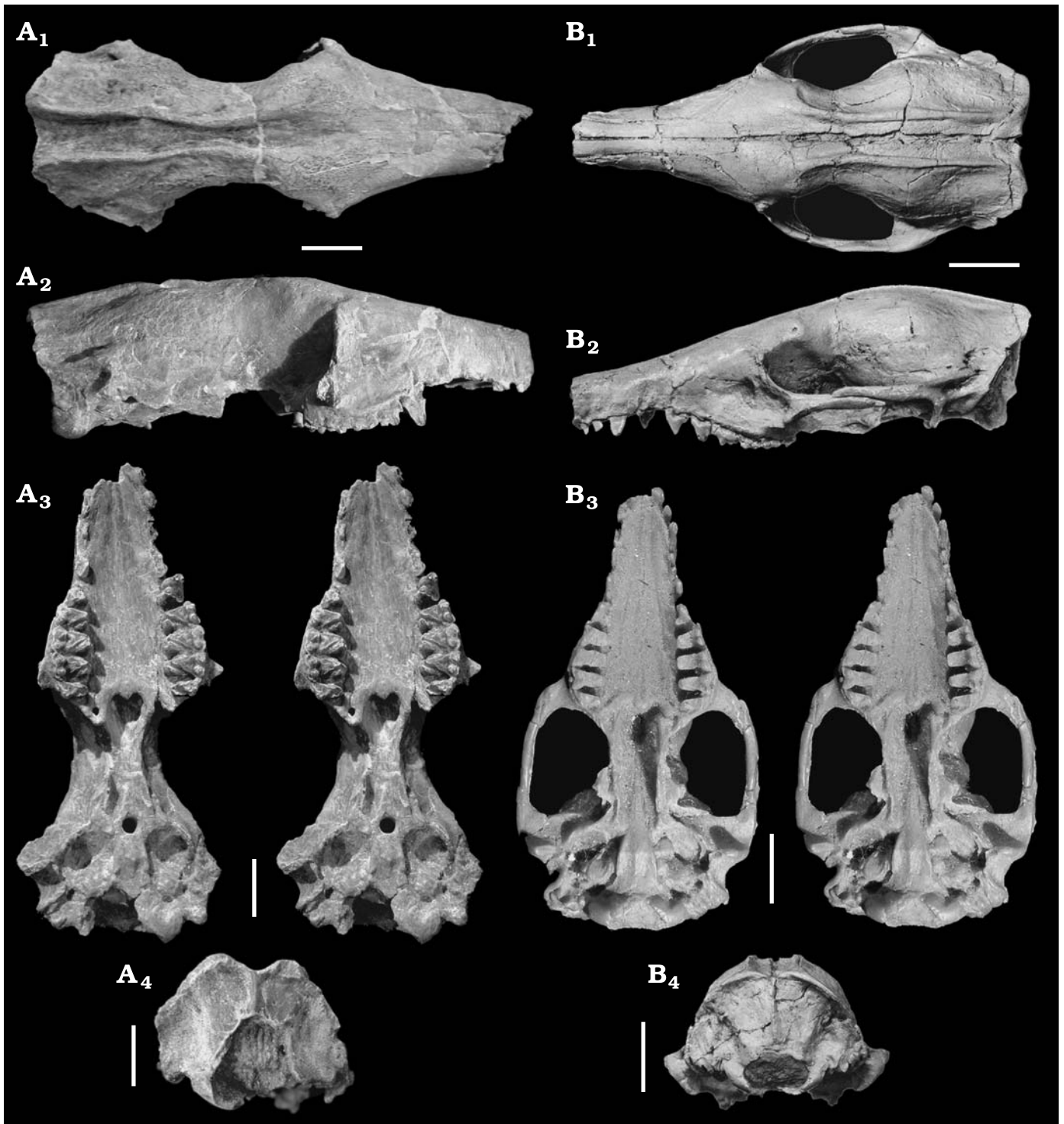
Fig. 1. Leptictid insectivore skulls. **A**. *Megaleptictis altidens* gen. et sp. nov., holotype (KUVP 2568), from the latest Eocene or earliest Oligocene of South Dakota's White River Group, compared to the common species of this time; A_1, skull in dorsal view, note the postorbital constriction of the parasagittal crests; A_2, lateral view, the teeth and rostrum are taller than in *L. dakotensis*; A_3, stereo pair, ventral view, palate shape, middle ear region, and general tooth features are similar to *L. dakotensis*; A_4, occipital view, the occipital region is blockier than in *L. dakotensis*. A portion of the supraoccipital region is broken away. **B**. *Leptictis dakotensis* Leidy, 1868 (F:AM 108194) from the earliest Oligocene of North Dakota's White River Group; B_1, dorsal view, the parasagittal crests are nearly straight and parallel; B_2, lateral view; B_3, stereo pair, ventral view; B_4, occipital view. Photographs (B1, B_2, and B_4) from Novacek (1986: fig. 2). Scale bars 10 mm.

specimen are I2, I3, C, P1, and P2. The dentaries are mostly complete, with heavy damage to the rami (Fig. 2B). The right dentary of KUVP 2568 has p3–m2 well preserved, but almost all of the posterior ramus is broken away. The left dentary is more complete with i2–m2 well preserved, and the base of i1 present, as well as the posterior portion of the m3
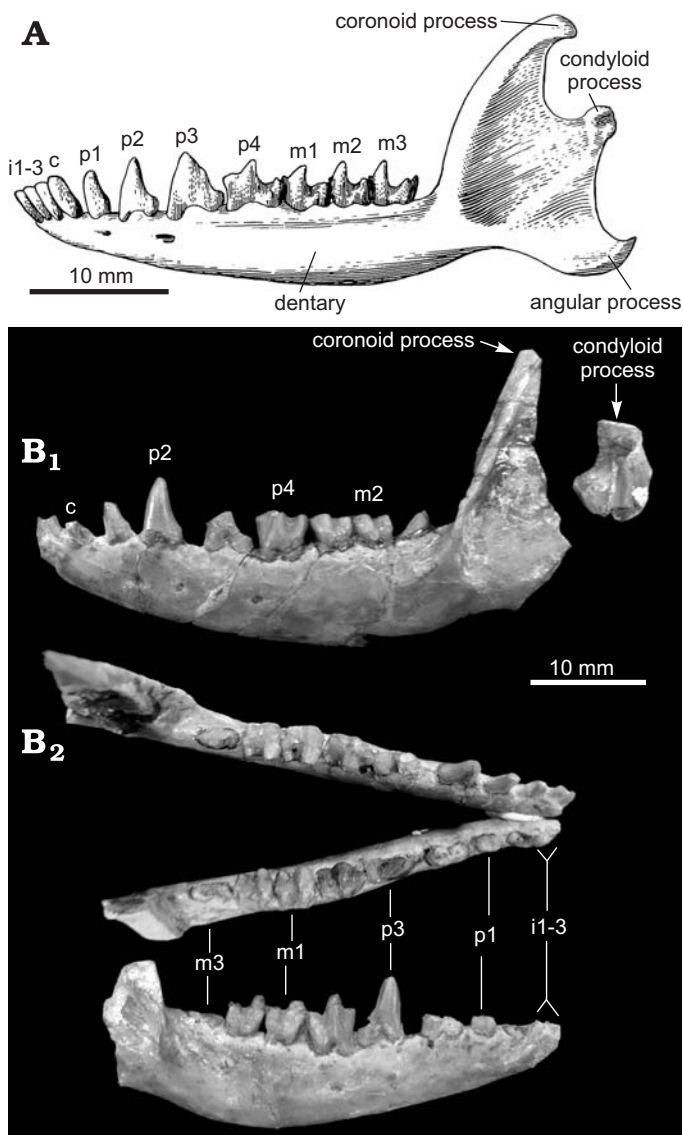
Fig. 2. Leptictid insectivore mandibles. **A**. *Leptictis dakotensis* Leidy, 1868 (F:AM 108194) from the earliest Oligocene of North Dakota's White River Group, left lateral mandibular drawing (modified from Novacek 1986: fig. 1). **B**. *Megaleptictis altidens* gen. et sp. nov., holotype (KUVP 2568), from the latest Eocene or earliest Oligocene of South Dakota's White River Group. B₁. Left dentary in lateral view; i2–m2 are well preserved, except for the fractured crown of p3; the base of i1 and posterior talonid of m3 are present; the posterior ramus is broken away, except for a portion of the condyloid region shown in its approximate position. Note the higher-crowned teeth of *M. altidens* and the flat wear of the p4–m2 trigonids. In contrast to the hook-like process of *L. dakotensis*, the coronoid process of *M. altidens* is triangular with a straight coronary ridge. B₂. Occlusal view of mandibles placed in articulation. B₃. Right dentary in lateral view; complete p3–m2 and the fractured bases of i2–p2 and m3 are present.

talonid. The left dentary has most of the ramus preserved, but the condyloid portion is a separate fragment, and the angle of the jaw is broken away.

The mandible of *Megaleptictis* mainly conforms to the unspecialized morphology of leptictids listed by Novacek (1986): the dentary is long, its ventral margin is convex, the

deepest portion of the jaw is at the level of m1, the mandibular condyle is wide and cylindrical, and the masseteric fossa is moderately deep. The dentary of KUVP 2568 differs in being relatively more robust, particularly below the molars, as one would expect with higher-crowned teeth. Most distinctly, the anterior edge of the coronoid process is straight, and its apex forms a slender triangle, while in *Leptictis dakotensis* the anterior edge is convex, and the coronoid apex is hook-like (Novacek 1986; Fig. 2A, B₁). *Leptictis dakotensis* possesses anterior and posterior mental foramina, which are located ventral to p1 and the anterior root of p3, respectively (Novacek 1986; Fig. 2A). In KUVP 2568, both dentaries have three mental foramina. On the left, the anterior and middle foramina are ventral to the anterior and posterior edges of p2, respectively, and the posterior mental foramen is ventral to the anterior edge of p4 (Fig. 2B₁). The right dentary differs in having the anterior mental foramen lying ventral to p1 and the posterior foramen ventral to the center of p4 (Fig. 2B₃).

The lower incisors (i1–i3) and canine are damaged in KUVP 2568, but they appear to be typical for leptictids. The sectorial premolars (p1–p3) are very tall; the left p2 crown height as measured on the lingual side is 5.5 mm, and the right p3 is 5.8 mm. The second premolar is twice as large as p1 and somewhat smaller than p3 (Fig. 2B, Table 1). These premolars lack cuspules, unlike in *Leptictis dakotensis*. There are small diastemata along i3–p4 similar to *L. dakotensis*; the largest (1.9 mm) in the mandible of KUVP 2568 lies between p2 and p3.

After accounting for heavy wear, the trigonids of p4–m2 in KUVP 2568 were likely erect and tall. The unworn height of p4 was likely around 4.5 mm, while in *Leptictis dakotensis* it is on the order of 3.5 mm (e.g., KUVP C-2225 and F:AM 108194). In Fig. 2, note how much taller the crown bases are in KUVP 2568 compared to *L. dakotensis*, as well as the flat, heavy wear of the trigonid and talonid cusps. The longest molariform tooth in KUVP 2568 is p4, but m1 is wider, so these two teeth are subequal in overall size. The fourth lower premolar has a well-defined paraconid, which is shorter and smaller than the protoconid and metaconid. The metaconid is the tallest cusp and is subequal in size to the protoconid. This trigonid morphology is similar to *Leptictis dakotensis*. The talonid has a large hypoconid, medium-sized entoconid, and a small hypoconulid with a twin cuspule between it and the entoconid. Except for the twinned cuspule, *Leptictis* has the same talonid morphology.

The lower molariform teeth of KUVP 2568 are slightly more compressed anteroposteriorly than in *Leptictis dakotensis*. In m1 and m2, the trigonid and talonid lengths are subequal, while in *L. dakotensis* the talonids are longer than the trigonids. In m1 and m2 of KUVP 2568, the paraconid is likely highly vestigial; it may have been lost, but the presence of the paraconid is difficult to discern owing to wear. As in *Leptictis*, the hypoconulids of p4 and m1 impinge on m1 and m2, respectively, creating indentations. In m1 and m2, the protoconid and metaconid are directly across from each other, and the entire trigonid is worn down to one slightly

Table 2. Skull comparisons of the contemporaneous leptictids *Megaleptictis*, *Blacktops*, and *Leptictis*. Measurements in mm. Abbreviations: H, height; L, length; W, width; ( ), estimate from little distorted or missing bone. [1] Measured from the nasofrontal suture to the occipital crest along the sagittal plane. [2] Measured at the anterior orbital margin. * Measurements for rostral ratio (broad versus narrow rostral morphology).

	Megaleptictis altidens (type) KUVP 2568	*Blacktops longinares* (type) UNSM 49038	*Leptictis* (*Ictops*) *dakotensis* (type) ANSP 11043	*Leptictis* cf. *dakotensis* AMNH 38915
rostral morphology	broad	narrow	broad	broad
parasagittal crests	parallel with a postorbital constriction	parallel	parallel	parallel
nasofrontal sutures	W-shaped	U-shaped	U-shaped	U-shaped
L basilar skull	(68)	(59)	–	(55)
L posterior skull[1]	46.0	37.8	–	35.5
H rostrum[2]	19.1	15.8	–	14.6
*L rostrum (nasal bone)	(32)	27.9	–	(25.5)
*W base rostrum[2]	26.3	18.2	(22)	(21)
*L/*W rostral ratio	(1.2)	1.53	–	(1.2)
W palate across I2s	(10)	6.1	–	7.7
W palate across M1s	22.3	15.0	(17)	16.5
W postorbital constriction	14.2	11.8	–	13.4
H occiput on sagittal plane	(11)	10.5	10.2	9.6
W occiput	(27)	21.5	22.9	23.0
W across occipital condyles	(18.4)	–	13.0	(13)
L upper tooth row	(38)	(31.3)	–	(31)
L P4–M3	13.5	12.3	12.3	(11)
L M1–M3	10.2	8.9	9.0	(8)

concave surface. The second molar is slightly smaller than m1; their talonids have a large hypoconid, medium-sized entoconid, and small hypoconulid, as seen in *Leptictis*.

The right m3 of KUVP 2568 is broken at the base, and the left m3 is broken away with just the posteriormost talonid preserved. It can only be observed that the preserved portions of m3 conform to *Leptictis* morphology (Novacek 1976, 1986: table 2): an elongate m3 outline with a bulbous hypoconulid.

On the left side of the KUVP 2568 skull, the bases of I2–P2 are present and exhibit no deviations from typical leptictid morphology (Fig. 1A$_2$, A$_3$). The P3 is typical in being sectorial with a somewhat isolated protocone abutting posterior to the paracone, yielding a triangular occlusal outline of the tooth (Fig. 3). P3 is unique in having a tall sectorial ridge, tall protocone, no cingula, no cuspules, and a small metacone; there is wear along the posterior tooth edge—it appears that an enlarged paracone dominates the sectorial portion of P3 and that the metacone is vestigial.

Except for their greater height, P4–M2 of KUVP 2568 are close in morphology to *Leptictis dakotensis*. The lingual crown height of P4 is 3.5 mm in KUVP 2568, while it is 1.7 mm in KUVP C-2225, *L. dakotensis* (both specimens have moderate wear). In KUVP 2568, the molariform teeth lack lingual cingula, have moderate ectocingula and precingula, have well-developed postcingula with hypocones, and have paracones that are slightly larger than the metacones (as is typical in leptictids). The protocones are all well worn and appear to be typical in shape and position. The precingula are situated centrally along the anterior tooth margins, while the postcingula meet the lingual edges of the teeth, being even

with the protocones. The precingula and postcingula have buccal edges that taper into the tooth walls and prominent lingual edges that are blocky to rounded in occlusal view (Fig. 3). The postcingula are tall next to the protocones (owing to the large hypocones), and they taper and slant buccally towards the tooth bases, while the precingula are nearly level and a little closer to the tooth bases in lingual view. *Leptictis dakotensis* has similar postcingula, but the precingula tend to be lens-shaped (tapered at both ends). Where there is less tooth wear on KUVP 2568, the precingula have a few cuspules, and the large hypocones of the postcingula have neighboring hypoconules that are nearly as large. Closer to the lin-
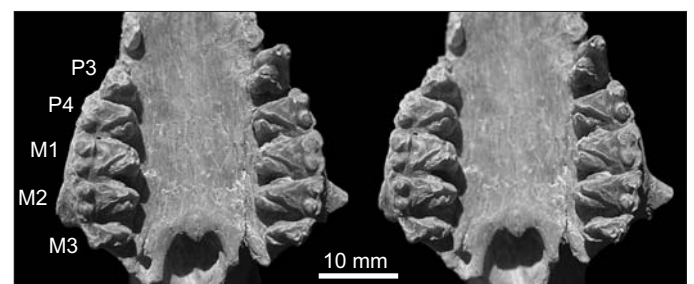

Fig. 3. Stereo pair of occlusal view of P3–M3 of the leptictid insectivore *Megaleptictis altidens* gen. et sp. nov., holotype (KUVP 2568), from the latest Eocene or earliest Oligocene of South Dakota's White River Group. Note the height of the teeth, particularly P3. Unlike *Leptictis dakotensis*, P3 has a small metacone and lacks cingula and cuspules. The upper molariform teeth are incipiently unilaterally hypsodont. Their postcingula are prominent as in *L. dakotensis*, but the ectocingula and stylar shelves are smaller. M1 and M2 are relatively wider than in *L. dakotensis*. M3 is similar in its size reduction and shape to *L. dakotensis*.
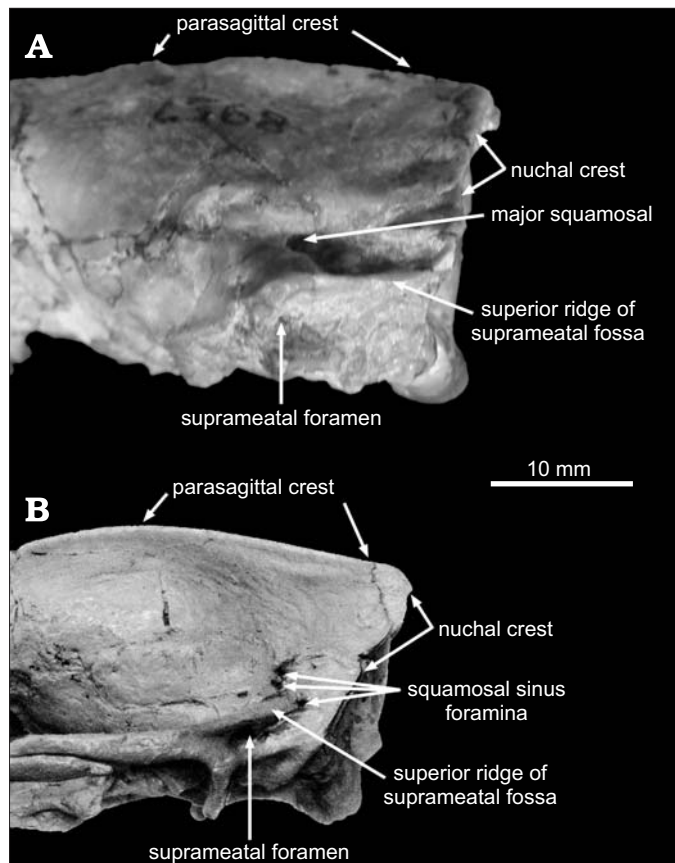
Fig. 4. Left squamosal regions of leptictid insectivores. **A**. *Megaleptictis altidens* gen. et sp. nov., holotype (KUVP 2568), from the latest Eocene or Early Oligocene of South Dakota's White River Group in oblique lateral view. The suprameatal fossa of *M. altidens* is larger than in *L. dakotensis*, as is the anterior venous foramen from the squamosal sinus. The dorsal ridge of the fossa extends posteriorly all the way to the nuchal crest, unlike in *L. dakotensis*. **B**. *Leptictis dakotensis* Leidy, 1868 (F:AM 108194) from the earliest Oligocene of North Dakota's White River Group in lateral view (modified from Novacek 1986: fig. 2).

gual tooth bases of P4–M2 and dorsal to the hypocone (or dorsal to the point between the protocone and hypocone), there is also a cuspule. The stylar shelves of P4–M2 in *L. dakotensis* are larger, and the ectocingula are larger and continuous from the paracones to metacones. In P4–M2 of KUVP 2568, the ectocingula are discontinuous, tapering to an end at the posterior paracones and are then moderately developed around the metacones. M1 and M2 are relatively wider and shorter in KUVP 2568 than in *L. dakotensis*.

M3 is also close in morphology to *Leptictis dakotensis*. It is similarly reduced, being about two-thirds the size of M2 (Fig. 3). The M3 precingulum and postcingulum are the same as in the other molariform teeth, yielding a bulbous outline to the lingual side of the tooth, as in *L. dakotensis*. On the M3s of KUVP 2568, the paracones and left metacone are broken away; the parastylar shelf is prominent, the metacone is reduced, and the ectocingulum is highly reduced, as in *L. dakotensis*.

In ventral view, the palate of KUVP 2568 conforms to *Leptictis dakotensis* morphology (Novacek 1986: fig. 14;

Figs. $1A_3$, 3), with the palatine bone extending anteriorly to P4 and having a large postpalatine foramen, small middle palatine foramen, and an apparently elongate anterior palatine foramen (there is some crushing in this region). The premaxillae are broken away at the incisive foramina.

In the basicranium of *Leptictis dakotensis*, the somewhat inflated entotympanic bulla covered most of the tympanic chamber (Novacek 1986), but preservation of this fragile bone is rare. The entotympanics are broken away in KUVP 2568, and there are no associated ectotympanic rings. The roof of the middle ear cavity is comparable to that of *L. dakotensis*, with the epitympanic recess and fossa for the tensor tympani being slightly deeper (Novacek 1986: figs. 20–23; Fig. $1A_3$, B_3). KUVP 2568 is missing the right occipital condyle and a portion of the supraoccipital bone just dorsal to the foramen magnum; its occipital region is blockier in outline than in *L. dakotensis* (Fig. 1A4, B4), with the petromastoid bone having a deeper fossa for neck muscle attachment. This region has at least three foramina—cracking and mineralization may be obscuring other foramina. Though the nuchal crest is broken along much of its edge, its prominence is slight and comparable in development to *L. dakotensis*.

The left postglenoid process of KUVP 2568 is chipped laterally, but appears to have been as broad and thick as in *Leptictis dakotensis*. Novacek (1986) stated that in leptictids the mandibular condyle does not fill the glenoid fossa, so that some horizontal motion is possible. The condyloid and glenoid in KUVP 2568 appear to form a tighter articulation than in *L. dakotensis*, but some horizontal motion is certainly possible since the glenoid fossa is open anteriorly. Just dorsal to the postglenoid process, running posteriorly to the nuchal crest, is the suprameatal fossa with an anteriorly positioned suprameatal foramen, as in *L. dakotensis* (Fig. 4). The suprameatal fossa is taller in KUVP 2568 than in *L. dakotensis*, and its ridged boundaries are more pronounced anteriorly and dorsally. The dorsal ridge runs the complete length to the nuchal crest (Fig. 4), while in *L. dakotensis* it tapers out a few millimeters anterior to the nuchal crest. The ventral ridge of the suprameatal fossa is the roof of the external auditory meatus. In ventral view, the concavity of the external auditory meatus is as in *L. dakotensis*, as is the short auditory canal. Dorsal to the suprameatal fossa on the right side of cranium of KUVP 2568, there are three foramina for the squamosal venous sinus, and the anterior one is quite large. On the left side, only this large squamosal sinus foramen is present (Fig. 4), but mineralization and preparation work may be obscuring any smaller openings. As described by Novacek (1986: figs. 2 and 17) in *L. dakotensis*, there are four foramina: three grouped posteriorly and one anteriorly, which lies dorsal to the postglenoid process. These three posterior ones are subequal in size and not as large as the anterior one in KUVP 2568. One might expect high individual variation in these foramina, but other specimens of *L. dakotensis* have three subequal foramina of medium size (about 0.7–1.0 mm in diameter), while KUVP 2568 has a major squamosal sinus foramen that is much larger (maximal diameter of 1.8 mm)

than neighboring foramina, including the suprameatal foramen; in *L. dakotensis*, the suprameatal foramen is much larger than the squamosal sinus foramina. A more pronounced feature of the posterior squamosal region dorsal to the suprameatal fossa is that it is deeply recessed in KUVP 2568, unlike in *L. dakotensis*.

The more anterior foramina along the lateral braincase cannot be described owing to cracking and some loss of bone, but the infraorbital region is well preserved. The infraorbital foramen is relatively larger in KUVP 2568 than in *Leptictis dakotensis*, and the posterior rostrum is taller, reflecting its higher-crowned teeth. The root of the zygomatic arch ventral to the infraorbital foramen has a shallow fossa, as in *L. dakotensis,* and anteriorly along the ventral rostrum, the alveolar processes are more pronounced in KUVP 2568 than in *L. dakotensis*.

From the orbit to the nuchal crest along the dorsal skull, KUVP 2568 has double parasagittal crests, as do all other known leptictids from the White River Group, including the unpublished genus "Frictops" from the latest Eocene (Chadronian NALMA; Novacek 1978). The parasagittal crests form the dorsal border of the temporal fossa. In KUVP 2568, the parasagittal crests differ from all other leptictids in having a long postorbital constriction (Fig. 1A$_1$), rather than being fairly straight and parallel as in *Leptictis* (Fig. 1B$_1$) and *Blacktops* (Meehan and Martin 2010), or wavy and posteriorly converging as in "Frictops" (Novacek 1978). Another differentiating trait of the dorsal skull is the shape of the nasofrontal sutures. In KUVP 2568, they are W-shaped, while *Leptictis* has broad U-shaped sutures (Fig. 5), as does *Blacktops* (Meehan and Martin 2010). "Frictops" also has W-shaped nasofrontal sutures, but they are more elongated, and "Frictops" is easily separated from *Megaleptictis* in being small-bodied for a White River leptictid and in possessing a much narrower snout and broader frontoparietal region (Novacek 1978).

Statigraphic and geographic range.—The type specimen, KUVP 2568, is from the lower or middle White River Group, southwestern South Dakota, which is latest Eocene or earliest Oligocene (Chadronian or Orellan NALMA). There are no known referred specimens.

Discussion

The large body size of *Megaleptictis altidens* and its uniquely higher-crowned teeth among leptictids indicate a different feeding ecology from other leptictid insectivores, though specific inferences can be difficult. Body size is a major factor in determining life history parameters (Calder 1984; Damuth and MacFadden 1990), and with a condylobasal skull length of approximately 68 mm, *Megaleptictis altidens* (KUVP 2568) is the second largest known leptictid from North America. The largest species from North America is *Leptictis douglassi* Novacek, 1976 (TMM 40688-6) with a p4–m3 length of 18.9 mm (Novacek 1976: table 2), while KUVP 2568 has a lower
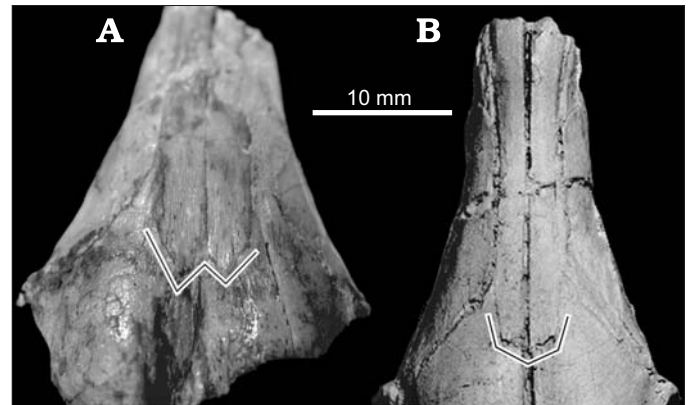

Fig. 5. Nasofrontal sutures of leptictid insectivores. **A**. *Megaleptictis altidens* gen. et sp. nov., holotype (KUVP 2568), from the latest Eocene or earliest Oligocene of South Dakota's White River Group compared to the common species of this time; rostrum in oblique dorsal view, showing the W-shaped nasofrontal sutures. **B**. *Leptictis dakotensis* Leidy, 1868 (F:AM 108194) from the earliest Oligocene of North Dakota's White River Group; rostrum in dorsal view, showing the U-shaped nasofrontal sutures (modified from Novacek 1986: fig. 2). White and black lines just posterior to the sutures outline their shape.

molariform series length of 16.7 mm (Table 1). *Leptictis douglassi* differs from *Megaleptictis altidens* in having a P3 with cuspules (including a prominent anterior one), a p4 with a prominent paraconid and deep prefossid, a p4 protoconid slightly anterior to the metaconid, greater wear on the metaconids than the protoconids (Novacek 1976), less anteroposteriorly compressed teeth, and more brachydont teeth. *Leptictis douglassi* occurs in the Late Eocene (late Duchesnean NALMA), just prior to White River Chronofauna (Chadronian, Orellan, and Whitneyan NALMAs). Among the species from the Chadronian and Orellan of North America, *Leptictis* condylobasal skull lengths range from about 50–61 mm (*L. haydeni* Leidy, 1868; *L. dakotensis* Leidy, 1868; *L. bullatus* Matthew, 1899*; L. acutidens* Douglass, 1901; *L. thomsoni* Matthew, 1903; *L. montanus* Douglass, 1905; and *L. wilsoni* Novacek, 1976); *Blacktops* skulls are 58–60 mm (*B. longinares* Meehan and Martin, 2010 and *B. latidens* Meehan and Martin, 2010); and the "Frictops" skull is 49 mm long (Matthew 1903; Douglass 1905; Novacek 1976, 1978; Meehan and Martin 2010). North American species of Cretaceous, Paleocene, and other Eocene genera (*Palaeictops* Matthew, 1899; *Myrmecoboides* Gidley, 1915; *Xenacodon* Matthew and Granger, 1921; *Gypsonictops* Simpson, 1927; *Prodiacodon* Matthew, 1929; *Stilpnodon* Simpson, 1937; *Leptonysson* Van Valen, 1967; and *Gallolestes* Lillegraven, 1976) are smaller-bodied than *Megaleptictis altidens* (Gidley 1915; Matthew and Granger 1921; Simpson 1927, 1937; Van Valen 1967; Lillegraven 1976; Novacek 1976, 1977). The largest known leptictid in the world is the Middle Eocene *Leptictidium tobieni* Koenigswald and Storch, 1987 from Messel, Germany, with a skull length of 101 mm (head and trunk length of 375 mm and tail length of 500 mm; Koenigswald and Storch 1987). All the species of the European Pseudorhyncocyonidae are large-bodied leptictids (skull lengths range from 67–101

mm; Sigé 1974; Koenigswald and Storch 1987), and apparently inhabited the subtropical to tropical forests of the Eocene. With the typical brachydont insectivorous teeth of leptictids, the large-bodied *Leptictidium nasutum* Storch and Lister, 1985 (skull length 89 mm; Sigé 1975; Koenigswald and Storch 1987) from the Eocene Messel deposits was likely a predator on the subtropical forest floor, and stomach contents from a few specimens include insect and small vertebrate remains (Koenigswald et al. 1988).

Another consideration in inferring mammal diet is snout morphology, which may yield additional information on feeding strategy (Jarman 1974; Janis and Ehrhardt 1988; Musser and Heaney 1992; Solounias and Moelleken 1993; Mathiesen et al. 2000; Freeman 2008). Meehan and Martin (2010) described two snout morphologies in leptictids from the White River Group, of which *Leptictis* and *Megaleptictis* have a broad snout with rostral length/width ratios of approximately 1.2, while *Blacktops* has a narrow snout with a ratio of 1.5 (Table 2). We suggested that the broad snout form fed more on small vertebrates, while the narrow snout form fed more in the leaf litter on arthropods and worms. Though broad-snouted, *Megaleptictis* clearly had a significant feeding difference, as indicated by its higher-crowned teeth (molariform teeth are about 30% taller than in other leptictids); the upper molars are starting to develop unilateral hypsodonty similar to rabbits (Lagomorpha: Leporidae). In the molariform teeth, there is heavy wear on the protocones and trigonids, while the metacones, paracones, and talonids have slight to moderate wear. Selection for such higher-crowned teeth and heavy wear suggest crushing of abrasive food and/or a high degree of grit on ingested food. In herbivores, tooth crown height is a factor of abrasiveness of vegetation and the grit content upon the vegetation (Stirton 1947; Janis 1988; Janis and Fortelius 1988; Williams and Kay 2001). The Eocene–Oligocene transition represents cooler, drier, and more open habitats becoming common at high and mid-latitudes, and increased hypsodonty in herbivores (e.g., rodents, horses, and artiodactyls) reflects this climatic shift (Martin 1993; Meehan 1998). If one were to conjecture, one possibility for the feeding ecology of *Megaleptictis* is a hunter of small vertebrates and digger for insect larvae and earthworms that are contaminated with soil particles in the drier, more open, savannah-like and scrub-like habitats that became more prominent during the latest Eocene–Early Oligocene (Retallack 1983, 1997). Another consideration is specialization on tough food stuffs that other leptictids rarely ingested, such as scorpions or millipedes. However, this seems unlikely, since modern insectivores that eat beetles or other hard-shelled arthropods puncture their exoskeletons and squeeze out the soft nutrients, and lack such high-crowned teeth and heavy wear.

Most insectivores ingest some plant matter, and some are quite omnivorous, so another possibility is that *Megaleptictis* fed on more plant material than other leptictids or most modern insectivores. There is leaf material associated with the abdominal region of a *Leptictidium nasutum* skeleton, but it is uncertain if this vegetation was part of the stomach remains or merely under the body when it was buried (Koenigswald et al. 1988). Among modern insectivores, the group with the highest-crowned teeth is sengis or elephant "shrews" (Macroscelidea). The Miocene fossil record of sengis shows much more diversity than modern forms, and teeth convergent to hyraxes suggest that, ancestrally, sengis were mainly herbivorous (Patterson 1965; Butler 1995). This implies that modern sengis secondarily shifted to a more insectivorous diet (Rathbun 1979), and have inherited taller teeth than expected for this niche. There is one living sengi that has truly hypsodont molars, the short-eared sengi (*Macroscelides proboscideus* Shaw, 1800), which is described as omnivorous, eating invertebrates, shoots, roots, berries, and seeds (Corbet and Hanks 1968; Kerley 1995; Unger and Schratter 2000). Besides being the most herbivorous (about 40% herbage by volume; Kerley 1995), as one might predict from its hypsodont molars, the short-eared sengi also occupies the most open habitat, the desert and semi-desert of southernmost Africa (Corbet and Hanks 1968; Rathbun 2009), where windblown and saltated grit on ingested vegetation would result in significant tooth wear. Sengis have a functional caecum, which also indicates a more herbivorous past, and the short-eared sengi has a longer large intestine, suggesting retention of a more herbivorous diet than other sengis (Kerley 1995; Leirs et al. 1995; Spinks and Perrin 1995).

The taller crowns and heavy, flat tooth wear observed in the leptictid *Megaleptictis altidens* could easily, and perhaps best, be explained by a significant herbivorous component similar to the short-eared sengi diet, with perhaps on the order of 40–50% herbage, rather than 0–15%, as is more typical in insectivores. A dietary shift to more herbage would make sense for an insectivore adapting to the expanding open habitats of the Late Eocene–Early Oligocene, where a drop in insect abundance would be associated with a marked dry season; Kerley (1995) hypothesized that the more arid-adapted sengis retained a more herbivorous diet for this reason. *Megaleptictis* evolving a larger body size is also consistent with (but not exclusive to) such a dietary shift.

Though speculative, we hope that these suggestions inspire studies on the functional morphology of small mammal rostra and dietary adaptations. Further avenues of interpreting diet would include isotopic analysis of tooth enamel (Vogel 1978; Bocherens et al. 1994; MacFadden 1998; Hopley 2006; Lee-Thorp et al. 2010) and dental microwear patterns, such as enamel pitting or scratching (Rensberger 1978; Covert and Kay 1981; Silcox and Teaford 2002; Organ et al. 2006; Firmat et al. 2010).

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