Chronostratigraphy and Paleontology of the Mid-Cretaceous Wayan Formation of Eastern Idaho, with a Description of the First Oryctodromeus Specimens from Idaho

Laurel J. Krumenacker
Brigham Young University - Provo

Follow this and additional works at: https://scholarsarchive.byu.edu/etd

Part of the Geology Commons

BYU ScholarsArchive Citation
https://scholarsarchive.byu.edu/etd/2286

This Thesis is brought to you for free and open access by BYU ScholarsArchive. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.
Chronostratigraphy and Paleontology of the mid-Cretaceous Wayan Formation of Eastern Idaho, with a Description of the First *Oryctodromeus* Specimens from Idaho

L.J. Krumenacker

A thesis submitted to the faculty of Brigham Young University in partial fulfillment of the requirements for the degree of Master of Science

Brooks B. Britt, Chair

Thomas H. Morris

Scott M. Ritter

Department of Geological Sciences

Brigham Young University

December 2010

Copyright © 2010 L.J. Krumenacker

All Rights Reserved
ABSTRACT

Chronostratigraphy and Paleontology of the mid-Cretaceous Wayan Formation of Eastern Idaho, with a Description of the First *Oryctodromeus* Specimens from Idaho

L.J. Krumenacker

Department of Geological Sciences

Master of Science

The mid-Cretaceous Wayan Formation of Idaho consists of floodplain-deposited siltstones and mudstones, with subordinate fluvial sandstones and conglomerates. Deposition occurred in a tectonic foredeep at the toe of the Sevier thrust complex. Measurement of two incomplete and one complete section indicates a thickness of roughly 1,344 meters in the study area. No laterally extensive marker beds are present but the lower Wayan contains distinct chert pebble conglomerates, and the middle Wayan may contain a higher relative abundance of fluvial sandstone. Known fossil localities are limited to the lower and middle portions of the formation.

The Wayan Formation, as currently defined, has a flora consisting of the ferns *Gleichenia* and *Anemia*, conifers, and angiosperms. This flora compares best with the Cenomanian aged Dakota Sandstone flora of Westwater, Utah. The vertebrate fauna is overwhelmingly dominated by the small burrowing ornithopod *Oryctodromeus* with other vertebrates being rare, consisting of a small dromaeosaurid theropod, iguanodontid grade ornithopods, and a large crocodilian similar to *Deinosuchus*. The fauna is most similar to the Cenomanian Blackleaf Formation of Montana. Prior to this report, only fragmentary dinosaurian remains had been reported from Idaho. The recovery of 10+ individuals of *Oryctodromeus*, some reasonably complete and partially articulated, provide significant insights into this genus, including an elongate femoral head projecting at roughly 40° from the femoral shaft, elongate cervical and dorsal centra, and abundant ossified tendons in the dorsal and caudal columns. Taphonomic evidence supports previous suggestions of adult/juvenile social groups and burrowing behavior in this taxon.

New detrital zircon U-Pb dates and palynological analyses support a latest Albian to Cenomanian age for the Wayan Formation, but provide little additional age resolution. The tightest age resolution is provided by faunal correlation using *Oryctodromeus*, a taxon previously known only from the Cenomanian-age Blackleaf Formation of southwestern Montana. Similar tectonic settings, ages, lithologies, and the presence of *Oryctodromeus* in both faunas suggest synonymy of the Wayan and Blackleaf Formation, with the Wayan having precedence.

Keywords: Wayan, Blackleaf, ornithopod, Cretaceous, Idaho, *Oryctodromeus*
ACKNOWLEDGEMENTS

Some specimens described herein were recovered as part of the author’s undergraduate research on Cretaceous vertebrates of Idaho while attending Idaho State University and as a volunteer with Caribou-Targhee National Forest. A portion of fieldwork was funded through Idaho State University undergraduate research grants R-2002-26, FY04-R13, and FY05-R19. Collection occurred on National Forest System lands and was conducted under permits ID34, ID40, ID40-01, and under a voluntary agreement for paleontological monitoring of Forest Service lands. Thesis research, some fieldwork, and fossil preparation were funded by the Warren van Pelt Scholarship, the David Jones Foundation, and the BYU Museum of Paleontology.

I sincerely appreciate Dr. Brooks Britt, my graduate advisor, whose subdued enthusiasm for ornithischians, assistance, insight, and encouragement greatly contributed this project. Dr. Thomas Morris and Dr. Scott Ritter provided valuable criticisms as part of my committee. Dr. Rod Scheetz provided valuable input on ornithopod osteology and phylogeny and provided valuable criticisms on the manuscript. Sincere thanks to my undergraduate advisor and mentor at Idaho State University, Bill Akersten, who started and encouraged my work in the Wayan Formation. Special thanks also to my friend Steve Robison, who provided driving and field adventures, constant help in the field, provided supplies, and participated in discovery of and collecting of *Oryctodromeus* specimens. Clint Boyd and Min Huh provided relevant papers. Jack Horner provided access to *Oryctodromeus* material at the Museum of the Rockies. Dave Varricchio provided insightful discussions and suggestions. Chris Brochu and Eric Allen helped assess and identify crocodyliform material. Dr. William Tidwell assisted in identification of the plant material. Thanks to my father, Dave Krumenacker, for helping collect BYU 19347. Gerald
Waanders and Dennis Braman performed palynological identifications and interpretations. Sierra Shulberg assisted in zircon processing and Garrett Schwanke provided assistance in the field. Mark Pecha and Alex Pullen provided assistance with zircon analysis. Ashley Scheetz assisted in specimen preparation. Adam McKean helped with technical preparation of this thesis and Mariah Chambers assisted with figures. Thanks especially to my wife Chantel, who has feigned enjoying fieldwork for my benefit.
In memory of my friend Shawn Rich Sorensen, who was an example of how to have faith in the hardest of times.
This thesis consists of two complete chapters, each with its own abstract, figures, tables and references.
1 TABLE OF CONTENTS

ABSTRACT .............................................................................................................................. II

ACKNOWLEDGEMENTS.......................................................................................................... III

1 TABLE OF CONTENTS .......................................................................................................... VII

2 CHAPTER 1: CHRONOSTRATIGRAPHY AND PALEONTOLOGY OF THE MID-CRETACEOUS WAYAN FORMATION OF EASTERN IDAHO ................................................................. 1

3 ABSTRACT ........................................................................................................................... 1

4 INTRODUCTION ................................................................................................................... 3

5 GEOLOGIC AND PALEONTOLOGIC BACKGROUND ................................................................ 4
  5.1 Geologic and geographic setting ....................................................................................... 4
  5.2 Description and lithologic character ................................................................................. 6
  5.3 Tectonic setting ................................................................................................................ 7
  5.4 Previous paleontological work ......................................................................................... 8

6 MATERIALS AND METHODS ............................................................................................. 9

7 STRATIGRAPHY .................................................................................................................... 9
  7.1 Stratigraphic framework and background ....................................................................... 9
  7.2 Localities of study ........................................................................................................... 10
    7.2.1 Schmitt and Moran (1982) measured section ............................................................... 12
    7.2.2 Tincup Canyon measured section ............................................................................. 12
    7.2.3 Miners Delight Creek measured section ................................................................... 13
    7.2.4 McCoy Creek measured section ............................................................................. 14

8 GEOCHRONOLOGY .............................................................................................................. 18
CHAPTER 2: AN OSTEOLOGICAL DESCRIPTION OF ORYCTODROMEUS
SPECIMENS FROM IDAHO, THE MOST ABUNDANT DINOSAUR OF THE WAYAN FAUNA,
AND THE FIRST OCCURRENCE OUTSIDE OF MONTANA

ABSTRACT

INTRODUCTION

GEOLOGY

AGE

SYSTEMATIC PALEONTOLOGY

Horizon and Locality

Revised diagnosis

Terminology and Methods

Description

Skull

Dentary

Dentary Teeth

Axial Skeleton

Cervical Vertebrae

Dorsal Vertebrae

Dorsal Ribs

Sacral Vertebrae

Caudal Vertebrae

Chevrons

Appendicular skeleton

Coracoid

Scapula

Humerus

Ulna

Manus

Ilia

Ischium

Pubis

Femur

Tibia

Fibula

Tarsus

ix
DISCUSSION ................................................................................................. 78

18.1 FUNCTIONAL MORPHOLOGY AND BEHAVIOR ........................................... 78

18.2 PALEOBIOGEOGRAPHY ........................................................................... 82

19 CONCLUSIONS AND SIGNIFICANCE ......................................................... 83

20 REFERENCES .............................................................................................. 83

CHAPTER 1 FIGURES AND TABLES

FIGURE 1 ........................................................................................................ 5
FIGURE 2 ........................................................................................................ 15
FIGURE 3 ........................................................................................................ 16
FIGURE 4 ........................................................................................................ 17
FIGURE 5 ........................................................................................................ 22
FIGURE 6 ........................................................................................................ 26
FIGURE 7 ........................................................................................................ 29
TABLE 1 ......................................................................................................... 34
TABLE 2 ......................................................................................................... 35

CHAPTER 2 FIGURES

FIGURE 1 ........................................................................................................ 53
FIGURE 2 ........................................................................................................ 69
FIGURE 3 ........................................................................................................ 73
FIGURE 4 ........................................................................................................ 79
FIGURE 5 ........................................................................................................ 81
FIGURE 6 ........................................................................................................ 83
CHAPTER 1: CHRONOSTRATIGRAPHY AND PALEONTOLOGY OF THE MID-CRETACEOUS WAYAN FORMATION OF EASTERN IDAHO

ABSTRACT

The mid-Cretaceous Wayan Formation of eastern Idaho consists of 1,344 m of highly variegated fluvial siltstone and mudstone, with subordinate sandstone and conglomerate. Deposition occurred in a tectonic foredeep associated with early events of the Sevier Orogeny. Measurement of one complete section, two incomplete sections, and incorporation of a previously measured incomplete section show an apparent lack of laterally continuous marker beds that permit regional correlation. Nonetheless, a dominance of coarse chert pebble conglomerates and coarse sandstones characterize the lower portion of the Wayan, while a predominance of fluvial sandstones over mudstones tentatively characterizes the upper-middle Wayan. Abundant calcareous nodules indicate a semi-arid, highly seasonal setting dominated the depositional environment.

Previous age estimates place the Wayan in the middle Albian stage of the Cretaceous Period. The first radiometric dates, recovered through detrital zircon analysis, indicate the base of the formation is no older than the Albian/Cenomanian boundary, while the top is early to middle Cenomanian in age. Palynologic data from three new localities compliments the radiometric dates and again suggests a middle Cretaceous age.

Fossils from the formation consist of a moderately diverse flora and a low diversity fauna. The macro-flora is known from one locality and consists of three fern species -- two species of *Gleichenia* and *Anemia*, as well as conifers and angiosperms. The Wayan flora is most
similar to the Cenomanian Westwater flora of the Dakota Formation of eastern Utah. Palynomorphs indicate conifers and ferns dominated the flora. These floral remains recovered suggest a setting of possible fern prairies and/or mixed angiosperm and conifer forests with a fern understory. Marine microplankton in some samples indicate a marine influence, suggesting the fluvial systems at times were low-lying and close to the Mowry Sea. With the exception of the small burrowing ornithopod *Oryctodromeus*, vertebrate fossils are rare but include a large crocodilian similar to *Deinosuchus*, a small dromaeosaurid theropod, and iguanodontid-grade ornithopods. The Wayan vertebrate fauna is most similar to the age-equivalent Blackleaf Formation of western Montana due to the presence of *Oryctodromeus* and a paucity of large dinosaurs.
4 INTRODUCTION

The Idaho/Wyoming Thrust Belt, located along the Idaho and Wyoming border, contains more than 3000 m of Lower to mid-Cretaceous terrestrial sediments deposited in a rapidly subsiding tectonic foredeep proximal to early Sevier event thrusts (Eyer, 1969; Wiltschko and Dorr, 1983; Dorr, 1985). In the vicinity of the Caribou Mountains of southeastern Idaho (Fig. 1) these sediments consist of the alternating fluvial and lacustrine stratigraphic packages: the Gannett Group, Smiths Formation, Wayan Formation, and Sage Junction Formation. One fluvial package in this series, the Wayan Formation, has received relatively little attention since its initial description (Mansfield and Roundy, 1916). The lack of attention is likely a function of poor exposures due to vegetative cover, limited aerial extent, and structural deformation. Previous work focused on regional descriptions that are now outdated (Mansfield, 1927; Mansfield, 1952) and stratigraphy and provenance (Schmitt and Moran, 1982). The Wayan Formation has been considered to be middle Albian in age, based on stratigraphy (Schmitt and Moran, 1982; Dorr, 1985), paleontology (Dorr, 1985), and palynology (Schmitt and Moran, 1982). Previously, the paleontology of the formation has been poorly known, consisting of a fragmentary and limited fauna (Dorr, 1985; Weishampel et al., 2002; Krumenacker, 2005) and a very limited flora (Andrews, 1943; Andrews and Kern, 1947; Crabtree, 1987; Wing and Boucher, 1998).

Recent paleontological work has resulted in the recovery of a modest vertebrate collection dominated by the remains of the small fossorial ornithopod *Oryctodromeus* (described below), with other vertebrates being rare (Dorr, 1985; Weishampel et al., 2002, Krumenacker, 2005; Krumenacker et al., 2007). Fortuitously, the search for fossil vertebrates has also
facilitated the discovery of the first foliage known from the Wayan Formation as it is currently defined.

The objectives of this study of the Wayan Formation are to revise and describe the fossil fauna and flora, describe the stratigraphic and geologic setting of fossil localities, and present new age data using palynomorphs and detrital U-Pb zircon dates.

5 GEOLOGIC AND PALEONTOLOGIC BACKGROUND

5.1 Geologic and geographic setting

The Wayan Formation crops out primarily in the Caribou Mountains of Bonneville and Caribou counties of southeastern Idaho, Idaho (Fig. 1A). In this area of Idaho Cretaceous strata (Fig. 1B) consist of alternating fluvial and lacustrine packages of the Early Cretaceous Gannett Group (in ascending order: Ephraim Conglomerate, Peterson Limestone, Bechler Formation, Draney Limestone, and Smoot Formation) which is overlain by the marginal-lacustrine Smiths Formation (Durkee, 1979). The Wayan overlies the Smiths and is itself overlain by the Sage Junction Formation. Farther to the north and east, in the Big Hole Mountains and Snake River Range, lateral equivalents of the Wayan, the marginal-marine Bear River Formation and the marine Aspen Formation crop out. To the southeast in Wyoming, Rubey (1973) defined three lateral equivalents of the Wayan Formation. In ascending order these are the variegated red beds of the Thomas Fork Formation, the fossiliferous freshwater deposits of the Cokeville Formation, and the variegated red beds of the Quealy Formation.
FIGURE 1. Study area and regional stratigraphy. Southeastern Idaho showing the three principle sites with stars (A), and, Cretaceous stratigraphy of the study area and correlative units (based on Dorr, 1985; Rubey, 1973; Dyman et al., 1989; Kirkland et al., 1999.)
5.2 Description and lithologic character

The Wayan Formation was originally described as 3,600 m of sandstone, shale, limestone, and conglomerate east of the small town of Wayan, Idaho (Mansfield and Roundy, 1916). No type section or reference section was, or has been, designated. In their description Mansfield and Roundy (1916) divided the Wayan into an upper and a lower unit (Mansfield, 1927). The lower unit consisted of, in ascending order: red soils, gray limestone with interbedded shale, calcareous redbeds, limestones and dark shale, redbeds and sandstone, dark shale overlain by massive limestone, sandstones, and sandstones and shales. The upper unit consisted of sandstone, shale, and some conglomerate. The lower boundary of the Wayan was poorly defined as the contact with the Tygee Sandstone, now the Smiths Formation (Rubey, 1973). The upper boundary was defined as the contact with overlying Tertiary-aged Wasatch and Salt Lake Formations (Mansfield and Roundy, 1916).

Rubey (1973) and Oriel and Platt (1980) recognized that much of the Wayan Formation, as originally described, included folded and faulted strata of the underlying Gannett Group (Eyer, 1969) and the Smiths Formation (Rubey, 1973). Likewise, the Sage Junction Formation of westernmost Wyoming (Rubey, 1973) has been recognized in southeastern Idaho (Oriel and Platt, 1980) and overlies the Wayan Formation as now defined (Schmitt and Moran, 1982; Dorr, 1985). The Sage Junction Formation is likely equivalent to the upper sandstones of the original Wayan (Mansfield and Roundy, 1916). Rubey (1973) defined the Smiths Formation as dark organic shales overlain by thick, tan, fluvial sandstones originally included in Mansfield and Roundy’s (1916) and Mansfield’s (1927) descriptions of the Wayan. Oriel and Platt (1980)
mapped and subdivided the Wayan utilizing Rubey’s (1973) newly defined Smiths and Sage Junction Formation. They defined the Wayan as: “Variegated red, purple, yellow and gray mudstone, siltstone, and sandstone; minor porcelainite, bentonite, and coal, about 1200 m thick”.

Schmitt and Moran (1982) considered the Wayan Formation to be mudstone-dominated with subordinate sandstones and minor conglomerates, limestones, and volcanic ashes. In addition, they described the provenance, general depositional setting, and stratigraphy of two incomplete sections in the lower part of the formation. Dorr (1985) summarized the lithology simply as highly color variegated siltstones and mudstones with abundant calcareous nodule horizons representing paleosols.

5.3 Tectonic setting

Deposition of the Wayan was directly related to early events of the Sevier Orogeny. During the Early and middle Cretaceous, the Paris and then the Meade Thrusts developed and migrated eastward in eastern Idaho (Wiltschko and Dorr, 1983; Dorr, 1985, DeCelles et al., 1993). Resultant crustal loading induced crustal subsidence and the development of a foredeep in easternmost Idaho (Dorr, 1985). Episodic uplift associated with these thrusts resulted in an Early to mid-Cretaceous clastic wedge more than 3 km thick in the Idaho and Wyoming Thrust Belt (Wiltschko and Dorr, 1983; Dorr, 1985). Earlier reports suggested that movement on the Paris Thrust only was responsible for generation of Wayan sediments (Wiltschko and Dorr, 1983; Dorr, 1985). More recent work (DeCelles et al., 1993) has shown that the Meade Thrust was active earlier than supposed, terminating in the early Late Cretaceous. And that the Crawford Thrust (DeCelles et al., 1993) was active much later than the Meade (DeCelles et al., 1993). Taken in conjunction with the age data presented below, this indicates that deposition of the
Wayan was actually caused by movement on the Meade Thrust and associated reactivation of the hindward Paris Thrust (DeCelles et al., 1993).

5.4 Previous paleontological work

Until recently, the Wayan has been considered to be relatively unfossiliferous (Dorr, 1985; Weishampel et al., 2002). The first fossils reported from the Wayan were an unidentifiable bone fragment and freshwater mollusks (Unio, Sphaerium, Viviparus, and Goniobasis; Mansfield, 1927). These fossils more likely belong to the Gannett Group and/or the mollusk-bearing sandstones of the Smiths Formation (Rubey, 1973) as currently defined. Nonetheless, rare freshwater gastropods molds and unionid bivalves are present low in the formation (pers. obs.) as it is currently defined.

Few fossil plants were reported from the Wayan Formation. Andrews (1943) reported conifer and cycad petrifactions associated with abundant false trunks of Tempskya (Andrews and Kern, 1947). Spackman (1948) reported dicotyledon petrifactions associated with Tempskya, and Wing and Boucher (1998) reported the angiosperm Sapindopsis.

Dorr (1983, 1985) reported the first significant vertebrate fossils, including a tooth he referred to Tenontosaurus and abundant dinosaur eggshell. Weishampel et al. (2002) reported isolated vertebrates, including possible neoceratopsian remains. Krumenacker (2005) and Krumenacker et al. (2007) summarized the vertebrate fauna and reported a small ornithopod now known to be Oryctodromeus (Krumenacker et al., in progress). The Wayan vertebrate fauna is summarized in Table 1.
MATERIALS AND METHODS

Three outcrop areas were utilized in this study: Tincup Canyon in Caribou County, and Caribou Basin and Jackknife Canyon in Bonneville County (Fig. 1A). The recessive nature of the formation, extensive vegetative cover, and structural deformation are such that no locality has previously yielded a complete stratigraphic. Each of the localities has been placed into a stratigraphic setting as conditions permit. Stratigraphic sections were measured with a Brunton and a Jacobs staff.

STRATIGRAPHY

7.1 Stratigraphic framework and background

Poor exposures and structural complexities have prohibited detailed stratigraphic resolution in the Wayan Formation (Schmitt and Moran, 1982; Weishampel et al., 2002). Schmitt and Moran (1982) conducted the most detailed study resulting in two incomplete measured sections limited to the lower and middle parts of the formation, the thickest being 585.6 m thick. Only one apparently complete and undistorted section of the Wayan is recognized (pers. obs.). It is in the western margin of Tincup Canyon (Fig. 1A), in Caribou County. Unfortunately this section is very poorly exposed due to abundant vegetative cover and outcrops are limited to partially vegetated roadcuts. The thickness of the formation at this locality is 1,344 m. While this seems anomalously thick for a terrestrial fluvial unit, it is comparable with thicknesses of laterally equivalent foredeep deposits in western Wyoming (Rubey, 1973). In addition, Huntsman and Platt (1985) mapped the geology of the areas surrounding Caribou Mountain of Bonneville and Caribou counties, and determined the Wayan Formation to be roughly 1300 m thick.
No marker beds have been recognized or described in the Wayan, however some general relations and observations are of note. Rubey (1973) defined three formations in the Western Wyoming Overthrust Belt that are equivalent to the Wayan based on stratigraphic relations and lithologic similarities. In ascending order these are the Thomas Fork, Cokeville, and Quealy Formations. The Thomas Fork and Quealy are southeastward extending variegated redbed tongues of the Wayan, while the Cokeville consists of monotonous gray to tan fossiliferous limestones, siltstones, and sandstones representing poorly drained lowland floodplain environments proximal to the encroaching Mowry Seaway (Rubey, 1973). In the mid-Wayan of eastern Tincup Canyon, Oriel and Platt (1980) mapped what they called the ‘Wayan Sandstone” and suggested it may be equivalent to the Cokeville Formation, located roughly 80 km to the southeast.

Below, I present data from four stratigraphic sections in the Wayan Formation, three of which were measured for this study. Fossil localities in the Wayan that are in a complete stratigraphic framework so far are limited to the lower and middle portions of the formation and occur in western Tincup Canyon.

7.2 Localities of study

Four stratigraphic sections are utilized in this paper, and a chart correlating each section is given in figure 6. The four sections are:

1) Schmitt and Moran (Fig. 2), Caribou Basin: This section begins at the base of the Wayan near a prominent vertical ridge of the Smiths Formation near 43° 08’ 59”N, 111° 14’ 56”, and ends near 43° 09’ 05”N, 111° 15’ 24”. This section is drawn based on information from Schmitt and Moran (1982).
2) Western Tincup Canyon: This is the only known area with an apparently complete and undeformed stratigraphic section. Unfortunately exposures are extremely poor for most of the section. Measurement was conducted in roadcut exposures along Idaho Highway 34. The base of the Wayan begins at 42° 58’ 19”N, 111° 15’ 11”. Here the base of the Wayan is marked by the first color variegated soils directly above massive sandstones of the Smiths Formation. The top of the Wayan is located at 42° 58’ 15”N, 111° 17’ 20” and is recognized by a meter-thick, medium to coarse-grained, thin bedded, silver gray sandstone typical of Wayan Formation sandstone. This unit is overlain by distinct massive tan sandstone and interbedded gray siltstone of the Sage Junction Formation.

3) Miners Delight Creek: Outcrops east of Miners Delight Creek (Dorr, 1985; Site K) in Caribou Basin. This site was selected because of the number of fossil localities in the area but the stratigraphic position of the section is uncertain. The section begins in silty soils at 43° 08’ 44”N, 111° 16’ 09” and ends in crossbedded sandstone at 43° 08’ 36”N, 111° 16’ 09”. The top of this section is roughly 40 m below the base of measured section 4.

4) McCoy Creek Section (fig. 4): North of McCoy Creek in Caribou Basin. The section begins in a deeply weathered gray horizon associated with a medium to coarse grained light-gray sandstone at 43° 09’ 41”N, 111° 17’ 18” and ends with the beginning of a covered interval at 43° 09’ 37”N, 111° 17’ 29”. Measured section 4 is above section 3, with roughly 40 m of cover separating them.
7.2.1 Schmitt and Moran (1982) measured section

The most detailed measured sections of the Wayan were presented by Schmitt and Moran (1982). In this study we utilize their thicker section (585.6 m) along the north side of McCoy Creek in Caribou Basin. This section (Fig. 2) spans the basal and lower middle of the Wayan Formation. While covered intervals are abundant, some details and trends are discernible. Medium to fine-grained sandstone with chert clasts comprise the exposed sediments in the lower 250 m while mudstone, siltstone, and minor sandstone comprise the balance of the section.

Significant fossils are limited to palynomorphs and macroscopic plant fragments from an organic shale designated unit 94 in the original description (Schmitt and Moran, 1982). This layer is 440 m above the base of the formation. A bone fragment was also found just below this unit by the same authors.

7.2.2 Tincup Canyon measured section

Tincup Canyon (Fig. 1A) is significant because (1) it presents the most complete and undeformed section of the Wayan Formation and (2) fossil localities are relatively common and can be related to a stratigraphic framework. Exposures, however, are poor due to extensive vegetative cover. For this reason a detailed section is not figured. However, the formation thickness here of 1,344 m is striking.

Exposed portions of the lower 100 m are dominated by chert pebble and calcareous mud rip-up clast conglomerate, with minor sandstone and invertebrate-burrowed red siltstone. Above 100 m, exposures are dominated by variegated mudstone and siltstone, with subordinate sandstone. About 1000 m into the section, sandstone is more abundant in exposures, possibly
representing layers equivalent to the Cokeville Formation of Wyoming and the Wayan Sandstone of Oriell and Platt (1980). Above 1100 m variegated mudstone and siltstone again dominate with some sandstone interbeds.

Fossils discussed here are restricted to materials collected in-situ. A large ornithischian rib (IMNH locality 2273, no specimen number) was recovered 133 m above the section base from a red-green mottled siltstone below a well-indurated siltstone channel. Elongatoolithidae eggshell fragments, possibly representing a theropod nest, occur in a gray, silty mudstone at 156 m. A partial *Oryctodromeus* skeleton (BYU 19344) is from a nodular siltstone at roughly 501 m. The largest known dinosaur from the Wayan, a partial ankylosaur skeleton, was found at 1036 m. Stratigraphically, the highest fossils are abundant semionotid fish teeth and Elongatoolithidae eggshell from a calcareous rip-up clast conglomerate at 1082 m.

### 7.2.3 Miners Delight Creek measured section

The Miners Delight section (Fig. 3) is 133 m thick and it begins some 40 m above the McCoy Creek sections. Together, these measured sections represent just over 400 m of strata. The beds are easily traced laterally through aerial photos; however a change in dip and poor intervening exposures obscures the exact thickness of the covered interval. The Miners Delight section is siltstone dominated with some sandstone beds. Siltstones are typically mottled and contain calcareous nodules indicative of numerous paleosols. The stratigraphic position is unknown, but the dominance of mudstone and siltstone, the lack of pebble conglomerates and thick sandstones, and the presence of *Oryctodromeus*, indicate this section pertains to the upper lower to middle Wayan.
Fossils are common in this section. *Oryctodromeus* (BYU 19345) and a small theropod tooth (described below) were recovered from a fine-grained, gray sandstone at the top of the section. *Oryctodromeus* (BYU 19347) also occurs in a red siltstone with sand stringers and abundant calcareous nodules near the base of the section. At the base of the section is a calcareous mud rip-up clast conglomerate associated with a sandstone channel. This lag produces abundant broken and abraded bone fragments.

7.2.4 McCoy Creek measured section

Measuring 268 m thick and dominated by semi-regularly alternating siltstone and sandstone, this section (Fig. 4) roughly overlies the Miners Delight measured section. The stratigraphic position is unknown, but due to the dominance of mudstone and siltstone, the lack of pebble conglomerates and thick sandstones, and the presence of *Oryctodromeus*, this section is tentatively referred to the upper lower to middle Wayan.

This interval contains the highest concentration of fossil localities of any of the measured sections. *Oryctodromeus* fossils are known from a silty, grey mudstone roughly 20 m above the section base, fine grained sandstones at 60 and 225 m, and red nodular siltstone at 150 and 255 m. A small iguanodontid ornithopod (BYU 19349, described below) is known from a mottled, green-gray calcareous mudstone 10 m above the section base. Petrified wood and plant foliage (described below) is known from a well-indurated grey mudstone 190 m above the section base.
FIGURE 3. Miners Delight Creek measured stratigraphic section.
FIGURE 4. McCoy Creek measured stratigraphic section.
8 GEOCHRONOLOGY

8.1 Sample localities

Four locations (Fig. 1A) produced enough zircons for sampling to help determine the ages of the top and bottom ages of the Wayan Formation and to date significant fossil localities. These localities are numbered to correlate with the palynological localities describe below and are as follows:

1) Iowa Creek, Caribou Basin, roadcut north of McCoy Creek Road, roughly 120 m above the base of the Wayan, locality is at 43° 08’ 51” N, 111° 14’ 52” W.

2) Roadcut in western Tincup Canyon northeast of Idaho Highway 34. Unit is a medium to coarse-grained, thin-bedded, light-gray sandstone defining the top of the Wayan in this area. Locality is 42° 58’ 16” N, 111° 17’ 19” W.

3) Unit 91 of Schmitt and Moran’s (1982) McCoy Creek measured section. This unit is a well indurated, gray mudstone one and a half meters above a gray-green to brown mottled siltstone. It occurs in a meander scar north of McCoy Creek in Caribou Basin, near 43° 09’ 06” N, 111° 15’ 17” W.

4) Outcrop north of McCoy Creek in Caribou Basin. This locality consists of a fine to medium-grained, muddy sandstone overlaying gray mudstone that produced a partial Oryctodromeus skeleton (BYU 19342). Locality is at 43° 09’ 41” N, 111° 17’ 20” W.
8.2 Methods

Samples were collected by digging to sufficient depth to obtain fresh, uncontaminated rock. Samples averaged 15 pounds and were stored in thick plastic bags. The samples were processed at BYU as follows (modified from Mori, 2009).

1. Washing: The surfaces of the rock fragments were cleaned under running water to eliminate surficial contaminants. Clay rich samples were held under running water to wash away contaminants and slough off a small amount of the sample surface. More durable samples were scrubbed with a wire brush under running water.

2. Drying: Wet samples were placed in stainless steel pans and dried in a low temperature oven at about 46 °C.

3. Crushing: Larger rock samples were broken down to a 2 cm or smaller fragments with a rock hammer on a clean steel anvil table. Resultant chips were reduced to powder in a roller mill.

4. Sorting: Grains in samples were sorted by a Wilfley Table into five groups by size and density. Samples were added to the Wilfley Table manually or via bin feeder. The coarse fractions were run through the Wilfley Table a second time to reduce the sample size prior to the next step.

5. Heavy liquid separation: Heavier minerals were separated from lighter minerals using liquid TBE (tetrabromoethane). First, the samples were put in a separator funnel and tetrabromoethane of appropriate amount was added. Samples were stirred every about 20 minutes at least three times. Then, the stopcock was opened to allow only the heavy fraction to pass through and be captured by filter paper in the underlying funnel. Samples and residual grains were then rinsed with acetone to remove the tetrabromoethane.
6. Magnetic separation: The heavy mineral concentrates were passed through a magnetic separator (Frantz Isodynamic Separator Model L-1) twice, each time increasing the strength of the magnetic field. The nonmagnetic fraction containing the zircons and magnetic fractions were stored in separate, labeled glass vials.

7. Picking: zircon crystals were handpicked by wet brushes, with care taken to select the most euhedral grains, with the assumption that such grains are most likely to represent the youngest grains in the sample (Kowallis, 1987).

8. Mounting: Select grains were mounted with zircon standard samples on double-faced tape and consolidated with resin plugs. They were polished so approximately half of the larger surfaces of the grains were exposed.

9. Analysis: The crystals were analyzed according to the standard practice in the Laserchron Lab of Dr. Gehrels at the University of Arizona. The processes of picking and mounting are summarized by Gehrels at:
http://www.geo.arizona.edu/alc/detrital%20zircon%20methods.htm

10. Age Calculations: Probability density curves were calculated using Isoplot 3.7 (Ludwig, 2008). When processing data, zircons with high uranium concentrations (>800 ppm), high U/Th ratio (>10), and concordance outside the range of ± 1000 % were excluded because high concentrations could indicate lead loss and anomalously young ages. Probability density curves, first used by Dodson et al. (1988), are drawn by combining probability distributions of data and errors of each grain in the sample. Here the age of the youngest grains and the peaks from the probability density curves are both used to estimate ages.
8.3 Results for lower Wayan (Iowa Creek)

Locality 1 (Iowa Creek), which is 120 m above the base of the formation, yielded an age of 99.3 ±2.5 -2.3 Ma. The result from Locality 1 indicates an age no older than late Albian for the base of the Wayan.

8.4 Results for middle (?) Wayan (DH2, Schmitt and Moran)

Localities 3 and 4 were the only localities tentatively from the middle of the formation to produce enough zircons for dating. Zircon sample 3, 440 m above the base of the formation, yielded a youngest crystal age of a minimum of 101.4 ± 3.7 Ma., and a peak age of 105.6 Ma. Zircon sample 4, which is in an unknown stratigraphic position in the mid-Wayan, yielded an age of 96.5 ± 3.1 Ma from the youngest crystal and a peak age (Figure 5) of 99.1 ±1.5/-1.3 Ma. This sample, being the youngest, indicates the middle Wayan is no older than the earliest Cenomanian. Locality 4 is particularly important due to its proximity to a well-preserved *Oryctodromeus*, BYU 19342.

8.5 Results for top of Wayan (West Tincup sandstone)

Locality 2 yielded an age of 97.55 ± 2 Ma. This indicates an age no older than early Cenomanian for the top of the Wayan.

8.6 Discussion

This study provides the first absolute ages for the Wayan Formation via detrital zircon LA-ICPMS analyses. Recovered dates indicate the formation ranges from the Albian-Cenomanian boundary to the middle Cenomanian. However, underlying beds were not dated and it is possible that zircons from the base of the Wayan were sourced from older strata. The lowest point sampled in the Wayan (Iowa Creek-Locality 1, 120 m above base) that yielded suitable
zircons for analysis appears to straddle the Albian-Cenomanian boundary (99.6 Ma.) with a maximum age of 101.8 Ma and a minimum age of 97.0 Ma. The top of the Wayan (Locality 2) has yielded a maximum age of 99.5 Ma and a minimum age of 95.5 Ma. These data slightly modify the age of the Wayan, making it slightly younger than the previously assigned middle Albian age, but it corresponds well with palynological and faunal data presented below.

![Probability density plot for U-Pb detrital zircon dates from location 7.](image)

**FIGURE 5.** Probability density plot for U-Pb detrital zircon dates from location 7.

9 PALEONTOLOGY

9.1 Palynology

9.1.1 Localities and methodology

Palynomorphs were collected at four locations (Fig. 1A) as indicated in the stratigraphic columns (Figures 2-4). These localities are numbered to correlate with the geochronologic localities described above (hence they are not consecutive) and are as follows:
3) Schmitt and Moran’s (1982) measured section unit 94, Caribou Basin: Outcrop is in a meander scar north of McCoy Creek, Caribou Basin at 43° 09’ 06” N, 111° 15’ 17” W. This unit is a black organic shale with plant fragments.

5) Miners Delight, Caribou Basin (Fig. 1A): Outcrop on the east side of Miners Delight Creek, Caribou Basin at 43° 08’ 44”N, 111° 16’ 10” W. Sample is a gray, silty shale.

6) Jackknife Canyon: Outcrop in meander scar north of Jackknife Creek, in Jackknife Canyon, Bonneville Canyon at 43° 02’ 53” N, 111° 08’ 06” W. Unit is a gray to green homogenous mudstone probably from the lower to middle portion of the Wayan.

Samples were processed and mounted by Gerald Waanders using standard palynological methods as outlined in Traverse (1988) with the exception of process ordering which was altered to: HCl, HF, followed by sieveing with a 10 micron screen before zinc bromide floating (“Chevron method”). Palynomorph identifications (Table 2) were made by Gerald Waanders and Dennis Braman.

9.1.2 Previous palynological results

Previous palynological work in the Wayan Formation is limited to the work by Schmitt and Moran (1982) who recovered palynomorphs along McCoy Creek from their unit 94, a black fissile shale with macroscopic plant fragments. Based on the presence of Taurocosporites spackmani and cf. Verricosisporites obscurilaesuratus they estimated the formation was middle Albian in age.
9.1.3 Palynoflora

In this study a moderately diverse palynomorphs assemblage (Table 2) was recovered from three localities, all thought to occur in the lower half of the Wayan Formation. The Schmitt and Moran (1982) sample is 440 m above the base of the formation while the other sites stratigraphic position are unknown due to complex folding of Wayan strata. However, these sites appear, due to proximity to the base of the formation and lack of faulting, to be in the lower half of the formation.

Palynomorphs include spores of pteridophytes or mosses, cysts of chlorophyte algae, and pollen of gymnosperms. The lack of definitive angiosperm pollen from the sample localities is problematic because angiosperm foliage is now known from the formation (described below). The absence may be due to the small sample size (Dennis Braman, pers. comm.) or processing. Overall, the Wayan palynoflora is dominated by gymnosperms with *Araucariacites australis* and *Classopolis classoides* being the most common. Individual sample yields can be summarized as follows: McCoy Creek: *Araucariacites australis* and pteridophyte spores pertaining to *Appendicisporites potomacensis*, *Cicatricosisporites imbricatus*, and *Deltoidospora* spp. The Jackknife Canyon sample is dominated by *Araucariacites australis*. The Miners Delight sample yielded common spores of the gymnosperms *Araucariacites australis* and *Classopolis classoides* and rare pteridophyte spores such as *Deltoidospora* spp. and *Verrucosisporites* sp. plus the marine acritarchs *Micrhystridium*, *Gingingodinium evitii*, and *Veryhachium reductum*. A discussion of the environmental implications of the palynoflora is given below.
9.1.4 Palynostratigraphy

Palynomorphs recovered do not permit precise age-resolution, but include common mid-Cretaceous forms (Dennis Braman, pers. comm.) such as *Eucommiidites minor*, *Liliacidites orbiculatus*, and *Triporoletes cenomanianus* from the McCoy Creek site and *Cingulatisporites distaverrucosus*, *Batiacasphaera microgranulata*, *Gingingodinium evitii*, and *Classopollis classoides* from the Miners Delight locality. The Jackknife Canyon sample yielded long ranging taxa indicative of an Albian to Cenomanian age (Gerald Waanders, pers. comm.). Thus, palynomorphs recovered from the Wayan Formation suggest a mid-Cretaceous age and agree with the geochronologic data.

9.2 Paleobotany

9.2.1 Previous paleobotanical work

Petrifactions constitute the bulk of the paleobotanical remains recovered from the Wayan Formation as it was originally defined. Reported fossils include false trunks of the Cretaceous tree fern *Tempskya* (Andrews, 1943; Andrews and Kern, 1947), the conifer *Cupressinoxylon* (Andrews and Kern, 1947), the cycadeoid *Cycadeoidea*, and the dicotyledon *Paraphyllanthoxylon* (Spackman, 1948). My observations over eight field seasons in the Wayan Formation show that all occurrences of *Tempskya* and associated petrifactions occur high in the section in horizons now assigned to the Sage Junction Formation as defined by Rubey (1973) and mapped as such by Oriell and Platt (1980) and Huntsman and Platt (1985). Thus no *Tempskya* is known to occur in the Wayan Formation as presently defined.
Foliage compressions pertaining to ferns (Wi

FIGURE 6. Correlation chart of stratigraphic sections. Correlations based on U-Pb detrital zircon dates; lithology, and *Oryctodromeus* occurrences. Stratigraphic positions of *Oryctodromeus* shown by BYU specimen numbers, detrital zircon samples with a Z, and fossil pollen/spores/cysts with “Palynomorphs”. Localities for stratigraphic sections shown in Figure 1.
ng and Boucher, 1998) and the dicotyledon angiosperm *Sapindopsis* (Crabtree, 1987; Wing and Boucher, 1998) have been reported from the Wayan Formation. Unfortunately, no localities were reported and the specimens have been misplaced. Therefore, the stratigraphic positions of these fossils cannot be ascertained and the possibility that they originated in the Sage Junction Formation must be considered.

### 9.2.2 New floral specimens

During this study a new locality bearing a small flora of ferns, conifers and angiosperms was discovered near McCoy Creek (Fig. 4). The foliage is curled haphazardly and three-dimensionally in a homogenous gray, well-indurated mudstone that is jointed perpendicular to bedding, making recovery of complete specimens difficult. This mudstone overlies a channel sandstone and becomes more platy up-section and then grades into silty redbeds typical of the Wayan. Wood petrifactions occur roughly one meter above the foliage horizon. Rare freshwater gastropods and ostracods also occur in this mudstone. Combined evidence suggests that this gray mudstone is a lacustrine deposit. The curled nature of the foliage suggests that the plants were buried in a viscous flow or that the horizon was trampled by vertebrates.

The compressions include complete and fragmentary specimens. Most of the foliage appears to have been preserved relatively intact. The fragmentation is largely a function of collecting and preparation of a highly fractured matrix. Ferns dominate the assemblage, with three pteridophyte (fern) taxa: a large and small form of *Gleichenia* (Fig. 7A and B), which occur in about equal numbers and dominate the assemblage, and the fern *Anemia* (Fig. 7C), which is much less common. All pteridophyte foliage is infertile.
Conifers represent a small proportion of the foliage recovered (~20%) and are represented by female cones (Fig. 7E), stems, and leaves (Fig. 7D). The stems and leaves compare favorably with *Pagiophyllum*. Three cones have been recovered, but their affinities are also uncertain. However, their morphology suggests an affinity with *Metasequoia* (William Tidwell, pers. comm.).

Angiosperms constitute roughly 50% of the assemblage, but due to the relatively large size of the leaves (Fig. 7F and G) and the geologic setting, none were recovered complete and none preserve diagnostic characters. For this reason, none of the taxa can be identified to genus. It appears that at least three taxa are present, all representing relatively broad-leafed taxa similar to *Magnolia*.

9.3 Vertebrate Paleontology

9.3.1 Previous work

Previous workers (Dorr, 1985; Weishampel *et al*. 2002; Krumenacker, 2005) have recovered a moderate diversity of vertebrate fossil materials, all of which were poorly represented (Table 1). Dorr (1985) reported an isolated tooth that he assigned to *Tenontosaurus* as well as an indeterminate large ornithopod vertebra centrum, an ankylosaur tooth, abundant dinosaur eggshell, as well as crocodilian and turtle remains. Weishampel *et al*. (2002) reported on possible neoceratopsian remains consisting of a partial pelvis, the proximal portion of a tail, and a skull roof fragment. In addition, they described an ankylosaur tooth, a proximal ornithischian caudal vertebra, an isolated large theropod pedal phalange, and theropod distal limb fragment. Krumenacker (2005) summarized the vertebrate fauna and reported a fragmentary
large crocodilian skull (described below) and remains from a small ornithopod form now known to be *Oryctodromeus* (see below).

More recent work by Montana State University, Brigham Young University, and Idaho State University has greatly enlarged our understanding of the Wayan vertebrate fauna. New

FIGURE 7. Carbonized plant compressions from the Wayan flora described in this paper. Partial fronds of two species of *Gleichenia* (A, B), partial *Anemia* frond (C), *Pagiophyllum*-like conifer branches showing minute leaves (D), *Metasequoia*-like female cone in cross-section (E), and fragmentary angiosperm leaves with elongate drip-point (F) and without, (G).
discoveries by MSU include: a partial skeleton of an ankylosaur, small ornithopod remains referable to *Oryctodromeus*, theropod eggshell, and other vertebrate remains (Dave Varricchio, pers. comm.). Work by the author facilitated the discovery of numerous partial skeletons of *Oryctodromeus*, as well as other vertebrate and paleobotanical remains. The material described below consists of the more fragmentary material from a number of different forms discovered partly in the course of the author’s undergraduate research. An overview of vertebrates collected as part of this thesis and preliminary research are presented below, osteological descriptions of *Oryctodromeus* materials from Idaho in presented in chapter 2.

### 9.3.2 Crocodilians

Eusuchia Huxley, 1875

Crocodylia Gmelin 1789, sensu Benton and Clark, 1988

Crocodyloidea Cuvier, 1807

**Referred Material:** BYU 18962, articulated left anterior and mid-portion of a skull consisting of a fragmentary pre-maxilla, maxilla, and ectopterygoid.

Little can be said of the affinity or morphology of this specimen due to its extremely fragmentary nature which was recovered in a heavily vegetated roadcut. As preserved, the specimen measures roughly 62 cm from the tip of the pre-maxilla to the preserved end of the ectopterygoid. The complete skull is estimated to have been roughly 1 meter in length. Alveoli are difficult to distinguish, but there appears to be a rough total of 25 on the left of the specimen. The robust crown of an *in-situ* premaxillary tooth measures 4.5 cm long. The extreme size of the
fossil and broad snout morphology suggests a relationship to the Late Cretaceous *Deinosuchus* or a large goniopholid (Chris Brochu, pers. comm.).

9.3.3 Ornithopods

Dinosauria Owen 1842

Ornithischia Seeley, 1887

Genasauria Sereno, 1986

Ornithopoda Marsh, 1871

Euornithopoda Sereno, 1986

Iguanodontia Dollo, 1888

Genus and species indeterminate

**Referred Material:** IMNH 15444, one indeterminate maxillary or dentary crown, missing most of the enamel, in a small block of rip-up clast conglomerate matrix.

Description: Exposed crown 6 mm high, 10.5 mm anteroposteriorly, and 6 mm labiolingually. Little detail is preserved on the crown, however, one patch of enamel is present on the described side. On the labial/lingual side a primary ridge is present and offset from the center of the crown, plunging ventrally to a corner of the crown. A single secondary ridge is present opposite of the primary ridge and plunges in the same direction.

Discussion: Iguanodontid remains are rare in the Wayan Formation, and, except for the remains described below, consist entirely of isolated teeth. One large isolated centrum is known from an indeterminate ornithopod (Dorr, 1985). The lack of detail on this specimen precludes detailed study or comparison.
Dinosauria Owen 1842
Ornithischia Seeley, 1887
Genasauria Sereno, 1986
Ornithopoda Marsh, 1871
Euornithopoda Sereno, 1986
Cf. Iguanodontia Dollo, 1888
Genus and species indeterminate

**Referred Material:** BYU 19349, associated dorsal (?), sacral (?) and caudal vertebrae, pes phalange with articulated ungual, indeterminate fragments. This specimen is heavily compacted, making discernment of details difficult.

Description: One fragmentary vertebral centrum with fragments of adjacent centra articulated with both ends, as well as another centrum fragment. These vertebrae are tentatively identified as sacral (or possibly proximal caudal) vertebrae. These centra are heavily dorsoventrally crushed with no details discernible dorsally. Ventrally the centrum has a deep sulcus extending anteroposteriorly. Two additional centra are interpreted as proximal caudal vertebrae. They are concave mediolaterally with transverse process origination above the neurocentral suture. Six distal caudal vertebrae are preserved. These centra are elongate (over three times as long as tall) with the articular ends having a round outline. The centra appear to have lateral grooves bordered by ridges dorsally and caudally, but this may be an artifact of crushing. Little detail is discernible of the neural spines or zygapophyses. These distal caudals are encased in a sheath of hypaxial and epaxial tendons similar to the condition in *Tenontosaurus*
(Ostrom, 1970). Tendons run from the dorsal portion of the centra down to the bottom of the centra over a distance of four vertebrae.

The pes phalange is very short and squat and anteroposteriorly compressed. The proximal articular surface is sub-circular and wider than tall, with a flattened ventral margin. The ungual is mediolaterally flattened and missing the tip. The overall form is intermediate between claw-like and hoof-like and is similar to *Camptosaurus* pes unguals.

Discussion: These remains likely pertain to a single individual based on size and their close association with much of the material *in-situ*. This specimen is referred to an undetermined iguanodontid because of the ornithopodan form of the caudals and the robust form of the pes phalange. These bones are similar to more derived iguanodontian ornithopods such as *Camptosaurus* (Gilmore, 1913) and *Iguanodon*, and distinct from more basal ornithopods such as *Orodromeus* (Scheetz, 1999) and *Oryctodromeus* (pers. obs.). This specimen is significant because it indicates the presence of a moderately derived iguanodontid that was a small taxon or subadult.

### 9.3.4 Dromaeosaurs

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Dromaeosauridae Matthew and Brown, 1922

Genus and species indeterminate
Referred material: BYU 19348, small tooth crown, found in association with an *Oryctodromeus* skeleton (BYU 19345).

Description: Tooth crown 6 mm tall and laterally narrow. The mesial portion of the crown lacks a distinct carina and serrations, while the posterior carina has eleven coarse serrations (giving a serration count of roughly 2 serrations per mm).

Discussion: Discounting abundant theropod eggshell, theropod remains are extremely rare in the Wayan Formation, with previously reported specimens consisting of a fragment of a tooth crown tentatively attributed to a dromaeosaurid (Krumenacker, 2005) and two theropod hind-limb elements (Weishampel *et al*., 2002). This tooth appears distinct from the larger tooth fragment previously reported due to serration count and size. This specimen is tentatively referred to the Dromaeosauridae due to the coarse serrations on the distal carina and lack of serrations on the mesial portion of the crown, which is typical of dromaeosaurids (eg. Ostrom, 1969; Norell and Makovicky, 2004).

<table>
<thead>
<tr>
<th>Osteichthyes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cf. Semionotidae (Krumenacker, 2005)</td>
</tr>
<tr>
<td>Chelonia (Dorr, 1985; Krumenacker 2005)</td>
</tr>
<tr>
<td>Archosauria</td>
</tr>
<tr>
<td>Crocodylia (Dorr, 1985; Krumenacker 2005, this report)</td>
</tr>
<tr>
<td>Dinosauria</td>
</tr>
<tr>
<td>Theropoda (Weishampel <em>et al</em>., 2002)</td>
</tr>
<tr>
<td>Dromaeosauridae (Krumenacker, 2005; this report)</td>
</tr>
<tr>
<td>Cf. Neoceratopsia (Weishampel <em>et al</em>., 2002)</td>
</tr>
<tr>
<td>Ornithopoda (Dorr, 1985; Weishampel <em>et al</em>., 2002)</td>
</tr>
<tr>
<td>Iguanodontidae (Dorr, 1985; this report)</td>
</tr>
<tr>
<td>Euornithopoda</td>
</tr>
<tr>
<td><em>Oryctodromeus</em> (this report)</td>
</tr>
<tr>
<td>Ankylosauria (Dorr, 1985; Weishampel <em>et al</em>., 2002)</td>
</tr>
</tbody>
</table>

**TABLE 1. Vertebrate fauna of the Wayan Formation.**
Spores and Pollen

*Acanthotritelles* sp. (MD)
*Appendicisporites* potomacensis (S)
*Apiculatisporis* sp. (MD)
*Araucariacites* australis (MD, S, J)
*Asteropollis vulgaris* (S)
Undifferentiated Bisaccates (S, J)
*Callialasporites* sp. (MD)
*Chonotritelles* fragilis (J)
*Cicatricosisporites* australiensis (J)
*Cicatricosisporites* imbricatus (S)
*Cicatricosisporites* venustus (S)
*Cingulatisporites* dista verrucosus (MD)
*Classopollis* classoides (MD, J)
*Cyathidites* australis (S)
*Deltoidospora* spp. (MD, S, J)
*Eucommiidites* minor (S)
*Exesipollenites* tumulus (MD, S, J)
*Gleicheniidites* senonicus (S, J)
*Khakisporites* sp. (MD)
*Liliacidites* orbiculatus (S)
*Lycopodiumsporites* austroclavatidites (MD)
*Lycopodiumsporites* sp. (S)
*Osmundacidites* wellmanii (S)
*Peronomonolites* allensis (S)
*Podocarpidites* sp. (S)
*Schizosporis* parvus (S)
*Taxodiaceae* (MD, S)
*Triletes?* sp. (S)
*Trilobosporites* minor (S)
*Triporolletes* cenomanianus (S)
*Tsiagaepollenites* sp. (MD)
*Verrucosisporites* sp. (MD)

Microplankton

*Micrhystridium* inconspicuum (MD)
*Micrhystridium* recurvatum (MD)
*Micrhystridium* spp. (MD)
Unidentified dinoflagellate cysts (MD)
*Tasmanaceae* (MD)
*Veryhachium* reductum (MD)

Marine Organisms

*Tasmanaceae* (S)

**TABLE 2. Palynomorphs taxa recovered from the Wayan Formation.**
9.4 Paleontological synthesis

Discounting the reports of *Tempskya* and associated plants that are now known to be from the overlying Sage Junction Formation, megascopic floral remains are rare and limited to what is reported above. The flora is similar to the Cenomanian age Westwater flora of the Dakota Sandstone of Utah (Rushforth, 1971; Tidwell, 1998). Both the Wayan flora and the Dakota Westwater flora contain the ferns *Gleichenia* and *Anemia*, as well as magnolian angiosperms.

Non-dinosaurian vertebrate remains are meager. Dorr (1985) and Krumenacker (2005) have reported unidentified turtle shell fragments as well as crocodilian remains. The crocodilian skull reported above represents the only crocodilian skeletal remains known to date. A scale and numerous crushing teeth from large semionotid fish are the only fish remains known.

Rivaling the abundance of *Oryctodromeus* in terms of individual element count is the abundance of theropod eggshell referred to the oofamily Elongatoolithidae (Krumenacker et al., 2007). The abundance of this eggshell, which can be found almost anywhere in the Wayan with diligent searching (pers. obs.), suggests an abundance of one or more coelurosaurian theropods. Despite the abundance of theropod eggshell, very few theropod skeletal remains are known. Weishampel et al (2002) reported an indeterminate theropod pedal phalange (possibly the proximal phalanx of digit III) which they compared to *Deinonychus antirrhopus*. However, this phalange is nearly twice the size of the equivalent digit in *Deinonychus* (Ostrom, 1969). A second theropod phalange was also reported, however this ‘phalange’ appears to be the distal end of a limb element, possibly a distal femur. A tooth fragment tentatively referred to the
dromaeosauridae (Krumenacker, 2005) and the small dromaeosaur tooth reported above are the only other theropod elements known.

Ornithopods dominate the Wayan Fauna, specifically through the relative abundance of the basal ornithopod *Oryctodromeus* which comprises over half of the vertebrate remains recovered from the Wayan (Krumenacker *et al*., 2008).

Large ornithopods are conspicuously rare, with *Tenontosaurus* being reported from a single tooth (Dorr, 1985). This referral must be viewed as tentative at best, due to the conservative nature of iguanodont grade teeth and the lack of post-cranial remains of *Tenontosaurus* in the Wayan. Dorr (1985) also reported an indeterminate larger ornithopod represented by a single large caudal centrum. The iguanodont grade tooth and associated axial remains described provide larger ornithopods in the fauna but little taxonomic data.

Weishampel *et al* (2002) reported two partial articulated individuals they tentatively referred to the neoceratopsia. These two fossils are IMNH 39294 and 40571. Specimen 39294 consists of a poorly preserved partial pelvis and proximal caudal vertebrae and 40571 of a series of articulated proximal caudal vertebrae. Preliminary comparison suggests 39294 may actually be from *Oryctodromeus* due to very similar size and morphology of the caudal vertebrae, however this observation is tentative. Nonetheless, the vertebrae from 40571 are very distinct from *Oryctodromeus*.

The only other ornithischians in the fauna are indeterminate ankylosaurs. Remains consist of isolated teeth (Dorr, 1985; Weishampel *et al*., 2002), an unreported small caudal vertebra (an unnumbered specimen observed in the IMNH collections), and an isolated scute in a block of rip-up clast conglomerate (again, an unnumbered specimen in the IMNH collections). A recently
collected partial ankylosaur skeleton currently under preparation at the Museum of the Rockies (Dave Varricchio pers. comm.) will be a significant contribution.

10 ENVIRONMENTS AND ECOLOGY OF THE WAYAN FORMATION

10.1 Geologic Insights

A detailed study of the paleoenvironments of the Wayan Formation has never been undertaken. Schmitt and Moran (1982) observed that the Wayan consisted primarily of meandering stream-related deposits, some overprinted by caliche development. Dorr (1985) compared the Wayan depositional environment to the modern Indogangetic Plain.

The stratigraphic columns described above and overall stratigraphic setting of the Wayan Formation provide additional insights on depositional environments that were prevalent in the Wayan depositional system, and on changing conditions in the foredeep at this time.

The underlying Smiths Formation represents lacustrine and fluvial environments in a well-watered environment (Durkee, 1979). The transition into the lower Wayan is marked with the appearance of coarse sandstones associated with pebble conglomerates (Schmitt and Moran section, Tincup Canyon measured section), which are rare higher in the formation. These lithologies indicate a steeper gradient (and therefore proximity to highlands) and/or higher energy fluvial environments with an availability of coarser sediments.

Pedogenically altered mudstones and siltstones with abundant calcareous nodules, dominate above the lower 100-250 m of the formation (Schmitt and Moran section, Tincup Canyon measured section). Horizons consisting of calcareous nodules are a diagnostic feature of
this formation. Nodules of various sizes are typically associated with variegated red beds are indicative of a monsoonal climate with fluctuating water tables similar to that postulated for the Morrison Formation and the Ruby Ranch member of the Cedar Mountain Formation (eg. Wing and Sues, 1992, Kirkland et al., 1999). The abundance of these lithologies indicates the majority of Wayan Formation paleoenvironments were dominated by floodplains subject to intermittent sedimentation and periods of depositional hiatuses (eg. Kraus and Bown, 1993). This drier setting may explain the dominance of Oryctodromeus in these sediments as modern burrowing vertebrates have been noted as preferring drier upland/inland soils (Voorhies, 1975).

The ‘Middle Wayan Sandstone’ as mapped by Oriel and Platt (1980) in eastern Tincup Canyon would represent a temporary increase in fluvial channel environments or sediment bypass perhaps related to the transgression of the Mowry Seaway, but this sandstone was not definitively recognized in this study due to vegetative cover in the area. However, a higher abundance of sandstone about 1000 m into the Tincup Canyon section (as described above) may represent this sandstone. About 1100 m into the Tincup section, pedogenic mudstone and siltstone again dominates the sequence and represents a return to the dry monsoonal climate that dominated Wayan paleoenvironments.

Overlying the Wayan is the sandstone-dominated Sage Junction Formation. The abundance of the tree fern Tempskya and the associated flora discussed above, and the higher abundance of fluvial channels and lack of pedogenic mudrock in this formation, indicates a more humid environment which was likely a function of the encroachment of the Mowry Seaway.
10.2 Faunal and Floral insights

An understanding of the Wayan Fauna is in the early stages. What is known at this point is that the preserved fauna is dominated by ornithischians, specifically *Oryctodromeus*. A larger iguanodontian ornithopod of unknown affinity is also present along with at least one ankylosaurian thyreophoran. Theropod body fossils are limited to teeth and fragmentary bones of large and small forms with sauropods remains being unknown. The abundance of theropod eggshell fragments indicates favorable nesting conditions and an environment favorable to the preservation of eggshell. Rare fish and snail remains, as well as moderately common turtle remains are indicative of permanent bodies of water, as is the large crocodilian, which suggests that prey was abundant near these water bodies. The paucity of vertebrate remains aside from *Oryctodromeus*, which is known to be fossorial, suggests that surficial conditions were generally not favorable to bone preservation. The burrowing habit of *Oryctodromeus* enhanced preservational potential and this may explain its dominance and the rarity of other vertebrate remains.

The presence of the ferns *Gleichenia* and *Anemia* suggest open and dry, possibly nutrient-poor substrates (Wing and Sues, 1992) in the Wayan. Wing and Sues (1992) suggest that forms such as these were major colonizers of open and possibly fire-disturbed habitat in tropical and sub-tropical environments. The presence of magnolian angiosperms and conifers suggests the presence of compositionally diverse forests.

Palynomorphs suggest a number of environmental settings (Gerald Waanders, pers. comm.). In the Jackknife Canyon sample, a freshwater deltaic to shallow lacustrine setting is suggested by a high organic content, a predominance of amorphous kerogens, and an absence of
marine forms. In contrast, a tidally influenced fluvial system is indicated by palynomorphs from the Miners Delight locality based on the presence of acritarchs and some dinoflagellate cysts. This was unsuspected for the Wayan Formation, which has previously been thought of as an entirely inland alluvial deposit with no noted marine influence (Dorr, 1985). The laterally equivalent Bear River Formation represents an environment more proximal to the Mowry Seaway, with the Wayan representing more inland areas. The Miners Delight sample is from a succession of moderately organic siltstone between fluvial sandstone and pedogenic mudstone. The absence of fully marine units and marine macrofossils in the Wayan suggests these siltstones were deposited by a tidally influence system. Schmitt and Moran’s (1982) unit 94 represents an extremely rare lithology in the Wayan Formation, a black carbonaceous shale with abundant plant fragments. A swampy to shallow lacustrine setting is suggested by the high organic content, a predominance of woody kerogens, and the absence of marine organisms (Gerald Waanders, pers. comm.).

One of the major findings of this study is that there are several environmental settings represented in the Wayan Formation – well-drained areas with evidence of monsoonal (seasonal) rainfall, and tidally, or otherwise marine influenced, waterways. In the well-drained environment *Oryctodromeus* likely burrowed to avoid predation and otherwise seek shelter. Coelurosaurian theropods nested, possibly preying on the abundant small ornithopods. Ferns adapted to fire or seasonally adverse conditions were abundant and grew in association with short-leaved conifers and magnolid angiosperms.
The Wayan Fauna is broadly similar at the family level to other Early and mid-Cretaceous faunas in western North America, with a typical euornithopod, ankylosaur, and theropod dominated assemblage like those found in part in the Mussentuchit Member of the Cedar Mountain Formation (Kirkland et al., 1999; Mori, 2009), the Willowtank Formation of Nevada (Bonde, 2008), and the Cloverly Formation of Montana and Wyoming (Ostrom, 1970). Unlike those faunas, sauropods are conspicuously absent from the Wayan Fauna. The presence of possible neoceratopsians is an important faunal component that is only known from teeth in equivalent faunas (eg. Kirkland et al., 1999).

The Wayan Fauna is most similar to the Cenomanian-age fauna of the Blackleaf Formation of southwestern Montana (Varricchio et al., 2007). This similarity is typified by the dominance of *Oryctodromeus* in both, which suggests similar ages and environments for both formations. As in the Wayan, large dinosaurs are rare in the Blackleaf Formation, being known only from isolated teeth (Varricchio et al., 2007). The similarities of the fauna and of the depositional setting also suggest similar taphonomic biases in the Wayan and Blackleaf and/or similar environmental preferences and settings for similar taxa. The close proximity of the two formations and their occurrence along the structural strike suggest that the Wayan and Blackleaf Formations were deposited in the same basin, and this fact, along with the faunal, chronological, and depositional environments suggest that the units should be considered a single formation. If this is the case, the Wayan name has priority, having been described in 1916 (Mansfield and Roundy), while the Blackleaf Formation was first named in 1959 (Cobban et al., 1959)
The only other fauna of similar age (Albian) and composition is from the Otway Group of southern Victoria, Australia (Weishampel et al., 2004). Numerous hypsilophodontids are reported from these rocks including *Leaellynasaura* and *Atlascopcosaurus* (Rich and Rich, 1999). The recent report of burrows in these the Otway Group (Martin, 2009) similar to *Oryctodromeus* burrows is noteworthy.

One final observation involves a unique locality in the Aptian Twin Mountains Formation, near Proctor Lake in Comanche County, Texas. While basal ornithopods are rare in this fauna, one locality has produced articulated and associated remains of dozens of hypsilophodont grade ornithopods (Winkler and Murray, 1989). This site occurs in pedogenic red mudstones and seems to represent a communal nesting site that was repeatedly utilized (Winkler and Murray, 1989). The dominance of hypsilophodontid grade ornithopods at this site is unique, as they are extremely rare in other known vertebrate localities in the formation.

12 SUMMARY

The Cretaceous age Wayan Formation of eastern Idaho is a thick accumulation of pedogenically altered sediments shed from highlands uplifted on the Meade and Paris thrusts in early movements of the Sevier Orogeny. Measurements indicate a thickness of 1,344 m in the Tincup Canyon area of Caribou County. Stratigraphic resolution is difficult due to the lack of recognized marker beds. However, the base of the Wayan may be recognized by a dominance of chert pebble conglomerates, while the upper middle Wayan may contain a higher relative abundance of sandstone versus variegated pedogenic mudstone and siltstone.

The Wayan contains a rare record of a mid-Cretaceous terrestrial community dominated by the burrowing ornithopod *Oryctodromeus*. Lesser known elements of the fauna include a
small dromaeosaurid theropod, iguanodontid ornithopods, and a large crocodilian. The flora included ferns such as *Gleichenia* and *Anemia* plus conifers, and angiosperms. The Wayan flora appears most similar to the Westwater Flora from the Dakota Sandstone of eastern Utah. The Wayan fauna is most similar to that of the Blackleaf Formation of southwestern Montana due to the dominance of *Oryctodromeus* and the rarity of larger dinosaur remains in both faunas.

Detrital zircon U-Pb dates support a latest Albian to Cenomanian age for the Wayan Formation, and palynological analysis suggests a mid-Cretaceous age as well. The dominance of *Oryctodromeus* in the Wayan and Blackleaf formations, similar ages, and possible deposition in the same basin indicate possibly synonymy for both, with the Wayan taking priority.

13 REFERENCES


CHAPTER 2: AN OSTEOLOGICAL DESCRIPTION OF *ORYCTODROMEUS*

SPECIMENS FROM IDAHO, THE MOST ABUNDANT DINOSAUR OF THE WAYAN FAUNA, AND THE FIRST OCCURRENCE OUTSIDE OF MONTANA
15 ABSTRACT

The earliest Late Cretaceous Wayan Formation of Idaho has previously produced a fragmentary but moderately diverse dinosaur fauna including theropods, ankylosaurs, possible neoceratopsians, iguanodontid-grade ornithopods, and small ornithopods. Recent field work in the formation has yielded substantial remains of *Oryctodromeus*, a small ornithopod that numerically dominates the assemblage. These specimens (1) increase the known distribution of this taxon, (2) indicate the Wayan and Blackleaf formations are time equivalent and may represent the same basin, and (3) and provide substantial osteological insights.

Newly recognized osteological characters include: elongate cervical and dorsal centra, over 55 elongate caudal vertebrae enveloped in hypaxial and epaxial tendons, and a femoral head projecting from the femoral shaft body at roughly 40° on an elongate neck.

The close field association of individuals representative of several ontogenetic stages, and commonly articulated specimens, some with fully articulated hands and feet, indicate the specimens were not subject to vertebrate scavenging or fluvial transport. These taphonomic points are interpreted as evidence the individuals died and were buried in burrows, as with the holotype and paratype specimens from Montana.

16 INTRODUCTION

In terms of vertebrates, Cretaceous strata in southeastern Idaho (Fig. 1) have long been considered to be relatively unfossiliferous. Until recently, only meager remains of fish, turtles, crocodilians, and dinosaurs had been reported from the Early Cretaceous Gannett Group (Dorr, 1985; Krumenacker, 2002; Krumenacker, 2005) and the mid-Cretaceous Wayan Formation
Figure 1. Vertebrate fossil locality map and regional stratigraphy. Map showing main vertebrate localities with stars (A). Cretaceous stratigraphy of the study area and correlative units (based on Dorr, 1985; Rubey, 1973; Dyman et al., 1989; Kirkland et al., 1999) (B).
(Dorr, 1985; Table 1). Subsequent work in the Wayan Formation has demonstrated the presence of a fairly diverse but poorly represented fauna with semionotid fishes, turtles, crocodilians, large and small theropods, ankylosaurs, possible neoceratopisans, a *Tenontosaurus*-like and indeterminate large ornithopods, and a basal ornithopod form that compares most favorably with *Oryctodromeus cubicularis* specimens from the Cenomanian-age Blackleaf Formation of Montana (Dorr, 1985; Weishampel *et al.* 2002; Krumenacker *et al.* 2007; Krumenacker *et al.* 2009, Varricchio *et al.*, 2007). In addition, abundant Elongatoolithidae eggshell (Dorr, 1985; Krumenacker *et al.*, 2007) occurs in the Wayan. While most of the above forms are only known from fairly fragmentary and indeterminate material, *Oryctodromeus* is represented by partial skeletons of over 10 individuals, making it the most common Wayan fossil found other than eggshell (Krumenacker *et al.*, 2008).

While none of the small ornithopods from the Wayan Formation includes the cranial and complete pelvic elements that provided the autapomorphies forming the diagnosis of *Oryctodromeus* (Varricchio *et al.*, 2007), direct comparison of Wayan specimens with the holotype and paratype specimens and additional undescribed Blackleaf *Oryctodromeus* material in the Museum of the Rockies (MOR) indicates the Idaho and Montana specimens are cogenetic.

Post-cranial elements of *Oryctodromeus* from the Wayan are moderately well represented, while skull elements are largely unknown. The purpose of this paper is to describe the osteology of the Wayan *Oryctodromeus* as represented by the Wayan materials, which provides substantial new insights into the osteology and habits of *Oryctodromeus*. 
16.1 GEOLOGY

The Wayan Formation occurs in the Caribou Mountains (Fig. 1A) of southeastern Idaho (Mansfield and Roundy, 1916; Mansfield, 1927; Mansfield, 1952; Schmitt and Moran, 1982) and is roughly age equivalent with the Mussentuchit Member of the Cedar Mountain Formation of Utah (Cifelli et al., 1997; Garrison et al., 2007; Mori, 2009), the Blackleaf Formation of southwestern Montana (Varricchio et al., 2007), and the upper Willow Tank Formation of Nevada (Bonde, 2008). The formation is dominated by mudstone and siltstone, with subordinate sandstone and rare conglomerate, tuff, and limestone (Mansfield, 1927; Mansfield, 1952; Schmitt and Moran, 1982). Relatively little geological work has been done on the Wayan due to poor exposures, complex structural deformation, and limited geographic extent. No complete sections have been described and only preliminary work in its sediments has been conducted (Schmitt and Moran, 1982). My measurement of an apparently undeformed section in western Tincup Canyon (Fig. 1A), Caribou County, Idaho, indicates a thickness of 1,344 m, a thickness roughly equal to laterally equivalent foredeep strata in westernmost Wyoming described by Rubey (1973).

Deposition occurred in a meandering fluvial system (Dorr, 1985; Schmitt and Moran, 1982) that Dorr (1983, 1985) compared to the modern Indogangetic Plain. Palynological evidence suggests that preserved paleoenvironments included floodplains, freshwater deltas, lakes, rare swamps, and tidally influenced streams (Gerald Waanders, pers. comm.). Abundant calcareous nodules throughout the formation suggest a highly seasonal monsoonal climate with long depositional hiatuses (Dorr, 1985). Based on paleogeographic reconstructions, regional stratigraphic relations, and a complete lack of marine macrofossils in the Wayan, deposition appears to have been some 20 or more km inland from the Mowry Sea, in an inland terrestrial...
environment. However, the presence of numerous marine microplankton (Gerald Waanders, pers. comm.) retrieved from two palynological samples indicates an inland marine influence for some stratigraphic intervals, probably due to tidal wedging into freshwater fluvial environments.

In the Wayan Formation, *Oryctodromeus* specimens are usually found in the variegated, mudstone and siltstone paleosols that typically contain caliche nodules, but specimens have also been recovered from fine-grained sandstone (pers. obs.). In contrast, *Oryctodromeus* remains are absent from coarser-grained sandstone and mud-clast conglomerate (Krumenacker *et al*., 2008). *Oryctodromeus* remains recovered from a known stratigraphic framework are limited to the middle portion of the Wayan Formation. *Oryctodromeus* fossils in the Wayan Formation typically consist of articulated to semi-articulated partial skeletons. Bones exhibit little to no abrasion or biologic modification (Krumenacker *et al*., 2008), suggesting rapid post-mortem burial. Some localities have produced remains of multiple individuals of various sizes.

16.2 AGE

The age of the Wayan has been relatively poorly constrained. Previous estimates of a middle Albian age were based on stratigraphic position and palynology (Mansfield, 1927; Schmitt and Moran, 1982; Dorr, 1985). Based on its stratigraphic position above the Gannett Group and below the Sage Junction Formation, and on its inferred intergrading relationship with the Bear River and Aspen Formations, the Wayan has been correlated with the Bear River Formation and the overlying Aspen Shale of eastern Idaho and western Wyoming (Schmitt and Moran, 1982; Dorr, 1985), which have been dated as Albian. Palynomorphs from the lower portion of the Wayan Formation include *Batiacasphaera microgranulata*, *Cingulatisporites distaverrucosus*, *Classopolis classoides*, *Gingodinium evitti*, *Eucommidites minor*, *Liliacidites*
orbiculatus, and Triporoletes cenomanianus, suggesting a mid-Cretaceous age for the lower Wayan Formation (Gerald Waanders, pers. comm.; Dennis Braman, pers. comm.). In addition, recent detrital zircon radiometric dating has indicated an age of 99.3 +2.5, -2.3 Ma (Chapter 1, Section 8.3) for the base of the Wayan (near the Albian/Cenomanian boundary) with the top of the formation dating at 97.55 +2, -2 Ma (Section 8.5). The occurrence of Oryctodromeus in both the Vaughn Member of the Blackleaf Formation and the Wayan Formation, the alignment of the two units along the structural trend, and their lithologic similarities suggest the units are part of the same basin. The uppermost Vaughn Member has yielded $^{39}\text{Ar}/^{40}\text{Ar}$ ages of 93-96 Ma (Zartman et al., 1995) and thus the member is approximately the same age the Wayan Formation.


17 **SYSTEMATIC PALEONTOLOGY**

DINOSAURIA Owen, 1942

ORNITHISCHIA Seeley, 1888

ORNITHOPODA Marsh, 1881 (*sensu* Butler et al. 2008)

EUORNITHOPODA Sereno, 1986

ORYCTODROMEUS sp. Varricchio *et al.*, 2007

Holotype- MOR 1636a from the Blackleaf Formation of Montana: fused premaxillae; posterior/occipital region of the braincase; three cervical, six dorsal, sacrum and 23 caudal
vertebrae; three dorsal ribs; scapulocoracoid; scapula; coracoid; humerus; ulna; radius; tibiae; distal fibula; and metatarsal IV.

Paratype- MOR 1636b from the Blackleaf Formation of Montana: includes cranial and postcranial materials found in association with the holotype and represents two juveniles with most linear dimensions measuring 55% to 65% those of the adult.

Referred materials from the Wayan Formation:

BYU 19342: partial skeleton consisting of five dorsal, four sacral, and at least fifty-five caudal vertebrae, chevron, partial left and right coracoids and scapulae, partial left humerus, right pubis fragment, ilium and ischium fragments, left femur, right femur head, distal left tibia with articulated astragalus and calcaneum.

BYU 19343: portions of three individuals of varying sizes: sacral vertebrae, caudal vertebrae, coracoid, humerus, pelvic fragments, two distal femora, two tibiae, two partial fibulae, two astragali, two calcanea, three partial to near complete articulated pedes.

BYU 19344: partial skeleton with partial dentary, dorsal, sacral, and caudal vertebrae, partial humerus, partial radius, distal tibia, partial metatarsal.

BYU 19345: partial articulated skeleton with one cervical vertebra, complete dorsal series, two fused sacral vertebrae, coracoid, scapulae, humerus, radius, partial ulna, carpal, metacarpals, partial femur, proximal tibia, fibula, and pes fragments.
BYU 19346: partial pelvis with five articulated sacral vertebrae, a partial posterior ilium, partial ischium, and a femoral head.

BYU 19347: partial skeleton with fragments of the dentary and maxilla, cervical, sacral, and caudal vertebrae, partial scapula, partial humerus, partial ulna, partial femora, partial tibiae, astragalus, and partial pes.

Horizon and Locality-The referred specimens from the Wayan Formation are from predominantly fine grained pedogenically altered silty mudstones in the latest Albian to early Cenomanian Wayan Formation of eastern Idaho. Localities are concentrated in two main areas (though specimens are known from elsewhere where the Wayan Formation crops out): the Tincup Canyon area of Caribou County, and the Caribou Basin area of Bonneville County (Fig. 1A). Referred specimen locality information is on file at BYU.

Revised diagnosis- Autapomorphic features of *Oryctodromeus cubicularis*: long paraoccipital processes indicating a skull with relatively broad proportions; basioccipital with a steeply sided ventral ‘box’ just rostral to the occipital condyle, seven sacral vertebrae, including two sacralized posterior dorsals and their ribs; large scapula with a sharply angled and narrow acromion process bearing a thin-edged laterally projecting scapular spine and a distinct posterior bend to the scapular blade; ilium with very short pre-acetabular and long post-acetabular portions; brevis shelf slopes mediolaterally and is visible laterally throughout its length; and long prepubic process with a transversely broad proximal portion possessing an elongate ventral fossa (Varricchio *et al.*, 2007).

The referred specimens from the Wayan Formation and newly prepared but undescribed Blackleaf Formation *Oryctodromeus* materials in the MOR provide the following additional
autapomorphies: elongate cervical centra about 1.6 times as long as high; posterior dorsal centra 1.4 times as long as high; squat sacral centra with transversely expanded articular faces with "W"- "U"- shaped cross section; elongate tail containing over fifty-five vertebrae encased in a sheath of hypaxial and epaxial tendons; distal two thirds of caudal vertebrae elongate with centrum length more than twice centrum height; coracoid with elongate ovoid fossa below the glenoid cavity; robust olecranon process; well-defined femoral head set on elongate neck projecting from the greater trochanter at 40°; laterally flattened greater trochanter; modest to weak anterior intercondylar groove on the femur; and bifid ascending process of the astragalus.

17.1 Terminology and Methods

In this description, the terminologies of Boyd and Gates (in prep), Scheetz (1999), and Varricchio et al. (2007) are used. Comparisons with *Orodromeus*, and *Oryctodromeus* were based on osteological descriptions (Scheetz, 1999; Varricchio et al. 2007) and direct specimen comparison. Comparisons to other genera were conducted through the literature.

Descriptions of the dentary teeth refer to a medial primary ridge which is the most distinct ridge on the crown. Cusps adjacent to the primary ridge (some supported by what are here referred to as secondary ridges) are referred to as denticles. Smaller denticles originating on these denticles are referred to as secondary denticles.

Descriptions are based on the specimens referred to above. When not otherwise specified, the description is based on the best represented specimen, BYU 19342.
17.2 Description

17.2.1 Skull

The skull of *Oryctodromeus* is incompletely known. Varricchio et al. (2007) illustrates the fused premaxillae and braincase of the holotype (MOR 1636a), and provided a brief description. Only the jugal, lacking the boss, is described for the juvenile paratype (MOR 1636b) (Varricchio 2007). The only skull elements known for the Idaho specimens are a partial dentary, a dentary fragment, and a possible maxilla fragment.

17.2.1.1 Dentary

Partial dentaries are known from BYU 19347 and BYU 19344. The latter consists of a bone fragment with a partial tooth while BYU 19344 (Fig. 2A) consists of the anterior one-fourth of the element and is the basis of this description. It contains six partial to complete tooth crowns.

In medial view the anteroventral portion of the dentary thickens and extends medially toward the predentary articulation, which is not preserved. The Meckelian groove runs ventrally and mesially through the contact area of the splenial. The tooth row is slightly inset from the lateral surface of the bone. Three nutrient foramina are preserved located slightly below mid-height of the dentary. This dentary differs little from those of other basal ornithopods such as *Orodromeus* (Scheetz, 1999) and *Hypsilophodon* (Galton, 1974).
17.2.1.2 Dentary Teeth

Teeth described here are from the dentary of BYU 19344 and consist of anterior dentary teeth braced labially by cyanoacrylate. The best preserved crown of BYU 19344 is shown in figure 2B. The single tooth in BYU 19347 is incomplete but is identical to those in BYU 19344.

As in Orodromeus (Scheetz, 1999) the crowns are triangular in medial and lateral view, distinctly constricted just above the root, slightly asymmetrical, and laterally compressed. Unlike Orodromeus however, Oryctodromeus teeth are nearly half again larger relative to the size of the dentary. In posterior crowns height exceeds the breadth, while on anterior crowns breadth exceeds height. The moderately developed cingulum is supported by a centrally placed bulbous primary vertical ridge that flares ventrally into the cingulum. The tooth apex is formed by the primary ridge. The mesial and caudal ridges of each tooth are comprised of prominent, dorsoventrally elongate denticles which number up to nine on each side of the crown. Denticles located mid-series on each side of the primary ridge descend farthest forming the longest secondary ridges which nearly reach the cingulum. Though no crown is perfectly preserved and none preserve a full set of denticles, the number of denticles on the mesial and caudal side of the crowns is similar. Secondary denticles are preserved on some primary denticles.

17.2.2 Axial Skeleton

The axial column is fairly well represented with the exception of cervical vertebrae, of which only three were recovered. A complete dorsal series with articulated ribs is preserved in BYU 19345. Sacral vertebrae are best represented in BYU 19342, which has four associated centra. The same specimen possesses a nearly complete caudal series, with at least 55 articulated and/or associated vertebrae.
17.2.2.1  Cervical Vertebrae

The holotype, MOR 1636a, bears 3 cervical vertebrae which were described simply as weakly opisthocoelous (Varricchio 2007). BYU 19345 has one poorly preserved and crushed cervical vertebra articulated with the dorsal column. BYU 19347 has two associated cervical centra. One of these (Fig. 2B,C,D), judged to be from the proximal cervical region, is well exposed and shows the centrum is platycoelus to slightly amphicoelus with the articular ends wider than high with an oblong heart shape (Fig. 3D), and has a pronounced ventral keel (Fig. 3C). The centrum is more elongate than in related forms, such as Zephyrosaurus (Rod Scheetz, pers. comm.) and Orodromeus (Scheetz, 1999), measuring 1.6 times as long as high. An undescribed Orodromeus-like basal ornithopod from Korea (Min Huh, pers. comm.) has similarly elongate centra. By comparison, the typical ratios in other basal ornithopod cervical vertebrae are 1.0 to 1.3. No other detail is discernible on this specimen.

17.2.2.2  Dorsal Vertebrae

Only six dorsal vertebrae are mentioned preserved in the holotype (MOR 1663a) but they were given only a cursory description (Varricchio et al., 2007). Specimen BYU 19342 has five dorsal vertebrae; two isolated centra and three in an articulated series (Fig. 2E, F). This series represents the last three dorsals as they are articulated with what is likely the first sacral. Specimen BYU 19345 contains an articulated series of vertebrae referred to the posteriormost cervical as well as fifteen dorsal vertebrae and two sacral vertebrae. Because some matrix was left on the specimen for stability, and the anterior-most vertebra (tentatively recognized as the posterior-most cervical) of the specimen is heavily crushed, details are less discernible, and assignment of specific positions of the vertebrae are tentative. The descriptions of dorsals 1-12 are based on BYU 19345, and dorsals 13-15 are based on 19342.
Like the cervical centra, the dorsal centra are elongate as in the undescribed Korean form (Min Huh pers. comm.) and slightly amphicoelus to platycoelus with moderately spool-shaped centra in ventral view. The anterior dorsal centra bear a ventral keel like that on the cervicals. The keel is less apparent on dorsal five and is absent by dorsal nine. The remaining posterior dorsal centra bear a poorly developed sulcus. Posteriorly in the series the centra become more robust. Posterior dorsals (Fig. 2E, F) exhibit roughened and rugose intervertebral muscle scars on the articular edges that are typical of basal ornithopod dorsal centra as in forms such as *Thescelosaurus* (Gilmore, 1915) and *Zephyrosaurus* (Rod Scheetz, pers. comm.). Beginning at dorsal three ossified epaxial tendons occur throughout the dorsal column of 44951.

The parapophyses and diapophyses are not visible in BYU 19345. By dorsal 13 of BYU 19342, the parapophyses and diapophyses merge into one articular facet. Transverse processes project dorsolaterally, originating just above the neurocentral suture and are longest in the first dorsal and decrease in length along the column. Transverse processes angle posteriorly in the anterior portion of the dorsal column, and more anteriorly in the posterior portion of the back vertebrae. Few details of the zygapophyses are discernible except that, in dorsal fourteen of BYU 19342 the prezygapophyses are of moderate size and are inclined roughly 30° from horizontal. Neural spines on the anterior dorsal vertebrae are narrower in lateral view and increase in width posteriorly in the series. Neural spines in the posterior dorsals flare slightly anteroposteriorly distally, as in *Orodromeus* (Scheetz, 1999), are roughly equal in height to the centra, originate just behind the anterior edge of the centra, and extend slightly beyond the posterior edge of the centrum.
17.2.2.3 Dorsal Ribs

Most dorsal ribs are represented in semi-articulation in BYU 19345 but details of the tuberculum and capitulum are not discernible. Ribs in this specimen are longest on dorsal 7 or 8. Varricchio and others (2007) describe this area (dorsal 6 or 7) as the transition area where the parapophyses and diapophyses begin to align in the horizontal plane. Ribs occur through dorsal 14 and are typical of small ornithopods.

17.2.2.4 Sacral Vertebrae

Isolated and associated sacral vertebrae are known for most specimens but no complete sacral series is represented by the Wayan material. BYU 19342 apparently preserves four associated sacral vertebra, with a partial probable first sacral in articulation with the dorsal series. In BYU 19345 the first two sacrals appear to be preserved in one massive, fused unit braced by ossified tendons more robust than in other portions of the vertebral column but obscuring individual centra and other features. In BYU 19346 three nearly complete and two incomplete sacral centra (possibly sacrals 2-6) are preserved. An articulated series of one and a half sacrals are known from BYU 19343. Sacral fragments are also known from BYU 19347. The entire sacrum is known for the holotype (MOR 1636a), but only briefly described and illustrated in lateral view (Varricchio et al., 2007). Unfortunately, no complete sacral series is known from the Wayan Formation, though isolated and associated sacral vertebrae are known for most specimens. Here, the sacrals from BYU 19342 and BYU 19346 are described, as they are the best preserved.

For BYU 19342 the first sacral (sacrodorsal) is largest of the four known, with a squat u-shaped cross section and a broad, nearly flat ventral surface with a very minor ventral groove. In
ventral view the centrum is shaped like a squat spool. The posterior portion of this centrum is incomplete. Three more sacral centra were closely associated with this specimen. These centra are wider than tall and have a“W” or “U”-shaped in cross section, as in an undescribed form from the Late Cretaceous of southern Utah (Boyd and Gates, in prep.). A moderate ventral sulcus is present on each centrum. In BYU 19346, a deep ventral sulcus is present on each sacral. Here, the most anterior sacral vertebra (second or third) is noticeably expanded transversely compared to later centra. Varricchio et al. (2007) described the third sacral in the holotype as bearing an abutment for the bracing of the pubis, as in Orodromeus and Zephyrosaurus (Scheetz, 1999).

17.2.2.5 Caudal Vertebrae

Caudal vertebrae are associated with most Wayan Formation Oryctodromeus specimens and most of these vertebrae are encased in a thick lattice of hypaxial and epaxial tendons that run parallel to the long axis of the centra, as in Hypsilophodon (Galton, 1974) and Tenontosaurus (Ostrom, 1970). Interestingly, the tail vertebrae in the holotype specimen (MOR 1636a) are described as bearing few ossified tendons, with a lack of a tendon lattice (Varricchio et al., 2007). No complete tail was found but BYU 19342 preserves at least fifty-five caudal centra and likely represents a nearly complete series. In this description proximal, mid, and distal caudals are distinguished by the length and height ratios of the centra and the presence/absence of transverse processes. Proximal caudals have centra that are taller than long with transverse processes, mid caudals have centra longer than tall, some with transverse processes, and distal caudals have centra at least twice as long as high with no transverse processes. As described here, the 55 caudal vertebrae of BYU 19342 are divided roughly into bins as follows based on morphology; 5 proximal, 9 mid, and 41 distal. The following descriptions are based on the nearly complete series of BYU 19342 and associated proximal and mid caudals from BYU 19343.
On proximal caudals (Fig. 2G, H) the dorsoventrally thick transverse processes attach just above the neurocentral suture and are angled up steeply and sweep slightly posteriorly. A complete right transverse process on a proximal caudal from BYU 19343 is roughly twice as long as the centrum is wide, as in *Orodromeus* (Scheetz, 1999). Centra are moderately laterally compressed, with their amphicoelus articular faces taller than wide. Laterally, centra are equidemensional, with length and height being roughly equal. On successive centra in the series the height decreases and length increases gradually. A weak ventral groove is present on the more anterior members of the proximal series while those farther back have a ventral keel. Chevron facets are present anteriorly and posteriorly with the latter being more pronounced. The neural spines are recumbent. Pre- and post-zygopophyses extend just beyond the centra and are of moderate size. The zygopophysial articular plane is about 45° from the horizontal.

Mid-caudals (Fig. 2I) have short transverse processes that originate on the neurocentral suture in more proximal centra and just below the neurocentral suture distally in the series. These processes sweep posteriorly and are more distal on the centra than on preceding vertebrae. Transverse processes are absent in the more distal mid-caudals. Although it cannot be confirmed with the Wayan material, the last transverse processes-bearing caudal in the holotype is number 19 on (Varricchio *et al*., 2007). Centra are amphicoelus with round to heart-shaped hexagonal ends, quickly elongate in the series, and bear a prominent ventral sulcus. Chevron facets become less distinct along the series and neural spines originate posteriorly and sweep over the proximal portion of the following vertebra with an anteroposteriorly flared tip. Prezygopophyses extend just beyond the centra and angle at 45° from the horizontal.
Distal caudals (Fig. 2J) are similar to those of *Zephyrosaurus* (Rod Scheetz, pers. comm.), being very elongate and amphicoelus. Centra have a distinct lateral ridge that gives them a hexagonal cross section and articular faces similar to those in *Tenontosaurus* (Forster, 1990) and *Zephyrosaurus* (Rod Scheetz, pers. comm.). The ventral sulcus persists but chevron facets are small. Neural spines are reduced and equal to the centra in height. These spines are positioned on the posterior-most portion of the centrum and do not extend beyond the centrum. Prezygopophyses extend just onto the next vertebra and angle by this point in the column to about 35°.

### 17.2.2.6 Chevrons

Despite the abundance of caudal vertebrae, only four chevrons were recovered. BYU 19343 has two chevrons associated with a proximal caudal centrum, and one chevron articulated with two mid-caudals. Proximally, the chevrons bear a single articular facet. The articulated chevron is longer than corresponding neural spines in contrast to the condition in ornithopods such as *Tenontosaurus* (Forster, 1990) where chevrons are equal in length to corresponding neural spines; and more similar to *Hypsilophodon* (Galton, 1974), where the mid-caudal chevrons are longer than the corresponding neural spines.
FIGURE 2. *Oryctodromeus* skull and vertebral elements. Dentary and teeth of BYU 19344, medial view (A). Cervical vertebra centrum of BYU 19347 in right lateral (B), ventral (C), and posterior (D) views. Posterior dorsal and possible first sacral vertebrae of BYU 19342 in right lateral (E) and ventral (F) views. Proximal caudal vertebrae of BYU 19343 in left lateral (G) and anterior (H) views. Mid-caudal vertebrae of BYU 19343 in left lateral (I) view. Distal caudal vertebra of BYU 19342 in right lateral (J) view.
17.2.3 Appendicular skeleton

17.2.3.1 Coracoid

Varricchio et al. (2007) figured the fused scapulocoracoid of the holotype, but the coracoid curves medially from the scapula preventing a full view of the element in their figure. This description is based on the nearly complete coracoid of BYU 44939. Four coracoids were recovered from the Wayan Formation.

The coracoid (Fig. 3A) is relatively large and robust with an ovoid outline similar to that of Orodromeus (Scheetz, 1999). The lateral and medial surfaces are nearly flat. The scapular articulation is thin and buttressed posteriorly by a transverse expansion with a large glenoid cavity bearing a centrally placed glenoid fossa. The coracoid foramen is placed well anterior of the scapula and fully enclosed, unlike Hypsilophodon (Galton, 1974); and is circular on the lateral surface and is a dorsoventrally elongated ellipse on the medial surface. As in Orodromeus (Scheetz, 1999), the sternal process is prominent, making the posterior border of the coracoids strongly concave. A shallow, elongate, ovoid fossa (referred to here as the ventral fossa) is located ventrally, between the sternal process and the glenoid fossa (Fig. 3B). Another shallow, circular fossa (referred to here as the lateral fossa) is present on the lateral side of the coracoid, located slightly anteroventrally of the glenoid (Fig. 3A).

17.2.3.2 Scapula

Six partial to nearly complete scapulae are known from the Wayan and compare favorably to the complete scapula of the holotype. The best preserved are associated with BYU 19345, BYU 19343, and BYU 19347; while BYU 19342 preserves portions preserved in
articulation with coracoids. Here descriptions are based on the right scapulae of BYU 19347 and BYU 19345.

The scapula (Fig. 3C) is strap-like and thin, with the distal ends missing. The expanded anterior end curves medially and is concave above the glenoid. The scapular blade has a strong posterior bend. The acromion process is prominently angled with a laterally projecting scapular spine similar in angle and form to other Orodromeus-like basal ornithopods. The ventral edge of the scapular neck is thick and rounded and becomes sharp posteriorly along the scapular blade.

17.2.3.3 Humerus

Two fragmentary and three nearly complete humeri are known from the Wayan Formation and compare favorably to the complete humeri of the holotype and paratype (MOR 1636a & 1636b). Near complete specimens are known from BYU 19344 and BYU 19345, while a proximal portion is known from BYU 19342 and fragments from BYU 19347. The best Wayan Formation specimen is a complete left humerus associated with 19343. Here descriptions are based on BYU 19343, BYU 19342, and BYU 19344.

In lateral and caudal views the humerus (Fig. 3D, E, F) is sigmoidal in shape. The humerus is widest at the proximal end and a well defined, raised head occurs centrally on the proximal end. The moderately developed deltopectoral crest is similar to that of Hypsilophodon (Galton, 1974) and emerges prominently as an outward swelling tubercle on the lateral margin, curves medially, and merges into the shaft about mid-length. The middle third of the shaft is ovoid in cross section. The distal end is bicondylar with an intercondylar groove which is most developed anteriorly.
17.2.3.4 Ulna

A radius and ulna are included in the holotype but were not illustrated nor described (Varricchio et al., 2007). Two ulnae are known from the Wayan, the proximal and possible distal ends in BYU 19347, and one in BYU 19345. Because the ulna for 19345 is articulated and embedded in matrix, this description is based on BYU 19347.

The ulna (Fig.3G, H) is triangular in dorsal view with a well-developed olecranon process. The shaft is oval in cross section. The tentatively assigned distal end is reniform and concave medially. In BYU 19345, the ulna is over 80% the length of the humerus.

17.2.3.5 Manus

A partial articulated manus (Fig. 5C) is preserved in BYU 19345. Tentatively, metacarpals II, III, IV, and V are/were present (II was only an imprint that was inadvertently removed during preparation). Proximally metacarpal IV is expanded, and III to a lesser degree. Metacarpals III and II are elongate and slender, similar to those of Dryosaurus (Galton, 1981) and Hypsilophodon (Galton, 1974). The metacarpals are 23% the length of the ulna. No other detail is discernible for the manus.

17.2.3.6 Ilium

A complete juvenile ilium is figured and described for the paratype (MOR 1636b) Varricchio et al. 2007). Fragments of ilia are known from BYU 19342 and BYU 19343, the anteriormost blade of the ilium is preserved in articulation in BYU 19345, and BYU 19346 preserves the posterior portion. The Wayan ilia fragments compare favorably to the paratype and do not provide additional information.
FIGURE 3. *Oryctodromeus* forelimb elements. Left coracoid of BYU 19343 in medial (A) and ventral (B) views showing ovoid lateral fossa and slit-like ventral fossa. Right scapula of BYU 19345 in lateral view (C). Left humerus of BYU 19343 in anterior (D), proximal (E), and medial (F) views. Left ulna of BYU 19347 in lateral (G) and proximal (H) views.
17.2.3.7 Ischium

Fragmentary ischium shaft fragments are known from BYU 19342 and the anterior two-thirds are preserved in BYU 19346, which is described below. No ischia have been described from the Blackleaf Formation materials.

The proximal portion flares forming the pubic and iliac peduncles and the posterior acetabulum. The lateral acetabular surface is distinctly concave. No other significant details are discernible from this specimen.

17.2.3.8 Pubis

Pubis shaft fragments are present in BYU 19343, and the anterior process and main body of the right pubis is preserved in BYU 19342, which is described here as it provides information on the previously undescribed prepubic process.

This process is dorsoventrally compressed proximal to the obturator foramen and main body of the pubis, with a flattened cross section. Anteriorly, it is more rounded and medially concave with a shallow groove running along its length. The main body of the pubis forms the anteroventral portion of the acetabulum and flares into flanges dorsally and ventrally, with the ventral flange being larger with a slight cotyle on the incomplete edge. Though incomplete, the overall morphology is very similar to Orodromeus and other related basal ornithopod forms. The flaring ventral edge and cotyle suggest a pubosacral articulation as in other Oryctodromeus specimens (Varricchio et al., 2007).
17.2.3.9  Femur

Most of the Wayan Formation specimens preserve at least partial femora. A well preserved, near complete left femur is known from BYU 19342, BYU 19345 has most of the left femur in sub-articulation with pelvic and sacral elements, a mid and distal right femur and loose right and left femoral heads occur in BYU 19347, and distal femora are associated with BYU 19343. The following description, based on BYU 19342 and BYU 19347 provides significant new information on the femur of *Oryctodromeus*.

The femur (Fig. 4A, B, C) is moderately robust in larger individuals such as BYU 19347 and BYU 19343, and slightly more gracile in juveniles, e.g. BYU 19342. The shaft is bowed anteriorly, as is typical in basal euornithopods (eg. Galton, 1974) and at mid-shaft is triangular in cross section. The prominent globular femoral head projects from the femoral shaft at an angle of 40 degrees, similar to the condition in a related but undescribed Korean taxon (Min Huh pers. comm) and is born on a distinct neck that angles steeply above and away from the greater trochanter. A deep sulcus for the ligamentum capitis femoris angles obliquely on the caudal portion of the head, as in *Orodromeus* (Scheetz, 1999) and *Hypsilophodon* (Galton, 1974). The greater trochanter is laterally flattened as in an undescribed form from the Kaiparowits Formation of Utah (Boyd *et al.* in press). The proximal portion of the lesser trochanter is missing, but the base is placed anteriorly and angles slightly laterally. A pendant triangular fourth trochanter projects posteromedially on the proximal portion of the shaft, as in other taxa, e.g. *Orodromeus*. A shallow pit for the insertion of the caudifemoralis muscle occurs medially on the shaft adjacent to the upper portion of the fourth trochanter. Distally, the lateral condyle is smaller than, and projects slightly farther posteriorly, the medial condyle. The flexor intercondylar groove is deep while the extensor intercondylar groove is more modest.
17.2.3.10 Tibia

Portions of tibiae are known for all specimens included in this study. A smaller left tibia and a larger right tibia (from two different individuals) are associated with BYU 19343 and are the basis for this description. Tibia/femur ratios of 1.19 are given for the juvenile paratype (MOR 1636b) and a tibia is known for the holotype (Varricchio et al., 2007) but was not described.

Tibiae (Fig. 4D, E) are gracile in comparison to femora, and bear a modest and rounded cnemial crest and a bifurcated lateral condyle, similar to Orodromeus but dissimilar to the southern Utah form (Boyd and Gates, in prep.). The mid-shaft is triangular in cross section. Astragali and a calcaneum are articulated on the two tibiae described here and obscure features of the distal end.

17.2.3.11 Fibula

Only two fibulae (Fig. 4F), both incomplete and lacking distal ends, have been found and both pertain to BYU 19343. A distal portion of the fibula is listed as part of the holotype, but was not described (Varricchio et al., 2007).

The fibula is a long, slender, simple element. The proximal head is anteroposteriorly expanded, concave laterally, and inclined posteriorly with a small flange on the posterior projection. The mid-shaft has a “D”-shaped cross section with the flat side medial, and changes to ovoid more distally, similar to Orodromeus.

17.2.3.12 Tarsus

Astragali (Fig. 4I, J) and calcanea are known for BYU 19347, BYU 19342, and BYU 19343. In BYU 19343, the specimen described below, the calcaneum is articulated on a left tibia
and a calcaneum and astragalus are articulated on a larger right tibia. A free right, loose calcaneum is also present. No ankle bones were previously reported for *Oryctodromeus*.

The astragalus is similar in form to *Orodromeus*, having a bifid ascending process that lies within the flexor groove of the tibia. The calcaneum fits firmly against the astragalus, and is roughly half the length of the astragalus and ovoid in lateral view.

### 17.2.3.13 Pes

Fully articulated left and right pes elements (from two different individuals – based on size) occur in BYU 19343. In addition this specimen has a third smaller partial articulated pes. Specimen BYU 19347 has an associated partial metatarsals and phalanges. Only the fourth metatarsal was found with the holotype, and a ratio of 0.58 metatarsal III/femur lengths was given for the juvenile paratype (Varricchio et al, 2007). BYU 19343 (Fig. 4G, H), described here, provides information on this previously undescribed unit of *Oryctodromeus*.

As in most ornithopods, the foot consists of five metatarsals, three of which are functionally weight bearing. The phalangeal formula is 2(?)−3−4−5−0. Proximally, metatarsal I is a thin blade, and distally becomes an ovoid shaft, as in *Orodromeus*. Metatarsal II and IV are equal in length, and shorter than metatarsal III. Proximally, metatarsal II is compressed mediolaterally to articulate with metatarsal III. In proximal view, the head of metatarsal III is wedge-shaped while the head of metatarsal IV is triangular. Distally, metatarsal IV diverges laterally at midshaft from metatarsal III, while metatarsal II diverges medially from metatarsal III near the distal third of metatarsal III. A small, centimeter-long, bladeiform element closely associated with one of the pedes of BYU 19343 is tentatively identified as metatarsal V. Phalange II-1 is distinctly elongate. Pedal unguals are roughly equal in proximal width and height, elongate,
triangular in cross-section, claw-like, and concave ventrally. Grooves flank both sides of the unguals and extend to the distal tips. Overall, the pes is similar to *Hypsilophodon* and other basal euornithopods.

### 18 DISCUSSION

#### 18.1 FUNCTIONAL MORPHOLOGY AND BEHAVIOR

Notable features of these new *Oryctodromeus* specimens include a number of previously undescribed features. The elongate cervical and dorsal centra are similar to the undescribed Korean form (Min Huh, pers. comm.). The extreme length of the tail, which comprised over half the body length, (the tail of 44920 would be nearly two meters long) is similar to *Tenontosaurus* (Ostrom, 1970; Forster, 1990). Elongate chevrons in the mid-caudal region of the tail indicate a deep tail, again similar to *Tenontosaurus* (Forster, 1990). A reconstruction of a complete *Oryctodromeus* individual with elements known from the Wayan is presented in figure 6.

The discovery of the holotype of *Oryctodromeus* within an infilled burrow provided the first evidence of fossorial behavior in a dinosaur and led to suggestions that other basal ornithopods may have been fossorial (Varricchio *et al.*, 2007; Boyd and Gates, in prep; Min Huh, pers. comm.). Evidence of such behavior was provided by Martin (2009) in the form of burrows closely matching the morphology of *Oryctodromeus* dens in the basal ornithopod-rich rocks of the Early Cretaceous Otway Group of Victoria, Australia. However, Boyd *et al.* (2010) have shown that most osteological correlates for fossorial behaviors in ornithopods are either restricted to *Oryctodromeus* itself or co-occur in presumably non-fossorial taxa such as *Thescelosaurus*. This complicates inferred fossorial behavior for any basal ornithopods.
FIGURE 4. *Oryctodromeus* hindlimb elements. Left femur of BYU 19342 in anterior (A), lateral (B), and proximal (C) views. Left tibia of BYU 19343 in lateral (D) and medial (E) views. Left fibula of BYU 19343 in lateral view (F). Right pes of BYU 19343 in lateral (G) and anterior (H) views. Left astragalus of BYU 19347 in medial (I) and proximal (J) views.
The abundant ossified tendons in the tail also complicate the inference of a fossorial habit, because the general consensus is that ossified tendons served to stiffen the vertebral column (Organ, 2006). If true, the stiff tail would hinder maneuverability in the tight confines of a burrow. The fossorial habit of *Oryctodromeus*, however, is well established, so it is possible that ossified tendons permitted significant tail flexion.

No vertebrate burrows have yet been observed in the Wayan Formation, but taphonomic evidence strongly suggests some *Oryctodromeus* specimens were preserved in burrows. The evidences are:

1. Preferential preservation - the overwhelming abundance of the genus relative to other vertebrates (except for eggshell),
2. High degree of articulation, including hands and feet (Fig. 5),
3. Absence of bone modification such as abrasion, breakage, weathering, and tooth marks,
4. “Pockets” yielding multiple partially articulated individuals of various ontogenetic stages,
5. Consistent occurrence in calcic paleosols.

Taken together, these features are consistent with individuals who were buried, often as congregations, in burrows.
FIGURE 5. Articulated Oryctodromeus, BYU 19345, from Wayan Formation in dorsal (A) and ventral (B) views. Detail of left manus (C).
18.2 PALEOBIOGEOGRAPHY

During the Cenomanian in eastern Idaho the Sevier Orogeny was well underway with the Meade Thrust inducing thrust loading and rapid subsidence of the foredeep that filled with Wayan and Blackleaf sediment (Wiltschko and Dorr, 1983; Dorr, 1985; DeCelles et al., 1993). *Oryctodromeus* lived within a narrow inland alluvial strip bordered by the active thrusting in the Paris Highlands to the west and the Mowry Seaway to the east.

The presence of *Oryctodromeus* in both the Wayan and Blackleaf faunas suggests age equivalence of the formations and, therefore, these stratigraphic packages likely represent the same elongate basin or generation of basin(s) adjacent at the toe of the Sevier thrust belt. Presently, these formations are separated by the volcanics of the Snake River Valley of eastern Idaho.

The Idaho *Oryctodromeus* specimens represent the first middle Cretaceous basal ornithopod genus reported between Montana and Utah, and fill in a gap in the geographic range of basal ornithopods. This description of Idaho’s first well represented dinosaur allows more detailed faunal comparisons with similarly aged faunas from the Western Interior of North America.
CONCLUSIONS AND SIGNIFICANCE

*Oryctodromeus* is the first Idaho dinosaur to be described in detail and provides substantial, new osteological data for the taxon. The Idaho specimens consist of numerous partial articulated specimens which sometimes occur in pods of multiple individuals, with the bones lacking evidence of surficial exposure – taphonomic characters that are consistent with the fossorial habit first recognized by Varricchio *et al.*, (2007). Thus the Wayan Formation provides additional evidence for burrowing by this small, basal ornithopod. The recognition that *Oryctodromeus* occurs in the Wayan Formation, which shares sedimentologic and tectonic position with the nearby Blackleaf Formation in Montana extends the range of the genus and suggests these formations were contemporaneous and deposited in the same foredeep trough. If subsequent work verifies this inference, the Wayan Formation would have priority.

REFERENCES


