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THE EARLIEST KNOWN NORTH AMERICAN BOVID, *NEOTRAGOCERUS*

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ABSTRACT—*Neotragocerus* represents the earliest recognized occurrence of the Bovidae in North America but is rare and poorly understood, known principally by scattered horn cores assigned to two species. Recently, the largest sample of *Neotragocerus* was discovered in the Fort Rock Formation of south-central Oregon where Eurasian immigrants co-occur. Horn cores, cranial fragments, dental material, and postcranial elements were found at five closely related sites and provide significant morphological data of this enigmatic ungulate. The specimens occurred in a ferruginous-stained basalt gravel that represents a paleochannel. Associated faunal elements indicate deposition during the Hemphillian NALMA, and ⁴⁰Ar/³⁹Ar dates from interbedded tephros, ranging from 6.11 + 0.08 to 5.74 + 0.01 Ma correspond with the Hemphillian assignment. *Neotragocerus* was a medium-sized bovid with relatively short horn cores, normally with dorsoventral ridges, ovate cross-section at the base, very short pedicles and a brachyselenodont dentition. Morphologies suggest assignment of *Neotragocerus* to the “Boselaphini,” the least derived tribe of living bovids or at least derivation from a “boselaphine” synapomorphic complex. The Hemphillian genus does not appear to be closely related to later occurring North American bovids, and a close Eurasian relative is not obvious. Based on the range of variation displayed by the Oregon specimens, *Neotragocerus improvisus* is retained, and *Neotragocerus lindgreni* is considered a nomen dubium.

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INTRODUCTION

Paleontological research in Upper Miocene rocks in the Pacific Northwest has been conducted since 1974 by parties under the direction of the first author. As a result, thousands of specimens have been retrieved (e.g., Martin, 1984, 1998, 2008, 2017). However, specimens of the earliest known bovid in North America, *Neotragocerus*, were seldom recovered until recently when 22 new Hemphillian localities were identified in the Poverty Basin of northern Lake County in south-central Oregon (Fig. 1). Five localities produced the largest significant sample of *Neotragocerus* recorded from North America.

Of the large terrestrial ungulates, ruminants are currently the most numerous and diverse, and cetartiodactyls, including ruminants, have been widely distributed since the late Eocene/Oligocene. Ruminants occur naturally worldwide except in Australia and Antarctica, and a great proportion are bovids that appear in Eurasia during the Miocene approximately 19–18 Ma (Gentry et al., 1999; Gentry, 2000; Vrba and Schaller, 2000; Kostopoulos, 2006) or possibly 17.1–15.3 Ma based on a mitochondrial phylogeny by Bibi (2013). The least derived bovids have been classified within the monophyletic Bovinae (Hassanin and Ropiquet, 2004; Fernández and Vrba, 2005), which includes the tribes: “Boselaphini,” a paraphyletic group of Miocene–Pliocene bovines including the Tragelaphini and Boselaphini sensu stricto (Bibi et al., 2009) appearing as early as 18–16 Ma depending upon the inclusion of *Eotragus*; the Tragelaphini (appearing approximately 9 Ma); and the Bovini (appearing 6–5 Ma,

Kostopoulos, 2006, or 8.3 Ma, Bibi, 2007). Not until the Late Miocene do bovids appear in North America in the guise of *Neotragocerus*, and not until the Early Pleistocene do bovids commonly occur in the western hemisphere (Janis, 2000; Mead and Czaplewski, 2009). Today, bovids are the most diverse group of ruminants and exist in a wide range of habitats from rainforests to woodlands, savannas, deserts, mountains, and arctic environments.

Here, we present a review of the earliest and least understood North American bovid, *Neotragocerus*, along with new remains from Oregon. The relationship of *Neotragocerus* to other bovids is poorly understood. *Neotragocerus* is a rare, enigmatic bovid that appeared in North America during the late early Hemphillian (Hh2) through the early late Hemphillian (Hh3; Tedford et al., 2004) and ranged from the Pacific Northwest to the Great Plains of North America.

The type species, *Neotragocerus improvisus*, was described by Matthew and Cook in 1909 (Fig. 2A). Skinner et al. (1977) suggested that the holotype, a single horn core (AMNH 14141), was derived from Cook’s Pliohippus Draw from the lower upper Hemphillian (Hh3) ZX Bar Locality in the Johnson Member of the Snake Creek Formation in Sioux County, Nebraska. From the same locality, two brachyodont upper dentitions with M¹-M³ (AMNH 14136, 14137) were considered provisionally as paratypes of *Neotragocerus improvisus* that “agree quite nearly with some of the brachyodont (sic) antelopes” (Matthew and Cook, 1909:414). Matthew (1918:223) reiterated, “The upper molars, provisionally referred to it, may not belong to this genus, but they are nearer to the antelope type than to any other.” On the supposition that the horn core was “goat-like” (Skinner et al., 1977:361) and that its dentition should therefore be hypsodont, they reassigned these brachyodont specimens and a tooth (AMNH 83458) found by Cook from the

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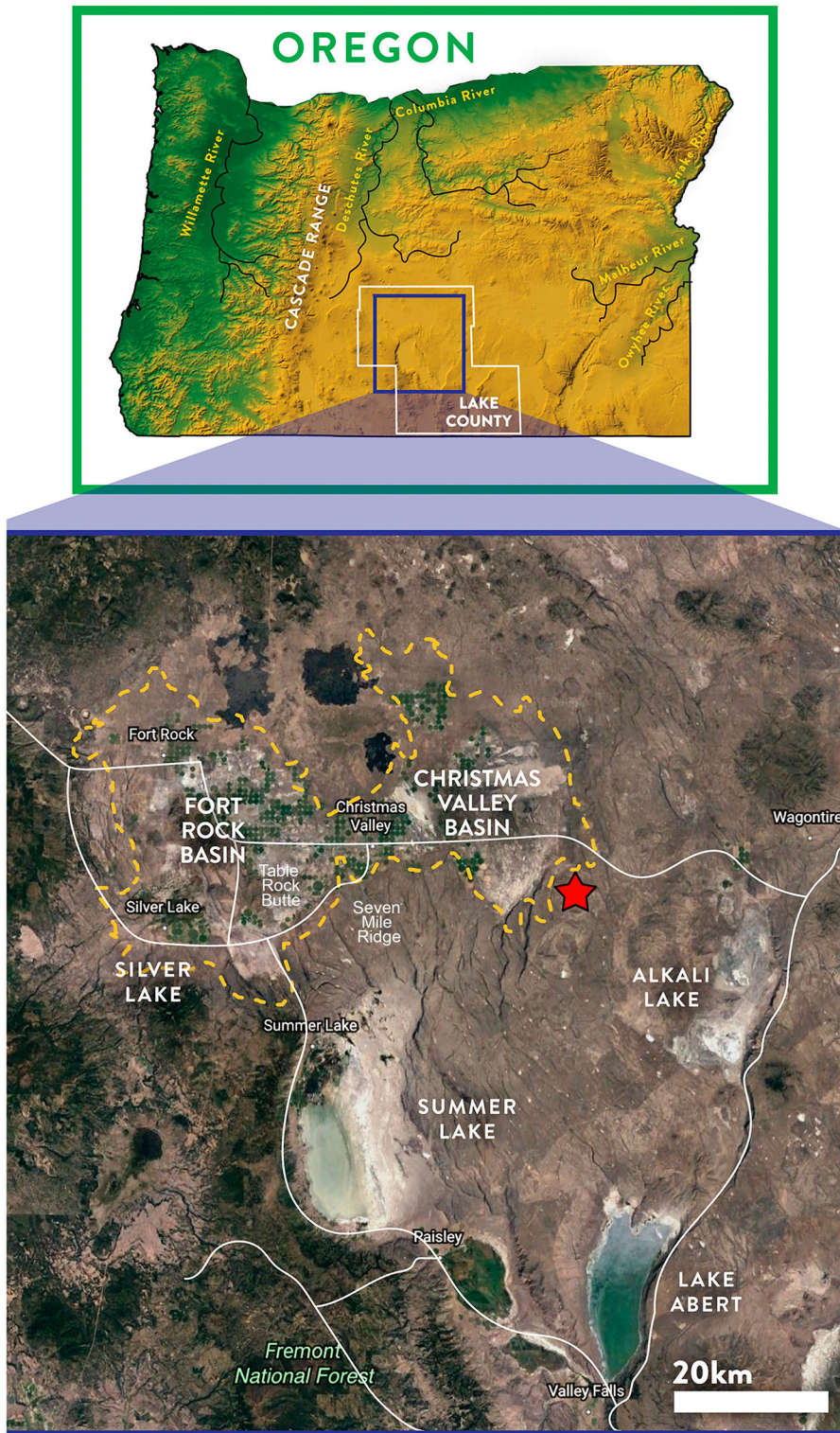


FIGURE 1. Area of investigation. Star denotes Poverty Basin localities containing new remains of *Neotragocerus* southeast of the Christmas Valley Basin in Lake County, Oregon.

same site to the cervid *Pediomeryx*. They probably modeled their removal of these specimens from *N. improvisus* on Frick's (1937) contention that the jaws were camelids. Another Hemphillian locality in Sioux County, Nebraska, that was cited to have produced *N. improvisus* (Sinclair, 1915; Skinner et al., 1977) is Princeton Locality 1000C. Like the dentitions discussed above,

Sinclair's lower jaw (PU 12106) was transferred from *Neotragocerus* to *Prosynthocerus* (protoceratid) by Frick (1937), although Matthew (1918) previously thought the p4 was too narrow to be that of a bovid or cervid and considered the dentary to be that of a camelid. Overall, a state of relative confusion has surrounded these brachyodont dentitions.

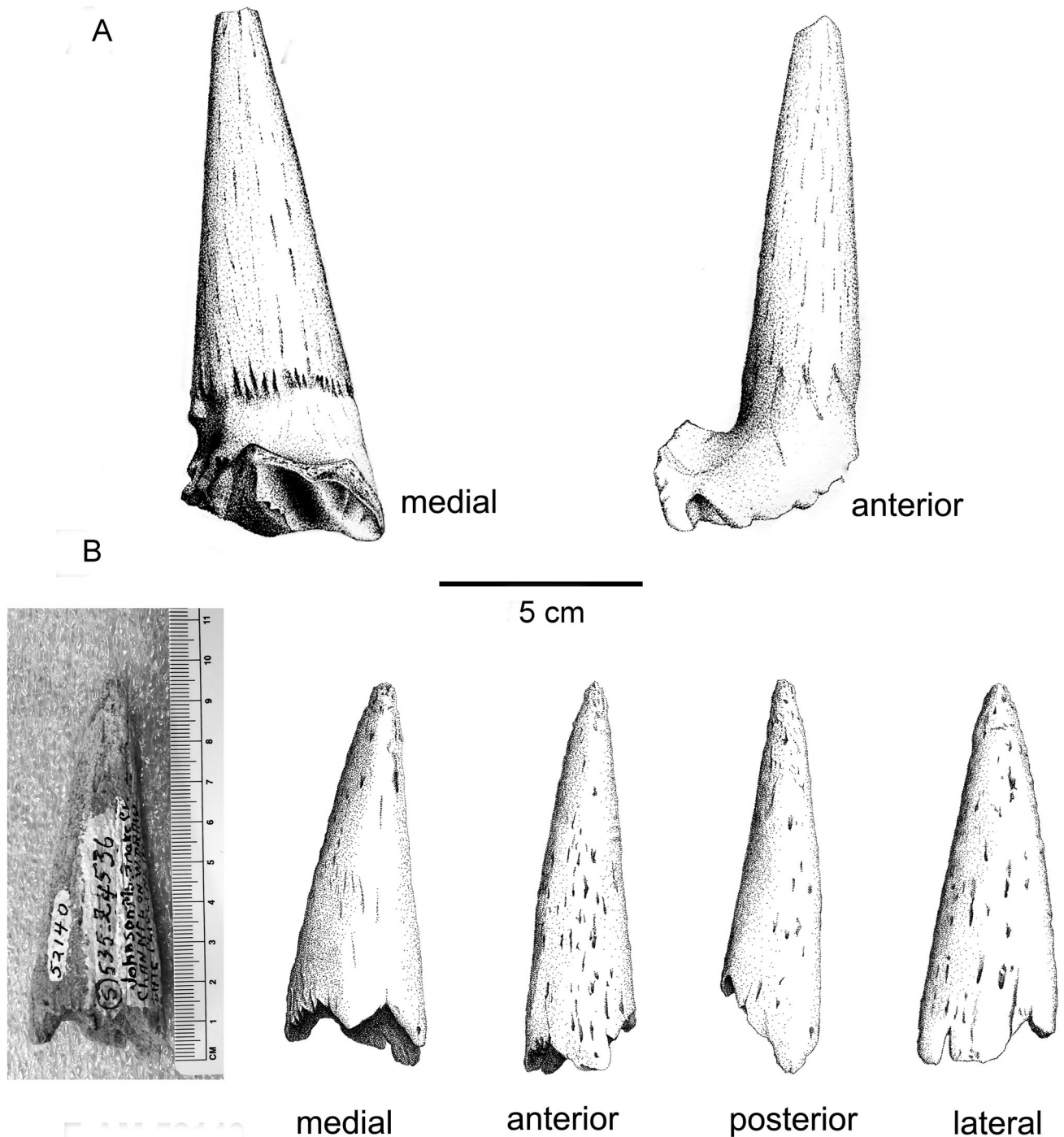


FIGURE 2. New illustrations of *Neotragocerus* from Miocene deposits of northwestern Nebraska. **A**, AMNH 14141, horn core, holotype of *Neotragocerus improvisus* Matthew and Cook, 1909; **B**, F:AM 52140, horn core of *Neotragocerus* sp. cf. *N. improvisus* (see Skinner et al., 1977).

Another specimen (Fig. 2B) assigned to *Neotragocerus improvisus*, a distal horn core fragment (F:AM 52140), was collected by Morris Skinner in 1947 from a channel of the lower Snake Creek Formation in northwestern Nebraska. Skinner et al. (1977:357) assigned the locality to the lower Johnson Member and its paleofauna from Aphelops Draw to the early Hemphillian. Tedford et al. (2004) and Morgan (2008) considered the assemblage as late early Hemphillian (Hh2).

A second species, *Neotragocerus lindgreni* (Fig. 3A), was described (Merriam, 1918) from deposits 4.8 km east of Boise,

in Ada County, Idaho. These deposits are considered part of the Chalk Hills Formation of the Idaho Group, which are considered Upper Miocene (e.g., Swirydczuk et al., 1981; Stearley and Smith, 2016). The holotype, USNM 3941, a single horn core, was diagnosed as more slender, longer, and showing slightly greater lateral compression than that of *N. improvisus* (Merriam, 1918:527).

A few other occurrences assigned to *Neotragocerus* include a left horn core, RAM P85.18.29 (Fig. 3B), from the Courtney West Pit, an upper Hemphillian locality in the Hand Hills,

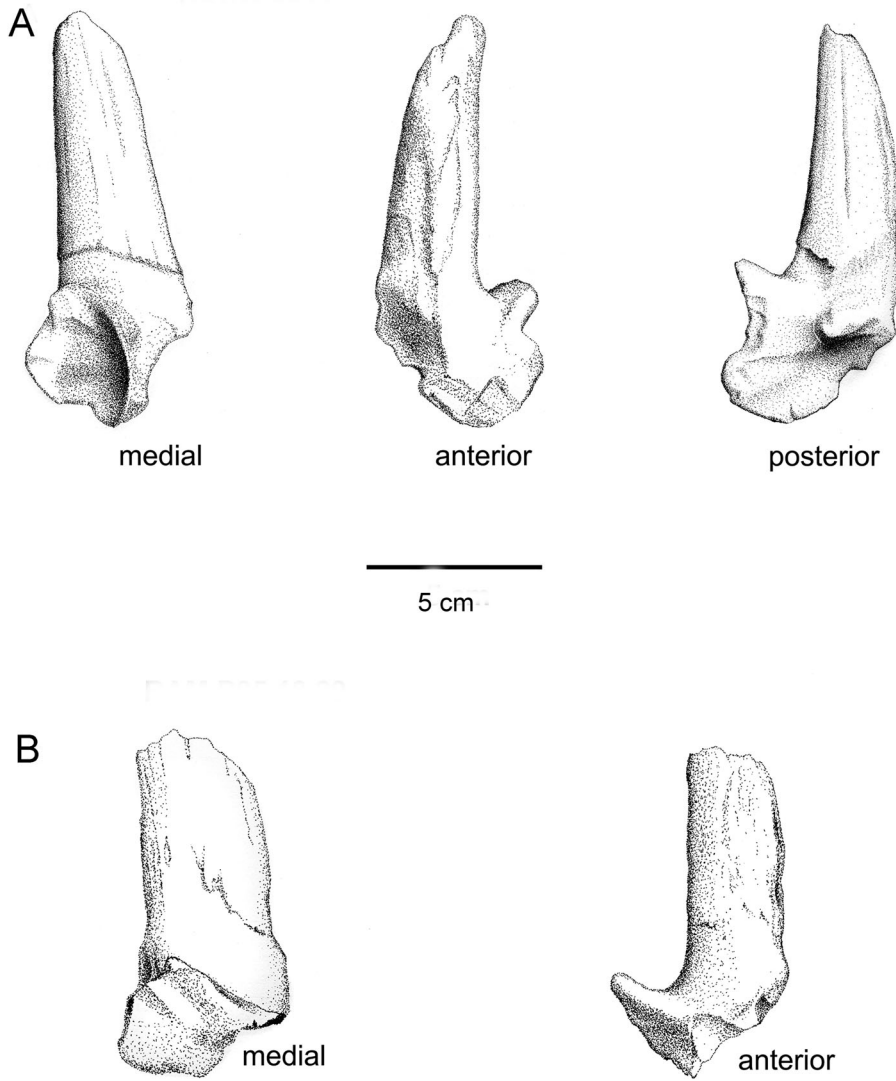


FIGURE 3. New illustrations of *Neotragocerus*. **A**, USNM 3941, horn core, holotype of *Neotragocerus lindgreni* from Miocene deposits of southern Idaho (Merriam, 1918); **B**, RAM P85.18.29, horn core of *Neotragocerus improvisus* from Miocene deposits near Drumheller, Alberta (Burns and Young, 1988).

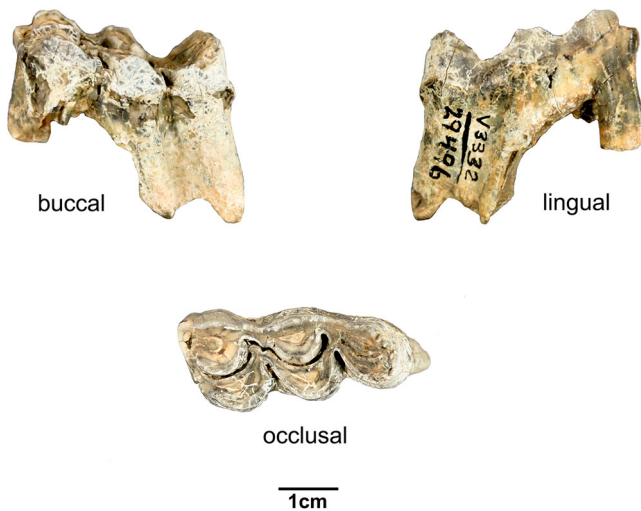


FIGURE 4. UCMP V29496, M₃ of cf. *Neotragocerus* sp. indet. from Miocene deposits of Cherry County, Nebraska.

26.5 km northeast of Drumheller, Alberta (Burns and Young, 1988). SBCM L2743-32, a proximal phalanx, was collected at the Mesquite Locality, a site in the Muddy Creek Formation of Clark County, Nevada, considered by Reynolds and Lindsay (1999) as ?*Neotragocerus* sp. and as having been deposited during the mid-Hemphillian. From UCMP Locality V-3332 in the Ash Hollow Formation near Valentine in Cherry County, Nebraska, ?*Neotragocerus* (Stirton and McGrew, 1935) was based on UCMP V29496, an M₃ (Fig. 4). The Ash Hollow Formation is normally considered to have been deposited during the late Clarendonian NALMA, and on the UCMP database, UCMP Locality V-3332 is considered upper Clarendonian. However, the Ash Hollow Formation has been illustrated from 6 Ma to approximately 12 Ma (e.g., Diffendahl et al., 1996; Tedford et al., 2004), an interval that would include much of Hemphillian time. Finally, on their biostratigraphic range chart, Janis et al. (1998) illustrated the range of *Neotragocerus* throughout the Hemphillian, although we know of no positively documented earliest Hemphillian occurrences thus far.

Overall, very few occurrences of *Neotragocerus* have been recorded in North America since its initial description (Matthew and Cook, 1909). Most occurrences are single

specimens, typically horn cores. During field investigations in northern Lake County in south-central Oregon during 2014–2016, five new localities were discovered that produced relatively numerous specimens of *Neotragocerus*. These localities lie within a square kilometer, occur within the Upper Miocene Fort Rock Formation as revised by Martin et al. (2018), and all specimens were apparently derived from the same lithostratigraphical unit, a ferruginous sand and basalt channel gravel (Fig. 5). One locality (ULGM V-32), the Megatylopus Locality, produced two partially articulated skeletons of *Megatylopus* (Martin et al., 2018), cyprinids, catostomids, *Oncorhynchus*, Felidae, Mammutidae, *Hypolagus*, *Teleoceras*, and *Hemiauchenia*, as well as *Neotragocerus*, represented by horn cores, cranial material, and postcranial elements. A second locality (ULGM V-51), the Mity Mite Locality, was dominated by *Neotragocerus* with many fewer camelids, canids, felids, and tayassuids. The third locality, Tylopus High (ULGM V-52), is aerially limited with only three specimens of *Neotragocerus* collected with a few rhinocerotid and giant camelid remains. Two other sites, Anything Goes (ULGM V-38) and 5PPL335 (ULGM V-57), produced three and seven *Neotragocerus* specimens, respectively, with similarly associated taxa.

As shown below, the Megatylopus Locality produced 14 *Neotragocerus* specimens, whereas the Mity Mite Locality produced approximately 60 specimens making this sample of *Neotragocerus* the largest heretofore discovered. Based on this significant collection, many questions concerning the anatomy of *Neotragocerus* can be answered, surprising features discovered, and additional questions raised.

GEOLOGICAL SOURCE AND AGE

The specimens analyzed were found in detrital deposits in southern Oregon that are considered part of the Fort Rock Formation delineated by Hampton (1964). The formation occurs in the Fort Rock-Christmas Valley Basin and extends to the south-east into the Poverty Basin (Fig. 1). Through this area, the Bonneville Power Administration undertook a major project to upgrade their power line. The fossils were discovered as part of the geological and paleontological analyses for this power line.

The localities that produced *Neotragocerus* were found in the Fort Rock Formation that lies between the Picture Rock Basalt and the Hayes Butte Basalt as mapped by Hampton (1964), although the Fort Rock Formation appears interbedded with the latter basalt (Walker et al., 1967; Walker and McHugh, 1980). The formation was described to consist of diatomite, marls, fluvial detritus (channels, overbank deposits, and levees), and volcanoclastic deposits (e.g., Fig. 5). Colbath and Steele (1982) noted diatomite in the lower portion of the formation and named these diatomaceous rocks as the Pettus Dam Member of the Fort Rock Formation. However, we noted diatomaceous units and marls interbedded throughout the formation, making the contacts of the Pettus Dam Member difficult to define. Fluvial and lacustrine units produced fossil invertebrates and vertebrates, particularly in the northern Poverty Basin. Hampton's (1964) geological map included some of the new fossiliferous localities but ended north of most sites. Martin et al. (2018) extended the formation 50 km south to include strata containing all of our new localities. Present correlations suggest the localities lie in the upper portion of the formation, which attains a maximum thickness of 305 m (1000 ft) (Hampton, 1964).

$^{40}\text{Ar}/^{39}\text{Ar}$ dates were obtained from interbedded tephra that occur above the ferruginous basalt gravel that produced the *Neotragocerus* specimens. These dates range from 5.84 ± 0.08 to 5.74 ± 0.01 Ma (Martin et al., 2018). In addition, a fluvially reworked tephra was derived from the gravel (Unit 1) at ULGM Locality V-32 where 14 specimens of *Neotragocerus* were collected. This waterlain tephra produced an $^{40}\text{Ar}/^{39}\text{Ar}$ date of 6.11 ± 0.08 Ma

from hornblende, which owing to its reworked nature, represents a maximum age of Unit 1 (Fig. 5). Although recent observations in its type area suggest that the Hayes Butte Basalt may be localized as are many volcanics in the Fort Rock Basin, those mapped as Hayes Butte Basalt appear interbedded above and within some fossiliferous units (see maps, Hampton, 1964; Walker and McHugh, 1980), but normally the principal flows lie suprajacent to the Fort Rock Formation; a date of 5.19 ± 0.05 Ma was derived from the highest flow in the study area. Collectively, these dates indicate a latest Miocene time of deposition for the fossiliferous units.

Typical late Hemphillian taxa occur in the Fort Rock deposits such as *Gaillardia*, *Pliotaxidea*, *Hypolagus*, *Teleoceras*, *Megatylopus*, *Dipoides*, *Castor*, and *Promimomys* (= *Prosomys*); and *Neotragocerus* first appears in the Hemphillian (Tedford et al., 2004). Thus, biostratigraphic correlations indicate the Fort Rock strata were deposited during the Hemphillian, and the radiometry coincides with dates previously determined for the Hemphillian (approximately 9.0–4.6 Ma, Tedford et al., 2004). Clearly, the Hemphillian represents a time of major Eurasian dispersal into North America. Evidence of this dispersal includes *Gaillardia*, *Castor*, *Promimomys*, and apparently *Neotragocerus* occurring together in the Fort Rock Formation during the lower upper Hemphillian (Hh3) in the Pacific Northwest.

NEOTRAGOCERUS OCCURRENCES IN OREGON

The five localities, ULGM V-32, V-38, V-51, V-52, and V-57, that produced the *Neotragocerus* specimens occur within the same lithostratigraphical unit (Fig. 5), a rounded basalt conglomerate and sandstone. The gravel contains clasts from pebble to large-cobble size in a coarse pumaceous and basaltic sand matrix. Cross-beds and cut and fill structures are common. The gravel has diagenetic ferruginous cement, caused by iron-rich groundwater percolating through the permeable sand and gravel deposits. The iron was apparently derived from the ubiquitous basalt, occurring either as flows or reworked clasts into fluvial deposits. Sedimentary structures clearly indicate a riparian channel environment of deposition, and the riparian habitat is reinforced by the occurrences of three families of fish.

Numerous *Neotragocerus* specimens were discovered from the five localities, particularly, the Mity Mite Locality (ULGM V-51). Nevertheless, all specimens were found as float, some with ferruginous pumaceous sandstone adhering (e.g., Fig. 6). Their positions on the surface of the channel deposits and with no other possible source units above positively indicates their source from the channel deposits. Moreover, other mammalian remains, including partial skeletons, were discovered in situ in the gravel (Martin et al., 2018).

The Mity Mite site produced medium-sized artiodactyl specimens with a few carnivore elements. Many cranial elements of *Neotragocerus* occur, including four horn cores. Within the artiodactyl assemblage, small camelid and tayassuid specimens could easily be differentiated, but no other artiodactyl specimens other than those of *Neotragocerus* could be distinguished. Therefore, the non-camelid/tayassuid postcranial elements were assigned to *Neotragocerus*. No cervid or antilocaprid elements were identified from the five localities with the possible exception of two fragmentary jaws (ULGM V8577 and V14830) that we believe also represent *Neotragocerus*.

All elements of *Neotragocerus* are exceedingly well preserved and had been eroded from their original positions. As expected, the dense podial elements were complete and unabraded, but elongate elements were represented by unabraded proximal or distal articulations. Bone preservation suggests the denser elements, horn cores and braincase fragments, had not been transported far in the channel and represent eroded elements remaining as lag on the present surface. Two cores separated

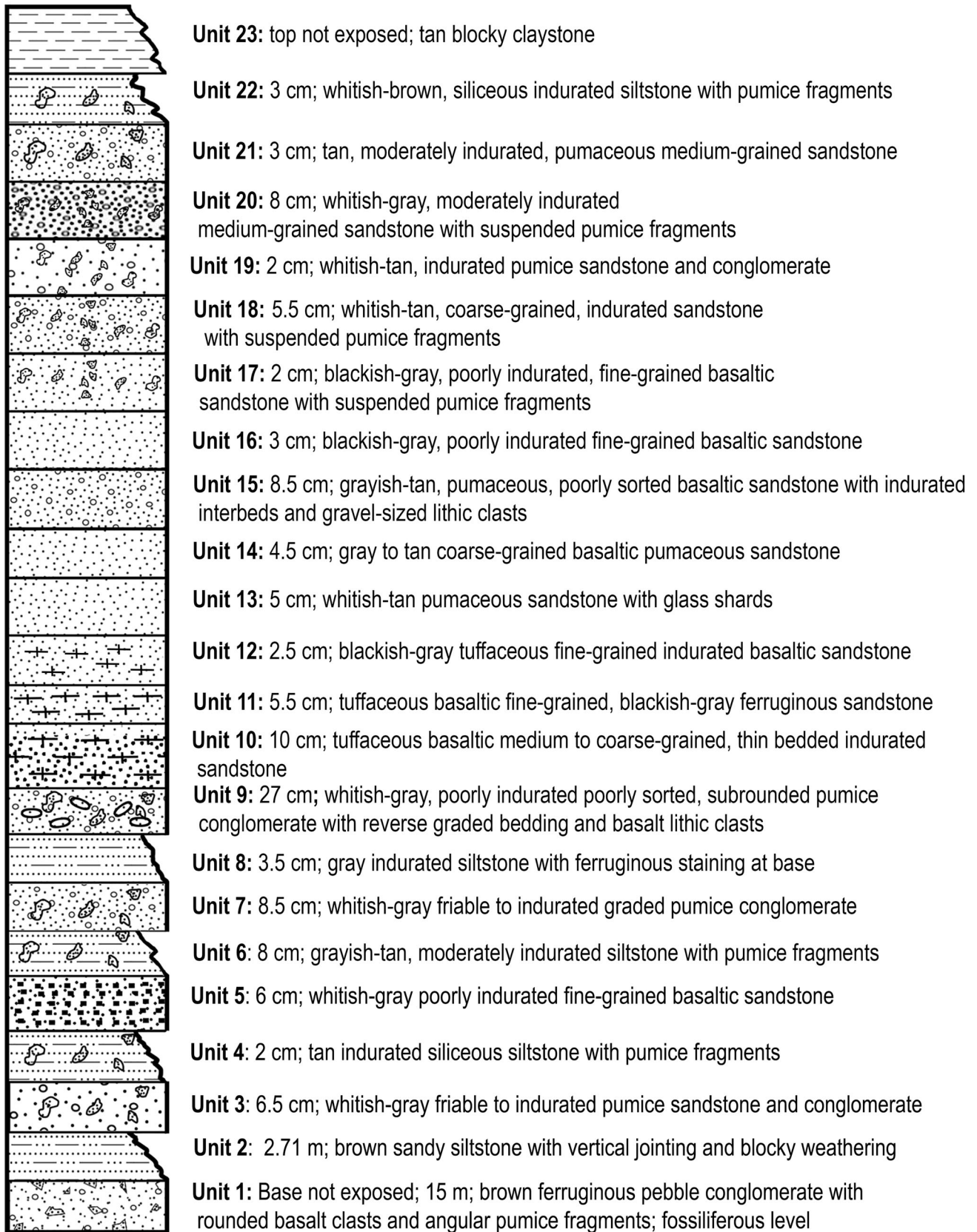


FIGURE 5. Measured section at the Megatylopus Quarry (ULGM Locality V-32) in northern Lake County, Oregon, illustrating the lithostratigraphical unit (Unit 1) from which specimens of *Neotragocerus* were derived.

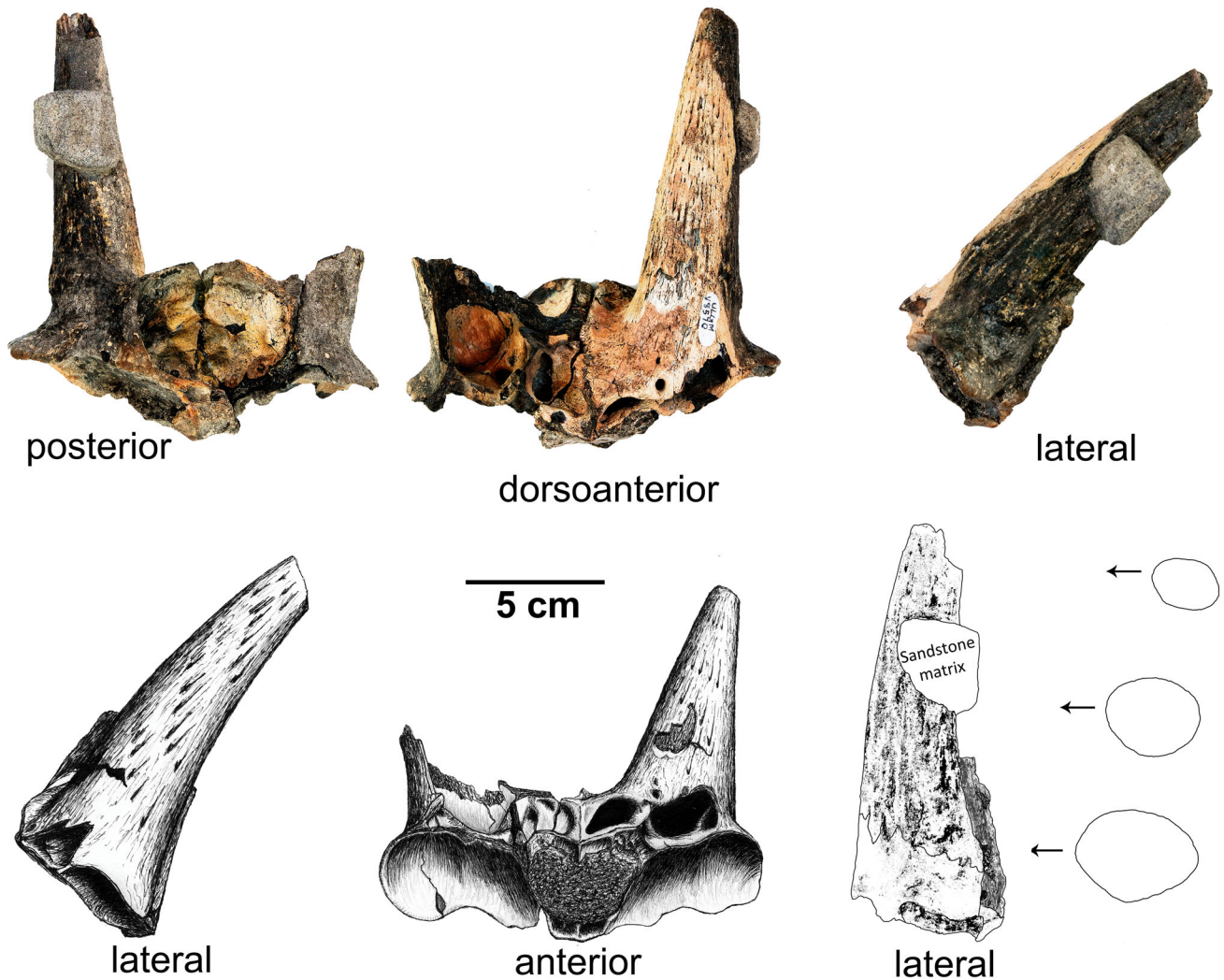


FIGURE 6. ULGM V8570, calvarium of *Neotragocerus* sp. aff. *N. improvisus* from the Miocene Fort Rock Formation at ULGM Locality V-51, transverse cross sections along the horn core are illustrated; anterior view and tilted lateral views are oriented in approximate life position; the anterodorsal and posterior views taken with horn cores oriented vertically.

by approximately 50 m were found to fit together, forming the first known calvarium of *Neotragocerus*, and indicate differential transport after exposure. Tooth enamel fragments and two fragmentary jaws with broken dentitions were recovered. Overall, the occurrences indicate an autochthonous assemblage, which upon erosion, were exposed for extended periods, perhaps for centuries, and indicate that the localities had not been previously collected, providing a relatively unbiased sample.

Abbreviations

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, NY, U.S.A.; **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **PU**, Princeton University Geological Museum, now housed at the Yale Peabody Museum, New Haven, CT, U.S.A.; **RAM**, Royal Alberta Museum, Edmonton, Alberta; **SBCM**, San Bernardino County Museum, Redlands, CA, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, CA, U.S.A.; **ULGM**, University of Louisiana Geology

Museum, Lafayette, LA, U.S.A.; **USNM**, United States National Museum, Washington, DC, U.S.A.

Abbreviations—**MN**, Mammifères Néogènes (Mein biochronological zones); **NALMA**, North American Land Mammal Age.

Measurements—Specimen measurements were taken in mm with dial calipers. Tooth anteroposterior length (**AP**), transverse width (**Tr**), and height (**h**) in millimeters represent maximum dimensions to obfuscate the effects of occlusal tooth wear. The terminology of the tooth crown elements follows that of Pilgrim (1937), Gentry (1994), and Suraprasit et al. (2016).

Material

Neotragocerus specimens listed below are a sample of disarticulated material from the Fort Rock Formation of northern Lake County, Oregon. These specimens were collected under the authorization of Oregon (OR) paleontological resources use permits, OR #50519, OR #50882, OR #50889, and OR #50945, issued to the first author under the auspices of the United States Bureau of Land Management. The specimens collected under this authority were curated into the systematic

paleontological collections at the Geology Museum of the University of Louisiana, Lafayette (ULGM).

Specimens by Locality

The fossil specimens of *Neotragocerus* from the Fort Rock Formation include the following (analysis of the postcranial elements will comprise a later contribution but are listed to illustrate the extent of the collection):

ULGM Locality V-32 (Megatylopus Locality)—Horn cores: ULGM V6294, V8519, V8520, V14828; cranial fragments: V8518, V8522 (frontal); tooth fragments: V14003, V14004; femur (proximal): V14006 (head), V6298; malleolar: V14007; astragalus: V13965, V13972; phalanx: V8521.

ULGM Locality V-38 (Anything Goes Locality)—Atlas fragment: ULGM V8677; radioulna (proximal): V8680; radioulna (distal): V8679.

ULGM Locality V-51 (Mity Mite Locality)—Calvarium: ULGM V8570; horn cores: V8571, V8572, V8573; cranial fragments: V8574 (frontal), V8576 (?squamosal); dentaries: V8577 (right w/ M₁-M₂), V14830 (right w/ M₃), V8578 (articular process); tooth fragments: V8579 (4), V11614 (5); atlas fragment: V8580; vertebral centra: V8581 (2), V11620; humerus (distal): V8582; scaphoid: V8583, V8584; ectocuneiform: V8585; lunar: V8586; pisiform: V8599; femur: V8589 (head); patella: V8590, V8591, V11615; tibia (distal): V8592; astragalus: V8594, V8595 (2 fragments), V8596 (4 fragments), V11617; calcaneum (proximal): V8593, V11616; calcaneum (distal): V14831; navicular-cuboid: V8597 (3), V8598 (3); metapodial (distal): V8600, V8601 (2 epiphyses), V8602; phalanges: V8603 (2), V11618, V8604 (proximal), V11619 (proximal).

ULGM Locality V-52 (Tylopus High Locality)—Horn core: ULGM V8557; cranial fragment: V8556 (frontal); tibia (distal): V8558.

ULGM Locality V-57 (SPPL335 Locality)—Tooth fragments: ULGM V8625 (2); humerus (distal): V8626; femur (distal): V8627; astragalus: V8628; metapodials (distal): V8629 (2).

DESCRIPTIONS

Calvarium

The medium-sized calvarium (V8570) consists of the frontals, left horn core, and basal portion of the right core (Fig. 6). Enough of the cores is preserved to indicate divergence of 10 degrees from the sagittal plane and slight posterior curvature. On V8570, the pedicle is indistinct below the horn core, although a small area of smooth bone occurs medially below the horn core. Lack of a distinct pedicle was considered characteristic of the “boselaphins” (Solounias, 2007). The dorsal portions of both orbits are preserved below the horn cores. The anterior edges of the cores lie well anterior to the anterior edge of the orbit. The posterior margin of the core is nearly confluent with the posterior margin of the orbit. Therefore, the entire orbit lies below the posterior two-thirds of the horn core insertion.

Well-developed frontal sinuses with relatively low complexity (low number of struts; Farke, 2010) are completely separated by the metopic suture. A prominent supraorbital strut trends from the supraorbital canal posteriorly and curves to the medial wall to form the medial portion of the frontal sinus, which invades the intercornal portion of the frontal. Laterally, the corneal diverticulum of the frontal sinus is large and resembles a low, rounded cone with the apex extending up into the horn core. A small pocket of the sinus extends laterally above the orbit. On the well-preserved left side, the supraorbital foramen, which includes two small rounded foramina at the base of the core, are not in a depression or fissure and invade the supraorbital strut, the bony division between the two large

frontal sinus vacuities, to form the supraorbital canal. The anteroventral of the two dorsal foramina (Fig. 6) is round and larger (4 × 4 mm); the smaller posterodorsal opening is ovate (1.0 × 1.5 mm). The larger supraorbital foramen connects via the supraorbital canal with the large circular foramen in the dorsomedial portion of the orbit. This connection on *Neotragocerus* can be demonstrated on V8571, a broken horn core with frontlet on which the supraorbital canal illustrates connection directly with the orbit. On V8571, two small foramina occur close together in the medial portion of the dorsal orbit rather than one as exemplified by V8570. The superior borders of the orbits of V8570 project laterally and exhibit distinct dorsally concave rims that extend 11 mm laterally from the rise of the horn core.

The frontals are raised above the level of the orbits and possess a convoluted metopic suture between the horn cores, which although broken, forms an elevated midline ridge; lateral grooves occur between the ridge and the horn cores (Fig. 6). The coronal suture is also convoluted indicating the strong suturing of the cranium. The vault for the frontal lobes of the brain is an ovate cavern between the horn cores and represents a mold illustrating the gyrification of the brain. No postcornal groove appears. The horn core bases are 25 mm apart, diverge from the midline, and are curved posteriorly; the oblique anteroposterior axis of the core forms an angle of 40° with the sagittal plane, and the anterior edge of the horn core is tilted approximately 45° from vertical. The more completely preserved horn core has an ovoid cross section wider anteriorly becoming narrower and rounded distally (Fig. 6). A low, rounded, straight anterior keel-like ridge represents the intersection of the rounded medial portion of the core and the more flattened anterior face. A similar but fainter rounded interface occurs between the flat anterior face and the lateral face. Both subduced structures extend the length of the core. The horn core has a slight but distinct posterior curve (Table 1; for index of curvature) but no steps or medial curvature occur (the only adult core from Oregon without medial curvature); a faint, blunt posterior ridge can be felt better than seen on ULGM V8570, although preservation hinders definitive determination.

Horn Core

Horn cores were relatively common in the Poverty Basin localities; portions of nine very similar cores were recovered from localities V-32, V-51, and V-52. A variety of sizes of horn cores were recovered, suggesting juveniles to large adults. In addition to the horn core on the calvarium, one core is broken about two-thirds its length (V8571; Fig. 7A) and two smaller fragmentary cores were recovered from Locality V-51. Of these, V8572 represents an adult specimen, whereas V8573 appears to represent a subadult, based on slightly smaller size and less ossification. Four horn cores were discovered at Locality V-32; V6294 (Fig. 7B) and V8519 (Fig. 8A) are missing only the tips. (Fig. 8B) is broken half way up its length, and V14828 is a basal fragment; all appear to represent adult individuals. A very small short core with part of the frontlet attached from Locality V-52, V8557 (Fig. 8C), represents a juvenile. Small size and poor ossification indicate the young age of the individual. The development of the groove between the horn core and metopic suture approaches the size of an adult, whereas the horn core itself is diminutive. V8557 represents the youngest known juvenile of *Neotragocerus*.

Larger adult specimens correspond to the descriptions of *Neotragocerus improvisus*, with some differences. The horn cores are approximately 120 mm long when adult, with a slight posterior curvature (all indices of curvature are over 100; Table 1), possess indistinct pedicles, exhibit only short medial elevations of the frontal, are characterized by coarse discontinuous longitudinal furrows over the entire core that appear deepest and wider anteriorly and laterally, are slightly mediolaterally

TABLE 1. Measurements of horn cores of *Neotragocerus* spp. **Abbreviations:** **AP base**, anterior-posterior at burr base; **Tr**, transverse at burr base.

Measurement	Specimen								
	ULGM V8590	ULGM V8571	ULGM V8519	ULGM V6294	ULGM V8520	ULGM V8557	AMNH 14141	USNM 3941	RAM P85.18.29
AP base	42.4	40.2	42.0	39.7	40.2	26.1	36.9	41.5	37.3
Tr base	31.0	-	32.8	29.8	30.7	17.8	25.5	29.3	25.6
AP at 70 mm	26.5	-	27.8	27.5	-	-	16.3	-	-
Tr at 70 mm	21.0	-	22.1	22.0	-	-	13.2	-	-
Compression Index ¹	73.1	-	78.1	75.0	76.4	68.2	69.1	70.6	68.6
Preserved length	110.0	82.6	118.5	117.7	67.2	29.1	93.4	62.5	69.7
Estimated length	125-130	115-120	120-125	120-123	115-120	-	115	-	-
Index of curvature ²	108.0	~109.0	113.6	104.2	-	97	-	-	-

¹, Index of Compression = Tr base × 100/AP base (Kostopoulos, 2005).

², Index of Curvature = length of anterior face × 100/length of posterior face (Kostopoulos, 2005).

compressed becoming more circular near the tip, are slightly curved medially (except V8570 which appears to be a variant), have a basal cross section of an anteroposteriorly elongate ovoid wider anteriorly, and exhibit variation in subdued keel-like ridges. V6294 and V8519 from Locality V-51 are the most complete cores with only the tips broken away. All relatively complete cores except V6294 have portions of the frontal attached; the metopic suture is at least twice as thick as the coronal suture, especially notable on V8571 and V8520. The groove between the raised metopic suture and the horn core varies from V to U-shaped, depending upon depth. The four most complete cores (V6294, V8519, V8520, and V8571) and that of the calvarium (V8570) are complete enough to display subdued longitudinal keel-like ridges. All cores except one exhibit a low, rounded anterior keel-like ridge. V6294 lacks a subdued anterior keel-like ridge, but the core appears shorter and less ossified than the others, suggesting a younger adult. Alternatively, V8571 from Locality V-51, which is similar ontogenetically, appears to possess an anterior keel-like ridge and a raised posterior ridge. V8520 from Locality V-32 represents the most robust horn core, but is broken with only the lower third of the core preserved. A raised anterior keel-like ridge on V8520 extends from the core base to fade near the break where the cross section becomes rounded, and a case may be made for the occurrence of very faint posterior ridge. Therefore, a relatively distinct but subdued anterior, straight keel-like ridge that terminates medial to the supraorbital foramen appears to be typical but varies dependent upon ontogeny. Moreover, a straight blunt posterior ridge may occur, and finally, a case may be made for a faint, rounded longitudinal third ridge on some horn cores. V8520, which appears to be ontogenetically the oldest individual in the sample, may possess a faint lateral ridge as do V8571 and V8570 producing a somewhat triangular cross section. Overall, keel-like ridges are variable but the anterior appears the most persistent. The posterior and lateral ridges are more variable, fainter, and their interpretation may be equivocal.

Another important character of the horn core is the variation of the pedicle, which ranges from indistinct to extremely short. Of the five most complete cores, V6294 and V8519 exhibit little evidence of a pedicle, V8570 and V8571 have a small area devoid of coarse striae low on the medial surface below the core, and V8520 exhibits a short pedicle except posteriorly. The juvenile core (V8557) exhibits a rudimentary, indistinct pedicle, as do V8573 and V14828. A very small area of compact bone appears medially at the base of the core of V8572, although this may be owing to poor preservation. Overall, only one specimen displays a very short pedicle, which is incomplete posteriorly.

The base of each horn core is invaded by the corneal diverticulum of the sinus frontalis, even that of the juvenile, V8557

(Fig. 8C), with a short core of only 29.1 mm. The sinus at this ontogenetic stage invades two-thirds the length of the small core and fills the core base. Adult cores, at approximately 120 mm, show the sinus invaded the core base up only to the approximate level as that exhibited by the juvenile. However, the circumference of the sinus is enlarged to fill much of the core diameter. Dimensions of the medial portion of the sinus frontalis are variable. This sinus on the calvarium is large and very deep, extending posteriorly nearly half the anteroposterior diameter of the horn core, whereas that of the large core, V8520, appears more shallow. That of V8571, a smaller adult core, presumably representing a younger individual, is shallow and large, but deeper, larger, and more complex than that of V8520. Therefore, significant variation in size and depth of the medial portion of the frontal sinus exists, but the sinus occurs in all horn cores. A distinctive small sinus pocket extends antero-lateral to the major cavern of the corneal diverticulum on V8570 and V8520. This opening lies just above the orbit below the lateral margin of the horn core base, evincing the complexity and extent of sinus invasion in *Neotragocerus*.

V8519 exhibits taphonomic alteration (Fig. 8A). Two deep, puncture-like gouges occur, one laterally about halfway up the length of the core and another depression posteriorly near the base of the core. Both are irregularly ovate and were formed prior to fossilization. These gouges resemble those on a core of *Miotragocerus monacensis* (BSPG 1921 I 54) from southern Germany (Fuss et al., 2015) and suggest evidence of carnivore activity, predation and/or scavenging.

Cranial Fragments

Various cranial fragments were found associated with the horn cores and postcranial elements. V8518, V8522, V8556, and V8574 are portions of frontal bones. V8522 is a fragment of the braincase containing a raised crest formed by fused convoluted sutures and large openings of the frontal sinus. Internally, the bone possesses the imprint of the cortical gyri and sulci of the cerebral cortex. V8574 resembles a frontal fragment containing portions of frontal sinuses. V8518 and V8556 are the most complete of the cranial fragments, including a significant portion of the braincase, the thickened frontal suture, and excavation for the large sinus frontalis that lies within the horn core that was broken away. V8576 appears to represent fragments of the squamosal, but they are too poorly preserved to be definitive.

Dentary

Relatively little of the dentary is preserved. V8577 and V14830 are fragments indicating a relatively narrow ramus. The

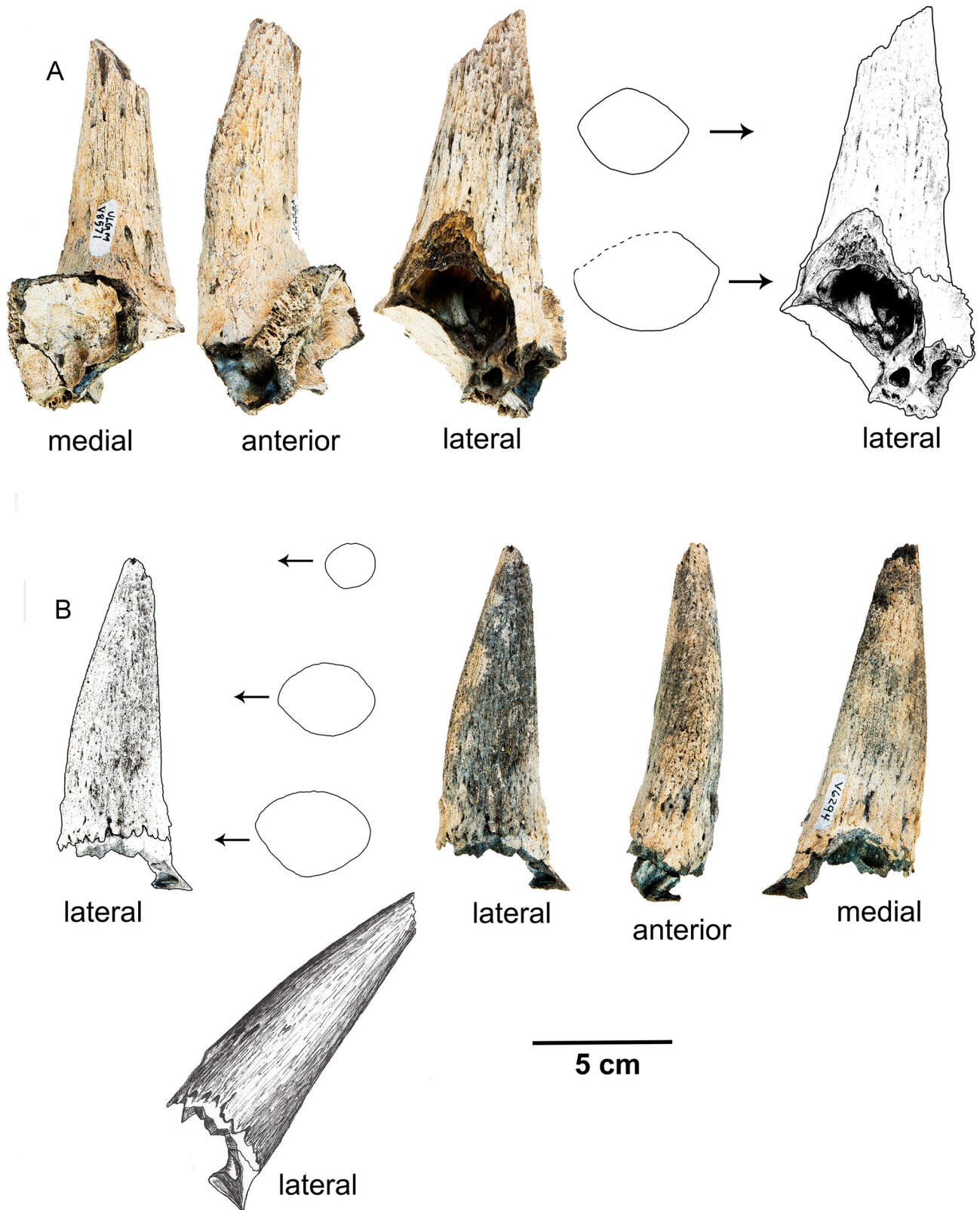


FIGURE 7. *Neotragocerus* sp. aff. *N. improvisus* from the Miocene Fort Rock Formation. **A**, ULGM V8571, right horn core from ULGM Locality V-51, transverse cross sections along the horn core are illustrated; **B**, ULGM V6294, left horn core from ULGM Locality V-32, tilted lateral view is in approximate life position; transverse cross sections along the horn core are illustrated.

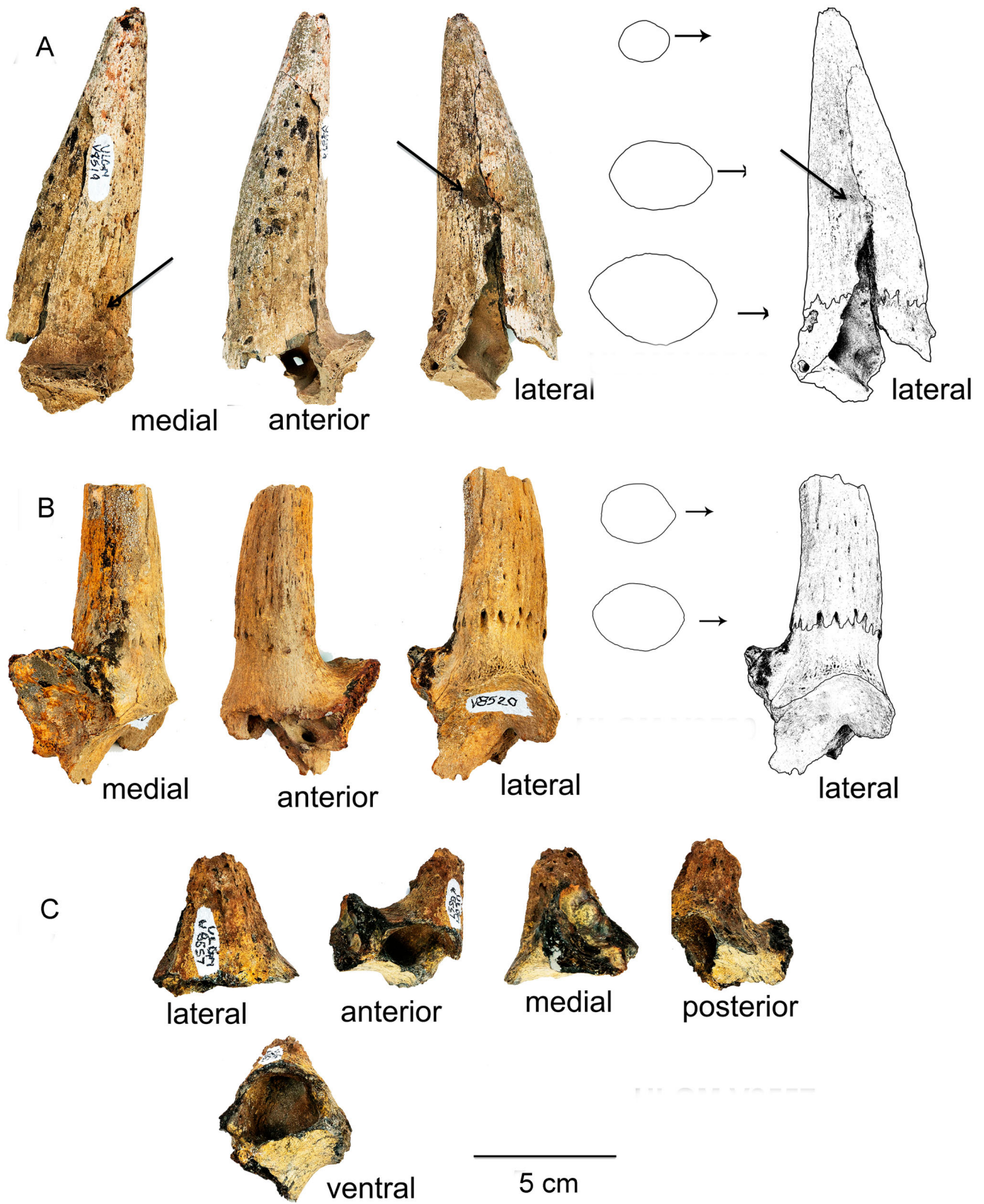


FIGURE 8. *Neotragocerus* sp. aff. *N. improvisus* from the Miocene Fort Rock Formation. **A**, ULGM V8519, right horn core from ULGM Locality V-32, arrows indicate gouges, suggestive of scavenging/predation; transverse cross sections along the horn core are illustrated; **B**, ULGM V8520, right horn core from ULGM Locality V-32, transverse cross sections along the horn core are illustrated; **C**, ULGM V8557, small juvenile left horn core and frontlet from ULGM Locality V-52.

ascending ramus is represented by V8578, an articular process with a portion of the coronoid process. The specimen is typical of selenodont artiodactyls with a thin coronoid process offset laterally from a delicate articular process.

Molars

Plesiomorphic bovid teeth are brachydont and can be difficult to distinguish from those of early cervids, except among other features, the absence of the *Palaeomeryx* fold of the lower molars in bovids (Pilgrim, 1939; Groves, 2007). No *Palaeomeryx* folds occur on the Oregon molars. Numerous brachyselenodont tooth fragments (V14003 and V14004 from Locality V-32; V8579 and V11614 from Locality V-51; and V8625 from Locality V-57) were found as float with the cranial and horn core specimens. Importantly, two partial dentaries with tooth remnants, V8577 (right dentary with M₁–M₂) and V14830 (right dentary with M₃) from Locality V-51, were recovered. The molars are at moderate stages of occlusal wear, although the M₃ appears more worn than the M₁–M₂. *Neotragocerus* is the predominant (79%) smaller artiodactyl in the assemblages, and none of the brachyselenodont teeth fragments resemble those of any other small ungulate occurring at the five localities. Therefore, the most parsimonious conclusion is that these brachydont teeth represent those of the most abundantly occurring artiodactyl, *Neotragocerus*.

The M₁–M₂ of V8577 (Fig. 9) are broken, bilobate, have broadly V-shaped slightly posteriorly slanted lobes, finely rugose lingual margins of lobes, and larger anterior lobes that are shorter transversely compared with their respective posterior lobes. The tooth crowns are occlusally worn, exhibit uncomplicated crescentic selenes, and possess a buccal wall deeply infolded almost to the lingual margin, forming a narrow transverse valley. The molars are moderately brachydont (see index of hypsodonty, Table 2; all are less than 100), have restricted crown necks and long roots, and subdued lingual ribs and stylids (although the metastylids appear somewhat more robust). A robust transverse accessory cuspule (ectostylid) lies at the base of the transverse valley on M₁; a small pillar-shaped cuspule occurs at the base of the valley on M₂. A faint basal cingulid exists on the anterior lobes, but no anterior transverse flange (goat-fold or anterior cingulid) occurs on either.

The M₃ of V14830 is broken with only a small posterior portion of the brachyselenodont anterior lobe surviving, the middle lobe

is nearly intact, but most of the crown of the posterior lobe is missing. The middle lobe has a posteriorly slanted, more rounded buccal margin compared with that of the M₁–M₂ of V8577, the crescentic fossettid curves gently posteriorly, and a subdued rib occurs on its lingual margin. A small accessory pillar lies in the transverse valley between the anterior and middle lobes; poor preservation prevents positive determination of the cuspid between the middle and posterior lobes. The transverse valley between the middle and posterior lobes is very narrow and extends nearly to the buccal tooth margin and the posterior end of the fossettid of the middle lobe. Therefore, the middle and posterior lobes are not widely separated compared with some other Miocene bovids. Although the crown is broken, the hypoconulid appears large, long, and forms a wide, inflated loop oriented obliquely rather than in line with the tooth row, similar to the M₃ specimens of the “*Boselaphini*” illustrated by Bibi (2007).

V14830 (Fig. 10A) exhibits some differences from the M₃, UCMP V29496 (Fig. 4), designated as ?*Neotragocerus* from Nebraska (Stirton and McGrew, 1935). The occlusal surface of UCMP V29496 is well worn, but the transverse width indicates similar overall size (Table 2). Moreover, the lingual tips of the lobes are not pointed but rounded, the posterior lobe is inflected, the external ribs are indistinct, and very small accessory pillars exist; all resemble those conditions of V14830. However, at the occlusal wear stage of UCMP V29496, the medial and posterior fossettids are joined. The remnant curved ends of the fossettids are preserved near the isthmus where the fossettids join and indicate the structure of fossettid terminations in earlier wear stages. Also, the valley between medial and posterior lobes is slightly wider than that of V14830, but not as great as in many other bovids. Both features appear to be the result of great occlusal wear. The inflection of the posterior lobe accounts for the relatively narrow transverse valley. These two features are decidedly different from many artiodactyls in which the lingual margin of the posterior lobe is in line with those margins of the anterior and medial lobes, creating the wide transverse valley. The similarity of V14830 and UCMP V29496 suggest they are congeneric, but the small sample size and no associated elements suggest a conservative reference as cf. *Neotragocerus* sp. indet. for the Nebraska specimen.

V8625 represents two halves of separate upper tooth fragments, and one (Fig. 10B) exhibits a very strong mesostyle, subdued rib, and some complexity of the selene. V8579, V11614, V14003, and V14004 are fragments principally of exterior tooth enamel with relatively subdued ribs.

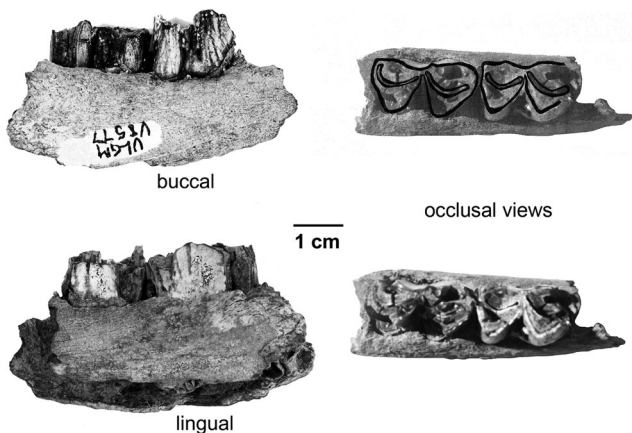


FIGURE 9. ULGM V8577, right dentary with M₁–M₂ of *Neotragocerus* sp. aff. *N. improvisus* from the Miocene Fort Rock Formation at ULGM Locality V-51.

TABLE 2. Measurements of ULGM teeth of *Neotragocerus*. **Abbreviations:** AP, tooth anteroposterior length; h, height; Tr, transverse width.

Specimen	A-P max	Tr	h	Hypsodonty Index*
M ₁ ULGM V8577	16.8	10.4	14.0	83.3
M ₂ ULGM V8577	20.0	11.3	12.5	62.5
M ₃ ULGM V14830	-	10.6 (middle lobe)	17.0	-
M ₃ UCMP V29496	45.0	10.7 (middle lobe)	7.5	23.0

*Index of Hypsodonty = Height of posterior lobe/occlusal length × 100 (Kostopoulos, 2005); differential wear greatly affects this index.

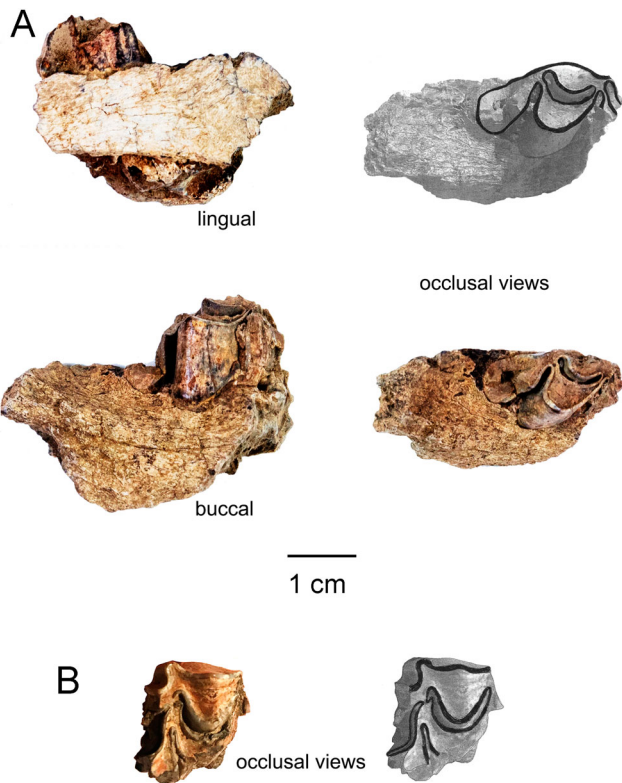


FIGURE 10. *Neotragocerus* sp. aff. *N. improvisus* from the Miocene Fort Rock Formation. **A**, ULGM V14830, right dentary fragment with broken M_3 from ULGM Locality V-51; **B**, ULGM 8625, upper molar fragment from ULGM Locality V-57.

COMPARISONS AMONG NORTH AMERICAN *NEOTRAGOCERUS*

The bovid specimens from Oregon exhibit both similarities and differences with previously known North American *Neotragocerus* specimens. The type specimen of *Neotragocerus improvisus* (AMNH 14141) from the lower upper Hemphillian (Hh3) of Nebraska is a nearly complete horn core, which as figured (Matthew and Cook, 1909:fig. 413; Frick, 1937:fig. 542), appears broken at the base on the medial edge. However, the actual specimen has the medial portion of a frontlet attached (Fig. 2A). The horn core is perfectly straight, approximately 115 mm high, has an ovoid cross section, exhibits no ridges or keels, lacks a distinct pedicle, displays cancellous structure of fine discontinuous longitudinal grooves extending from the base to the core tip, the base of the core is invaded by the frontal sinus, and the frontal exhibits a raised metopic suture, which creates a midline ridge that forms the medial edge of a distinct groove between the ridge and the horn core. Many of these features are found among the Oregon horn cores. However, all those from Oregon are curved posteriorly and most are curved medially unlike the condition of *N. improvisus*. All but one exhibits a subdued anterior keel-like ridge that appears more similar to the subdued keels of *Sporadotragus*, *Miotragocerus valenciennesi*, or *Palaeoryx majori* (e.g., Kostopoulos and Karakütük, 2015; Kostopoulos (2005:figs. 12–14, 23) and unlike the distinct, sharp keels of taxa such as *Strepsiptax* or *Tragoptax* (e.g., Pilgrim, 1937; Khan et al., 2011; Kostopoulos and Karakütük, 2015). Many Oregon specimens also display posterior ridges and possibly even lateral ridges. Although the Oregon specimens display some variability of these ridges, most possess at least a

subdued anterior ridge and medial curvature, and all cores are curved posteriorly, suggesting an apomorphic condition. Of course, if specimens are recovered from the type area in Nebraska that exhibit curved horn cores with keel-like ridges, that hypothesis may require re-evaluation.

The broken horn core (F:AM 52140) from the upper early Hemphillian (Hh2) Aphelops Draw in Nebraska has not been previously described. Unfortunately, owing to the Covid pandemic, we could only inspect photographs that suggest a relatively straight core (Fig. 2B; orientations based on photographs may be equivocal) that is similarly constructed and of similar size (preserved length = 96 mm) as AMNH 14141. F:AM 52140 appears poorly preserved, exhibits an ovate cross section, longitudinal striations, but little indication of longitudinal subdued ridges. The base of the core is missing, so a pedicle or sinus could not be ascertained. Based on characters observable from the photographs, the specimen is herein regarded as *Neotragocerus improvisus*.

The second North American species, *Neotragocerus lindgreni*, from the Upper Miocene of Idaho is a portion of frontal with attached horn core (USNM 3941) that is broken distally and degraded along the lateral edge (Fig. 3A). It resembles the Oregon horn cores and that of *N. improvisus* in an ovate cross section, lack of distinct pedicle, longitudinal grooves, and distinct groove between the horn core and raised metopic ridge, which clearly indicates *Neotragocerus* as defined in North America. *Neotragocerus lindgreni* was differentiated from *N. improvisus* by being more slender and with slightly greater mediolateral compression (Merriam, 1918:527). However, direct comparison of the type specimens indicates that the reverse is actually the case; *N. lindgreni* is less slender and less compressed. Moreover, these particular features fall within the range of variation of the Oregon specimens, which are extremely limited stratigraphically and geographically, indicating a coherent sample. A posterior keel-like ridge occurs on USNM 3941, but the lateral side of the core is heavily abraded. Lateral views suggest the core is straight as with *N. improvisus* and unlike those of the Oregon specimens, particularly in the lack of posterior curvature. Given these considerations, *N. lindgreni* appears similar to *N. improvisus*. However, it must be noted that this specimen is poorly preserved, especially laterally. Degradation of this face provides an illusion of medial curvature, but the preservation is too poor for certainty. Overall, this specimen is so poorly preserved that many salient features of the Oregon specimens are indeterminable. Therefore, insufficient characters are available to diagnose *N. lindgreni*, which is considered a nomen dubium (see Systematic Paleontology).

The Miocene *Neotragocerus* specimen from Alberta, RAM P85.18.29, collected from the Courtney West Pit, in the Hand Hills, northeast of Drumheller (Burns and Young, 1988), is a frontlet with horn core broken about half way up its length (Fig. 3B). The preserved frontal exhibits a wide groove between the horn core and the raised metopic ridge. The frontal sinus invades the core. Core ornamentation appears coarse, no definite ridges or keels are observed, some mediolateral compression appears, no posterior curvature occurs, and no definite pedicle could be differentiated. These features are most similar to those of *N. improvisus*.

A specimen mentioned but not described (Reynolds and Lindsay, 1999) from the mid-Hemphillian portion of the Muddy Creek Formation in eastern Nevada questionably assigned to *Neotragocerus* was considered to be from the mid-Hemphillian. This specimen, SBCM L2743-32, is a proximal phalanx and will be discussed further in a forthcoming contribution concerning the postcranial elements of *Neotragocerus*.

Overall, all known *Neotragocerus* cranial specimens from North America appear closely related based on core and frontal morphology. Only relatively minor differences can be

observed among previously described specimens. The collection from the Hemphillian of Oregon provides the first understanding of the potential intraspecific range of variation. Posterior and typically medial curvature of the cores, lack of significant medio-lateral compression, and common appearance of subdued keel-like ridges appear to separate the Oregon specimens from those previously known in North America. These features may indicate intraspecific variation, but until such characters are found on *N. improvisus*, this cannot be unequivocally ascertained.

DISCUSSION OF PREVIOUS ASSIGNATIONS OF *NEOTRAGOCERUS*

Because no apparent ancestors for *Neotragocerus* exist in North America, comparisons must be extended to the Old World bovids where a great diversity exists. In fact, G.G. Simpson (1945:287) stated, “With the possible exception of some rodents, [Bovidae] is the most difficult of all mammalian families from a taxonomic point of view.” Contradictory characters of *Neotragocerus* are in line with this viewpoint. The genus has been variously assigned to the Antilopinae (Frick, 1937), the Bovini (Kostopoulos, 2006), Caprini and “Rupicaprini” (Masini and Lovari, 1988; Harrington, 1971), but excluded from the “Rupicaprini” and particularly from the Caprini (Mead and Taylor, 2005), and from the Caprini and Bovini (Webb, 1998).

Considering these assignments, Frick (1937) included *Neotragocerus* within the Antilopinae but provided no rationale. The Antilopinae is comprised of the tribes Neotragini and Antilopini (Gentry, 1992). The Neotragini are polyphyletic (Gentry, 1990; Solounias, 2007; Hassanin et al., 2012), quite small, have upright horn cores that are slightly divergent, straight or slightly curved anteriorly, usually without keels or ridges, have postcornual fossae, usually are without basal pillars on molars (although Gentry, 2010, states no basal pillars exist on the molars of Neotragini), and labial lobes of lower molars strongly angled (Gentry, 1990, 2010). The Oregon *Neotragocerus* specimens are larger with more robust cores that normally curve slightly posteriorly and medially, lack postcornual fossae, have distinct basal pillars, and labial lobes of the lower molars that are not strongly angled unlike those of the Neotragini. Authors such as Gentry (1990, 2000), Gentry and Heizmann (1996), and Solounias (2007) suggested that *Homoiodorcas* Thomas 1981 could represent an ancestral form for the Antilopini, and therefore could be related to *Neotragocerus*. However, *Homoiodorcas* has been characterized as small, having horn cores large for the size of the skull with a convex anterior profile, cross section at base oblique, as if the lowest part of the anterolateral surface had been pressured to provide a slight inward tilt (Gentry, 1990, 2010). In addition, Gentry (2010:fig. 38.8) illustrated constriction of the horn core at the base and a postcornual depression, both of which do not appear on the Oregon specimens. Derivation of *Neotragocerus* characteristics from a *Homoiodorcas*-like progenitor appears improbable. If *Neotragocerus* were a member of the Antilopini, frontal sinuses that extend into the horn cores would not be expected (Solounias, 2007; Farke 2010). The Antilopini also possess distinct, prominent horn core pedicles, the dentition is normally hypsodont, lack basal pillars on the molars, and the hypoconulid on the M₃ is enlarged. Thus, *Neotragocerus* does not appear to be a member of the Antilopini.

Another alternative for assignment of *Neotragocerus* was within the Bovinae, which includes principally the Bovini, Tragelaphini, Tragoportacini, and Boselaphini sensu stricto (Kingdon, 1982; Bibi et al., 2009; Hassanin et al., 2012). The polyphyletic “Boselaphini” that included most of the Miocene–Pliocene bovids was revised to include the Tragoportacini, the Late

Miocene *Miotragocerus*–*Tragoportax* and allies, and the Boselaphini sensu stricto that includes the living *Boselaphus* and *Tetracerus*. The Bovini seems possible for assignment of *Neotragocerus* (Kostopoulos, 2006), whereas the other tribe (Allard et al., 1992) of the Bovinae, the Tragelaphini, appears less likely. The Tragelaphini are spiral-horned bovids now confined to southern Africa and appear to have been derived from the “Boselaphini” approximately 9 Ma (Kostopoulos and Koufos, 2006; Bibi, 2013). The high pedicle and spiral horns of the Tragelaphini separate them from *Neotragocerus*. Alternatively, the Bovini are more similar; this group also diverged from the “Boselaphini,” and the earliest known bovin comes from the Upper Miocene of the Siwaliks (Bibi, 2007; Gentry et al., 2014). This timing late in the Miocene (Hassanin and Ropiquet, 2004; Kostopoulos, 2006; Bibi, 2007) makes their affiliation possible. More derived Bovini are characterized by hypsodonty, a low, wide cranium, loss of horn core keels with the possible exception of the third keel, horn cores more divergent and positioned posterior to the orbit as the frontal overrides the parietal, cores less upright that trend transversely from their insertion, and exhibit a prominent pedicle (e.g., Gentry, 1990). Therefore, *Neotragocerus* may be a “boselaphin” with indistinct keel-like horn core ridges or a bovin with relict ridges. At our present state of knowledge, horn core position and structure of *Neotragocerus* suggest the former.

Various authors (Harrington, 1971; Masini and Lovari, 1988) have regarded *Neotragocerus* as a member of the “Rupicaprini” based on the contention that the fossil taxon is related to *Rupicapra*, the chamois, and *Oreamnos*, the mountain goat. Moreover, they have contended that *Neotragocerus* may have given rise to *Oreamnos*, although they prefer a later Quaternary dispersal of *Oreamnos* from Asia. These authors and others (e.g., Gliozzi and Malatesta, 1980) follow Thenius and Hofer (1960) in their contention that all three genera were derived from an ancestor similar to *Pachygazella grangeri* from China. However, *P. grangeri* exhibits stout cores with distinct pedicle, round cross-section at base, inserted backwards behind the orbits, swollen frontals, midline suture in a deep hollow (Gliozzi and Malatesta, 1980:fig. 6), and therefore appears more derived than *Neotragocerus*.

The simple horn cores of *Neotragocerus* suggest a relatively primitive bovid, and the monophyletic Boselaphini sensu stricto (Bibi et al., 2009) includes the living Indian bovids, *Boselaphus tragocamelus*, the nilgai, and *Tetracerus quadricornis*, the four-horned antelope (chousinga), that also exhibit horn cores with rounded cross sections, although the latter has faint indication of ridges (Pilgrim, 1939). However, the concave anterior horn core geometry does not correspond with that of *Neotragocerus*. Spassov and Geraads (2004:341) noted that the presence of an anterior keel was the only “constant feature” for fossil taxa included within the “Boselaphini,” and Bibi et al. (2009) utilized the Tragoportacini for the monophyletic group with keeled horn cores and triangular core cross section, among other characters (Bibi, 2009). Solounias (2007) indicated that little or no pedicle development was considered a principal defining character of the “boselaphins,” which would include the tragoportacines. Khan et al. (2011) noted that early “boselaphins” were characterized by horn cores inserted above the orbits. Additional “boselaphin” characters include horn cores relatively far apart somewhat similar to those of *Miotragocerus gaudryi* (Spassov and Geraads, 2004), *M. monacensis* (Fuss et al., 2015), or *Sporadotragus parvidens* (Kostopoulos and Karakütük, 2015), skull relatively broad across the orbits, large frontals with internal sinuses, horn cores inserted immediately above the posterior portion of the orbit, projecting rims above orbits, face only little angled downward against the cranium, supraorbital pits relatively simple and widely separated above and anterior to the orbits, supraorbital foramina rounded, not slit-like as in

later bovids, some backward shift of cores over time, core divergence and backward tilt variable, cores straight with slight lateral compression, curved medially or with slight torsion, cross section primitively circular or ovoid, progressively assuming a triangular shape with two strong primary keel-like ridges, the third angle rounded or sharp, no transverse ridges, brachydont or incipiently hypsodont dentition, premolar series relatively unreduced, upper molars quadrate with external styles and ribs, molars with basal pillars, lower molars generally without anterior transverse folds (goat folds), and teeth with rugose enamel (Pilgrim, 1939; Gentry, 1990). Based on these characters, the Oregon *Neotragocerus* appears closely aligned with the “Boselaphini” in possessing cores with slight posterior and medial curvature, slight lateral compression, no torsion or demarcations (steps), horn cores normally with anterior keel-like ridges, cores inserted above the posterior portion of the orbits, and significantly, the lack of a typical pedicle or its rudimentary formation.

The affinity of *Neotragocerus* with Miocene representatives of the “Boselaphini” is problematic. The relatively simple horn cores with relatively faint keel-like ridges appear plesiomorphic, more like living boselaphins and unlike most Old World fossil tragoportacins (Bibi, 2009; Bibi et al., 2009) from the later Miocene such as *Miotragocerus*, *Austroportax*, *Sivaceros*, *Sivoreas*, *Protragocerus*, *Kipsigicerus*, and *Tragoportax* that normally have long, strongly compressed horn cores characterized by anterior step-like indentations and well-formed keels (Solounias and Moelleken, 1992). Even some species of *Miotragocerus*, a genus with diverse morphology that probably requires revision (Hartung et al., 2020:281), that have relatively simple, compressed shorter horns, such as *M. monacensis*, *M. pannoniae*, or *M. abyssinicus*, exhibit greater differences in degree of horn core compression, demarcations, prominent anterior keels, posterior groove(s), no posterior curvature, and no raised ridge between horn cores (see Spassov and Geraards, 2004; Bibi, 2011; Fuss et al., 2015; Hartung et al., 2020). Other Miocene “boselaphins” with cores exhibiting distinct keels, strong mediolateral compression, great divergence, and/or torsion differ from *Neotragocerus* and include *Pachyportax*, *Plioportax*, *Samokeros*, *Selenoportax*, and *Sivaportax*. *Parabos* and *Phronetragus* appear to have horn cores that originate behind the orbits and are strongly inclined posteriorly unlike those of *Neotragocerus*. Fossil “boselaphins” with relatively simple horn cores are relatively uncommon and include such taxa as *Elachistoceras*, which is much smaller and exhibits a weak goat fold, and *Eotragus*. *Eotragus* from the late Early Miocene has often been considered a basal bovid from which the Boselaphini appear to have been derived (Solounias et al., 1995). In particular, the horn cores appear rather plesiomorphic in being relatively short, normally without keels, with greater bone mass at the base of the anterior portion of the horn core than at its posterior base, a medium-sized pedicle, and normally concave anteriorly and convex posteriorly similar to the living boselaphins. *Neotragocerus* likewise possessed relatively straight cores, but without a distinct pedicle and with the reverse curvature from *Eotragus* and *Tetracerus*, i.e., the anterior margin being convex and the posterior margin being concave from lateral view. Neither *Eotragus* nor *Neotragocerus* exhibit distinct keels as do most “boselaphins,” whereas the lack of a distinct pedicle in *Neotragocerus* does mirror the condition of the “Boselaphini.”

Although North American faunal evidence suggests that *Neotragocerus* entered North America from Asia, Chen and Zhang (2009) stated that the faunal composition of Miocene Chinese bovids differed from other areas of Eurasia. The Chinese bovids were dominated principally by the Hypsodontinae and endemic taxa of the Caprini, whereas the Eurasian Miocene bovids were dominated by *Eotragus*, “Boselaphini,” Tragoportacini, Bovini, spiral-horned Antilopinae, and primitive caprins. Clearly, the eastern Asian Late Miocene–Early Pliocene bovid

assemblages are dominated by caprins with fewer “boselaphins” and bovins. The dominance of caprins suggests that the North American immigrant could be a member of this group. If so, the morphologies of *Neotragocerus* suggest a very plesiomorphic member of the caprins. Typical caprin characters such as hypsodonty, long cores, lateral curvature, lack of medial curvature, absence of basal pillars on the molars, and transverse folds on the anterior of the lower molars (Gentry, 1992) are all absent in *Neotragocerus*.

Therefore, all these comparisons and assignments leave a quandary. *Neotragocerus* has plesiomorphic synapomorphies that appear to indicate ancestry to a number of bovid groups, but assignment to any one is premature. Even so, the contention that *Neotragocerus* dispersed from Eurasia seems most parsimonious given other Hemiphillian immigrants and the lack of North American ancestors. However, *Neotragocerus* cannot be assigned with confidence to any East Asian group, but most likely represents a relict “boselaphin,” a morphotype from which other bovids may have been derived.

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen 1848

Suborder RUMINANTIA Scopoli 1777

Superfamily BOVOIDEA Gray, 1821, sensu Simpson, 1931

Family BOVIDAE Gray, 1821

Subfamily BOVINAE Gray, 1821

Tribe “BOSELAPHINI” Knottnerus-Meyer, 1907, sensu Simpson 1945

Genus *NEOTRAGOCERUS* Matthew and Cook, 1909

Type Species—*Neotragocerus improvisus*.

Emended Generic Diagnosis—A moderately sized bovid with straight to gently posteriorly curved horn cores; with slight mediolateral compression; some with slight medial curvature; indistinct pedicle; porous surface characterized by coarse discontinuous longitudinal striae; slight divergence; cross section elliptical becoming more narrow and rounded toward the tip; no steps or transverse ridges; dorsoventral keel-like ridges variable; orbit lying below the posterior two-thirds of the horn core insertion; well-developed frontal sinuses that extend into the basal horn core and laterally to above the orbit; supraorbital foramen relatively simple; frontals with a convoluted metopic suture forming a midline ridge; well-defined grooves between the ridge and the horn cores; no postcornual groove. Dentition brachyselenodont with restricted crown necks and long roots, ectostylids, simple selenes, subdued ribs, narrow transverse valleys, and rugose enamel; upper molars with prominent styles; lower molars with less prominent stylids and no goat fold. M₃ middle lobe posteriorly slanted with rounded buccal margin, transverse valley between the middle and posterior lobes narrow extending nearly to the buccal tooth margin, middle and posterior lobes are not widely separated, and large hypoconulid, forming wide, inflated loop oriented obliquely to the axis of the tooth row.

Comparative Differentiation—*Neotragocerus* differs from *Austroportax*, *Kipsigicerus*, *Miotragocerus*, *Protragocerus*, *Sivaceros*, *Sivoreas*, and *Tragoportax* in the lack of well-formed keels, normally long, strongly compressed horn cores, and anterior step-like indentations (demarcations). *Neotragocerus* differs from *Pachyportax*, *Plioportax*, *Samokeros*, *Selenoportax*, and *Sivaportax* in the lack of horn cores with distinct keels, wide divergence, strong mediolateral compression, and/or torsion. *Neotragocerus* differs from *Parabos* and *Phronetragus* in the lack of horn cores that originate behind the orbits and strongly inclined posteriorly and from *Elachistoceras*, which has a weak goat fold and is much smaller. *Neotragocerus* differs

from *Eotragus*, which has horn cores with concave anterior margins and convex posterior margins.

Discussion—*Neotragocerus lindgreni* Merriam, 1918:526–527, fig. 2 is herein considered a nomen dubium (see *Neotragocerus* sp. indet. below).

NEOTRAGOCERUS IMPROVISUS Matthew and Cook,
1909
(Figs. 2A–B, 3B)

Holotype—AMNH 14141, horn core with attached frontlet.

Referred Specimens—RAM P85.18.29, horn core with frontlet; F:AM 52140, broken horn core.

Questionably Referred Specimens—AMNH 14136, maxillary fragment with M¹–M³; AMNH 14137, upper molars; SBCM L2743-32, proximal phalanx.

Diagnosis—Medium-sized bovid; horn cores straight and short with finely striated surface, delicate overall structure, indistinct pedicle; brachyselenodont molars.

Type Locality—Pliohippus Draw from the upper Hemphillian ZX Bar Locality, Sioux County, Nebraska.

Occurrences—Pliohippus Draw, ZX Bar Locality, Johnson Member of the Snake Creek Formation, Nebraska (Skinner et al., 1977); Aphelops Draw, lower Johnson Member of the Snake Creek Formation, Nebraska (Skinner et al., 1977); Courtney West Pit, Hand Hills, 26.5 km northeast of Drumheller, Alberta (Burns and Young, 1988); Mesquite Locality, Muddy Creek Fm., Clark County, Nevada (Reynolds and Lindsay, 1999).

Age—Hemphillian NALMA (9.0–4.75 Ma).

NEOTRAGOCERUS sp. aff. *N. IMPROVISUS*
(Figs. 6–11)

Referred Specimens—ULGM V8570, calvarium; ULGM V8571, V6294, V8519, V8520, V14828, V8557 (juvenile), V8572, V8573, horn cores; V8518, V8522, V8556, V8574, V8576 cranial elements; V8577, right dentary with M₁–M₂; V14830, right dentary fragment with M₃; V8579, V8625, V11614, V14003, V14004, tooth fragments; V8578, dentary articular process.

Localities—Megatylopus Locality, ULGM locality V-32; Mity Mite Locality, V-51; Tylopus High Locality, V-52; Anything Goes Locality, V-38; and 5PPL335 Locality, V-57.

Occurrences—Fort Rock Formation.

Age—Early late Hemphillian (Hh3) NALMA (6.8–5.7 Ma).

Discussion—The paucity of *Neotragocerus improvisus* from the type area in Nebraska presents a dilemma. The principal distinguishing feature of *Neotragocerus improvisus* described by Matthew twice in the original description (Matthew and Cook, 1909:413) and reiterated in 1918 is the lack of horn core curvature. He specifically utilized the lack of posterior horn core curvature to differentiate the taxon. In contrast, horn cores from Oregon are larger, more divergent, and curved both posteriorly and medially. Matthew and Cook's type specimen is small, delicate, and not well ossified, suggesting a young adult. The large sample of *Eotragus* from Sansan in France (Made, 2012) includes younger individuals with straight cores and older adults normally with curved cores and variations in between. Therefore, the Nebraska specimen may only be a variant based upon ontogeny. However, two cores in the Oregon sample (V6294 and V8571) appear to be of similar ontogenetic development as the Nebraska specimen, and they both exhibit curved horn cores. The straight core versus curved core differences may be the result of intraspecific variation rather than ontogenetic differences. However, until more specimens are available, the Oregon specimens are considered at least to have affinities with the Nebraska specimens.

NEOTRAGOCERUS sp. indet.
(Fig. 3A)

Referred Species—*Neotragocerus lindgreni*.

Referred Specimen—USNM 3941, horn core with attached frontlet.

Locality—“Idaho Group,” 4.8 km east of Boise, Ada County, Idaho (Merriam, 1918).

Occurrence—Chalk Hills Formation of the Idaho Group.

Age—Hemphillian NALMA (9.0–4.75).

Discussion—*Neotragocerus lindgreni* Merriam, 1918:526–527, fig. 2 is herein considered a nomen dubium. The type specimen is poorly preserved, and Merriam's (1918) diagnostic characters of being more slender, longer, and perhaps showing slightly greater lateral compression than that of *N. improvisus* (Merriam, 1918) are incorrect; the reverse is actually the case. These characters are valid at a generic level but are not diagnostic at species level.

cf. *NEOTRAGOCERUS* sp. indet.
(Fig. 4)

Referred Specimen—UCMP V29496, left M₃, designated as ? *Neotragocerus* (Stirton and McGrew, 1935).

Locality—UCMP Locality V-3332, Cherry County, Nebraska.

Occurrence—Ash Hollow Formation.

Age—?late Clarendonian or Hemphillian NALMA.

DISCUSSION

Neotragocerus appears best aligned with the “Boselaphini,” which appeared in the Early Miocene before 17.5 Ma (MN 4) in Pakistan (Kostopoulos, 2006), about 17.5 Ma in Namibia (Morales et al., 2003), and slightly later in France (Sansan) and dispersed across Europe, Asia, and Africa by the Middle to Late Miocene (Vrba, 1985; Gentry, 2010). “Boselaphins” became some of the most dominant bovids in the Late Miocene of Africa, Eurasia, and particularly the Indian Subcontinent (Khan et al., 2009; Patnaik, 2013; Khan et al., 2014). This expansive Eurasian bovid group was in place when the Bering connection to North America opened in the Late Miocene. Evidence of the Eurasian influence in the New World is recorded by the occurrences of *Gaillardia*, *Castor*, and *Promimomys* in Oregon and elsewhere (Martin, 2008, 2017; Martin et al., 2018). These occur in the late Hemphillian NALMA, and ⁴⁰Ar/³⁹Ar radiometric dates between 6.0–5.5 Ma of their generic co-occurrence have been derived from the McKay Reservoir Formation and the Fort Rock Formation in northern and southern Oregon, respectively (Martin et al., 2018). Of these, *Castor* has been found earlier in the early Hemphillian Rattlesnake Formation (7.30–7.05 Ma) of central Oregon (Samuels and Zancanella, 2011). This coincides with the late early Hemphillian, Hh2 (Tedford et al., 2004), dated approximately 7.5–6.8 Ma. Therefore, based on current knowledge, the latter dates represent an interval when dispersal to North America occurred and correspond with what is currently known for *Neotragocerus*. *Neotragocerus* specimens derived from lower upper Hemphillian deposits in Nevada and Aphelops Draw, Nebraska, correspond with the suggested Hh2 dispersal. However, the M₃ from Cherry County, Nebraska, which is considered cf. *Neotragocerus* sp. indet., may be late Clarendonian. Alternatively, Tedford et al. (2004) illustrated the Ash Hollow Formation ranging well into Hemphillian time.

The specimens of *Neotragocerus* from Oregon represent the most westerly occurrence of the bovid in North America. Webb (1998) suggested the distribution of *Neotragocerus* to be mainly the High Plains and Idaho. However, these specimens coupled with the occurrence in Nevada (Reynolds and Lindsay,



FIGURE 11. Reconstruction of *Neotragocerus* sp. aff. *N. improvisus* from the Miocene Fort Rock Formation of southern Oregon.

1999), indicate widespread geographic distribution of *Neotragocerus* across western North America by the end of the Miocene.

The Oregon sample of *Neotragocerus* provides the basis for initial interpretations of the habit of this medium-sized bovid. Some larger bovids, particularly with hypsodont dentitions, can traverse across varied niches and exploit varied habitats and diets. Their size can correlate with a lower metabolic protein requirement than that of smaller bovids (e.g., Khan et al., 2009). The brachydont dentition of *Neotragocerus* indicates habitat preferences containing softer vegetation such as browse. Medium size based on available osteological elements suggests that *Neotragocerus* would most likely be classified in ecological Category C of Janis (1982), open canopy woodland browsers, or a habitat of Light Cover utilizing the four-category habitat scheme of Kappelman et al. (1997) of plains, light cover, heavy cover, and forest (DeGusta and Verba, 2003). The restricted occurrence of the Oregon specimens to paleochannel deposits where such habitats would have occurred adds credibility to this contention.

Neotragocerus has short, relatively straight horn cores, with an ovate cross section (Fig. 11). Bovids with similar horn cores of short horn length (~ reach) and undeveloped catching arch are associated with dodging and stabbing intraspecific fighting behavior (e.g., Geist, 1966). Extant taxa that exhibit this fighting style include *Boselaphus*, *Sylvicapra*, *Neotragus*, *Oreotragus*, and *Oreamnos* (Lundrigan, 1996) and provide a model for the behavior of *Neotragocerus*.

CONCLUSIONS

1. The ULGM collection from Oregon represents the largest sample of *Neotragocerus* from North America and provides the first evidence of its range of morphological variation.
2. The ULGM specimens were found in the Fort Rock Formation of south-central Oregon. $^{40}\text{Ar}/^{39}\text{Ar}$ dates from tuffs within the fossiliferous detrital units range from 6.11 ± 0.08 to 5.74 ± 0.01 Ma and indicate deposition during the Late Miocene Epoch.
3. The *Neotragocerus* remains from Oregon were associated with typical Hemphillian taxa such as *Gaillardia*, *Pliotaxidea*, *Dipoides*, *Castor*, *Teleoceras*, *Megatylopus*, and *Promimomys* (= *Prosomys*). The temporally restricted occurrence of *Promimomys* and probably *Gaillardia* coupled with the

radiometric dates indicate an early late Hemphillian (Hh3) time of deposition.

4. *Neotragocerus* represents dispersal into North America from Eurasia during the Hemphillian along with *Gaillardia* and *Promimomys*; all three taxa co-occur in the Fort Rock Formation of northern Lake County, Oregon. These occurrences in the Pacific Northwest provide additional evidence of the path of dispersal via an early Bering land connection.
5. The occurrences of *Neotragocerus* in Nevada and at Aphelops Draw in Nebraska suggest a late early Hemphillian (Hh2) time for the first appearance of bovids in North America.
6. The Oregon sample represents the most northwesterly occurrence of *Neotragocerus* and indicates its geographic range throughout western North America during the Late Miocene.
7. The association of dental elements with the horn cores in Oregon suggests that the earlier assignments of dentitions by Matthew and Cook (1909) may have been correct.
8. Oregon specimens exhibiting relatively simple horn cores with slight medial and posterior curvature and brachydont dentition suggest assignment to the “Boselaphini” but are unlike most Late Miocene medium-sized tragoportacins such as most species of *Miotragocerus* or *Tragoportax*, exhibiting triangular, greatly laterally compressed horn core cross sections with sharp posteroexternal keel and unlike the large “boselaphins” such as *Selenoportax* or *Pachyportax* (Khan et al., 2014). They appear more closely related to the living boselaphins, although they are distinctly different. The relatively late occurrence of a taxon with such plesiomorphic characters suggests a relict “boselaphin,” and may represent a morphotype that gave rise to other bovids. *Neotragocerus* represents evidence of the penetration of the “Boselaphini” into the New World during the Miocene.
9. *Neotragocerus* does not appear closely related to any known fossil or extant North American Bovidae.
10. The Oregon horn cores that curve posteriorly and normally medially are unlike those of *Neotragocerus improvisus* or *Neotragocerus lindgreni*, which were described as perfectly straight (Matthew and Cook, 1909; Merriam, 1918).

Moreover, the specific characters utilized by Merriam (1918) to diagnose *N. lindgreni*, relative slenderness, length, and compression are valid at the generic level but not at the specific level. Therefore, *Neotragocerus lindgreni* is considered a nomen dubium.

11. The diminutive, short horn core (V8557; Fig. 8C with part of the frontlet attached from locality V-52) of *Neotragocerus* represents the first known North American bovid calf.
12. The frontal sinuses of *Neotragocerus* are large, bipartite, not complex, invade the base of horn core, and extend over the orbits. This Late Miocene taxon evinces frontal sinuses in the “Boselaphini” in North America.
13. Short, relatively straight ovate horn cores of *Neotragocerus* indicate a dodging/stabbing intraspecific competitive behavior.
14. The medium size of *Neotragocerus* suggests a habitat of Light Cover (Kappleman et al., 1997). Size coupled with a brachydont dentition with simple occlusal structures indicate habitat preferences containing softer vegetation, a browsing folivorous habit, and suggest an open canopy woodland browser (ecological Category C of Janis, 1982). The occurrence of the Oregon specimens in riparian deposits adds credibility to these contentions.

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