# AN ORNITHISCHIAN DINOSAUR FROM THE SUSTUT BASIN, NORTHERN BRITISH COLUMBIA, CANADA. 

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#### Abstract

In 1971, dinosaur bones were discovered during uranium exploration in the Sustut Basin in northern British Columbia, Canada, and were donated to Dalhousie University in Nova Scotia in 2004. Although dinosaur bones have been reported from British Columbia previously, this specimen is the earliest recorded discovery of dinosaur bones from the province. The specimen also represents one of the westernmost discoveries of dinosaur bones in Canada. The bones were collected from loose blocks in a talus slope, near the intersection of Birdflat Creek and Sustut River.

The fossils are encased in a hard siltstone that shares characteristics with both the Early Albian to Late Cenomanian Tango Creek Formation and the Late Campanian to late Early Maastrichtian Brothers Peak Formation, making a more precise age estimate for this specimen difficult. Bones collected include the right humerus, a radius, the distal portion of the right tibia and fibula, several pedal phalanges including two unguals, and several unidentifiable fragments. A small block of matrix removed from the tibia contains additional small bones, but further preparation is not possible at this time.

Comparison of the material with specimens at the Royal Ontario Museum and descriptions in the literature indicates that a relatively small (less than three metres in length), bipedal ornithischian is represented. General features of the tibia and phalanges are consistent with the ornithopod Thescelosaurus, but a low deltopectoral crest on the humerus matches closely with Stegoceras and other pachycephalosaurs. The specimen may represent a new taxon unique to British Columbia.


Keywords: Dinosauria, Ornithopoda, Iguanodontia, Pachycephalosauria, systematics, palaeoecology, palaeobiogeography, Cretaceous, intermontane basin

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### 1.0 INTRODUCTION

### 1.1 Background

In 1971, Kenny Flyborg Larsen, an economic geologist, discovered fossil bones (Fig. 1.1) in the Sustut Basin of Northern British Columbia (Fig. 1.2). As he was prospecting for thorium, his scintillometer registered above-background levels of radiation in a talus pile near the junction of Birdflat Creek and Sustut River. This radiation was emitted by the fossil bones. Larsen recorded the discovery in his field notes and collected the loose bones from the rubble. The bones remained in his possession until 2004, when they were donated to the Earth Sciences Department at Dalhousie University.


Figure 1.1: The Sustut dinosaur specimen, prior to further preparation for this study. There are at least 14 bones represented by this material.


Figure 1.2A: Location of the Bowser and Sustut Basins (in red) in northern British Columbia, Canada.
Modified from Ferri (2003).

Figure 1.2B: Geographical relationship between the Bowser and Sustut Basins. Modified from Mustard (2003).

Figure 1.2C: Map sheet NTS 94 D shows the location of the Sustut River and Birdflat Creek junction (in blue) in the southern Sustut Basin.
Modified from Mustard (2003).

Figure 1.2D: Enlargement of highlighted area in Fig. 1.2C. The collection site is located near the intersection of Birdflat Creek and Sustut River. Modified from National Topographic Series sheet 94 D, 1986, and Evenchick et al. (2003).

### 1.2 Vertebrate Palaeontology Of British Columbia

A brief overview of the fossils, and especially the vertebrate fossils, of British Columbia assists in understanding the significance of the Sustut Basin dinosaur discovery. Rolf Ludvigsen provides a thorough, yet concise, overview of British Columbia's palaeontology in his book Life in Stone: A Natural History of British Columbia's Fossils (1996). The book provides coverage of many invertebrate, vertebrate, microfossil, and palaeobotanical discoveries. As with most places in the world, invertebrates and microfossils are more abundant in the fossil record than are vertebrate remains. Characteristic invertebrates of British Columbia include trilobites, ammonoids, bivalves, and insects, as well as the Burgess Shale fauna made famous in 1989 by Steven Jay Gould's book Wonderful Life: The Burgess Shale and the Nature of History. Plant fossils such as carbonized leaves and petrified trunks are also abundant in the province.

Less common, though just as important to our understanding of evolution and biodiversity, are British Columbia's fossil vertebrates. British Columbia has several localities with abundant and well-preserved fish fossils. Triassic fish fossils have been found at Wapiti Lake (Neuman, 1996), and fish fossils have also been recovered from various Cenozoic localities around the province (Wilson, 1996; Carlson and Klein, 1996). Cenozoic mammal fossils are also abundant in British Columbia (Harington, 1996; McAnnally, 1996).

Mesozoic marine reptiles are well represented in British Columbia. The first elasmosaur from the west coast of Canada was discovered on Vancouver Island and dubbed the Puntledge Elasmosaur (Ludvigsen, 1996). Another group of marine reptiles, the mosasaurs, which had long tails and paddle-like limbs, are represented by Tylosaurus and are also found on Vancouver Island (Ludvigsen, 1996). Pink Mountain has been the site of
discovery for more than 60 ichthyosaur specimens, as well as several thallatosaurs (Nicholls and Manabe, 2001). Several new ichthyosaur species have been named, most notably Shonisaurus sikkanniensis (Nicholls and Manabe, 2004), the largest ichthyosaur yet discovered in the world, at over 21 metres in length. Many ichthyosaurs have also been discovered at Williston Lake and are summarized in McGowan (1997).

Until quite recently, discoveries of dinosaur bones were exceptionally rare in British Columbia. A single phalanx of an ornithopod dinosaur was found by accident in 1979 in a display of coal pebbles at the offices of Crow's Nest Industries Ltd (Sampson and Currie, 1996), in the town of Fernie (Fig. 1.3, site A). The exact location where it was collected is unknown, but it may have come from Jurassic or Cretaceous strata. It has been heavily abraded, and is broken and incomplete. As such, it is difficult to glean any precise details about the dinosaur it likely belongs to, but it most closely resembles the ornithopod dinosaur Camptosaurus (Sampson and Currie, 1996). In 1992, a tooth was discovered on Vancouver Island (Fig. 1.3, site B) and eventually identified in 1994 as a theropod tooth (Ludvigsen, 1996). The tooth is 1 cm long and was found in Upper Cretaceous deep marine sediments; it was likely washed into the ocean by a river, or a carcass may have floated out to sea and been


Figure 1.3: Dinosaur fossils in British Columbia. A - A single phalanx was found in 1979 in an office in Fernie.
B - A single tooth was found in 1992 near Courtenay, Vancouver Island.
C - Many dinosaur tracks have been found along the Peace River Canyon.
D - Dinosaur tracks have also been found near Michel, Fernie and Elkford. E - A single dinosaur footprint was found in the Bowser Basin in 2004.
F - Dinosaur footprints and numerous dinosaur bones have been found near Tumbler Ridge since 2002.

* Sustut collection site, discovered in 1971. Map modified from Ferri, 2003.
scavenged by fish or marine reptiles (Ludvigsen, 1996).
Although dinosaur bones are rare in British Columbia, the province has long been an important location for dinosaur trackway and footprint sites. Dinosaur tracks were abundant along the Peace River Canyon (Fig. 1.3, site C), but many of the best sites are now submerged under a lake between the W.A.C. Bennett and Peace Canyon dams (Sampson and Currie, 1996). Prior to the construction of the W.A.C. Bennett Dam, more than fifty tracks were studied by staff from the Royal Ontario Museum, and many were preserved through casting (Sampson and Currie, 1996). Likewise with the construction of the Peace Canyon Dam, palaeontologists from the Royal Tyrrell Museum of Palaeontology salvaged many tracks prior to the completion of the dam (Sampson and Currie, 1996). In that case, over 1700 footprints were documented (Sampson and Currie, 1996), about two hundred were cast, and ninety were collected and are now in museum collections (Cannings and Cannings, 1999). Dinosaur tracks have also been found in coal mines near the towns of Michel, Fernie and Elkford (Fig. 1.3, site D) (Sampson and Currie, 1996). The most recent discovery was of a single ornithopod dinosaur footprint in the Bowser Basin (Fig. 1.3, site E) during the summer of 2004 (Evenchick et al., 2005). The tracks at these various sites represent several ichnogenera: Amblydactylus, Irenesauripus, Irenichnites, and Tetrapodosaurus (Sampson and Currie, 1996). These ichnogenera indicate that hadrosaurs, smaller ornithopods, large, medium-sized, and small theropods, and ankylosaurs were present British Columbia from the Late Jurassic to Early Cretaceous (Sampson and Currie, 1996).

Even though dinosaur tracks had been known in British Columbia since 1922 (Sampson and Currie, 1996) only two dinosaur bones had been recorded from the province. This would change in 2002. After two young boys discovered an ankylosaur trackway and
vertebrate bone while tubing down Flatbed Creek near the town of Tumbler Ridge (Fig. 1.3, site E), a prospecting trip to the nearby Quality Creek Canyon was organized in 2002 (McCrea and Buckley, 2004). During this trip, vertebrate bones were discovered in a loose block of rock that had slid down the steep cliffs surrounding the river; McCrea and Buckley (2004) describe this discovery in detail. The bones were excavated during the summer of 2003 and are currently in preparation (pers. comm., Buckley, 2005). Dinosaur vertebrae and ribs were collected, as well as a phalanx, fibula, possible pelvic bone and possible ossified tendons; these may be from a medium-sized ornithopod (McCrea and Buckley, 2004). A theropod tooth and ankylosaur scute were also discovered. Non-dinosaurian vertebrate fossils included crocodilian scutes, fish bones, and a partial turtle carapace. Large fossilized tree logs were also found at the site. The fossils are all found within the Kaskapau Formation, which is Upper Cretaceous (Turonian) in age.

### 1.3 Significance

As discussed above, dinosaur skeletal material has rarely been recovered from British Columbia. The Sustut dinosaur is the first dinosaur specimen collected from the Sustut Basin, and seems to be the first dinosaur body fossil ever discovered in British Columbia: the Sustut dinosaur was discovered in 1971, while the hadrosaur phalanx was discovered in 1979 (Sampson and Currie, 1996), the theropod tooth in 1992 (Ludvigsen, 1996), and the Tumbler Ridge material in 2002 (McCrea and Buckley, 2004). The Sustut specimen is, aside from the isolated theropod tooth, the westernmost dinosaur yet discovered in Canada. This specimen may represent a new genus or species. Dinosaur assemblages along the west coast of North America are poorly known at present, and as such, the Sustut dinosaur may shed new light on
the palaeobiogeography of North American dinosaurs. The specimen's occurrence in an intermontane basin amid the newly accreting terranes of British Columbia leads to questions regarding the origin of dinosaurs in British Columbia, and whether endemic faunas were developing in this region.

### 1.4 Objectives

The main objective of this study is to describe the fossil material collected by Larsen and determine which taxon is represented. Information from Larsen's field notes as well as the matrix surrounding the bones will be used to narrow down the location of the original collection site, and the geological formation, environment of deposition, and age will be considered. The significance of this new specimen to dinosaur biogeography will be briefly considered.

### 2.0 GEOLOGICAL BACKGROUND AND LOCATING THE COLLECTION SITE

### 2.1 Introduction

Dinosaurs living in Mesozoic British Columbia would have found themselves in a tectonically active area. The province formed as a series of offshore terranes accreted to the west coast of ancestral North American continent. Mountain chains developed, with periods of intense volcanism, and isolated areas were occasionally inundated by seawater. In this chapter, I will briefly review the tectonic history of British Columbia, and describe the sedimentary environments and palaeogeographic settings of the Bowser and Sustut Basins. Finally, I will attempt to relocate the original fossil collection site, using Larsen's field notes and information from the matrix surrounding the bones.

### 2.2 Canada West Of The Rockies

Until the early Palaeozoic, the west coast of North America was a passive margin formed from the Neoproterozoic breakup of the supercontinent Rodinia (Dickinson, 2004). Much of western North America was then extended westward as a series of exotic terranes accreted to the edge of the continent. British Columbia thus began to form in the midPalaeozoic as a series of island arcs rose from the ocean floor, far to the south of their current position based on palaeomagnetic and palaeontological data (Coney et al., 1980). Other pieces of British Columbia are continental in origin and represent pieces of displaced ancestral North America (Cannings and Cannings, 1999). The Kootenay terrane (Fig. 2.1) is an example of one of these displaced continental fragments (Cannings and Cannings, 1999).

Several terranes accreted to ancestral North America during the Palaeozoic, but here I will focus on Mesozoic terrane accretion.

The Quesnellia Arc (Fig. 2.1) was originally considered an oceanic structure with no genetic relationship with ancestral North America (Dickinson, 2004). It was originally thought to have amalgamated with another volcanic arc called Stikinia, forming the Intermontane Superterrane (Cannings and Cannings, 1999). However, new research indicates that it may have been a


Figure 2.1: Simplified terrane map of British Columbia showing some of the major terranes. Map modified from Ore Systems Consulting (1998) and Geological Survey of Canada (2004).
magmatic arc along the North American margin (Dickinson, 2004). In Canada, the backarc region of Quesnellia was flooded by seawater (Dickinson, 2004), forming the Slide Mountain Terrane (Cannings and Cannings, 1999).

West of Quesnellia is the Cache Creek Terrane (Fig. 2.1), which forms a suture zone between the Triassic-Jurassic continental margin and the accreted terranes to the west (Dickinson, 2004). The Cache Creek Terrane represents a series of thrust panels of seafloor containing fossils of Permian Tethyan affinities (Coney et al., 1980). Blueschists that formed as a result of subduction metamorphism are Late Triassic (230 to 210 Ma) (Dickinson, 2004).

When the Cache Creek Terrane accreted, the subduction zone 'jammed' and was forced to retreat westward (Dickinson, 2004).

Stikinia (Fig. 2.1) accreted to North America by the Middle Jurassic, and includes Upper Triassic to Middle Jurassic volcanics, volcaniclastics, and associated plutons (Dickinson, 2004). Two more major island arcs lay off the west coast of British Columbia at this time. The Alexander Terrane (Fig. 2.1), which likely lay near the Arctic during the midPalaeozoic, and Wrangellia (Fig. 2.1) joined to form the Insular Superterrane (Dickinson, 2004). The two arcs had amalgamated by the Carboniferous, and had accreted to North America by the Middle Jurassic (Dickinson, 2004).

Changes in the subducting plates at 85 Ma resulted in a shift to transform motion of the west coast along the Northern Rocky Mountain Trench and the Fraser and Queen Charlotte-Fairweather Faults (Cannings and Cannings, 1999). This resulted in 'smearing' of many of the accreted terranes. Wrangellia is a good example of the displacement many of the terranes experienced. Although Wrangellia probably occupied about 7 latitudinal degrees originally, transform motion resulted in pieces of Wrangellia being displaced over a latitudinal spread of 24 degrees at present, from Oregon through British Columbia to Alaska (Schermer et al., 1984).

### 2.3 The Bowser And Sustut Basins

The Bowser and Sustut Basins (Fig. 1.2 A and B) have been described by Gabrielse (1991), Gabrielse et al. (1991), and Yorath (1991), and the following is a summary of their descriptions. The two basins lie within the Intermontane Belt, a topographically low area (with the exception of the Skeena Mountains), bounded to the east by the Omineca Belt and to the west by the Coast Belt. The Omineca Belt includes the Cassiar, Omineca and Columbia Mountains and spans the boundary between the edge of Ancestral North America
to the east and the accreted terranes to the west. The Coast Belt includes the Coast and Cascade Mountains and formed as the Insular Superterrane accreted to the Intermontane Superterrane (which had previously docked with North America).

Within the Intermontane Belt, the stratified rocks are not usually metamorphosed higher than greenschist facies. Broad folds are characteristic of volcanic sequences, while tight folds and thrust faults are common within sedimentary units. A series of dextral strikeslip faults of Late Cretaceous and Tertiary age trend northwest. The underlying terranes in this region are overlapped by sediments eroded from units uplifted during times of compression associated with terrane accretion. The Bowser and Sustut Basins are two such overlap assemblages.

In the Mid Jurassic, the Cache Creek Terrane was thrust onto Stikinia, and marine sediments were deposited in the Bowser Basin. From the Late Jurassic to Early Cretaceous, contraction of these terranes resulted in uplifted source areas for the Bowser Basin. Cretaceous to Tertiary sediments in the Sustut Basin indicate the collapse of the Bowser Basin eastern margin (Bustin and McKenzie, 1989) along with uplift of the Omineca Belt during Albian to Campanian (Lower to Upper Cretaceous) time, and uplift of the Bowser Lake Group during Campanian to Maastrichtian time (Upper Cretaceous) (Gabrielse et al., 1991). The Late Cretaceous record for the Sustut Group also records evidence of active volcanism, with tuffs possibly derived from volcanoes in the Intermontane and Omineca belts. During the Late Cretaceous, transform motions began to occur in the Canadian Cordillera, resulting in northward displacement. Palaeopoles from the Intermontane and Insular Superterranes suggest that at 100 Ma the terranes were 2400 km south of their current position, and that they reached their current position by approximately 80 to 50 Ma through
transform motion. This contrasts with fossil evidence (leaves and palynomorphs), which suggests that much less displacement occurred after the Bajocian (Middle Jurassic).

The Bowser Basin occupies $4900 \mathrm{~km}^{2}$ and is as much as 3500 m thick in some areas. Sediments include deposits from Late Bajocian to Early Oxfordian (Middle to Upper Jurassic), with possible Lower Cretaceous rocks near the top. The basin is bounded by the Stikine Arch to the north, the Skeena Arch to the south, the Omineca Belt to the east, and the Coast Belt to the west. The Middle Jurassic to Lower Cretaceous Bowser Lake Group consists of marine sediments, with some nonmarine sediments (the Groundhog Coal Measures) towards the top of the group. Relatively abundant fossils include: belemnites, pelecypods, and ammonites in the Ashman Formation; belemnites in the McEvoy unit; abundant poorly preserved plant fossils, rare bivalves and ammonites, and locally abundant shoreline coquinas in the youngest strata; and abundant woody material and pelecypods near the southwest margin. In 2004, a fossil turtle shell and dinosaur footprint were discovered by members of the Integrated Petroleum Resource Potential and Geoscience Studies of the Bowser and Sustut Basins project (Evenchick et al., 2005).

The Sustut Group unconformably overlies the Bowser Lake Group, with rocks of mid-Albian age along the northern and eastern margins of the Bowser Basin. The Sustut Basin contains nonmarine sediments 300 to 2600 m thick. The age of the sediments ranges from mid-Albian to Maastrichtian, with possible early Tertiary sediments. Occupying a narrow belt between the Skeena and Omineca Mountains, it extends from Takla Lake in the southeast to Stikine River in the northwest. Fossil leaves are relatively abundant within the Sustut Group. The lithology of the Sustut Group will be discussed in detail in the following section.


Numerical time scale is from Harland 4 t al ( 1900 .
WITHMD Hiatus
Figure 2.2: Stratigraphy of the Spatsizi River area, representative of other regions in the vicinity of the Bowser and Sustut Basins. This stratigraphic column shows the relationships between the Sustut and Bowser Lake Groups and their respective formations. Image from Evenchick and Thorkelson (2004).

### 2.4 The Sustut Group

The Sustut Group has been described in detail by Eisbacher (1974) and Bustin and McKenzie (1989). Located between Takla Lake to the southeast, Skeena River to the north, the Omineca Mountains to the east and the Skeena Mountains to the west, it represents an Upper Cretaceous nonmarine assemblage, divided into two formations: the Tango Creek Formation and the Brothers Peak Formation.

### 2.4.1 The Tango Creek Formation

The Tango Creek Formation unconformably overlies the Bowser Lake Group. It ranges in thickness from about 500 m in the east to 1400 m in the west (Yorath, 1991). It is generally characterized by interbedded sandstone, mudstone, and pebble conglomerate, with occasional thin seams of lignite (Yorath, 1991). Eisbacher (1974) summarized ages previously given for the Tango Creek Formation, based largely on fossil leaves and pollen. Ages generally ranged from Cenomanian to Palaeocene. The Integrated Petroleum Resource Potential and Geoscience Studies of the Bowser and Sustut Basins project (2005) conducted a study in 2001 that revised the age of this formation as Barremian or Early Albian to Late Campanian. The Tango Creek Formation is informally divided into the Niven and Tatlatui Members.

The Niven Member is composed of interbedded sandstones and mudstones with a polymictic basal conglomerate. Sandstones are sub-quartzose, feldspathic arenites, and are more abundant than mudstones. Red mudstones and quartz-pebble conglomerates are located higher within this member. Yorath (1991) describes the 'lower Tango Creek Formation' as rich in detrital mica and quartz. Gabrielse et al. (1991) also notes that muscovite is common through the lower Sustut Group, possibly originating from a metamorphic source in the Omineca Belt.

Eisbacher (1974) described the Tatlatui Member as consisting of dark grey mudstones and chert-pebble arenites, with the mudstones being more abundant. Within the mudstone, layers of calcite concretions were common. Higher within the member, thin seams of lignite are locally abundant.

Bustin and McKenzie (1989) subdivided the Tatlatui Member into fine-grained and coarse-grained lithofacies. The fine-grained lithofacies are largely made up of interbedded mudstone, siltstone, and fine-grained sandstone. Mudstone is commonly brown, grey or black, and thinly laminated. Siltstones are green or grey, thinly bedded, and locally carbonaceous. Sandstones are brown or grey, parallel-bedded, and have common carbonaceous lenses and mudstone rip-up clasts.

The Tatlatui Member coarse-grained lithofacies consist of orthoconglomerates and coarse to medium-grained sandstones. Conglomerates are grey, massive or thick-bedded, pebbly, poorly sorted, and with sharp or channel bases. Carbonaceous fragments and mudstone rip-up clasts are common as in the fine-grained lithofacies, but large (up to 3 m long) log impressions, and calcareous sandstone concretions are also present. Sandstones are light to dark grey and contain chert, quartz, and volcanic and sedimentary fragments, and are cemented by calcite, quartz, or clay.

Sediments in the Niven Member were likely deposited in meandering streams and in flood events that resulted in overbank deposits (Bustin and McKenzie, 1989). Within the basin, topography probably did not exceed 50 m , but to the east elevations as much as 150 m may have existed (Bustin and McKenzie, 1989).

The Tatlatui Member was deposited in an alluvial plain with a low gradient, with meandering rivers carrying a large load of suspended sediments (Bustin and McKenzie, 1989). Seasonal freshwater lakes were common. Splays and sheet flood deposits are recorded by the fine-grained lithofacies of Bustin and McKenzie (1989). Lignite near the top of the unit indicates the development of floodbasin swamps. Bustin and McKenzie (1989) considered the coarse-grained lithofacies to indicate the presence of braided streams.

Eisbacher (1974) considered the Bowser Basin to be a significant source of sediments for the Tatlatui Member. In contrast, Bustin and McKenzie (1989) contend that the Omineca Belt to the east and the Cache Creek Terrane were the main sources of sediment. The Tatlatui Member could thus record uplift of either the Bowser Basin or the Omineca Belt and the formation of an alluvial plain or distal alluvial fan in the Sustut Basin.

### 2.4.2 The Brothers Peak Formation

The Brothers Peak Formation conformably and unconformably overlies the Tango Creek Formation, and ranges in thickness from 300 m to 1500 m (Yorath, 1991). The formation is characterized by conglomerates, sandstones, mudstones, and ash-fall tuffs. Eisbacher (1974) summarized ages previously assigned for the Brothers Peak Formation based on fossil leaves and K-Ar dating. The age estimates ranged from possible Palaeocene to Eocene. The Integrated Petroleum Resource Potential and Geoscience Studies of the Bowser and Sustut Basins project (2005) conducted a study in 2001 that revised the age of this formation as Late Campanian to late Early Maastrichtian. The Brothers Peak Formation is informally divided into the Laslui and Spatsizi Members.

Bustin and McKenzie (1989) subdivided the Laslui Member into upper and lower divisions that include both coarse and fine-grained lithofacies. The coarse-grained lithofacies consists of orthoconglomerates and coarse to fine-grained sandstone. Conglomerates have erosional bases and fine upwards, are massive to thick-bedded, and contain clasts of black, red, green and grey chert, quartz, volcanic fragments, sedimentary fragments, and granitic fragments. Sandstones are dark brown to grey, fine upwards, and are cemented by quartz, calcite, or clay. Common to both the conglomerates and sandstones are mudstone rip-up
clasts, carbonaceous fragments, and log impressions. The fine-grained lithofacies consists of rhythmically interbedded fine-grained sandstone, siltstone, and mudstone. The lower Laslui is characterized by dark grey, black, and green carbonaceous mudstone, siltstone, and finegrained sandstone with orthoconglomerate. The upper Laslui is characterized by interbedded mudstone, siltstone, fine to very-fine grained sandstone, and tuffs. The tuffs, which are bluegreen and buff coloured, locally make up as much as $25 \%$ of the upper Laslui Member, and are associated with bentonite beds.

The Laslui Member most likely represents a flood-plain environment with highenergy braided river complexes (Bustin and McKenzie, 1989). Mudflows and debris flows were responsible for the conglomerates. Tuff beds probably formed in small lakes or ponds, after volcanic ash was carried by floods to the alluvial plain. The Bowser Lake Group became a more important sediment source than in the Tango Creek Formation. Volcanic fragments probably eroded from the Takla Group and Hazelton Group to the southwest. Tuffs probably originated far away from the Sustut Basin in a long-lived active volcanic center possibly represented by the Brian Born Formation to the southwest.

The Spatsizi Member is a monotonous succession of cyclic, fining upward sandstone and mudstone sequences and thick intervals of homogeneous dark mudstone. The sandstones are dark grey to green, have sharp or channeled bases, and contain pebble lag deposits, carbonaceous fragments, and calcareous concretions. They are composed primarily of plagioclase, volcanic rock fragments, K-feldspar, chert, mica, and metamorphic rock fragments. The mudstones are black to dark grey or green, massive or thick-bedded, and locally carbonaceous.

The Spatsizi Member records deposition from braided streams, followed by the submergence of the alluvial plain and the deposition of mudstones in lacustrine environments. Major sources for the sediments were probably the Bowser Lake Group, Takla Group, and Hazelton Group.
2.5 The Bone Matrix

The sediments that remained on some of the fossil bones (the 'matrix') are a dark grey sandy siltstone with a carbonate cement and carbonaceous fragments. The largest pieces of matrix were removed from the distal end of the tibia and the articulated phalanges. Bedding is difficult to distinguish on most samples.

Two thin sections of the matrix were prepared. The material for the thin sections was a relatively large block of matrix on which articulated toe bones were preserved. The thin sections were cut after the bones had been removed. One sample was cut perpendicular to the indistinct bedding, while the other was cut parallel to the bedding.

The fine-grained, poorly sorted matrix includes some very large grains with diameters of 2 to 5 mm . These large grains have ill-defined edges and contain smaller grains, and may represent altered or relict grains, or the beginning of concretions. Thin fractures are present both parallel to and cutting bedding. They are filled with colourless isotropic material that is difficult to identify in thin section.

Minerals present include quartz, feldspar, and micas. There also appear to be volcanic rock fragments. Quartz is the most abundant clast type, and the large (up to 0.25 mm ), colourless quartz grains appear to be unstrained and do not suggest a metamorphic provenance or subsequent deformation. The brown biotite grains are coarse and likely
sedimentary in origin, and there are biotite-rich patches within the sample. A 'stringy' mica of uncertain type (possibly muscovite or illite) has a feathery appearance with ill-defined boundaries, which may represent incipient cleavage. Minor chlorite is also present. There are sandier lenses that are rich in accessory minerals such as possible zircons. A large lithic clast is likely igneous in origin, and exhibits a crystalline texture with feldspar and a green mineral which may be epidote. However, this clast does not resemble the volcanic fragments that are also present. There appears to be less than $1 \%$ mafic material visible in the thin sections.

### 2.6 Locating The Original Collection Site

The following is an excerpt from Larsen's field notes from 1971, which were generously provided during an interview on February 3, 2005; a copy of the original notes is provided in Appendix A. Larsen was working for Uranerz Mining and Exploration Co. Ltd. (that has since been bought by Cameco), prospecting for uranium during the 1971 field season (pers. comm., 2005). Unfortunately, the original field maps have since been lost. However, several pieces of information from Larsen's notes have helped pinpoint the location of the fossil material.

Kenny Flyborg Larsen
Field Notes 1971
Friday, August 3
Airborne Time 1 $3 / 4$ Hours.
Boys in Sustut River Area
$13 / 4$ hours of helicopter borne radiometric surveying in the Sustut river - Birdflat Creek area. Looked @ several good sections of interbedded sandstone (greywacke), mudstone, conglomerate and bitumen rich siltystene shales. Occ. petrified logs, bones ect. [sic] may show weak radioactivity - Thin ( mm to rarely cm . seams of bitumen likewise are occ. weakly radioactive. The scarecity[sic] of radioactive
material and the low grade does not appear to make this section economically favourable.

Total hours - Helicopter to date. 48.2 hours

Saturday, August 4

Total Airborne Radiometric time - 1 hour

RAIN \& heavy fog. - Cleared slightly at $1^{00}$ PM. Crew stayed in Camp - packed up all geochem samples. Ken went airborne radiometric - down Atika River Valley to Junction with Sustut river. Suspicious anomaly 9 min flying time ( 30 knots) from Atika river Junction in Sustut river canyon - will check this out again tomorrow Sunday.

- The anomaly is about 1200 CPS - max 1500 CPS - some 30 feet above tree tops previous background was about 4-600 CPS.

Checked out fossil bone location again - collected several more bones appear to be from Cretaceous giant sloth - one toe with claw bone well preserved Will send entire collection to G.S.C. if they are interested.

During the interview, Larsen also described in more detail the location of the bone discovery. The bones were found in a rubble pile near the intersection of Sustut River and Birdflat Creek, in a BC Rail cut which ran alongside the river. The talus slope was located on one side of the railway, and the river on the opposite side (Fig. 2.1). Larsen described the area as rich in bituminous material, and that the bitumen seams were all slightly radioactive.

In an email from May 20, 2005, Larsen further described the area. He recalled fishing on an island near some rapids in the Sustut River, and indicated the location on an air photo that I provided (Fig. 2.3). He stated that the island was relatively close to the bone locality. He also emphasized that no other radioactive fossil bones were found anywhere else in the area during his work there, but admitted that he and his crew were looking for larger radioactive signatures.

With additional geological information, it is possible that the location of the Sustut bones (both geographically and geologically) can be narrowed down more precisely. The intersection of Sustut River-Birdflat Creek can be found on NTS Map Sheet 94D, McConnell

Creek Area. Several airphotos also show this intersection (Fig. 2.3). The intersection falls within the Sustut Basin, where rocks of the Sustut Group outcrop (Fig. 2.4). The Sustut Group is divided into the lower Tango Creek Formation and the upper Brothers Peak

Formation.


Figure 2.3: Composite air photo showing the intersection of the Sustut River and Birdflat Creek, in NTS Map Area 94-D McConnell Creek Area. Annotations indicate major features from Larsen's 1971 field notes and subsequent interviews in 2005.


Figure 2.4: Distribution of outcrops of the Tango Creek Formation (orange) and Brothers Peak Formation (yellow), modified from the composite air photo in Fig. 2.1 and Evenchick and Porter (1993). Variations of outcrop distributions by other authors show only the Tango Creek Formation or Brothers Peak Formation outcropping in this area (e.g. Integrated Petroleum Resource Potential and Geoscience Studies of the Bowser and Sustut Basins, 2005 and MINFILE Database, 2005).

The matrix surrounding the dinosaur's bones is a dark grey, sandy siltstone, with carbonaceous fragments and cemented by carbonate. Thin sections contained poorly sorted, angular grains. Quartz, feldspar, biotite, muscovite or illite, volcanic rock fragments, and chlorite were present. Log impressions were found near the bones.

Carbonaceous fragments are found in the Tatlatui Member (Tango Creek Formation), and Lower Laslui and Spatsizi Members (Brothers Peak Formation). Carbonate cement is found in the Lower Laslui, Upper Laslui, and Spatsizi Members. The Niven Member (Tango Creek Formation) is rich in mica and quartz, but these are present in the Spatsizi Member as well. Volcanic rock fragments are also present in the Lower and Upper Laslui Member and the Spatsizi Member. Log impressions are recorded from the Lower Laslui Member. These characteristics suggest that the dinosaur bones may have originated from the Lower Laslui Member of the Brothers Peak Formation. However, the presence of abundant micas in the thin sections correlates with descriptions of the Niven Member (Tango Creek Formation), which is said to be rich in muscovite. It is thus difficult to say with certainty from which formation within the Sustut Group the bones were collected, and therefore difficult to assign an age to this dinosaur.

### 2.7 Summary

Consideration of sedimentological evidence and field records demonstrate the dinosaur bones were found in mid to Late Cretaceous terrestrial rocks of the Sustut Basin in northern British Columbia, more than 1000 kilometres from the more famous dinosaur assemblages of Alberta. This area represents a floodplain environment, with high-energy braided river complexes depositing sediments eroded from the Bowser Lake Group, the

Takla Group, and the Hazelton Group. Mudflows and debris flows were common, as were flood events. An active volcanic center to the southwest produced volcanic ash sporadically, which settled in lakes and ponds within the basin.

### 3.0 METHODS

### 3.1 Collection Techniques: Radiological Instruments And Digging For Dinosaurs

As explained previously, the bones were collected from a talus slope near the Sustut River and Birdflat Creek confluence in the Sustut Basin, British Columbia. However, Larsen's field notes do not explain the precise location of the collection site, and no field maps remain to provide additional information. The bones are radioactive and were detected by Larsen's scintillometer while he was prospecting for thorium. A similar method could be employed to prospect for additional fossils in the Sustut basin. Radioactive fossil vertebrates are also found in the Morrison Formation in Utah, the Hagerman Fossil Beds in Idaho, and at several locations in South Africa (Jones et al., 1998; Carman, 1988).

Jones et al. (1998) summarized the process in which vertebrate bones may become enriched with uranium. Igneous rocks are believed to be the ultimate source of the uranium, which is released into groundwater during weathering. Uranium ions are mobile if the groundwater is oxidizing, and bond with oxygen to form uraninite in a reducing environment. Decaying organisms may provide this reducing environment. The uranium may be incorporated into the crystal structure of other minerals as those minerals grow and replace the original organic material of the bone. It is also possible for uraninite to precipitate into cracks and voids within the bone. Using a modified scintillometer, Jones et al. (1998) developed a technique for radiological surveying of fossil vertebrates that was able to successfully locate the missing in situ skull of a theropod dinosaur at Dinosaur National Monument in Utah. The abandoned quarry was mapped using the scintillometer, and data was entered into a spreadsheet that corresponded to the grid of the quarry. Background
radiation was subtracted so that only elevated radiation levels remained. Their hypothesis was that the elevated radiation levels represented concentrations of uranium, which could indicate subsurface fossil bone. Further excavation proved that the technique was successful, as the elevated levels of radiation corresponded to the missing theropod skull. The authors note that this form of radiological surveying could be useful in remote areas where field time is limited, as the surveying reduces time spent digging in unfossiliferous locations, and helps to define bone boundaries.

Radiological surveying could potentially be useful in the Sustut Basin. It is possible that the source of the uranium is a large igneous body located near the site where the bones were recovered. Access to the Birdflat Creek and Sustut River areas is restricted to a few trails and rail grade (National Topographic Series sheet 94 D, 1986; National Topographic Series sheet 94 D/6, 1985). Since the precise location of the collection site within this area is unknown, a scintillometer could be used to identify areas with higher-than-background radiation. If such trials were successful, a more precise line survey could be undertaken, using the surveying technique developed by Jones et al. (1998). These techniques could provide an affordable way to prospect in the Sustut River-Birdflat Creek area for additional vertebrate fossils.

### 3.2 Preparation Techniques

The dinosaur's bones are preserved in a hard, black siltstone that has proven to be extremely difficult to remove without endangering the bone. Most of the bones were recovered by Larsen with little to no siltstone matrix remaining on the bone surface. Larsen did not attempt to remove any of the remaining matrix (pers. comm., Larsen, 2005).

However, the tibia had a large piece of matrix near the distal end, which in turn contained smaller bones. The articulated phalanges and ungual were almost completely removed from the matrix, articulated on a block of matrix with all but the plantar side free from the rock. These phalanges were relatively easy to remove from the underlying


Figure 3.1: Tools used for vertebrate fossil preparation include dental tools, hammers, chisels, and brushes. A magnifying lamp (upper right corner) was also useful. matrix and the bones suffered only clean fractures during removal; these were easily repaired later on.

To remove the bones from the matrix, a small cold-steel chisel, a small craft hammer, assorted dental picks, and brushes were used (Fig. 3.1). Cloth bags filled with rice were placed underneath the bones during chiseling to prevent damage to the bones from the hard surfaces of desks and tables. A magnifying lamp was used to illuminate and magnify the bone during preparation, and a hand lens was also used to examine the surface of the bone. While chiseling, small pieces of matrix were removed, and care must be taken not to let the surface of the bone flake away with the matrix. The bones were stored in cardboard boxes filled with foam and cotton batting, and the removed matrix was saved and stored in a separate bag after each preparation session.

Chure (1993) highlights the health risks associated with preparing radioactive fossil vertebrate bone. The greatest risk comes from inhaling the radioactive dust, which can lead to cancer with prolonged exposure. The risks associated with directly handling radioactive bones themselves are usually negligible. Dr. Sandy Grist (Fission Track Lab Manager, Dalhousie University Earth Sciences) tested the radioactivity of the dinosaur bones to ensure that they were safe for handling. Background radiation in the Life Sciences Centre at Dalhousie University is approximately 20 to $40 \mu \mathrm{R} /$ hour. The $\beta$ radiation for each bone or group of bones was tested using a Victoreen Radiation Meter. Only the humerus was measured with the $\beta$ shield on (which measures all other radiation); under this setting, the radiation of the humerus was approximately $20 \mu \mathrm{R} /$ hour, which is equivalent to background radiation. The bones were then tested with the $\beta$ shield off, with the bone less than one centimetre from the device. The results are given in Table 3.1 below.

| Table 3.1: $\beta$ radiation emitted by the Sustut specimen, using a Victoreen Radiation Meter. Background <br> radiation on the day of testing was 20 to $40 ~$ $\mathrm{R} /$ hour. |  |
| :--- | :--- |$|$| Bone | Radioactivity $(\mu \mathrm{R} / \mathrm{hour})$ |
| :--- | :--- |
| Humerus | $\sim 100$ |
| ?Ulna | $\sim 100$ |
| Radius | $\sim 125-130$ |
| Indeterminate Bone 1 (?skull) | $\sim 90$ |
| Articulated digit | $\sim 40$ |
| Disarticulated phalanges | $\sim 60-70$ |
| Tibia/fibula | $\sim 70-80$ |
| Matrix block | $\sim 30-40$, maximum 60 |

None of the bones emit enough radiation to harm a person during short-term
handling. However, to minimize the risks of radioactive exposure, the preparation areas were always kept well ventilated, all surfaces were cleaned to remove chips of matrix after the session was over, and hands were always thoroughly washed after each preparation session.

Removing the matrix from the bones without damaging the bones proved to be a difficult task. It is not always clear whether one is looking at bone or rock. X-rays of the tibia
and fibula were taken, in the hopes of being able to delineate the boundary between rock and bone more effectively. Chloe Younger (Curator, Dalhousie University Earth Sciences) assisted with the use of the X-ray machine in the Department of Earth Sciences, which is normally used to X-ray sediment cores. An arrow (marked on a piece of material visible on the developed X-ray film) was placed underneath the tibia inside the X-ray machine. If the arrow was visible on the developed film, the X-rays had penetrated through the bone. Several X-rays were taken, with differing exposure times, but the arrow was never visible on the developed film. This indicated that the X-rays were unable to penetrate the bones. It was too difficult to differentiate between the rock and bone, and the technique proved unsuccessful.

Certain fossils can be prepared by dissolving the matrix with acid (Rutzky et al., 1994). A technique involving hydrogen peroxide, water, and chiseling has been successful at removing the matrix without damaging the bone. An eyedropper is used to soak specific areas of the bone with peroxide, and then water is used to further soften the matrix. The softened matrix can then be removed using the chisel and picks. The method is slow, but makes differentiating between matrix and bone somewhat easier. It also has the added benefit of reducing the amount of dust generated by the preparation process.

Either before or after collection, most of the bones had suffered numerous breaks. Larsen had repaired some of these breaks using an unidentified adhesive resembling hot glue or epoxy. Some of the bones had been slightly misaligned during repair, so an attempt was made to remove the adhesive and reset the bones. Some epoxies can be softened using steam. A cappuccino machine was used to create and direct steam in a controlled manner, and protective gloves and tongs were used to hold the bones in place (Fig. 3.2). This method was
ultimately unsuccessful, since the glue did not soften even after several minutes of direct immersion in the steam.

The remaining breaks were repaired using Vinac donated by Tim Fedak (Dalhousie University Biology and Fundy Geological Museum). Vinac is polyvinyl acetate, and is used by many museums to repair fossils because it is reversible, easy to work with, and strong (pers. comm., Fedak, 2005). It is safe to use in a well-ventilated area, and Material Safety Data Sheets are available for further handling information.


Figure 3.2: Using a cappuccino maker to remove glue. Gloves are used to handle the larger bones (A), while tongs are used for the smaller bones (B). The steam is not visible in the photos.

Measurements of length, width, and thickness were made after the bones had been cleaned and repaired. The measurements were taken using a Vernier caliper (except for the tibia, which was larger than the caliper; a clear plastic ruler was used instead). The margin of error for each measurement is $\pm 1 \mathrm{~mm}$. Each measurement was made three times, and the results were averaged.
3.4 Research Visit At The Royal Ontario Museum

I visited the Vertebrate Palaeontology Collections at the Royal Ontario Museum in Toronto from July 25 to 27, 2005. Dr. Kevin Seymour is the Head of Vertebrate Palaeontology Collections at the museum, and graciously lent his time to show me around the collections department, set up a workspace, and answer questions. The purpose of the visit was to examine first-hand a variety of dinosaur bones and casts. Special attention was paid to the limb bones of ornithischians, but bones from all groups of dinosaurs, as well as crocodilians, turtles, and champsosaurs were also observed. Several hundred digital photographs of numerous specimens were taken, descriptions of the bones were noted, and relevant literature was acquired from the museum's reprint collection. A complete listing of all observed specimens is given in Table 3.2 on the following page. This important part of the thesis research provided an opportunity to observe comparative specimens (most notably the small ornithopod Parksosaurus warreni) and improve my familiarity with dinosaur anatomy.

Table 3.2: Specimens observed at the Royal Ontario Museum.

| ROM catalogue numb | er Specimen name | Notes |
| :---: | :---: | :---: |
| Ornithischian Dinosaurs |  |  |
| 3082 | Hypsilophodontid | Ungual |
| 3586 | Hypsilophodontid | Ungual |
| 36533 | Hypsilophodontid | Ungual |
| 45957 | Hypsilophodontid | Femur; Australian, cast |
| 45960 | Hypsilophodontid | Femur; Australian, cast |
| 45961 | Hypsilophodontid | Tibia; Australian, cast |
| 45966 | Hypsilophodontid | Tibia; Australian, cast |
| 45968 | Hypsilophodontid | Tibia; Australian, cast |
| 45970 | Hypsilophodontid | Femur; Australian, cast |
| 45971 | Hypsilophodontid | Tibia; Australian, cast |
| 46253 | Laosaurus minimus | Pes; cast |
| 46240 | Othnielia rex | Pes; cast |
| 804 | Parksosaurus warreni | Skeleton; type specimen of Thescelosaurus warreni |
| 5687 | ?Thescelosaurus sp. | Tibia |
| 49590 | Camptosaurus sp. | Ungual |
| 49589 | Camptosaurus sp. | Ungual |
| 49593 | Camptosaurus sp. | Phalanx |
| 44643 | Iguanodon sp. | Ungual; cast |
| 03508 | Juvenile hadrosaurid | Humerus |
| 633 | Edmontosaurus sp. | Tibia |
| 00801 | Edmontosaurus annectens | Pes |
| 869 | Lambeosaurus lambei | Pes; type specimen of Corythosaurus frontalis |
| 1935 | Edmontonia rugosidens | Humerus |
| 1930 | Euoplocephalus tutus | Humerus |
| Saurischian Dinosaurs |  |  |
| ? | Therizinosaurus cheloniformis | Ungual; cast |
| 1790 | Struthiomimus altus | Pes |
| R9951/26354 | Baryonyx walkeri | Ungual; cast |
| 49543 | Allosaurus fragilis | Radius, ulna |
| 36242 | Tyrannosaurid | Ungual |
| 31810 | Tyrannosaurid | Ungual |
| 807 | Albertosaurus sarcophagus | Humerus; type specimen of Albertosaurus arctunguis |
| Crocodilians |  |  |
| R4415 | Alligator mississippiensis | Humerus, femur, tibia, pes |
| Turtles |  |  |
| 50780A | Geochelone sp. | Tibia |
| 51239 | Geochelone sp. | Tibia |
| 52906 | Hesperotestudo ?crassiscutata | Ungual |
| Champsosaurs |  |  |
| 806 | Champsosaurus albertensis | Humerus, radius, ulna; type specimen |

### 4.0 DESCRIPTION OF THE FOSSIL MATERIAL

### 4.1 General Comments

The bones are solid and are not deformed, although many are missing either the distal or proximal ends. The bones recovered by Larsen include the right humerus, right radius, left tibia, left fibula, seven pedal phalanges (including two unguals), a possible hip girdle fragment, a possible ulna, and several small bones encased in a block of matrix.

No bones from the skull, pectoral girdle, pelvic girdle, axial skeleton (vertebrae and ribs), or manus are preserved. A tooth or plant fragment may have been recovered from matrix surrounding one of the bones, but further preparation is impossible with the available equipment.

I will follow the positional terms used by Weishampel et al. (2004) in The Dinosauria, $2^{\text {nd }}$ Edition. The following terms will be important to remember while reading this chapter:

- cranial: towards the head (anterior)
- caudal: towards the tail (posterior)
- dorsal: the top of the animal
- ventral: the underside of the animal
- palmer: refers to the underside of the manus
- plantar: refers to the underside of the pes
- proximal: towards the centre of the body
- distal: away from the centre of the body
- medial: towards the sagittal line
- lateral: away from the sagittal line
4.2 Humerus
Dimensions (in millimetres):
Length: 101 (minimum)
Proximal width: 36
Proximal thickness: 20
Distal width: 33
Distal thickness: 16

The proximal end of the right humerus (Figs. 4.1 - 4.6) has been abraded, and the distal end has broken off, making the total length and distal width of the humerus unknown. Comparison with the pachycephalosaurian Stegoceras validum (Gilmore, 1924a) suggests the Sustut humerus may have been as long as 130 mm , while comparison with the basal ornithopods Thescelosaurus neglectus (Gilmore, 1915) and Parksosaurus warreni (Parks, 1926) suggests a maximum length of around 119 mm and 112 mm , respectively. The maximum proximal width is 36 mm . Although the humeral head is abraded, it appears to have been small and weakly developed (Fig. 4.1). It is unclear if it was situated in the center of the proximal articular surface. The proximal end is slightly expanded relative to the shaft, and the distal end of the preserved portion of the bone also shows that the bone was beginning to expand again (Fig. 4.1).

The deltopectoral crest is poorly developed in this specimen, and is nearly nonexistent (Fig. 4.1). The deltopectoral crest is cranially directed, is thickest near the proximal end of the humerus, and eventually merges with the rest of the humerus. The shaft is bowed only slightly. The medial face has a rounded, relatively shallow depression that is deepest near the proximal end and extends 62 mm down the shaft; the depression does not extend completely to the proximal edge of the bone (Fig. 4.1). The shaft is elliptical in cross section at the distal end, but with a slightly flattened medial surface (Fig. 4.6).


Figure 4.1: The right humerus, medial view. Note the reduced deltopectoral crest and weak curvature of the shaft. Scale bar equals 10 mm .


Figure 4.2: The right humerus, lateral view. Scale bar equals 10 mm .


Figure 4.3: Right humerus, caudal view. Scale bar equals 10 mm .


Figure 4.4: Right humerus, cranial view. Scale bar equals 10 mm .


Figure 4.5: Right humerus, proximal view. Scale bar equals 10 mm .


Figure 4.6: Right humerus, distal view. Scale bar equals 10 mm .

### 4.3 Radius

Dimensions (in millimetres):
Length: 136
Proximal width: 32
Proximal thickness: 19
Distal width: 25
Distal thickness: 27
Minimum diameter of shaft: 14
The complete right radius is preserved (Figs. 4.7-4.12), and is 136 mm long. The proximal end is somewhat expanded but badly damaged. The shaft is slender and slightly sigmoidal. The proximal end has a flattened, elliptical cross-section, while the shaft has a triangular cross-section with pronounced edges. The distal end of the radius is thick and less abruptly expanded than the proximal end. It has a rounded, triangular shape in crosssection.


Figure 4.7: The right radius, lateral view. Scale bar equals 10 mm .


Figure 4.8: Right radius, caudal view. Scale bar equals 10 mm .


Figure 4.9: Right radius, medial view. Scale bar equals 10 mm .


Figure 4.10: Right radius, cranial view. Scale bar equals 10 mm .


Figure 4.11: Right radius, proximal view.
Scale bar equals 10 mm .


Figure 4.12: Right radius, distal view.
Scale bar equals 10 mm .

### 4.4 Tibia

Dimensions (in millimetres)
Length: 212 (minimum)
Distal width: 90
Proximal width: 26
Proximal thickness: 38
Only the distal portion of the left tibia is preserved (Figs. 4.13-4.18). This fragment is 212 mm long. Comparison of the tibia to Parksosaurus warreni (Parks, 1926), which has a similar distal width $(93 \mathrm{~mm})$ and overall morphology, suggests the Sustut tibia may have been as long as 312 mm . Comparison with the tibia of the related but smaller Thescelosaurus neglectus (Gilmore, 1915), which has a distal width of 77 mm , suggests the Sustut tibia may have been as long as 350 mm . The distal end of the tibia is expanded, and two malleoli are visible on the caudal side as flat planes, which meet at a low angle offset from the midline of the shaft (Fig. 4.13). This produces a sharp edge on the caudal side of the tibia, which is discernable for 80 mm up the shaft. The outer malleolus is approximately 64 mm wide, while the inner malleolus is approximately 46 mm wide. The outer malleolus has a slight concavity near the angle with the inner malleolus, on the caudal side.

The cranial side of the distal end of the tibia is covered in a hard matrix that is impossible to remove with the available equipment without damaging the bone. The morphology of the cranial side is therefore unknown (Fig. 4.14). The caudal surface is convex when viewed laterally or medially (Fig. 4.15).

The shaft of the tibia is round but slightly triangular in cross section at the broken proximal end (Fig. 4.17). The shaft becomes more triangular in cross section towards the distal end, before the tibia expands into the inner and outer malleoli.

### 4.5 Fibula

Dimensions (in millimetres)
Length: 203 (minimum)
Proximal width: 19
Proximal thickness: 10
Distal width: 15
Distal thickness: 26
The left fibula is preserved in close articulation with the left tibia (Figs. 4.13-4.18).
The proximal end is also missing, and the preserved portion is 203 mm long. Comparison with Parksosaurus warreni (Parks, 1926) suggests a length of 330 mm for the Sustut fibula. The shaft of the fibula at the broken end has a round, elliptical cross section (Fig. 4.17). It is narrow and curves cranially towards the distal end (Fig. 4.16).

The distal end is slightly expanded and lies on the cranial face of the outer malleolus of the tibia (Fig. 4.14). The distal tip of the fibula is flattened. No fusion with the tibia is observed.


Figure 4.13: Distal portions of left tibia and fibula, caudal view. Eroded ankle bones may be preserved at the distal end of the tibia. The fibula lies alongside the tibia. Scale bar equals 50 mm .


Figure 4.14: Distal portion of left tibia and fibula, cranial view. At the distal end, some edges of bone under the matrix may represent eroded portions of ankle bones. The fibula lies next to the tibia. Scale bar equals 50 mm .


Figure 4.15: Distal portion of left tibia and fibula, medial view. Note the curvature of the distal tibia.


Figure 4.16: Distal portion of left tibia and fibula, lateral view. Scale bar equals 50 mm .


Figure 4.17: Right tibia and fibula, proximal view. The bones have been broken perpendicular to the long axis. Scale bar equals 10 mm .


Figure 4.18: Right tibia and fibula, distal view. Bone and matrix are difficult to differentiate at the distal end of the tibia. Approximate bone outlines are indicated by a dashed line. Scale bar equals 10 mm .
4.6 Pes

| Table 4.1: Measurements of the pedal elements (in millimetres) |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Length | Proximal <br> transverse <br> width | Distal <br> transverse <br> width | Proximal <br> vertical height | Distal vertical <br> height |
| Digit II, <br> phalanx I | 40 | 23 | - | 18 | - |
| Digit II, <br> phalanx II | 29 | 23 | 22 | 21 | 17 |
| Digit II, <br> phalanx III | 29 | 26 | 24 | 22 | 18 |
| Digit IV, <br> phalanx I | 29 (minimum) | 17 | - | 14 | - |
| Digit IV, <br> phalanx II | 22 | 19 | 18 | 16 | 12 |
| Digit IV, <br> phalanx III | 23 | 20 | 18 | 20 | 14 |
| Digit IV, <br> phalanx IV | 25 | 20 | 21 | 19 | 16 |

Larsen recovered articulated phalanges from two separate digits, for a total of 7 bones. Comparison with measurements in Parks (1926) suggests that these represent elements from digit II (phalanges I, II, and III), and digit IV (phalanges I, II, III, and IV). Comparison with Parksosaurus warreni (Parks, 1926) suggests that these bones were originally part of the right pes, based on the relative lengths of the condyles: the outer condyles are longer than the inner condyles in $P$. warreni.

Digit II (Figs. 4.19, 4.20) was found articulated on a block of matrix. Unfortunately, the bones have been glued together and repaired using a non-reversible glue. Therefore, the distal and articular surfaces are generally not visible. Digit II has three phalanges including the ungual. The ungual has a triangular outline when viewed dorsally, with a pointed tip. It appears curved and claw-like, but the plantar side has been broken. The ungual is not laterally compressed, which indicates it may have been more hoof-like than claw-like, with a flattened plantar side. Lateral grooves are present but badly eroded, and appear to have been shallow. The articular end is not visible.

The phalanx that articulates with the ungual, phalanx II, has the usual features associated with phalanges. The distal end and proximal ends are raised with respect to the middle of the bone, giving the bone an hour-glass outline when viewed laterally. The distal end is pulley-like. Lateral pits are present but poorly preserved. The outer condyle is longer than the inner condyle. The distal and articular ends are not visible. The next phalanx, phalanx III, is similar to phalanx II. The articular side is visible but badly eroded, and the articular facets are poorly defined (Fig. 4.20).

Digit IV (Figs. 4.21-4.32) consists of four phalanges, including the ungual. The proximal two phalanges were previously glued and so the articulating ends are not visible. The distal two phalanges articulate well with the proximal two phalanges, indicating that these were separated during erosion of the encasing sediments, or during collection.

While the distal tip of the ungual is missing, the ungual otherwise had a triangular outline similar to the ungual in digit II (Fig. 4.21). Shallow lateral grooves are partially visible (Figs. 4.21, 4.24), and the ventral side is missing as in digit II. The articular surface is visible and shows two adjacent facets, with the medial articular facet slightly smaller than the lateral articular facet (Fig. 4.25).

Phalanx II of digit IV is similar to the phalanges in digit II. The articular surface is preserved, and shows facets with a similar arrangement to those on the ungual (Fig. 4.26). The medial facet is smaller than the lateral facet. Lateral pits are shallow and poorly preserved (Figs. 4.29, 4.30). Phalanges III and IV are similar in appearance to phalanx II (Figs. 4.31, 4.32). The articular end is not visible on phalanx III, and is poorly preserved on phalanx IV.


Figure 4.19: Digit II, medial view showing three articulated phalanges including ungual.
Scale bar equals 10 mm .


Figure 4.20: Digit II, lateral view showing three articulated phalanges including ungual. Scale bar equals 10 mm .


Figure 4.21: Digit IV, ungual, dorsal view. Scale bar equals 10 mm .


Figure 4.23: Digit IV, ungual, lateral view. Scale bar equals 10 mm .


Figure 4.22: Digit IV, ungual, plantar view. Scale bar equals 10 mm .


Figure 4.24: Digit IV, ungual, medial view. Scale bar equals 10 mm .


Figure 4.25: Digit IV, ungual, articular (proximal) view. The interior facet is smaller than the exterior facet. Scale bar equals 10 mm .


Figure 4.26: Digit IV, phalanx II, articular (proximal) view. The interior facet is smaller than the exterior facet. Scale bar equals 10 mm .


Figure 4.27: Digit IV, phalanx II, dorsal view. Scale bar equals 10 mm .


Figure 4.29: Digit IV, phalanx II, medial view. Scale bar equals 10 mm .


Figure 4.28: Digit IV, phalanx II, plantar view. Scale bar equals 10 mm .


Figure 4.30: Digit IV, phalanx II, lateral view. Scale bar equals 10 mm .


Figure 4.31: Digit IV, phalanges III and IV, dorsal view. Scale bar equals 10 mm .


Figure 4.32: Digit IV, phalanges III and IV, plantar view. Scale bar equals 10 mm .

### 4.7 Indeterminate Bones

Several bones recovered by Larsen cannot be identified at this time. Two of these are fragments of otherwise well-preserved bones. The others are found in a block of matrix that cannot be prepared further with the available tools.

Indeterminate Bone 1 (Figs. 4.33-4.36) is extremely thin and flat, with thicknesses ranging from 6 to 15 mm . It is 98 mm long and 33 mm wide. It is strongly curved in several directions. It is badly broken on almost all edges, making identification difficult. Based on its thin, curved shape, this fragment may represent a bone from the lower jaw. Other flat bones include the scapula, pubis, ischium, ilium, and parts of the vertebrae.

Indeterminate Bone 2 (Figs. $4.37-4.42$ ) is 78 mm long, 32 mm wide, and ranges from 7 to 22 mm thick. One end of the fragment has a triangular outline with a pronounced notch, while the other end is thin and flattened. The long axis of the fragment is bowed. Both ends of the bone are broken off, again making identification difficult. The cross sections of the two ends are similar to those of a right ulna, which this fragment may represent.

A block of matrix was removed from the cranial face of the distal end of the tibia, and further preparation revealed that several small bones are encased in this block (Fig. 4.43). Complete preparation was impossible with the available equipment and time. At least two bones are present within the block. These may represent additional phalanges, or possibly parts of the astragalus, calcaneum, or tarsals.


Figure 4.33: Indeterminate Bone 1. This bone could be a fragment of the skull, but it is too poorly preserved to determine exactly.

Scale bar equals 10 mm .


Figure 4.34: Indeterminate Bone 1, reverse side of Figure 4.33. Scale bar equals 10 mm .


Figure 4.35: Indeterminate Bone 1, top view of Figure 4.33.
Scale bar equals 10 mm .


Figure 4.36: Indeterminate Bone 1, bottom view of Figure 4.33. Scale bar equals 10 mm .


Figure 4.37: Indeterminate Bone 2. This bone fragment may represent part of an ulna. Scale bar equals 10 mm .


Figure 4.38: Indeterminate Bone 2, reverse side of Figure 4.37. Scale bar equals 10 mm .


Figure 4.39: Indeterminate Bone 2. Scale bar equals 10 mm .


Figure 4.40: Indeterminate Bone 2, reverse side of Figure 4.39. Scale bar equals 10 mm .


Figure 4.41: Indeterminate Bone 2, top view of Figure 4.37. Scale equals 10 mm .


Figure 4.42: Indeterminate Bone 2, bottom view of Figure 4.37. Scale equals 10 mm .


Figure 4.43: This block of matrix contains several small bones, one of which became visible after a few hours of preparation.

Scale bar equals 10 mm .

### 5.0 TAXONOMIC ASSIGNMENT

### 5.1 What Is A Dinosaur?

In order to assign the Sustut dinosaur to a particular taxon, we should first understand what a dinosaur is and is not, and understand how dinosaurs are grouped. The Dinosauria, $2^{\text {nd }}$ Edition (edited by Weishampel et al., 2004) provides a good overview of these topics; the reader is referred to this book for a more in-depth discussion of dinosaur systematics and evolution.

Vertebrate animals all share a backbone composed of vertebrae, and most have a distinct head and tail. Vertebrata includes the numerous types of fishes, the 'amphibians' and 'reptiles', as well as birds and mammals. Within the vertebrates, Tetrapoda includes those animals with the pelvis attached to the vertebral column, and four limbs. Tetrapoda includes all vertebrates except fishes.

Within the tetrapods, the amniotes ("reptiles", birds, and mammals) are those animals with an amniotic egg. The Amniota is divided into three major lineages. These divisions are based on the number of postorbital fenestrae (in other words, the number of holes behind the eye socket). The Anapsida have no fenestrae, and include the turtles and their extinct relatives. The Synapsida have only one postorbital fenestra, and include modern mammals (monotremes, marsupials, and placentals), plus their extinct relatives. Diapsids have two postorbital fenestrae, and include the extant Sphenodon (tuatara), crocodilians, birds, lizards, and snakes, and their extinct relatives. Recently, there is some debate as to whether turtles belong in the Diapsida.

Diapsida is in turn divided into two major lineages, one leading to modern snakes and lizards (Lepidosauromorpha), and one leading to modern birds and crocodiles (Archosauromorpha). The Archosauromorpha includes several extinct lineages, as well as the Archosauria.

Archosauria is a major grouping of tetrapods, characterized by the presence of yet another hole in the head, the antorbital fenestra (found in front of the eye socket). One branch of the Archosauria, the Crurotarsi, leads to crocodiles, while the other, the Avemetatarsalia, leads to birds. Avemetatarsalia includes the group Ornithodira, which consists of the Pterosauria and Dinosauromorpha. Dinosauromorpha in turn is composed of the Dinosauriformes and the Dinosauria proper.

Dinosauria (Fig. 5.1) is a monophyletic group that is divided into two main lineages, the Saurischia and Ornithischia, based on the morphology of the hip. The Saurischia include the carnivorous theropods, extinct and modern birds, the giant, long-necked sauropods, and the prosauropods. The Ornithischia is first divided into the Thyreophora and Cerapoda. Thyreophorans include the Stegosauria (plated dinosaurs) and Ankylosauria (armoured dinosaurs). The Cerapoda is in turn broken into the Ornithopoda and Marginocephalia. The ornithopods include the Heterodontosauria, Iguanodontia, and Hadrosauria (duck-billed dinosaurs), as well as a group of dinosaurs correctly referred to as 'basal ornithopods' but frequently referred to as hypsilophodontids. The basal ornithopods will be important later in this chapter. Marginocephalia is again divided into the Pachycephalosauria (dome-headed dinosaurs) and Ceratopsia (horned dinosaurs).


Figure 5.1: Simplified cladogram showing the major lineages of the Dinosauria. The Saurischia consists of the theropods (the carnivorous dinosaurs) and the sauropodomorphs (the prosauropods and sauropods, or long-necked dinosaurs). The ankylosaurs (armoured dinosaurs) and the stegosaurs (plated dinosaurs) together form the Thyreophora. The Ornithopoda consist of hadrosaurids, iguanodontians, and basal ornithopods. The hadrosaurids are the duck-billed dinosaurs. Iguanodontians are characterized by a large thumb spike. The basal ornithopods include more primitive forms, with unresolved phylogenetic relationships. Pachycephalosaurians have large domed skulls, and the ceratopsids are the horned dinosaurs; together these form a group called the Magrinocephalia.

### 5.2 Cretaceous Mammals

Larsen, in his field notes from the 1971 field season, believed that the bones might represent a Cretaceous sloth. Sloths are members of the Xenarthra, along with anteaters and armadillos (Delsuc et al., 2004). The earliest xenarthran originated about 58 Ma , and sloths are thought to have diverged from anteaters about 55 Ma (Delsuc et al., 2004). This date is based on molecular data, as the fossil record of early xenathrans is poor (Delsuc et al., 2004). It is therefore unlikely that the Sustut specimen represents a sloth, as originally speculated.

Mammals are known from Dinosaur Provincial Park in Alberta, Canada, and are representative of many mammals present in North America at the same time (Fox, 2005). All of these mammals are small, and most are mainly known from teeth, tooth fragments, or incomplete jaws (Fox, 2005). Present in these Late Cretaceous sediments were members of the extinct multituberculates, and the extant marsupials and placentals (Fox, 2005). The largest Mesozoic mammal comes from Liaoning, China (Hu et al., 2005). Repenomamus giganticus, a carnivorous early mammal that ate the young of neighbouring dinosaurs, lived during the Early Cretaceous and was over one metre long (Hu et al., 2005). The Sustut dinosaur is much larger than any known Mesozoic mammal, and the overall morphology of the specimen's unguals, tibia, and humerus is inconsistent with those of Mesozoic mammals.

### 5.3 Anapsids And Non-Dinosaurian Diapsids

During the Mesozoic, there were other relatively large terrestrial and marine vertebrates, such as crocodilians, turtles, ichthyosaurs, plesiosaurs, mosasaurs, and champsosaurs. Several of these (the ichthyosaurs, plesiosaurs, mosasaurs, and champsosaurs)
can be ruled out based on the limb morphology: these animals had developed flippers, and did not have claw or hoof-like unguals.

The Royal Ontario Museum has a large collection of modern crocodilian bones (Alligator mississippiensis, ROM R4415). A. mississippiensis has a flexed tibia (Fig. 5.2) and a flexed humerus with a strongly developed deltopectoral crest. The claws are sharp and recurved, but not overly laterally compressed (Fig. 5.4). The tibia and humerus from the Sustut Basin do not exhibit crocodilian morphology.

The Royal Ontario Museum also has several specimens of fossil turtles. Geochelone (ROM 50780A and 51239) and Hesperotestudo (ROM 52906) are both giant land tortoises similar to the Galapagos tortoise (Auffenberg, 1966). The tibia of Geochelone is robust, with broad, round distal and proximal ends (Fig. 5.3). The ungual of Hesperotestudo is wide, strongly dorsoventrally compressed, and flat on the plantar side (Fig. 5.5). These bear no resemblance to the comparatively slender Sustut tibia and conical, slightly recurved unguals.

### 5.4 Saurischians And Ornithischians

### 5.4.1 Overview

Sauropods, stegosaurs, ankylosaurs, and ceratopsids all tend to have robust 'hourglass-shaped' humeri, with broadly expanded proximal and distal ends (Upchurch et al., 2004; Galton and Upchurch, 2004b; Vickaryous et al., 2004; Dodson et al., 2004). Many species within these groups have prominent deltopectoral crests. The theropods, iguanodontians, and hadrosaurids have more slender humeri compared to the quadrupedal forms mentioned above (Clark et al., 2004; Holtz, 2004; Holtz et al., 2004; Horner et al.,


Figure 5.2: Alligator mississippiensis (ROM R4415) left tibia.


Figure 5.3: Geochelone sp. (ROM 51239) left tibia.


Figure 5.4: Unguals of Alligator mississippiensis (ROM R4415) in A) dorsal and B) medial or lateral views.


Figure 5.5: Pedal ungual of ?Hesperotestudo crassicutata (ROM 52906) in A) dorsal B) medial or lateral and C) articular views.

2004; Makovicky et al., 2004; Makovicky and Norell, 2004; Norell and Makovicky, 2004; Norman, 2004; Osmolska et al., 2004; Tykoski and Rowe, 2004). In larger forms, the humeri may be robust, while smaller forms like the ornithomimids, oviraptorosaurs, troodontids, and dromaeosaurs have rod-like humeri (Makovicky et al., 2004; Osmolska et al., 2004; Makovicky and Norell, 2004; Norell and Makovicky, 2004). In all of these forms, the deltopectoral crest is prominent. The basal ornithopods have small, relatively slender humeri, with somewhat reduced deltopectoral crests (Fig. 5.6) (Norman et al., 2004).

Pachycephalosaurians have reduced, almost nonexistent deltopectoral crests (Fig. 5.6) (Maryanska et al., 2004).

The radius of many dinosaurs (and many other vertebrates, for that matter) is a simple, rod-like bone. The ends may be gently expanded. A possible ulna preserved in the Sustut specimen is insufficient for comparison with other groups.

The tibia and fibula differ strongly between the quadrupedal and bipedal dinosaurs. Theropods and most basal ornithopods were obligatory bipeds (did not use the forelimbs for locomotion), and in general have slender, straight tibiae and fibulae that may be modestly flared at the proximal and distal ends (Clark et al., 2004; Holtz, 2004; Holtz et al., 2004; Makovicky et al., 2004; Makovicky and Norell, 2004; Norell and Makovicky, 2004; Norman et al., 2004; Osmolska et al., 2004; Tykoski and Rowe, 2004). The sauropods have massive, boxy tibiae and fibulae (Upchurch et al., 2004). The stegosaurs, ankylosaurs, and ceratopsids have massive, hourglass-shaped tibiae and fibulae that flare strongly at the proximal and distal ends (Galton and Upchurch, 2004b; Vickaryous et al., 2004; Dodson et al., 2004).


Figure 5.6: Comparison of humeri from various archosaurs. A) Sustut dinosaur, B) Stegoceras validum (after Sues and Galton, 1987), C) Parksosaurus warrenae, ?left humerus (ROM 804), D) juvenile hadrosaur, right humerus (ROM 03508); E) Alligator mississippiensis, left humerus (ROM 51679), F) Edmontonia rugosidens, right humerus (ROM 1935). Scale bar in A and B equal 10 mm . Scale bar in $F$ equals 10 cm .

Theropod dinosaurs, in general, have sharp, laterally compressed claw-like unguals (Fig. 5.7) (Clark et al., 2004; Holtz, 2004; Holtz et al., 2004; Makovicky et al., 2004; Makovicky and Norell, 2004; Norell and Makovicky, 2004; Osmolska et al., 2004; Tykoski and Rowe, 2004). Many sauropods also exhibit this condition (Upchurch et al., 2004). Stegosaurs, ankylosaurs, iguanodontians, hadrosaurids, and ceratopsids, on the other hand, developed blunt, round, dorsoventrally compressed hoof-like unguals (Galton and Upchurch, 2004b; Vickaryous et al., 2004; Dodson et al., 2004; Norman, 2004; Horner et al., 2004). The basal ornithopods and pachycephalosaurians have unguals that fall somewhere in between generally conical in shape, and usually without excessive lateral compression (except in the case of some basal ornithopods) or dorsoventral compression (Maryanska et al., 2004; Norman et al., 2004). In general, the unguals of pachycephalosaurians and basal ornithopods are not strongly recurved and may exhibit a flattening of the palmer or plantar side (Maryanska et al., 2004; Norman et al., 2004).

With this very rough overall description of the morphology of certain bones among dinosaur groups, we can compare a few key points and narrow the taxonomic assignment. The Sustut humerus is small and slender, with a small deltopectoral crest, therefore it is unlikely that the Sustut specimen represents a sauropod, stegosaur, ankylosaur, ceratopsid, theropod, iguanodontian, or hadrosaurid dinosaur. However, the basal ornithopods and the pachycephalosaurians do exhibit a similar humerus morphology.

The Sustut tibia and fibula morphology resembles more closely a bipedal form (theropod, basal ornithopod, or pachycephalosaurian) than the more quadrupedal forms (sauropods, stegosaurs, ankylosaurs, and ceratopsids).


Figure 5.7: Diversity of theropod unguals. Tyrannosaurid pedal ungual (ROM 36242) in A) dorsal B) medial or lateral and C) articular views; D) Baryonyx walkeri manual ungual (ROM 26354, cast); E) Therizinosaurus cheloniformis manual ungual (catalogue number unknown, cast).

The Sustut unguals are not strongly compressed, either laterally or dorsoventrally, and do not appear to be strongly recurved. They are conical, and more claw-like rather than hoof-like. This morphology excludes taxonomic assignment to theropods and sauropods (which have compressed, claw-like unguals), and stegosaurs, ankylosaurs, iguanodontians, hadrosaurids, and ceratopsids (which have depressed, hoof-like unguals). The unguals do resemble those of the basal ornithopods and pachycephalosaurians, which have conical and only slightly recurved (if at all) claw-like unguals.

This suggests that the Sustut dinosaur is a basal ornithopod or pachycephalosaurian. Although representing two distinct branches of the dinosaur family tree (the Ornithopoda and Marginocephalia), these two groups share a similar overall morphology in the postcranial skeleton. Both forms are relatively small, herbivorous, bipedal animals.

### 5.4.2 Basal Ornithopods

Norman et al. (2004) list 19 valid genera of basal ornithopods (excluding heterodontosaurids), and 8 nominia dubia (species of uncertain validity, usually due to a lack of appropriate fossil material). Several of these lack material appropriate for comparison (such as genera based on teeth or skull material only): Atlascopcosaurus, Fulgurotherium, Qantassaurus, Dianchungosaurus, Geranosaurus, Hypsilophodon wielandi, Laosaurus celer, Nanosaurus, Phyllodon, and Siluosaurus. This leaves possible comparisons to Agilisaurus, Anabisetia, Bugenasaura, Gasparinisaura, Hypsilophodon, Jeholosaurus, Leaellynasaura, Notohypsilophodon, Orodromeus, Parksosaurus, Thescelosaurus and the as yet unnamed Proctor Lake hypsilophodontids. Most recently, Barrett et al. (2005) proposed the new genus Hexinlusaurus for Yandusaurus multidens, a taxon from the Jurassic of China. Zan et al.
(2005) described the skeleton and skull of the primitive ornithopod Changchunsaurus parvus, also from China. Additional information regarding each of these taxa can be found in Appendix B.

### 5.4.2.1 Hypsilophodon and Other Small, Gracile Basal Ornithopods

Hypsilophodon foxii is one of the best-described basal ornithopods. Numerous specimens have been recovered from the Isle of Wight, England, and these are thoroughly described and reviewed by Galton (1974a), a summary of which follows. H. foxii is a small, bipedal, herbivorous dinosaur. The humerus of $H$. foxii has a moderately pronounced deltopectoral crest and a centrally located humeral head, and the shaft is oval in cross section. The humerus has a maximum recorded length of 159 mm , and maximum proximal width of 41 mm . The radius is slender and the shaft has a roughly triangular cross section; the maximum length is 114 mm . The radius of $H$. foxii compares well with the Sustut radius (Fig. 5.8). At the distal end of the tibia in $H$. foxii, the two malleoli form a sharp edge where they meet, similar to what is observed in the Sustut specimen. The tibia and fibula are slender, but there is great individual variation among different specimens with regards to the shape of the shaft in cross section. The Sustut tibia is considerably larger than that of the largest $H$. foxii, with a distal width of 91 mm compared to 56 mm in $H$. foxii. The maximum length of the tibia is 242 mm in $H$. foxii. The proximal ends of the phalanges in $H$. foxii bear two facets side-by-side, and the unguals are pointed, somewhat compressed, and claw-like. Here the Sustut specimen differs from $H$. foxii, with unguals that are dorsoventrally rather than mediolaterally compressed.


Figure 5.8: Comparison of the Sustut radius (right) to the radius of Hypsilophodon foxii (left), in A) lateral view, B) caudal view, C) medial view, D) cranial view. H. foxii modified from Galton (1974a). Scale bar equals 10 mm .

Observation of casts of the pes of Othnielia rex (ROM 46240) (Fig. 5.9) and Laosaurus minimus (ROM 46253) (Fig. 5.10) show that these two dinosaurs were small, gracile animals. The unguals are not strongly compressed and are not very recurved. The phalanges are similar to those from the Sustut Basin, although more slender. Gilmore (1924b) figured the tibia of $L$. minimus, and gave a maximum distal width of 30 mm . The Sustut specimen is much larger and more robust than these two species, and is not likely a specimen of $O$. rex or $L$. minimus.

There are several unguals from unidentified basal ornithopods ('hypsilophodontids') in the Royal Ontario Museum's collections (ROM 36533, 3586, and 3082). Although these bear a range of morphologies, they are in general more claw-like than hoof-like, but only slightly recurved if at all (Figs. 5.11, 5.12, 5.13). These unguals compare well with those from the Sustut Basin.

Also at the Royal Ontario Museum are casts of the tibiae of Leaellynasaura, a small basal ornithopod from Australia. These are exceptionally small, slender bones (Fig. 5.14), and are clearly distinct from the Sustut specimen.

### 5.4.2.2 Thescelosaurus, Parksosaurus, and Bugenasaura

Thescelosaurus neglectus was first discovered in 1891 but remained unprepared and undescribed until 1913, when Gilmore rediscovered the 'neglected marvellous lizard' (Gilmore, 1913). The humerus, radius, ulna, tibia, fibula, and many pedal phalanges were recovered, as well as other postcranial material. Galton (1974b) further supplemented Gilmore's original description. The humerus has a proximal width of 65 mm (Gilmore, 1915), much larger than the proximal width of the Sustut humerus ( 36 mm ). The shaft is


Figure 5.9: Left pes of Othnielia rex (ROM 46240, cast) in A) medial and B) lateral views.


Figure 5.10: Left metatarsus and pes of Laosaurus minimus (ROM 46253, cast). A) Reassembled elements, dorsal view. B) Digit IV disassembled, medial view.


Figure 5.11: Manual or pedal ungual, hypsilophodontid (ROM 36533) in A) dorsal B) medial or lateral and C) articular views.


Figure 5.12: Left manual or pedal ungual, hypsilophodontid (ROM 3586) in A) dorsal B) medial and C) articular views.


Figure 5.13: Pedal ungual, hypsilophodontid (ROM 3082) in A) dorsal B) medial or lateral and C) articular views.


Figure 5.14: Casts of tibiae from small hypsilophodontids (possibly Leaellynasaura) from Australia (ROM 45971, 45966, 45968, 45961). The tibia on the far right was diseased or injured.
approximately oval beneath the deltopectoral crest, with a concave medial face (Gilmore, 1915). The deltopectoral crest is less prominent than that of H. foxii, but is stouter (Galton, 1974b). Gilmore (1915) notes that the humerus of T. neglectus is similar to Camptosaurus. The radius is similar to $H$. foxii but is more robust, with a length of 149 mm , proximal width of 30 mm , and distal width of 22 mm (Gilmore, 1915). The tibia and fibula are similar to those of Camptosaurus; the tibia has a length of 300 mm and distal width of 77 mm (Gilmore, 1915). The tibia as figured by Gilmore (1915) has a straight shaft with no distal curvature. The joints of the phalanges are strongly keeled, and the phalanges have welldefined lateral pits (Gilmore, 1915). The unguals are slightly curved, depressed rather than laterally compressed, and have well-defined lateral grooves (Gilmore, 1915).

Thescelosaurus warreni was first described by Parks (1926), however Sternberg (1940) placed the type specimen of $T$. warreni into a new genus, Parksosaurus warreni. P. warreni is known from a relatively complete skeleton (ROM 804). Comparison of the type specimen to the Sustut dinosaur shows several similarities, as well as some striking differences. The arm bones were badly crushed and not suitable for comparison, but the tibia is of a similar size (distal width is 93 mm ) to the Sustut specimen ( 91 mm ). The tibia of $P$. warreni is also expanded at the distal end (Fig. 5.15), and the two malleoli also appear as two flat planes on the posterior side of the tibia. However, observation of the type specimen shows that the shaft of the tibia of $P$. warreni is straight, not curved as in the Sustut specimen, and the tibial shaft of $P$. warreni is not as strongly triangular in cross section. The fibula is of a similar size, with a maximum posterior diameter of 24 mm for $P$. warreni (Parks, 1926) and 26 mm for the Sustut specimen. P. warreni differs markedly in the morphology of the pes, particularly the unguals (Fig. 5.16). The unguals are laterally


Figure 5.15: A) Caudal view of the left and right tibiae (with articulated ankle bones and fibulae) from Parksosaurus warreni (ROM 804). These compare well with the Sustut tibia shown in caudal view in (B). Scale bar in B equals 50 mm (both photographs are at approximately the same scale).


Figure 5.16: A) Right pes of Parksosaurus warreni (type specimen, ROM 804) in dorsal view, left pes in B) dorsal and C) medial (emphasizing digit I) views, and ungual in D) articular view. Note the long toes and laterally compressed, curved claws. Also note the arrangement of the articular facets in D (redrawn from Parks 1926). Scale in D equals 10 mm .
compressed, curved, and claw-like. Most significantly, the articular end of the unguals have distinctive articular facet arrangements (Fig. 5.16). The articular facets of the Sustut unguals are side-by-side, whereas the articular facets of $P$. warreni are arranged approximately one above the other (Parks, 1926). The ungual morphology precludes assignment of the Sustut specimen to $P$. warreni.

Thescelosaurus edmontonensis was described by Sternberg (1940), and includes a humerus, tibia, fibula, a phalanx and ungual. The humerus as figured by Sternberg (1940) has a low deltopectoral crest. The humeral head overhangs the posterior border (Sternberg, 1940), a feature not exhibited by the Sustut specimen. The humerus is 215 mm long and has a proximal width of 65 mm . The tibia of T. edmontonensis is broader distally than in $T$. neglectus (Sternberg, 1940). In T. neglectus, the distal fibula lies on the side of the tibia, in contrast to the fibula of T. edmontonensis, which lies on the cranial face (Sternberg, 1940). The phalanx and ungual are identical to T. neglectus. Galton $(1974 b, 1995)$ reassessed the validity of T. edmontonensis and found it to be a junior synonym of T. neglectus.

Morris (1976) described ?Thescelosaurus garbanii based on several vertebrae, and portions of the left leg including the pes, tarsus, tibia, fibula, and part of the femur. Although the tibia and pedal phalanges are not discussed, photographs show that the tibia is similar in morphology to $T$. neglectus and $P$. warreni, the phalanges are robust, and the unguals are conical, depressed, and not greatly recurved. Interestingly, Morris (1976) comments on the similarity of the tibia and fibula with the pachycephalosaurian Stegoceras. Galton (1995) found the ankle region of ?T. garbanii to be diagnostically different from T. neglectus and referred this specimen to a new genus, Bugenasaura infernalis. Galton (1995) erected the genus Bugenasaura based on a skull referred to Thescelosaurus sp. (Morris, 1976). Again
highlighting the postcranial similarities between pachycephalosaurians and basal ornithopods, Galton (1995) noted that the hind limb of B. infernalis could belong to the pachycephalosaurian Stygimoloch spinifer, for which the postcranial skeleton was unknown at the time.

A very large isolated tibia was assigned to ?Thescelosaurus sp. by Russell (1968). Examination of this bone at the Royal Ontario Museum (ROM 5687) showed that there were few distinctive features to suggest that this represents a specimen of Thescelosaurus (Fig. 5.17). The length of the bone is 513 mm , and it has a distal width of 154 mm (Russell, 1968).

Hilton et al (1997) described a hind limb from a basal ornithopod dinosaur from the Early Cretaceous of California. This specimen was broadly comparable to Parksosaurus and Thescelosaurus in terms of size and morphology. The tibia is 239 mm long (Hilton et al., 1997), smaller than the Sustut tibia, which measures at least 240 mm in length.

Recently, a new specimen of a possible Thescelosaurus was described (Fisher et al., 2000). This specimen is of note because it contains a concretion within the chest cavity that may represent the first fossilized dinosaur heart. Unfortunately, because most of the focus on this specimen has been related to this concretion, little has been discussed regarding its referral to Thescelosaurus (Fisher et al. (2000) say only that the skeleton "closely resembles that of the hypsilophodontid Thescelosaurus" (p. 504) and indicate that it is not referable to Bugenasaura).

A fourth dinosaur closely allied with T. neglectus, $P$. warreni, and B. infernalis is Gasparinisaura cincosaltensis, from Argentina (Norman et al., 2004). G. cincosaltensis is closely related to these dinosaurs based on characters of the skull and ilium (Norman et al., 2004). The Sustut specimen differs from G. cincosaltensis based on the morphology of the


Figure 5.17: A) The Sustut tibia in caudal view. B) The distal portion of the Willow Creek ?Thescelosaurus tibia in caudal view. Note the large size difference (the Sustut tibia is to scale with the Willow Creek specimen).
tibia: in G. cincosaltensis, the two malleoli are approximately equal in width (Norman et al., 2004), while the inner malleolus is smaller than the outer malleolus on the Sustut specimen.

To summarize the complex history of the taxonomy of Thescelosaurus: T. neglectus is considered the only valid species of Thescelosaurus. T. warreni is referred to $P$. warreni. T. edmontonensis is a junior synonym of T. neglectus. ?T. garbanii is referred to $B$. infernalis. Other specimens of Thescelosaurus such as that described by Russell (1968) are fragmentary and should probably be referred to Ornithopoda incertae cedis.

The Sustut radius, tibia, fibula, phalanges, and unguals are generally consistent with T. neglectus. Although the tibia and fibula of $P$. warreni compare well with the Sustut specimen, the arrangement of the articular facets are significantly different. The differentiation of $B$. infernalis from T. neglectus and $P$. warreni is based on the structure of the ankle, which is probably not preserved in the Sustut specimen. The Sustut humerus is not similar to any of the above taxa. The Sustut tibia is unique in its distal convexity on the caudal face, a feature not observed in any of the above taxa.

### 5.4.3 Iguanodontians

Some iguanodontians are of a similar size and overall morphology to the basal ornithopods, so these will be considered as well. Norman (2004) lists 22 valid genera and 6 nominia dubia. Craspedodon, Fukuisaurus, Shuangmiaosaurus, Acanthopholis, Albisaurus, Anoplosaurus, Kangnasaurus, Loncosaurus, and Tichosteus are not represented by appropriate material for comparison. Iguanodontians that can be compared to the Sustut specimen include: Tenontosaurus, Rhabdodon, Zalmoxes, Dryosaurus, Planicoxa, Valdosaurus, Camptosaurus, Draconyx, Altirhinus, Eolambia, Equijubus, Iguanodon,

Jinzhousaurus, Lurdusaurus, Muttaburrasaurus, Nanyangosaurus, Ouranosaurus, Probactrosaurus, and Protohadros. All but a few of these are large, robust dinosaurs with proportions dissimilar to those in the Sustut dinosaur. A few, especially Dryosaurus, are similar in general morphology to the basal ornithopods. Additional information about each of these taxa can be found in Appendix B.

Two species of Dryosaurus are recognized: D. altus and D. lettowvorbecki. These are described in detail by Galton (1981). The maximum proximal width of the humerus of $D$. altus was about 57 mm , and of $D$. lettowvorbecki, 38 mm . The humerus of both species has a low deltopectoral crest, but is still larger than that seen in the Sustut humerus. The maximum distal width of the tibia of $D$. altus was 131 mm , and of $D$. lettowvorbecki, 44 mm . The tibia as figured by Galton (1981) is similar to that in $T$. neglectus and $P$. warreni, with a slender shaft and malleoli that meet at a sharp edge. Because Dryosaurus is a Jurassic form, it is unlikely that the Sustut dinosaur is a representative of this taxon. However, a relationship with Dryosaurus can neither be dismissed nor confirmed with the available material from the Sustut Basin.

### 5.4.4 Pachycephalosaurians

Maryanska et al (2004) list 16 valid genera and 1 nominum dubium of pachycephalosaurians. Again, several of these lack material appropriate for comparison, such as: Yaverlandia, Ornatotholus, Gravitholus, Heishansaurus, Micropachycephalosaurus, Prenocephale, Sphaerotholus, Stegoceras edmontonense, Tylocephale, "Troodon" bexelli, and Wannanosaurus. This leaves for comparison Stenopelix, Goyocephale, Homalocephale, Pachycephalosaurus, Stegoceras validum, and Stygimoloch. Most recently, Averianov et al.
(2005) named a new pachycephalosaurian, Ferganocephale adenticulatum. This taxon is based on isolated teeth and is therefore not comparable to the Sustut material. Additional information can be found in Appendix B.

Many pachycephalosaurians have been named exclusively on the basis of isolated frontoparietal domes, the thickened 'skullcaps' that are distinctive of many of this group. A few species have fragmentary postcranial remains. The best-preserved postcranial material for a pachycephalosaurian comes from a specimen of Stegoceras validum recovered from Dinosaur Provincial Park in Alberta (Sues and Galton, 1987). This specimen includes a humerus, radius, ulna, and ungual, which can be compared to the Sustut specimen, as well as a complete skull and other postcranial material. The humerus of $S$. validum is slightly bowed, with a poorly developed deltopectoral crest (Sues and Galton, 1987). It is a close match to the Sustut humerus (Fig. 5.6). The radius of $S$. validum is oval in cross-section and has a greater midshaft diameter than the ulna; this differs from the Sustut radius, which is triangular in cross-section (Sues and Galton, 1987). The unguals are slender and only slightly curved, and are not laterally compressed (Sues and Galton, 1987), and compare well with those from the Sustut Basin.

Postcranial remains have also been recovered for Goyocephale lattimorei (Perle et al., 1982), a Late Cretaceous species from southern Mongolia. In this pachycephalosaurian, the humerus is slightly bowed, with a thick but weakly projecting deltopectoral crest, and a depression below the proximal articular surface (Perle et al., 1982). The phalanges are described as robust. The unguals are asymmetrical, conical in shape, with a flat plantar side (Perle et al., 1982). These features are similar to what is seen in the Sustut specimen.

The humerus of Homalocephale calathocercos (Maryanska and Osmolska, 1974), another Late Cretaceous form from Mongolia, is unknown. The tibia and fibula are preserved, however. Maryanska and Osmolska (1974) describe the tibia as strongly broadened distally, with a slender shaft. The figures in Maryanska and Osmolska (1974) seem to show that the two malleoli do not form a distinct edge on the caudal face of the distal tibia; this differs from the distinct edge seen on the Sustut tibia. Only one phalanx was recovered from H. calathocercos, phalanx I of digit IV from the left pes (Maryanska and Osmolska, 1974). This phalanx is short and distally constricted, with a shallow proximal articular surface with no distinct facets (Maryanska and Osmolska, 1974).

Hou (1977) described a humerus and tibia for Wannanosaurus yansiensis. The tibia is described as slender and of a general ornithischian form. The humerus is small, with a weak deltopectoral crest and shallow depression on the medial face. Figures in Hou (1977) show it to be strongly curved craniocaudally.

### 5.5 A Basal Ornithopod Or Pachycephalosaurian In The Sustut Basin

The Sustut dinosaur most closely resembles a large basal ornithopod, such as Thescelosaurus, Parksosaurus, or Bugenasaura. Parksosaurus can be definitively eliminated based on the morphology of the unguals. Bugenasaura cannot be compared with the Sustut dinosaur based on the available material. Thescelosaurus neglectus is a close match based on the morphology of the unguals, tibia, and fibula, and is similar in size. The Sustut radius also closely matches the radius of Hypsilophodon foxii, although the simple, rod-like radius bone tends to be similar in many dinosaurs.

The Sustut humerus seems to tell a different story, however. The reduced deltopectoral crest is a very close match to pachycephalosaurians such as Stegoceras and Goyocephale (Fig. 5.6), although it is dissimilar to the humerus of Wannanosaurus. A reduced deltopectoral crest is also considered a diagnostic feature by Sues and Galton (1987), which means that the presence of this character is a strong indication that the animal is a pachycephalosaurian. However, the humerus of Notohypsilophodon, a basal ornithopod, is also described as lacking a deltopectoral crest (Martínez, 1998), so this feature may not be unique to pachycephalosaurians (this paper is not published in English and no figures were available for study, so Notohypsilophodon was not considered further). The Sustut humerus does not closely match any basal ornithopods, all of which seem to have more pronounced deltopectoral crests. The closest match among the basal ornithopods is Thescelosaurus edmontonensis (Sternberg 1940), a species now considered a junior synonym of T. neglectus (Galton, 1995). The Sustut tibia is more similar to that of Thescelosaurus than to any pachycephalosaurians, but the tibia of Homalocephale is comparable.

The Sustut tibia also has a unique feature: it is curved at the distal end so that the caudal face is convex. The tibiae of Parksosaurus, Thescelosaurus, and most other dinosaurs have straight shafts. Interestingly, a figure by Holtz et al. (2004) shows a distal curvature in the tibia of Allosaurus fragilis and these authors also note that the tibia of the theropod Chilantaisaurus tashuikouensis is similar. Figures in Madsen (1976) do not show curvature in the distal tibia of $A$. fragilis. The tibia of C. tashuikouensis as figured by Show-Yung (1964) is curved distally, but the convexity is on the cranial face rather than the caudal face, and is not as pronounced.

The Sustut specimen shares characteristics with both basal ornithopods and pachycephalosaurians. Overall, the proportions of the Sustut specimen are similar to $T$. neglectus (Fig. 5.18). The apparent combination of features from both pachycephalosaurians and basal ornithopods, and the unique distal curvature of the tibia, suggests that the Sustut specimen may represent a new taxon. The Sustut dinosaur resembles a basal ornithopod similar to $T$. neglectus, with a modified humerus and unique tibia, or a pachycephalosaurian similar to $S$. validum, with a tibia similar to T. neglectus with a unique distal curvature.

### 5.6 Limitations To The Taxonomic Assignment

Although the Sustut Basin dinosaur bones are preserved remarkably well, a lack of diagnostic features makes it difficult to assign the specimen to a specific taxon. Many dinosaurs are classified on the basis of unique features of the skull, and occasionally using characters from the vertebrae, shoulder girdle, or pelvic girdle. Taxonomic assignments based on fragmentary limb bones are challenging, because the limbs of many dinosaurs are very similar.

The presence of features seemingly from two different groups of dinosaurs (basal ornithopods and pachycephalosaurians) may be due to the similar postcranial skeleton shared by these two groups. The main differences between these two groups lie in the construction of the skull. The Sustut material was collected from a talus slope, so it is also possible that the specimen is a chimaera, an individual artificially 'constructed' from two different individuals. Therefore, the humerus may come from a pachycephalosaurian and the leg bones may come from a basal ornithopod. However, this seems unlikely for one main reason: several of the Sustut Basin elements were still preserved in their life position when Larsen


Figure 5.18: Rigorous skeletal reconstruction of the Sustut dinosaur showing only known elements. The general body shape is modelled after T. neglectus as figured by Paul (2000).
donated them to Dalhousie University. The fibula was still attached to the tibia, and several phalanges were still articulated as well. It therefore seems likely that a nearly complete skeleton was eroding out of a cliff face, and that the bulk of the specimen was simply not collected.

The Sustut humerus resembles a pachycephalosaurian humerus because it lacks a prominent deltopectoral crest. It is possible that the crest has simply been eroded away sometime after fossilization and exposure to the elements. Again, this seems unlikely, because no obvious weathering seems to have occurred on that area of the bone.

Finally, the Sustut tibia may be an individual variation, pathology, or a result of postfossilization deformation. Deformation seems unlikely because clasts in thin sections of the surrounding matrix showed no obvious deformation, and none of the other bones seem to show unusual deformation. Variation and pathology cannot be discounted without comparison to other individuals of whichever taxon the Sustut specimen represents.

Despite these reservations, there appears to be strong evidence in favour of the hypothesis that the Sustut dinosaur represents a new taxon of basal ornithopod or pachycephalosaurian, with a similar body shape to Thescelosaurus neglectus. The main limitation to assigning the specimen to an existing or new taxon is the lack of appropriate material for comparison with known taxa.

### 6.0 PALAEOGEOGRAPHIC SETTING AND IMPLICATIONS FOR BIOGEOGRAPHY

### 6.1 Comparison With Canadian Dinosaur Faunas And Palaeoecology

We can look at other dinosaur faunas through the Cretaceous to appreciate the palaeoenvironment of the Sustut Basin, and what other dinosaurs may have shared the landscape. The following is a summary of Canadian dinosaur distributions from Weishampel et al. (2004). Early Cretaceous dinosaurs of Canada are found in British Columbia and Alberta. In both cases, the fossil record consists only of trackways of theropods, ornithopods, and ankylosaurs. Late Cretaceous dinosaur localities are much more abundant, with fossils from Alberta, British Columbia, Saskatchewan, the Northwest Territory, and the Yukon Territory. Manitoba has Cretaceous bird fossils, but here I will focus on non-avian dinosaurs.

Alberta has the greatest concentration and diversity of dinosaur fossils in Canada. Almost all major groups of dinosaurs are represented by skeletal material in this province. Many of Alberta's geological formations contain similar dinosaur faunas, usually including theropods, ankylosaurs, basal ornithopods, hadrosaurids, and ceratopsids. Small theropods included Dromaeosaurus, Saurornitholestes, and Troodon. Ornithomimids such as Struthiomimus and Ornithomimus are often present, as are the oviraptorosaurs Chirostenotes and Caenagnathus. Large theropods included Daspletosaurus, Gorgosaurus, Albertosaurus, and Tyrannosaurus. Ankylosaurs such as Euoplocephalus, Edmontonia, Panoplosaurus, and Ankylosaurus were often part of the diverse dinosaur fauna. Basal ornithopods included "Laosaurus" minimus, Orodromeus makelai, Thescelosaurus neglectus, and Parksosaurus warreni. Hadrosaurids were the most diverse group, and included Brachylophosaurus,

Hypacrosaurus, Prosaurolophus, Gryposaurus, Maiasaura, Corythosaurus, Lambeosaurus, Parasaurolophus, Edmontosaurus, and Saurolophus. Pachycephalosaurians were less diverse, but included Stegoceras validum and Stegoceras edmontonensis, as well as Pachycephalosaurus. Finally, ceratopsids were represented by Leptoceratops, Anchiceratops, Chasmosaurus, Monoclonius, Centrosaurus, Styracosaurus, Montanoceratops, Arrhinoceratops, Pachyrhinosaurus, Triceratops, and Torosaurus. Eggs, trackways, and coprolites are also frequently discovered in Alberta.

From this we can surmise that the Sustut dinosaur probably shared its environment with a variety of theropods, ankylosaurs, hadrosaurids, and ceratopsids. We also see that Thescelosaurus and Stegoceras are frequently found in similar deposits, strengthening the hypothesis that the Sustut specimen is similar to one of these two taxa.

Brinkman (1990) studied microfossil localities in Dinosaur Provincial Park and found that Thescelosaurus was present in lower exposures within the park, corresponding to a more inland habitat, probably the areas of the coastal plain farthest from the shoreline. Brinkman et al. (1998) conducted another study of microfossil localities, this time from Dinosaur Provincial Park in Alberta, the South Saskatchewan River area, and Unity, Saskatchewan. They found that pachycephalosaurian remains decreased upwards through the transgressive sections of these localities, suggesting that these dinosaurs preferred more inland habitats. A study by Carpenter and Young (2002) of the Denver Basin in Colorado found that Thescelosaurus was more common in sediments interpreted to represent a coastal plain, while Pachycephalosaurus is found in sediments representing a more upland environment. In common among these three studies are the presence of Thescelosaurus and
pachycephalosaurians in more upland environments, consistent with the terrestrial, intermontane Sustut Basin.

It is clear that the Sustut dinosaur represents a herbivorous ornithischian, so which plants were present in the Sustut Basin is of interest. Eisbacher (1974) summarizes many of the fossil plants that have been recovered from the basin, and the Mesozoic species are highlighted in Table 6.1. Numerous flowering plants are represented, as well as a gymnosperm (pine) and cycadeoid (extinct seed-bearing, non-flowering plant).

| Table 6.1: List of plant fossils (macrofossils and palynomorphs) summarized in <br> Eisbacher (1974). Only Mesozoic species are shown. Plant type was found using the <br> Paleobiology Database (http://paleodb.org). |  |
| :--- | :--- |
|  |  |
| Species | Type of plant represented |
| Plant Macrofossils | flowering plant |
| Araliaephyllum parvidus | flowering plant |
| Cercidiphyllum arcticum | flowering plant |
| Dicotylophyllum sp. | flowering plant |
| cf. Fraxinus sp. | flowering plant |
| Platanus cf. P. raynoldsi integrifolia | cycadeoid (seed plant, non-flowering) |
| Pseudocycas unjiga |  |
| Palynomorphs | flowering plant |
| Alnus sp. |  |
| cf. Baculatisporites sp. | flowering plant |
| Cicatricosisporites sp. |  |
| cf. Compositae |  |
| Deltoidospora sp. | flowering plant |
| Monosulcites sp. | gymnosperm (seed plant, non-flowering) |
| cf. Picea |  |
| Pinus sp. |  |
| Triletes sp. |  |

### 6.2 Implications For Dinosaur Biogeography

The Sustut Basin specimen is the westernmost dinosaur discovered in Canada to date.
The location in the Sustut Basin is more than 1000 km west of Dinosaur Provincial Park in
Alberta, and more than 200 km west of Tumbler Ridge in British Columbia. As such, it
provides new information on the distribution of dinosaurs in North America and dinosaurian biogeography.

Dinosaurs evolved during the Late Triassic when Pangaea was still intact, therefore, many dinosaurs were global in distribution and there were no distinct biogeographic provinces (Russell, 1993). Ornithopods are believed to have arisen during this time, as well as theropods, sauropodomorphs, and stegosaurs (Russell, 1993). However, ornithischians were rare until the Early Jurassic (Sereno, 1997).

Central Asia became isolated from Pangaea during the Middle Jurassic, allowing dinosaurs in Central Asia to evolve separately from those elsewhere in the world (Russell, 1993). Russell (1993) holds that the pachycephalosaurians, as well as ceratopsids, troodontids, oviraptorosaurs, and therizinosaurs originated in Central Asia. There is some debate regarding a possible European origin for pachycephalosaurians (Sereno, 1997, and references within).

During the Early Cretaceous, Central Asia appears to have lost its isolation from North America and Europe (Russell, 1993). Groups characteristic of North America and Europe, such as ornithomimids, dromaeosaurs, and iguanodontians, began to appear in Central Asia (Russell, 1993). Groups characteristic of Central Asia also began to appear in North America: troodontids, tyrannosaurids, hadrosaurids, and ankylosaurs (Russell, 1993). By the Late Cretaceous, the Central Asian and North American faunas were so similar that they were effectively one large biogeographic province (Russell, 1993). Dispersal of dinosaurs from one continent to the other is thought to have occurred by a land bridge between Asia and North America, across the Bering Strait (Russell, 1993).

Evidence for a faunal interchange route across the Bering Strait has been strengthened by the discovery of dinosaurs and other terrestrial vertebrates in Alaska. The Prince Creek Formation of the Alaska Arctic Coastal Plain contains remains of tyrannosaurids, troodontids, ornithomimids, dromaeosaurs, hadrosaurids, basal ornithopods (including Thescelosaurus), pachycephalosaurians, and ceratopsids (Gangloff et al., 2005; Weishampel et. al., 2004). These dinosaurs lived at a palaeolatitude of $70^{\circ}$ to $80^{\circ}$ north from the mid to Late Cretaceous (Gangloff et al., 2005). This is the northernmost record for a pachycephalosaurian, with the next most northern known fossils found in the lower Horseshoe Canyon Formation in Alberta, at $53^{\circ}$ to $55^{\circ}$ north (Gangloff et al., 2005).

Unique Cretaceous dinosaur faunas may also have been developing along the west coast of North America. Hilton et al. (1997) described a partial hind limb of a basal ornithopod from the Early Cretaceous of California. The authors describe the specimen as similar to Parksosaurus and Thescelosaurus in terms of size and overall morphology, but note that there are some unique features, such as the proportions of the tibia and metatarsals, which do not precisely match any of the known basal ornithopods. This specimen, along with other unique Late Cretaceous Pacific Coast dinosaurs, has led the authors to suggest that distinct dinosaur faunas were present on either side of the Rocky Mountains during the Cretaceous.

Pachycephalosaurians and basal ornithopods are present in Asia, North America, and in the potential interchange zone in Alaska. Because the Sustut specimen is so incomplete, little can be said at present regarding its affinities to either Asian or North American forms. However, interesting future work could involve further exploration for, and description of, additional specimens from the Bowser and Sustut Basins. Additional specimens would elucidate which taxa are found in the Sustut Basin. It is possible, and likely, that the Sustut

Basin could have harboured a unique, endemic fauna independent of that found in Alberta. It would also be interesting to determine dinosaur dispersal routes into the Sustut Basin. Dinosaurs were present in British Columbia, in the Bowser Basin, by at least the Jurassic. The ancestors of the Sustut dinosaur may have migrated from Asia through Alaska and down into the Sustut Basin, or may have moved westward from Alberta later in the Cretaceous.

### 7.0 CONCLUSIONS

An ornithischian dinosaur specimen collected from the Sustut Basin in 1971 represents the first abundant dinosaur skeletal material discovered in British Columbia, and is one of the westernmost dinosaur discoveries in Canada. The specimen was collected near the intersection of Sustut River and Birdflat Creek. Outcropping in this area are mid to Late Cretaceous terrestrial sedimentary rocks of the Sustut Group. The Tango Creek Formation and Brothers Peak Formation make up the Sustut Group, and are both composed of varying siltstones, sandstones, and mudstones, with less common tuffs and conglomerates. The specimen was collected from a talus pile, and the original collection maps are lost, therefore the exact location of its collection site is unknown. It is also unknown which formation the specimen originated from, making its exact age unknown.

Several bones in relatively good condition were collected from the talus pile, including a humerus, radius, possible ulna, tibia, fibula, several pedal phalanges, and several indeterminate bone fragments. The humerus has a very low deltopectoral crest. The radius is a slender, rodlike bone. The distal end of the tibia is moderately expanded, and the two flat malleoli make a sharp edge where they meet. The distal end of the tibia is curved, with the convexity on the caudal side. The fibula lies against the cranial face of the tibia. Ankle bones may be preserved but are too badly eroded to provide diagnostic information. Two pedal digits are represented by seven phalanges, including two conical, moderately curved, slightly depressed unguals.

The tibia, fibula, and pes are consistent with a large basal ornithopod such as Thescelosaurus or Parksosaurus. The Sustut dinosaur is not a Parksosaurus based on the
morphology of the unguals. The humerus matches closely with that of Stegoceras, a pachycephalosaurian. The distally curved tibia may be unique to the Sustut taxon. Overall, the Sustut dinosaur was probably similar in overall size and morphology to Thescelosaurus neglectus, but may have shared affinities with the pachycephalosaurians. It is unclear if the Sustut Basin specimen represents a new taxon.

Remains of Thescelosaurus and Stegoceras are often found in the same deposits in the Late Cretaceous of North America. Previous studies have suggested that Thescelosaurus inhabited the areas of the coastal floodplain farthest from the coast, while Stegoceras may have preffered more inland habitats. The Sustut Basin likely included various large and small theropods, ankylosaurs, hadrosaurids, basal ornithopods, pachycephalosaurians, and ceratopsids. It is unclear which of the variety of flowering plants, gymnosperms and cycadeoids known from the Sustut Basin may have supported the Sustut dinosaur.

The discovery of dinosaur bones in the Sustut Basin may lead to a greater understanding of dinosaur biogeography in North America. During the Cretaceous, Asian dinosaurs migrated to North America via a land bridge in the Bering Strait. Further discoveries in the Bowser and Sustut Basins may reveal that the dinosaurs were more closely related to either Asian or North American taxa. This could shed light on dispersal patterns during dinosaur migrations between these two continents. The Sustut Basin may also have been home to a unique endemic fauna of dinosaurs that were evolving independently on the west coast of North America, separated from the interior faunas of Alberta and the Midwest states by the active mountain building to the east.

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## APPENDIX A: ORIGINAL FIELD NOTES

These are Kenny Larsen's original field notes from the 1971 field season. They were obtained during an interview with Larsen in January 2005. Important points have been highlighted in yellow.


## APPENDIX B: TAXON COMPARISON LISTS

The following is a summary of basal ornithopod, iguanodontian, and pachycephalosaurian taxa, and whether or not they are comparable to the Sustut dinosaur. "Unlikely" means that the taxon cannot be completely discounted, but that there is evidence to suggest that it is not comparable to the Sustut dinosaur. "Indeterminate" means that there is a lack of appropriate material for comparison, that the material is undescribed, or that the material is published in another language. "No" means that the taxon differs from the Sustut dinosaur and can be discounted. Taxa that are similar to the Sustut specimen are discussed in Chapter 5. The information in these tables is summarized from The Dinosauria, $2^{\text {nd }}$ Edition (Weishampel et al., 2004), unless otherwise stated.

| Taxon | Notes |
| :--- | :--- |
| Basal Ornithopods | Unlikely: almost all taxa are from South Africa |
| Heterodontosaurids |  |
| "Hypsilophodontids" | Unlikely: known only from Jurassic sediments |
| Agilisaurus | No: dorsal margin of humerus is convex (Coria and Calvo, <br> 2002) |
| Anabisetia | Indeterminate: maxilla and teeth only |
| Atlascopcosaurus | See Chapter 5 |


| Taxon | Notes |
| :--- | :--- |
| Iguanodontians | Nominum dubium; Indeterminate: vertebrae only |
| Acanthopholis | Nominum dubium; Indeterminate: scrap only |
| Albisaurus | No: unguals depressed, hooflike |
| Altirhinus | Nominum dubium; Indeterminate: vertebrae only |
| Anoplosaurus | No: unguals flattened |
| Camptosaurus | Indeterminate: teeth only |
| Craspedodon | Unlikely: known only from Jurassic sediments |
| Draconyx | Unlikely: known only from Jurassic sediments; see Chapter <br> $\mathbf{5}$ |
| Dryosaurus | Unlikely: large, robust taxon |
| Eolambia | Indeterminate: skull and vertebrae only (You et al., 2003) |
| Equijubus | Indeterminate: skull only |
| Fukuisaurus | No: hoof-like unguals |
| Iguanodon | Unlikely: large, robust taxon |
| Jinzhousaurus | Nominum dubium; Indeterminate: tooth only |
| Kangnasaurus | Nominum dubium; Indeterminate: femur only |
| Loncosaurus | No: massive, robust taxon (Taquet and Russell, 1999) |
| Lurdusaurus | No: large, robust taxon |
| Muttaburrasaurus | Unlikely: large, robust taxon |
| Nanyangosaurus | No: unguals depressed, hooflike |
| Ouranosaurus | No: unguals depressed |
| Planicoxa | No: elongate forearm; hoof-life unguals (Norman, 2002) |
| Probactrosaurus | Unlikely: large, robust taxon |
| Protohadros | No: unguals depressed |
| Rhabdodon | Indeterminate: skull only |
| Shuangmiaosaurus | No: large deltopectoral crest on humerus (Winkler et al., <br> 1997) |
| Tenontosaurus | Nominum dubium; Indeterminate: vertebrae only |
| Tichosteus | Indeterminate: no comparable material |
| Valdosaurus | No: prominent deltopectoral crest |
| Zalmoxes |  |


| Taxon | Notes |
| :--- | :--- |
| Pachycephalosaurians |  |
| Ferganocephale | Indeterminate: teeth only |
| Goyocephale | See Chapter 5 |
| Gravitholus | Indeterminate: dome only |
| Heishansaurus | Nominum dubium |
| Homalocephale | See Chapter 5 |
| Micropachycephalosaurus | Indeterminate: skull fragments, vertebrae, sacral girdle, <br> femur, and proximal tibia only (Dong, 1977) |
| Ornatotholus | Indeterminate: dome only |
| Pachycephalosaurus | Indeterminate: skull only |
| Prenocephale | Indeterminate: skull, ribs, pelvis, femur only |
| Sphaerotholus | Indeterminate: dome only |
| Stegoceras validum | See Chapter 5 |
| Stegoceras edmontonense | Indeterminate: skull fragments only |
| Stenopelix | Unlikely: known only from Europe |
| Stygimoloch | Indeterminate: insufficient description of postcranial <br> material |
| Tylocephale | Indeterminate: skull only |
| "Troodon" bexelli | Indeterminate: parietal only |
| Wannanosaurus | No: humerus strongly curved (Hou, 1977); see Chapter 5 |
| Yaverlandia | Indeterminate: skull fragment only |

## APPENDIX C: RECONSTRUCTING THE SUSTUT DINOSAUR

In Chapter 5, a rigorous skeletal rescontruction of the Sustut dinosaur is shown modelled after Thescelosaurus neglectus. Skeletal reconstructions show the shapes and proportions of the skeletal elements in a particular species of dinosaur, as well as an outline of the muscles and body shape, usually in black. If some of the bones are not known yet, educated guesses are used to fill them in. A rigorous skeletal reconstruction, on the other hand, shows the overall shape of the animal, but only the bones that are actually known at present. The rigorous skeletal reconstruction of the Sustut dinosaur took many hours to complete. The steps to creating this picture are shown below.

Step 1: Find a reconstruction of Thescelosaurus neglectus
Once I determined that the Sustut dinosaur was most similar in body shape to Thescelosaurus neglectus, I searched for suitable skeletal reconstructions of that dinosaur. Gregory S. Paul is a noted dinosaur artist and has created numerous accurate skeletal drawings. Some of these are featured in The Scientific American Book of Dinosaurs (2000). Both Thescelosaurus neglectus and Parksosaurus warreni are included in this book.


Figure C.1: Thescelosaurus by Paul (2000).

Step 2: Create a conversion chart
I measured Paul's drawing of T. neglectus and compared it with measurements of $T$. neglectus in Parks (1926). Paul's drawing is only about 9.4 cm long. I wished to create a drawing 25 cm long, so I set up a conversion chart:

$$
\text { Sustut dinosaur } \rightarrow \text { Paul's drawing }(9.4 \mathrm{~cm}) \rightarrow \text { my drawing }(25 \mathrm{~cm})
$$

I first scaled the Sustut dinosaur's measurements to Paul's 9.4 cm long T. neglectus. Then I scaled up to a proportionately-sized drawing 25 cm in length.

Step 3: Sketch drawing of Thescelosaurus
In this step, I repeated the conversion process of Step 2, but using T. neglectus instead of the Sustut dinosaur. Then I drew a sketch of $T$. neglectus with a length of 25 cm . I sketched the head and spinal column first. Then, using a ruler, lines were constructed to indicate the lengths and positions of the limb bones. The shapes of the limb bones were sketched over these lines, as well as the scapula and pelvic girdle. I roughly sketched ribs and vertebrae to fill out the body shape. Finally, the outline of the muscles was added.


Figure C.2: Sketch drawing of T. neglectus.

Step 4: Sketch drawing of the Sustut dinosaur
I used the sketch of T. neglectus from Step 3 to trace the outline and limb bones of $T$. neglectus to provide a base for the Sustut dinosaur's bones. Using the proportions from Step 2, I sketched the Sustut bones onto the T. neglectus outline. The arm had to be heavily modified since the Sustut humerus is much shorter than that of $T$. neglectus.


Figure C.3: Sketch drawing of the Sustut dinosaur.

Step 5: Clean-up drawing of the Sustut dinosaur
I traced the outline of the picture from Step 4. In the clean-up picture, only the lines needed for the final image were saved.


Figure C.4: Clean-up drawing of the Sustut dinosaur.

Step 6: Digitizing the image
I scanned the picture from Step 5 to the computer and edited in Adobe Photoshop Elements. In this image-editing program, I increased the contrast and used the burn tool to darken the lighter pencil lines that did not scan well. I then coloured everything black except for the bones, which were left white. Many hours were spent touching up the image until the final image was complete. I added a scale bar based on the scale bar in Paul's original reconstruction. Finally, a few lines of text were added, and the skeletal reconstruction was complete.


Figure C5: Final digitized image.

