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Investigating Sexual Dimorphism in Ceratopsid Horncores

by

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A THESIS

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Abstract

Evidence for sexual dimorphism was investigated in the horncores of two ceratopsid dinosaurs, *Triceratops* and *Centrosaurus apertus*. A review of studies of sexual dimorphism in the vertebrate fossil record revealed methods that were selected for use in ceratopsids. Mountain goats, bison, and pronghorn were selected as exemplar taxa for a proof of principle study that tested the selected methods, and informed and guided the investigation of sexual dimorphism in dinosaurs. Skulls of these exemplar taxa were measured in museum collections, and methods of analysing morphological variation were tested for their ability to demonstrate sexual dimorphism in their horns and horncores. Skulls and isolated horncores of *Triceratops* and *Centrosaurus* were measured in museum collections, and analysed with the methods applied to the exemplar taxa. Considerable morphological variation was found in both species, and was suggestive of dimorphism in *Centrosaurus*, but was deemed not to be attributable to sexual dimorphism.
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# Table of Contents

Abstract .......................................................................................................................... ii

Acknowledgements ...................................................................................................... iii

Table of Contents .......................................................................................................... iv

List of Tables ................................................................................................................ vii

List of Figures and Illustrations ................................................................................... ix

List of Symbols, Abbreviations, Nomenclature .............................................................. xii

Chapter 1: Introduction ................................................................................................. 1

1.1 Preamble .................................................................................................................. 1

1.2 Ceratopsid Dinosaurs ............................................................................................. 1

  1.2.1 Morphological Variation in Ceratopsids ......................................................... 2

1.3 Horns ...................................................................................................................... 4

1.4 Sexual Dimorphism ............................................................................................... 5

1.5 Prospectus .............................................................................................................. 10

Chapter 2: Evidence for Sexual Dimorphism as Manifested in the Vertebrate Fossil Record .... 11

2.1 Introduction ........................................................................................................... 11

  2.2.1 Fishes .............................................................................................................. 16

  2.2.2 Amphibia ....................................................................................................... 21

  2.2.3 Testudines .................................................................................................... 22

  2.2.4 Sauropterygia ............................................................................................... 23

  2.2.5 Ichthyosauria ............................................................................................... 24

  2.2.6 Archosauria ................................................................................................. 24

  2.2.7 Mammalia .................................................................................................... 37

2.3 Discussion ............................................................................................................. 57

  2.3.1 Methods ....................................................................................................... 58

2.4 Conclusions .......................................................................................................... 60

Chapter 3: Selection of Exemplar Taxa for the Study of Sexual Dimorphism in Ceratopsids .... 86

3.1 Introduction ........................................................................................................... 86

  3.1.1 The Merit of Models ................................................................................... 87

  3.1.2 The Selection of Bovids and Pronghorn ....................................................... 87
3.2 Relevant Characteristics of the Exemplar Taxa

3.2.1 The Occurrence and Degree of Sexual Dimorphism in Bovids

3.2.2 Exemplar Taxon 1: *Oreamnos americanus*

3.2.3 Exemplar Taxon 2: *Bison bison*

3.2.3 Exemplar taxon 3: *Antilocapra americana*

3.3 Conclusions

Chapter 4: Sexual Dimorphism in Bovids

4.1 Introduction

4.1.1 Objectives

4.2 Materials and Methods

4.2.1 Material

4.2.2 Measurements

4.2.3 Ageing

4.2.4 Analysis of Data

4.3 Results

4.3.1 Mountain goats

4.3.2 Bison

4.3.3 Pronghorn

4.4 Eigenshape Analysis

4.4.1 Eigenshape Analysis – Methods

4.4.2 Eigenshape Analysis – Results

4.5 Discussion

4.5.1 Discussion of Methods

4.6 Conclusions

Chapter 5: Investigating Sexual Dimorphism in Ceratopsid Horncores

5.1 Introduction

5.1.1 Distribution and Abundance

5.1.2 Horns and Horncores

5.2 Materials and Methods

5.2.1 Material

5.2.2 Taxonomy
List of Tables

Table 2.1 Summary table of studies with High confidence of sexual dimorphism. 62
Table 2.2. Summary table of studies with Moderate confidence of sexual dimorphism. 69
Table 2.3. Summary table of studies with Low confidence of sexual dimorphism. 74
Table 2.4. Summary table of studies with Poor confidence of sexual dimorphism. 77
Table 2.5. Summary table of studies with thorough methodologies for investigating sexual dimorphism. 82
Table 4.1 Mountain goat horn measurement descriptions and codes 149
Table 4.2 Bison horn measurement descriptions and codes 149
Table 4.3 Pronghorn horn measurement descriptions and codes 150
Table 4.4 Equality of means tests – Mountain goat variables 151
Table 4.5 Equality of means tests – Mountain goat variables, scaled data 153
Table 4.6 Performance of predictor variables as indicators of dimorphism, all 3 taxa 155
Table 4.7 Loadings for principal components 1 and 2 of mountain goat principal components analysis 156
Table 4.8 Equality of means tests – Bison variables 157
Table 4.9 Equality of means tests – Bison variables, scaled data 159
Table 4.10 Equality of means tests – Pronghorn variables 164
Table 4.11 Equality of means tests – Pronghorn variables, scaled data 163
Table 5.1 Centrosaurus ontogenetic stages 224
Table 5.2 Triceratops ontogenetic stages 225
Table 5.3 Ceratopsid skull measurement descriptions and codes 226
<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.4</td>
<td>Centrosaurus horncore measurement descriptions and codes</td>
<td>226</td>
</tr>
<tr>
<td>5.5</td>
<td>Triceratops horncore measurement descriptions and codes</td>
<td>227</td>
</tr>
<tr>
<td>5.6</td>
<td>Measurement data of Centrosaurus specimens</td>
<td>228</td>
</tr>
<tr>
<td>5.7</td>
<td>Measurement data of Triceratops specimens</td>
<td>232</td>
</tr>
<tr>
<td>5.8</td>
<td>Coefficient of variation and bimodality coefficient values for Centrosaurus measurement data</td>
<td>236</td>
</tr>
<tr>
<td>5.9</td>
<td>Dataset for first Centrosaurus principal components analysis</td>
<td>236</td>
</tr>
<tr>
<td>5.10</td>
<td>Variable loadings for principal components 1, 2, and 3 of first Centrosaurus principal components analysis</td>
<td>237</td>
</tr>
<tr>
<td>5.11</td>
<td>Dataset for second Centrosaurus principal components analysis</td>
<td>238</td>
</tr>
<tr>
<td>5.12</td>
<td>Variable loadings for principal components 1, and 2 of second Centrosaurus principal components analysis</td>
<td>238</td>
</tr>
<tr>
<td>5.13</td>
<td>Coefficient of variation and bimodality coefficient values for Triceratops measurement data</td>
<td>239</td>
</tr>
<tr>
<td>5.14</td>
<td>Dataset for first Triceratops principal components analysis</td>
<td>240</td>
</tr>
<tr>
<td>5.15</td>
<td>Variable loadings for principal components 1, 2, and 3 of first Triceratops principal components analysis</td>
<td>240</td>
</tr>
<tr>
<td>5.16</td>
<td>Dataset for second Triceratops principal components analysis</td>
<td>241</td>
</tr>
<tr>
<td>5.17</td>
<td>Variable loadings for principal components 1 and 2 of second Triceratops principal components analysis</td>
<td>241</td>
</tr>
</tbody>
</table>
### List of Figures and Illustrations

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.1</td>
<td>Mountain goat horn and horncore measurement dimensions</td>
<td>138</td>
</tr>
<tr>
<td>4.2</td>
<td>Bison horn sheath measurement dimensions</td>
<td>139</td>
</tr>
<tr>
<td>4.3</td>
<td>Bison core measurement dimensions</td>
<td>140</td>
</tr>
<tr>
<td>4.4</td>
<td>Pronghorn horncore measurement dimensions</td>
<td>141</td>
</tr>
<tr>
<td>4.5</td>
<td>Pronghorn sheath measurement dimensions</td>
<td>142</td>
</tr>
<tr>
<td>4.6</td>
<td>Representative bison age classes</td>
<td>143</td>
</tr>
<tr>
<td>4.7</td>
<td>Frequency histogram of mountain goat left horncore basal length</td>
<td>144</td>
</tr>
<tr>
<td>4.8</td>
<td>Bivariate scatterplot of mountain goat horn basal width and $M^2$ length</td>
<td>145</td>
</tr>
<tr>
<td>4.9</td>
<td>Scatterplot of principal components 1 and 2 from mountain goat principal components analysis</td>
<td>146</td>
</tr>
<tr>
<td>4.10</td>
<td>Hierarchical cluster analysis dendrogram of mountain goat principal components analysis</td>
<td>147</td>
</tr>
<tr>
<td>4.11</td>
<td>Shape variation in mountain goat horn sheaths from eigenshape analysis</td>
<td>148</td>
</tr>
<tr>
<td>5.1</td>
<td><em>Centrosaurus</em> skull measurement dimensions</td>
<td>195</td>
</tr>
<tr>
<td>5.2</td>
<td><em>Triceratops</em> skull measurement dimensions</td>
<td>196</td>
</tr>
<tr>
<td>5.3</td>
<td>Line plot of <em>Triceratops</em> horncore lengths</td>
<td>198</td>
</tr>
<tr>
<td>5.4</td>
<td>Eigenshape outline of <em>Triceratops</em> postorbital horncore ventral curvature</td>
<td>199</td>
</tr>
<tr>
<td>5.5</td>
<td>Eigenshape outline of <em>Triceratops</em> postorbital ventral curvature resampled</td>
<td>200</td>
</tr>
<tr>
<td>5.6</td>
<td>Frequency histogram of <em>Centrosaurus</em> occipital condyle circumference</td>
<td>201</td>
</tr>
<tr>
<td>5.7</td>
<td>Bivariate scatterplot of <em>Centrosaurus</em> occipital condyle height and width</td>
<td>202</td>
</tr>
</tbody>
</table>
**List of Figures and Illustrations Continued**

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.8</td>
<td>Bivariate scatterplot of <em>Centrosaurus</em> occipital condyle height and width, with horncore curvature labelled</td>
<td>203</td>
</tr>
<tr>
<td>5.9</td>
<td>Bivariate scatterplot of <em>Centrosaurus</em> basal horncore width and basal horncore length, with convex hulls</td>
<td>204</td>
</tr>
<tr>
<td>5.10</td>
<td>Bivariate scatterplot of <em>Centrosaurus</em> average horncore height and basal horncore width</td>
<td>205</td>
</tr>
<tr>
<td>5.11</td>
<td>Bivariate scatterplot of <em>Centrosaurus</em> anterior horncore height and posterior horncore height</td>
<td>206</td>
</tr>
<tr>
<td>5.12</td>
<td>Bivariate scatterplot of <em>Centrosaurus</em> basal horncore width and basal horncore length, with labels</td>
<td>207</td>
</tr>
<tr>
<td>5.13</td>
<td>Hierarchical cluster analysis dendrogram of <em>Centrosaurus</em> basal horncore width and basal horncore length</td>
<td>208</td>
</tr>
<tr>
<td>5.14</td>
<td>Scatterplot of principal components 1 and 2 from first <em>Centrosaurus</em> principal components analysis</td>
<td>209</td>
</tr>
<tr>
<td>5.15</td>
<td>Scatterplot of principal components 1 and 2 from second <em>Centrosaurus</em> principal components analysis</td>
<td>210</td>
</tr>
<tr>
<td>5.16</td>
<td>Bivariate scatterplot of <em>Triceratops</em> occipital condyle height and occipital condyle width</td>
<td>211</td>
</tr>
<tr>
<td>5.17</td>
<td>Bivariate scatterplot of <em>Triceratops</em> average basal horncore height and occipital condyle circumference</td>
<td>212</td>
</tr>
<tr>
<td>5.18</td>
<td>Bivariate scatterplot of <em>Triceratops</em> average basal horncore circumference and occipital condyle circumference</td>
<td>213</td>
</tr>
<tr>
<td>5.19</td>
<td>Bivariate scatterplot of <em>Triceratops</em> average basal horncore width and occipital condyle circumference</td>
<td>214</td>
</tr>
<tr>
<td>5.20</td>
<td>Bivariate scatterplot of <em>Triceratops</em> horncore spread at tips and average ventral horncore length</td>
<td>215</td>
</tr>
</tbody>
</table>
List of Figures and Illustrations Continued

Figure 5.21 Bivariate scatterplot of *Triceratops* average ventral horncore length and average basal horncore width 216

Figure 5.22 Scatterplot of principal components 1 and 2 from first *Triceratops* principal components analysis 217

Figure 5.23 Scatterplot of principal components 2 and 3 from first *Triceratops* principal components analysis 218

Figure 5.24 Scatterplot of principal components 1 and 2 from second *Triceratops* principal components analysis 219

Figure 5.25 Scatterplot of principal components 2 and 3 from second *Triceratops* principal components analysis 220

Figure 5.26 Hierarchical cluster analysis dendrogram of second *Triceratops* principal components analysis 221

Figure 5.27 Scatter plot of the first and second axes from the *Triceratops* eigenshape analysis 222

Figure 5.28 Bivariate scatterplot of *Triceratops* average ventral horncore length and average basal horncore circumference 223
List of Symbols, Abbreviations, Nomenclature

All abbreviations or acronyms are explained in the thesis before their first use.
Chapter 1: Introduction

“In the Ceratopsia perhaps more than in any other group of reptiles, fossil or recent, the skull has become greatly modified and specialized in certain directions” (Hatcher et al., 1907).

1.1 Preamble

This thesis was initiated and designed with the intention of investigating the perceived absence of sexual dimorphism in horned dinosaurs, or ceratopsians. In order to work toward this goal in an informed manner, a review of the occurrence of sexual dimorphism in the vertebrate fossil record was undertaken, and a proof of concept study was conducted wherein samples of extant horned mammals were examined as ceratopsian analogues. Only after these initial steps were taken could the subject of horned dinosaurs be meaningfully approached. As a result, there are many topics with which to potentially begin this thesis, but it seems most appropriate to start at the conceptual beginning, and to then expand upon the development and completion of this study in the order just explained. The ultimate subjects of this thesis are the large-bodied horned dinosaurs, the ceratopsids, and it is with them that the motivating questions lie.

1.2 Ceratopsid Dinosaurs

The Ceratopsidae, the clade of large, derived ceratopsians, is defined as the phylogenetic cluster that contains the most recent common ancestor of *Centrosaurus* and *Triceratops*, and all of its descendants (Dodson et al., 2004). It is divided into two monophyletic lineages (subfamilies), the Chasmosaurinae, which includes *Chasmosaurus* and *Triceratops*, and the Centrosaurinae, which includes *Centrosaurus* and *Styracosaurus* (Lehman, 1990). The Ceratopsidae arose and radiated...
during the Late Cretaceous and, with the exception of \textit{Sinoceratops} from China (Xu et al., 2010), and possibly \textit{Turanoceratops} from Uzbekistan (Sues and Averianov, 2009; but see Farke et al., 2009), is known exclusively from western North America (Farke et al., 2011).

Ceratopsids are readily identifiable by their large size relative to other ceratopsians, their obligate quadrupedality, and their elaborate cranial outgrowths, which include nasal and postorbital horns or bosses, and large, caudally-projecting frills that are extensions of the parietal and squamosal bones, and which may be variously adorned with spikes, hooks, and bumps.

The Ceratopsidae has recently been the subject of renewed interest from the palaeontological community, and 20 new ceratopsid taxa have been erected in the past 26 years. This contrasts with the preceding 36 years in which not a single new taxon was named (Farke et al., 2011; Ryan et al., 2012). This newfound diversity has brought to light a wealth of novel shapes and sizes of horns, frills, and spikes, and this variation in morphology has provided new impetus for investigation.

\textit{1.2.1 Morphological Variation in Ceratopsids}

Chasmosaurines tend to be larger than centrosaurines, attaining total body lengths of 8 m and skull lengths of up to 2.5 m (Sereno et al., 2007), whereas centrosaurines typically measure about 5 m in total length with skulls up to 1.5 m in length (Dodson et al., 2004). Postcranially, chasmosaurines and centrosaurines have similar skeletal anatomy, although there are diagnostic differences in the form of the olecranon process, and in features of the pelvis and sacrum, among others (Lehman, 1990).

Disregarding size, the two clades are readily distinguishable on the basis of a suite of characters largely related to the morphology and anatomy of the skull. These include a long, low
snout in chasmosaurines (preorbital region length/height = 1.4 to 3.0) and a deep, short snout in centrosaurines (preorbital region length/height = 1.2 to 1.4) (Lehman, 1990). Chasmosaurines have long frills (0.94 to 1.70 times basal skull length), with elongate, triangular to blade-like squamosals that extend caudally for most of the length of the frill, whereas centrosaurines are characterized by short frills (0.54 to 1.00 times basal skull length) with stocky, quadrangular squamosals that contribute to only the proximal portion of the frill, leaving the parietal to contribute the overall length (Lehman, 1990; Ryan and Evans, 2005). Centrosaurines also develop an autapomorphic ‘step’ between the proximal and caudal portions of the squamosal bone (Dodson, 1986; Ryan, 2008).

The most interesting aspects of cranial variation, however, are expressed in the outgrowths of the nasal, postorbital, and parietal bones, and it is variation in these features that provides important interspecific differences, including most of the species-specific diagnostic characters (Sampson et al., 1997; Ryan and Evans, 2005; Sampson et al., 2010). As mentioned, the parieto-squamosal frill differs in form between the ceratopsid subclades, but it also differs between each genus in each lineage in terms of the accessory spikes and hooks that adorn the parietal. These parietal features are highly diagnostic (e.g. Ryan and Russell, 2005). The cranial horns are also quite variable; in general, chasmosaurines typically exhibit large post-orbital horncores and small nasal horncores, whereas centrosaurines are often characterized by large nasal horncores or bosses and diminutive supraorbital horncores (Dodson, 1997; Sampson et al., 1997; Ryan and Evans, 2005).

In addition to these cranial features, ceratopsids possess, both relatively and absolutely, the largest skulls ever exhibited by terrestrial animals (Sereno et al., 2007). These two factors (high morphological variability in cranial outgrowths despite an otherwise highly conservative
skull structure, and enormous overall skull sizes) suggest an evolutionary history marked by strong selection acting on the cranial region, and identify cranial characters as features that may be disproportionately informative about the evolutionary history of the clade. This observation is what spurred this thesis, as it raised the question of whether any of the observed intraspecific variation is attributable to sex, and whether sexual selection comprised some part of that presumed ‘strong selection on the cranial region’. In order to address these questions in a manageable, but still meaningful, scope, the horns alone were chosen for investigation, because they are more readily measured and contextualised than are parietal features, and because horns have been well-studied in living vertebrates. My approach is restricted to investigating the potential for sexual dimorphism. Exploring the broader aspects of sexual selection in ceratopsid evolution would be a fascinating, but much more involved, endeavour (Padian and Horner, 2011; Knell et al., 2012).

1.3 Horns

Horns and horn-like structures are widespread throughout the evolutionary history of terrestrial vertebrates and invertebrates alike (Emlen, 2008). Among extant taxa, examples of horned animals (or those with horn-like appendages) include rhinoceroses, chameleons, horned lizards, beetles, and the ‘horned’ ruminants: bovids, cervids, giraffids, and pronghorn (Emlen, 2008; Davis et al., 2011). Much work has been undertaken to explore the evolution, development, and function of these structures. For example, Emlen et al. (2005) demonstrated more than two dozen instances of gains and losses of exaggerated horns in *Onthophagus* beetles, despite sampling only 2% of the genus, and Wasdik et al. (2010) demonstrated that the development of these horns is regulated by the *Hox* gene Sex combs reduced. The growth and structure of rhinoceros horns has been investigated using CT scanning and histology (Hieronymus, et al., 2006), and Berger
and Cunningham (1998) studied the role of horns in the social structure of rhinoceroses. In ruminants, the evolutionary origins of horn-like appendages continues to be an active topic of research (Davis et al., 2011), and much work has been conducted to enhance understanding of the controls of horn growth cycles in bovids (O’Gara and Matson, 1975) and pronghorn (O’Gara et al., 1971), and antler growth in cervids (Bubenik and Bubenik, 1990). Another large body of research encompasses the selection pressures that influence horn form and presence in male and female bovids (Kitchener, 1985; Lundrigan, 1996; Jorgensen, 2007; Stankowich and Caro, 2009).

This wealth of information and ongoing research provides the context for my investigation of horns in relation to sexual dimorphism in ceratopsids. From this abundance of analogous horn-like structures, the horns of bovids and pronghorn were selected for the proof of concept study. More information about these animals, and about why they were selected as analogues, is provided in Chapter 3.

1.4 Sexual Dimorphism

The term ‘sexual dimorphism’ is so commonly employed in the language of biology that it occurs approximately 65 times in Andersson’s landmark book *Sexual Selection* without ever being defined beyond “traits that differ between males and females” (Andersson, 1994). As sexual dimorphism is a core concept in this thesis, I cannot proceed without exploring the term further and defining it as it applies to my studies and to the area of biology in which they lie. In doing so I would be remiss to not review some of the debate surrounding the term that is currently taking place in the palaeontological literature (Padian and Horner, 2010, 2011; Knell and Sampson, 2011; Knell et al., 2012).
Padian and Horner (2010, 2011) state that ‘true sexual dimorphism’ requires a discrete structure to be present in one sex but not the other. Knell and Sampson (2011) appear to disagree; they do not provide their own definition, but seem to consider relative size differences between the sexes as being an example of sexual dimorphism. The source of Padian and Horner’s (2010, 2011) definition is unclear, but their repeated use of the term ‘sexual dimorphism’ in the context of sexual selection creates the impression that these two terms are inextricably intertwined. They are not. More importantly, Padian and Horner’s (2011) use of the term, when attempting to explain Darwin’s definition of sexual selection, creates the impression that Darwin defined sexual dimorphism in the manner that they employ it, which he did not:

Darwin cannot be ‘wrong’ about the definition of [sexual selection], despite the protests or confusion of later authors, because he invented it, and his empirical basis for it is entirely valid; he was not ‘imprecise’ (pace Carranza, 2009). Myriad examples prove the presence of distinct, monosexual characters in species that are used to attract mates and repel rivals (Darwin, 1871; Andersson, 1994). Thus, the only possible definition of sexual selection requires sexual dimorphism (and not simply allometric sexual differences: Padian & Horner, 2010). (p.1).

In fact, Darwin did not use the term sexual dimorphism at all. Rather Padian and Horner (2010, 2011) apply their definition of the term to the manifold examples provided by Darwin in his effort to illustrate structures that have been modified by, and employed in, the process of sexual selection (Darwin, 1871). Darwin does, however, use the term ‘dimorphic’ fourteen times in *The Descent of Man* (1871), and it is very clear that he is referring to two distinct forms of a structure, or colours, within a single sex, without intermediate forms or gradations between them. Darwin’s (1871) meaning is best demonstrated by the following passage, “In *Siagonium* we have a case of dimorphism, for the males can be divided into two sets, differing greatly in the size of their bodies and in the development of their horns, without intermediate gradations”. Darwin (1871) mentions in a subsequent footnote that “the dimorphism is not strict”, as he “noticed one
male specimen of *Stagonium* in an intermediate condition” in the collections of the British Museum (Darwin, 1871). From these quotes (and other examples in *The Descent of Man*) it is justifiable to conclude that a definition of ‘sexual’ dimorphism that would have been acceptable to Darwin would have been in reference to the sexes possessing distinct morphologies or morphological traits, without intermediate gradation. This is essentially the same definition advanced by Padian and Horner (2010, 2011), and it matches the original meaning of the term ‘dimorphic’, as derived from Greek: “[< Gk. *Dimorphos*, having two forms: *di-* , two + *morphē*, shape.]” (Soukhanov and Ellis, 1988).

However, it is worth noting that Darwin clearly understood the meaning of the term dimorphic and used it several times correctly, but did not once use it in reference to the differences between the sexes that he was describing. Padian and Horner (2010, 2011) insist that he was referring to dimorphic structures, although presumably just not stating it. I would argue instead that Darwin was referring to sexual differences because he clearly understood the term “dimorphic” and did not use it. Indeed many of the examples that he discusses are not, strictly-speaking, dimorphic.

Many researchers in the paleontological, paleoanthropological, and neontological fields who actively study sexual dimorphism do not hold to this traditional definition of discrete, non-gradational dimorphism. Rather, my readings on the topic reveal that it is considered to be an intraspecific (and intrapopulational where appropriate) morphological difference between males and females of the same ontogenetic stage, and one that is statistically detectable if based upon quantifiable traits (Bennett, 1992; 2003; Andersson, 1994; Thoren et al., 2006; Bonduriansky, 2007; Fairbairn, 2007; Stuart-Fox and Moussalli, 2007; Chenoweth et al., 2008; Cheng et al., 2009; Isles, 2009; Lawler, 2009; Losos, 2009; Chen et al., 2010; Johnson and Wade, 2010;
Meachen-Samuels and Binder, 2010; Tomkins et al., 2010; Barden and Maidment, 2011; Djordjevic et al., 2011; Kelaita et al., 2011; Mihlbachler, 2011; Hallsson and Bjorklund, 2012; Knell et al., 2012). A prominent and oft-cited example is the sexual difference in the relative size of canine teeth, with males possessing significantly larger teeth than females, as seen in baboons (*Papio sp.*) (Thoren et al., 2006). Many authors (probably including Knell and Sampson [2011]) would consider this to be sexual dimorphism, as would I – for reasons explained below.

Padian and Horner (2010, 2011) argue that instances such as that of baboon canines, just described, do not represent sexual dimorphism, and they are probably, technically, correct. However, there is currently a considerable field of research dedicated to unraveling the evolutionary causes and mechanisms that lead to sexual differences (including both discrete sexual dimorphism and allometric sexual differences, and much more) (e.g. Andersson, 1994; Fairbairn et al., 2007; Bonduriansky, 2007; Ketola et al., 2012). A time will no doubt arrive when subsets of this field become sufficiently specialised to benefit from a careful re-examination of terminology, but, for now, distinguishing allometric sexual differences (such as canine teeth or body size) from strict sexual dimorphism would create a terminological schism that would only complicate the discussion, rather than clarify it. Forcing authors to distinguish between ‘baboons exhibit sexually dimorphic canines’ and ‘baboons exhibit sexual differences in relative canine size’ would bring little additional clarity to the topic. I feel that holding to a strict definition of sexual dimorphism, as advocated by Padian and Horner (2011), solely out of deference to the traditional derivation of the word “dimorphic”, is counterproductive to the progress of the discussion of sexual differences that is occurring today. As a result, sexual dimorphism is used throughout this thesis to refer to significant (statistically demonstrable) morphological differences between males and females of the same ontogenetic stage. Where
appropriate, ‘discrete sexual dimorphism’ is used to refer to structures present in one sex but not the other.

Sexual size dimorphism (SSD) is the term applied specifically to sexual dimorphism in average adult body size; that is, a sex-based difference in adult body mass or dimensions (Fairbairn, 2007). Sexual size dimorphism is a phenomenon that occurs widely in extant vertebrates, with male-biased SSD predominating among birds and mammals (endothermic vertebrates in general), and female-biased SSD predominating among “reptiles” and amphibians, and poikilotherms in general (Fairbairn, 2007).

Sexual shape dimorphism is a subset of sexual dimorphism that relates to differences in relative body proportions between the sexes, and the term is applicable to such instances as pelvic canal dimensions that differ between the sexes in *Pteranodon* or *Alligator mississippiensis* (Bennett, 1992; Prieto-Marquez et al., 2007), femoral head dimensions that differ between the sexes in *Kentrosaurus aegypticus* (Barden and Maidment, 2011), and differences in plastron concavity between the sexes in some turtles (Djordjevic et al., 2011). As a subset of sexual dimorphism it will not receive separate treatment in the literature review, but I explore shape dimorphism in bovids and ceratopsids separately from size-based dimorphism.

One final word on sexual dimorphism: although many dimorphic structures are useful as sex-identifying features, they are not necessarily always able to be applied in this way. If one finds a red deer skull with antlers attached, it is surely male. However one would not know this without already knowing something about antler growth in red deer, and would be mistaken to draw a similar conclusion about an antlered caribou skull. For extinct taxa then, the hope is of course to find a ‘key’, a trait that permits assignment to sex, even in isolated specimens. It is
important to remember, however, that recognising sexually dimorphic structures does not necessarily yield the ability to assign sex to a specimen without additional information.

1.5 Prospectus

Sexual dimorphism is a widespread phenomenon in the extant biota, and is a feature that has clearly arisen many times in the past. To study it effectively in fossil species requires an understanding of its occurrence and how it is measured in living animals. Horn-like structures occur across a broad taxonomic spectrum and can vary from sexually monomorphic to discretely sexually dimorphic. As a result, the horns of ceratopsid dinosaurs provide an ideal focal structure for investigating the potential for the presence of sexual dimorphism in these extinct animals. To facilitate this, it is worthwhile to examine which methods of investigating sexual dimorphism have been previously employed for fossil species and to understand what kinds of structures or features have been reported to be dimorphic. To this end, the following chapter presents a review of the occurrences of sexual dimorphism in the vertebrate fossil record. This will provide the background context for the exploratory studies that follow, and ultimately allow a critical appraisal of the evidence gleaned from ceratopsian remains.
Chapter 2: Evidence for Sexual Dimorphism as Manifested in the Vertebrate Fossil Record

“Sexual dimorphism should be attributed to fossil species only when statistical significance and stratigraphic control have been demonstrated. Claims made in the absence of such evidence should be regarded with scepticism,” (Mallon and Holmes, 2006).

2.1 Introduction

Sexual dimorphism occurs widely in extant vertebrates, being evident in fishes, amphibians, squamates, birds, and a broad range of mammals (Darwin, 1871; Andersson, 1994; Fairbairn et al., 2007). Not surprisingly, it has also been reported for numerous extinct lineages, and sexual size dimorphism (SSD) and discrete sexually dimorphic traits have been advocated for many fossil species, as is shown in the body of this chapter. However, instances of sexual dimorphism appear to occur less frequently in the fossil record than in extant groups. This is not surprising, but merits some discussion. It is reasonable to make the assumption that the same selective regimes conducive to the evolution of sexual dimorphism in recent taxa were present in the past. As a result, the paucity of sexually dimorphic fossil species is most likely due to the nature of the fossil record rather than to the nature of the animals themselves. This is discussed briefly before returning to the main focus of this chapter – a review of studies of sexual dimorphism in the vertebrate fossil record.

2.1.1 The Challenges of the Fossil Record

There are several challenges that complicate the study of sexual dimorphism in the fossil record and these have long been recognised by palaeontologists (e.g. Kurtén, 1969; Olson, 1969;
Gingerich, 1981a; Chapman et al., 1997). Generally speaking, these relate to the determination of species, the determination of age, the determination of sex, and the nature of fossilization. I discuss each of these in turn.

Fossil species are typically defined using the morphospecies concept (Benton and Pearson, 2001). This complicates the recognition of sexual dimorphism because the morphological variation that may exist between the sexes can be of a similar nature to the variation that distinguishes closely related species. Thus, intersexual morphological variation must be distinguished from interspecific variation, and recognised within the scope of intraspecific expression. A good example of a paleontological study that has addressed this problem is Gingerich’s (1981a) study of *Adapis*. However, things are not always as clear cut, and distinguishing between sources of morphological variation can prove extremely challenging, as is well illustrated by the history of the taxonomy of *Triceratops*. Since the erection of the genus in 1889 by Marsh, 16 species of *Triceratops* have been described. Several of these were no doubt poorly characterised, but they lingered in the taxonomic nomenclature nonetheless. Finally, after nearly a century, a review of the genus by Ostrom and Wellnhofer (1986) found support for only a single species (*T. horridus*), and a subsequent review by Forster (1996) found support for only two species (*T. horridus* and *T. prorsus*). Forster (1996) stated that the possibility of these two species representing a single sexually dimorphic species could not be ruled out, an idea supported by Lehman (1998), although stratigraphic evidence does not seem to support this (Scannella and Fowler, 2009). Lehman (1998) and Dodson et al. (2004) also argued for a single species. The range of morphological variation in the genus *Triceratops* is great enough to represent 16 species (at least at first glance), and simultaneously small enough that all of the observed variation can be subsumed within the confines of a single dimorphic species. In
essence, as the number of species decreases the degree of intraspecific variation encapsulated by the remaining species increases. It is this plasticity in species-specific morphology that challenges the identification of sexual dimorphism – had anyone attempted to identify sexual dimorphism in a species of *Triceratops* prior to 1986 they would have been working with a limited subsample of the total morphological variation, and after 1996 they could potentially have been working within the confines of a single sex of one species (although unlikely).

If a species’ diagnosis is robust, specimens must then be assessed for age; that is, at what ontogenetic stage did they die? Size alone is an unreliable indicator of age, especially for taxa with resource-dependent growth (for example in snakes [Forsman and Lindell, 1996]), and even for taxa with indeterminate growth (Halliday and Verrell, 1988), so alternate means of assessing age are required. Tooth eruption patterns have been extensively studied in mammals and can be used to assess the maturity of mammalian specimens, but are of little use for other clades. Skeletal indicators of maturity, such as the fusion of sutures or the appearance of horns, can be difficult to establish for extinct species because they require assumptions to be made regarding the timing and process of bone formation, and may reflect arbitrary life stages (Sampson et al., 1997). Osteohistology is frequently used to study growth rates and ontogenetic processes in fossil taxa (e.g. Lee and Werning, 2008; Tumarkin-Deratzian, 2010; Botha-Brink and Smith, 2011; Horner and Lamm, 2011; Kohler et al., 2012) and is becoming increasingly valuable to the field of paleontology as techniques and knowledge improve, but reliable osteohistological indicators of maturity have yet to be definitively established. Also, these methods currently require destructive sampling, which is not always possible or practical (but see Curtin et al. [2012] for advancements in ontogenetic staging in elephantids and non-invasive sectioning of bones using X-ray computed tomographic imaging).
Again, *Triceratops* serves as an example of some of the challenges presented by ontogeny. Horner and Goodwin (2006) proposed an ontogenetic series for *Triceratops* that was divided into four stages and that was based upon transformations in the postorbital and nasal horns, the postorbital sinuses, the nasal bones, the frill margin and epoccipitals, and the occipital condyle. This growth series is largely dependent on transformations of secondary structures (other than the occipital condyle) to establish its stages, meaning that sexual variation in those structures, if present, could result in the assignment of males and females to different growth stages and thereby limit our ability to contrast them. This is particularly concerning if significant ontogenetic transformations are thought to occur in those structures (Scannella and Horner, 2010). Many secondary sexual structures only develop in males at the onset of sexual maturity and remain unexpressed or rudimentary in females. As a result, distinguishing juvenile or subadult males from adult females can sometimes be challenging without ontogenetic information. Smith and Fisher (2011) provide a good example of the usefulness of ontogenetic information in a study of tusk morphology in *Mammut americanum*.

Finally, although it is almost always possible, although not always simple, to establish the sex of an extant animal, determining the sex of a fossil specimen is often not possible. Without the preservation of the reproductive organs or the occurrence of exceptional death circumstances, such as a gravid female or mating pair, a single specimen often reveals no clues useful in establishing its sex. As a result, sexual dimorphism cannot typically be detected by direct comparison of the sexes (unless closely related extant taxa are available that provide a starting point for investigation, and even then these may be misleading), but rather must often be inferred through study of the variation within a sample of similarly-aged individuals of a single species. The discovery of an exceptional fossil may then provide additional support for the hypothesis of
sexual dimorphism, as has occurred on rare occasions (Voorhies and Stover, 1978; Cheng et al., 2004; Lu et al., 2011).

For most clades however, such exceptional fossils are rare, and confounding the determination of sex is the poor preservation of non-mineralised structures (such as horn sheaths, feathers, air sacs, dewlaps, or manes) in the fossil record. This has two significant implications. First, the loss of information regarding soft-tissue structures is immense, because knowledge of the absence of such structures is infinitely more informative than absence of knowledge regarding their presence. This is so obvious that it seems hardly worth mentioning at first. But imagine, for a moment, the state of dinosaur paleontology if feathers had never been preserved in Lagerstätten. Our ignorance of most soft tissue details is important to bear in mind if sexual dimorphism is to be considered in the absolute sense (i.e. a structural presence/absence dichotomy) and if hypotheses are to be proposed based on the absence of sexual dimorphism in a lineage (e.g. Padian and Horner, 2010). The second implication is that mass-based sexual size dimorphism (SSD), readily measurable in living samples, is largely hidden in fossils. The difference in mass becomes detectable only as a difference in skeletal dimensions, which, due to the scaling relationships between length, area, and body mass, is but a fraction of the mass difference, and is therefore much harder to detect. For statistical purposes, this means that a much larger sample would be required to detect the discrepancy in bone circumference or length than in body mass. For example, adult male mountain goats (*Oreamnos americanus*) can be 40-60% heavier than adult females and yet only 5% and 7% larger than females in shoulder height and chest girth, respectively (Cote and Festa-Bianchet, 2004).
Despite these challenges inherent to the study of fossil organisms, there have been many successful (and even more less-than-successful) studies of sexual dimorphism across a wide taxonomic range of fossil vertebrates. The following review documents published accounts of sexual dimorphism in the vertebrate fossil record. It is not an exhaustive survey, but serves as a reference source for future investigations of this topic. It has been organised by vertebrate taxon, from fish to mammals. This review fulfills two main objectives with respect to this thesis. Firstly, it documents the various methods that have been employed by authors when assessing sexual dimorphism, in order to reveal which methods may be most applicable to the investigation of dimorphism in ceratopsid horns. Secondly it permits some understanding of how broadly sexual dimorphism occurs in the vertebrate fossil record and to highlight what factors, if any, seem to influence this distribution.

To make the content and conclusions of this chapter more readily accessible, Tables 2.1 – 2.4 provide a brief summary of each study that is detailed in this chapter. They comprise four categories into which the studies have been assorted by the level of confidence that I attribute to their demonstration of sexual dimorphism (Table 2.1 = High, Table 2.2 = Moderate, Table 2.3 = Low, Table 2.4 = Poor Confidence.)

2.2 Instances of Sexual Dimorphism in the Vertebrate Fossil Record

2.2.1 Fishes

Sexual dimorphism in extant fishes often occurs as sexual size dimorphism (SSD), and the degree of SSD expressed in ceratioid anglerfish is the most extreme example known in vertebrates, with some females thousands of times more massive than males (Pietsch, 2005).
There are many occurrences of secondary sexual structures as well, including kype in salmon (Witten and Hall, 2003) and bizarre cranial appendages in the chimaeras. The fossil record is no different, showcasing many instances of SSD and interesting sexually dimorphic structures, such as jointed ethmoid claspers and elaborate dorsal fin spines.

i) Chondrichthyes

All extant male chondrichthians possess modified pelvic fins that function as intromittent organs to facilitate internal fertilization (Long et al., 2009). These ‘claspers’ evolved fairly early in the chondrichthyan lineage, possibly by the Devonian (Long et al., 2009), and as a result can be used to assign sex in many extinct chondrichthyan taxa. Claspers are also useful as ontogenetic indicators because they become calcified in sexually mature individuals (Lund, 1990). Because claspers function essentially as sex organs, they are considered morphologically to be primary, not secondary, sexual structures (Lund, 1990) and by definition they render all extant chondrichthians sexually dimorphic. As a result I do not focus on cases of sexual dimorphism in chondrichthians attributed to claspers. However, claspers provide an effective means to sex and age specimens, and are a useful tool for studying other aspects of sexual dimorphism.

Elasmobranchii: The Upper Mississippian Bear Gulch deposits of Montana entomb a marine fauna rich in chondrichthians that has been extensively studied by Richard Lund (1982, 1985a, 1985b, 1986, 1990). Within stethacanthid elasmobranchs, adult and subadult males possess a first dorsal fin and a dorsal fin spine that is often elaborate in form and denticulation, but these are absent in females. Lund (1985a, 1985b, 1986, 1990) described at least five species from Bear Gulch exhibiting such dimorphism. The best known examples are Falcatus falcatus (Lund, 1985a) and Damocles serratus (Lund, 1986), the males of which carried anteriorly-projecting,
denticulated dorsal fin spines. One particular specimen of *F. falcatus* preserves a male and female in close association, with the dorsal spine of the male overlying the open mouth of the female (Lund, 1985a), suggesting that females may have grasped the spine during courtship or copulation. Complete growth series are lacking for most stethacanthid species, but juveniles are known of *F. falcatus*. Sexed adult and subadult specimens include ten males and one female, and eleven males and one female, for *F. falcatus* and *D. serratus*, respectively (Lund, 1990).

Additional dimorphic features observed in the Stethacanthidae include specialised patterns of squamation in males, such as increased denticulation on the dorsal surface of the head, and elongation of the rostrum in males. All dimorphic features manifest at the onset of sexual maturity, as assessed by degree of clasper calcification (Lund, 1990).

The selachimorph elasmobranch *Heteropetalus elegantulus* is known from a complete growth series and the shape of the dorsal fin, and the fin’s posterior radials, are reported to be sexually dimorphic (Lund, 1990).

**Holocephali:** The chondrenchelyid *Harpagofututor volsellorhinus*, from Bear Gulch, exhibits sexual dimorphism in dramatic fashion (Lund, 1982, 1990). Males may be slightly smaller than females in size, but they possess paired ethmoid (cranial) claspers that are “without parallel among known chordates.” (Lund, 1982). These neomorphic structures extend postero-dorso-laterally from the ethmoid region of the male cranium and are multi-jointed, bifurcated, denticulated, and heavily calcified in sexually mature males (Lund, 1982, 1990). They are thought to have been strong, well-muscled, and mobile, and to have functioned directly in aiding in copulation (Lund, 1982). Furthermore, the preservation of pigments associated with the internal organs allowed for confirmation of assigned sexes by permitting the comparison of the arrangement of internal anatomy with that of extant chondrichthyans (Grogan and Lund, 1997).
The related *Chondrenchelys problematica*, from the Lower Carboniferous of Scotland, lacks ethmoid claspers but exhibits dimorphism in the form of the pectoral fins, with males possessing enlarged fins and hypertrophied radials and basal elements (Lund, 1982). These dimorphic features were recognised by direct comparison of fossil specimens, with males identified by the presence of pelvic claspers (Lund, 1982).

Another holocephalian from Bear Gulch, *Echinochimaera meltoni*, is known from a range of specimens covering the spectrum from juveniles to adults, and exhibits SSD and marked sexual dimorphism (Lund, 1990). Adult males are approximately twice as long as adult females, and males possess four pairs of short supraorbital denticles (whereas females exhibit only one), a pair of prepelvic tenaculae, an enlarged and denticulated dorsal spine, and considerable denticulation of the integument between the second dorsal fin and the tail (Lund, 1990).

Although fossil chondrichthyans present some interesting features unknown in the extant biota, the use of claspers to aid in the detection of sexual dimorphism is the first of many instances of extant-based inference of sexual dimorphism – that is, making deductions about the structures of fossil organisms in light of knowledge of related extant taxa. Without *a priori* knowledge of the association between males, internal fertilisation, and claspers, it is unlikely that sex could have been assigned to fossil chondrichthyans, even with the probable recognition of claspers as being sexually dimorphic.

ii) Osteichthyes

*Actinopterygii*: The Eocene lake deposits along the Horsefly River, British Columbia, have yielded large numbers of the catostomid fish *Amyzon aggregata*. Studying a collection of 85 specimens, Wilson (1984) identified strong peaks in the population’s size-frequency distribution
as year classes. Sexual dimorphism was then proposed to account for increased variability in body depth that appears during the fish’s second year of growth. This suggestion is based on trends observed in morphological data and is not supported by statistical tests. Wilson (1984) suggested that the deeper bodied morph is female.

Similar to the modified pelvic fins of chondrichthyans, modified anal fins are known to function as intromittent organs in some extant bony fish, but these structures are not widespread and merit noting here. Several species of *Peltopleurus*, a genus of small actinopterygian known from the Middle and Upper Triassic of Europe and China, exhibits dimorphic anal fins (Lombardo, 2003; see also Burgin, 1990, 1992). These have been described in detail for *P. nuptialis* by Lombardo (2003) and for *P. lissoccephalus* by Burgin (1990). In the putatively male morph the modified anal fin bears an enlarged lateral scute that covers the proximal segments of the anterior fin rays and possesses an additional segment of hooked fin rays. This fin structure is suggested to be analogous to the gonopodia of some cyprinodontids (such as guppies) (Burgin, 1990). Unfortunately numbers of each sex are not reported, and sex ratios are not established. The case for sexual dimorphism is supported by a difference in ornamental tubercles; specimens with modified anal fins have larger tubercles on the rostral and nasal bones whereas the unmodified morph exhibits smaller tubercles, these being present only on the nasal (Lombardo, 2003). These tubercles are suggested to be secondary sexual traits. Similar dimorphism, related to the distribution of cranial tubercles, has also been suggested for the Middle Triassic genera *Meridensia, Aetheodontus, Luganoia* and *Besania* (Burgin, 1990).

Anglerfish (suborder Ceratioidei) exhibit the most extreme sexual size dimorphism in vertebrates, and present a rather unique case in the study of sexual dimorphism in the vertebrate fossil record. No fossil anglerfish were known until 1980, when a single specimen was recovered
from the Upper Miocene Puente Formation of the Los Angeles Basin, California (Pietsch and Lavenberg, 1980; see also Carnevale and Pietsch, 2009). Less than 3 cm in standard length, the fish was assigned to *Acentrophyne* and recognised as a metamorphosed female by the presence of a lure (illicium) (Pietsch and Lavenberg, 1980). Since then, nine more fossil specimens have been found, all from the Puente Formation, attributable to five genera (*Borophryne*, *Chaenophryne*, *Linophryne*, *Oneirodes*, and *Leptacanthichthyes*), representing two ceratioid families (Linophrynidae and Oneirodidae) (Carnevale et al., 2008). Their morphology is so conservative (the authors reported that, “no relevant morphological change has characterized these taxa in at least the last eight million years.” [Carnevale et al., 2008]) that the specimens could be tentatively assigned to extant species, with all specimens being identified as metamorphosed females (Carnevale et al., 2008). These species even appear to have inhabited the same restricted biogeographic region in the Miocene that they do today (Carnevale et al., 2008). As members of living species, sex can be attributed to these fossils by direct comparison with extant specimens, and sexual dimorphism is presumed to have been present in these Miocene populations despite no males having yet been found. This assessment is supported phylogenetically as these two families are nested within Ceratioidea, the monophyletic status of which is primarily supported by their extreme sexual dimorphism (Carnevale et al., 2008). This represents an extreme case of extant-based inference of sexual dimorphism and depends entirely on our understanding of the life history and morphology of living ceratioids.

### 2.2.2 Amphibia

Reports of sexual dimorphism in fossil amphibians are rare, despite an abundance of known sexual dimorphism in extant amphibians (Shine, 1979).
Anura: Holman (2003) stated that variable development of the medial crest on the distal humeral condyle in *Scotiophryne pustulosa*, a discoglossid frog from the Late Cretaceous of western North America, was probably attributable to sexual dimorphism. Similar variation was reported by Venczel and Csiki (2003).

2.2.3 Testudines

Cryptodira: Sexual dimorphism in tail length, the degree of plastral kinesis, and body size (carapace length) has been reported for the Eocene carettochelyid turtle, *Alaeeochelys crassesculpta* (Joyce et al., 2012). Fifty-one specimens of *A. crassesculpta* have been recovered from the Eocene Messel Pit in Germany, and twelve are preserved as closely-associated pairs, previously hypothesised to be mating pairs. Joyce et al. (2012) corroborated this suggestion by documenting consistent differences in nine individuals from six of the pairs. By comparison with related extant turtles, Joyce et al. (2012) suggested that the sex with greater carapace length, relatively shorter tail, and a straighter suture between the hyoplastral and xiphiplastral plates, is the female. A plot of the ratio of cumulative caudal column length/pygal width over caudal vertebra number reveals two distinct trajectories, with ‘male’ tails elongating more quickly than those of ‘females’ and having more caudal vertebrae, resulting in a greater overall tail length. Carapace length was measurable on both individuals in five of the pairs, with ‘males’ found to be, on average, 17% smaller than ‘females’. Female-biased SSD occurs in the majority of extant turtle species (Cox et al., 2007).
2.2.4 Sauropterygia

**Pachypleurosauria:** Sexual dimorphism is well supported in the pachypleurosaurus. Sander (1989) and Reippel (1989) proposed sex as the explanation for marked dimorphism in the humeri of four species: *Neusticosaurus peyeri*, *N. edwardsii*, *N. pusillus*, and *Serpianosaurus mirigiolensis*. The pattern of dimorphism is similar in all four taxa, involving differences in humeral length and width as well as in the relative development of the ectepicondylar and supinator ridges, anterior proximal trochanters, and articular facets, with a larger, more robust morph exhibiting greater development of these features and a smaller, more gracile morph exhibiting less strongly developed features (Sander, 1989).

Similar humeral dimorphism was reported for *Keichousaurus hui* by Lin and Reippel (1998), and was extensively documented by Cheng et al. (2004, 2009). Study of 70 nearly complete skeletons revealed that the following three ratios best quantified dimorphism: 1) Maximum distal width of the humerus/minimum width of the humeral shaft; 2) Maximum humeral length/standard length; and 3) Maximum humeral length/maximum femoral length (Cheng et al., 2009). Frequency histograms of these ratios are clearly bimodal. The gracile morph, sex ‘x’, is thought to be female, a hypothesis that is strongly supported by the presence of embryos within the abdominal cavities of two sex ‘x’ specimens (Cheng et al., 2004). Juvenile specimens were found to be morphologically similar to, and indistinguishable from, females, suggesting that males deviate from a common growth trajectory prior to attaining sexual maturity (Cheng et al., 2009). A principal components analysis (PCA) was performed using 16 measurements from 65 specimens. A bivariate plot of principal component 1 against principal component 2 revealed two groups corresponding to the inferred sexes (Cheng et al., 2009). A discriminant function analysis of the dataset provided additional support for the existence of
sexual dimorphism, assigning specimens to their presumed sex 91% of the time, with the majority of incorrectly assigned individuals recognised as being immature. The three most predictive variables for assigning sex were minimum width of the femoral shaft, neck length, and minimum width of the humeral shaft (Cheng et al., 2009). The authors reported that their sample also suggested slight sexual size dimorphism, with females being smaller than males in snout-vent length (Cheng et al., 2009). Of the 70 individuals, the study revealed 22 – 24 males, the rest being identified as female or juvenile (Cheng et al., 2009).

2.2.5 Ichthyosauria

Despite multiple specimens having been identified as pregnant females (e.g. Maxwell and Caldwell, 2003), sexual dimorphism remains unknown in ichthyosaurs (Calloway, 1997).

2.2.6 Archosauria

i) Crurotarsi

Phytosauria: Zeigler et al. (2002) examined a collection of nine skulls of *Pseudopalatus*, a phytosaur from the early mid-Norian Canjilon quarry in New Mexico. They identified two morphs that varied in the form of the snout and narial crest. One morph has a slender snout and smaller narial crest and is suggested to be female, whereas the putative male morph has a more robust snout and a narial crest that is taller and considerably longer, extending further distally along the snout (Zeigler et al., 2002). Three ‘male’ skulls yielded an average length only slightly greater than that of four ‘female’ skulls, but exhibited narial crests nearly twice the length of the crests of females. Ziegler et al. (2002) reject the hypothesis that the morphs represent distinct species, due to the lack of any additional morphological variation in the skulls, and because the
specimens are all from the same quarry, and potentially, the same population (Ziegler et al., 2002). However, Nesbitt and Stocker (2008) reviewed the skulls and considered them to represent two species, *P. buceros* and *P. pristinus*, due to differences in snout length and the medial extent of the squamosal. Additional specimens or a more detailed morphological description of both morphs may help to resolve this.

**Eusuchia**: Sexual size dimorphism is common in extant crocodilians, and is well documented. Males are typically larger than females and grow faster (Cox et al., 2007; Grigg and Gans, 1993). Given its prevalence in extant species, it is possible that SSD was present in extinct crocodylians. However, without a means to sex specimens SSD would remain difficult to demonstrate.

Prieto-Marquez et al. (2007) reported weak sexual dimorphism in *Alligator mississippiensis*, with the female pelvic canal being slightly deeper and narrower than that of the male. Statistical support for these observations was provided; it is important to note however, that this detection of dimorphism relied on *a priori* knowledge of sex. The authors state that without a relatively large sample size the presence of this dimorphism would be “statistically difficult to prove”. Indeed, in reality, without the *a priori* knowledge of sex, it would be virtually impossible to demonstrate. The degree of overlap between the sexes is such that sex could be correctly assigned by pelvic dimensions only slightly better than by chance (Prieto-Marquez et al., 2007). It is possible that similar sexual dimorphism existed in fossil crocodilians, but if so, it is unlikely to be easily demonstrated.

A similar case was reported by Bonnan et al. (2008) who found very weak sexual dimorphism in femur shape in *A. mississippiensis*. Again, the detection of the dimorphism required a large sample size and *a priori* knowledge of sex, meaning it would be virtually undetectable in the fossil record.
ii) Pterosauria

Sexual dimorphism has been well documented in pterosaurs, representing some of the best defined instances of sexual dimorphism in archosaurs. Bennett (1992) demonstrated a well-defined bimodal size distribution in a very large sample of two species of *Pteranodon* from the Smoky Hill Chalk Member of the Niobrara Formation. He found support for two size classes in dimensions of the long bones and metacarpals, a less numerous larger class, and a smaller, more numerous class. He also found associated dimorphism in the size of the pelvic canal, and the size of the cranial crest. Individuals in the larger size class had relatively narrow pelvic canals and large crests, whereas the smaller size class had relatively large pelvic canals and small crests (Bennett, 1992). Furthermore, these size morphs are present in both species. The smaller morph, with a large pelvis and small crest is hypothesised to be female, with the pelvic canal proportioned to allow the passage of eggs, and the male morphs are interpreted as developing large crests via sexual selection. This study relied on a very large sample, with some 450 specimens contributing measurements (Bennet, 1992).

Strong evidence of sexual dimorphism in the pterosaur *Darwinopterus* was advocated following the discovery of an adult in direct association with an egg (Lu et al., 2011). Recovered from the Jurassic Tiaojishan Formation of Liaoning, China, the fossil allowed for the identification of the animal as female and, in turn, provided evidence of sexual dimorphism in *Darwinopterus*, and in pterosaurs as a whole (Lu et al., 2011). Similar to the situation in *Pteranodon*, the authors identified two morphs, with females having a smaller body size, a relatively large and less completely fused pelvis, and no cranial crest. These morphological differences would be recognisable on their own, as they were in *Pteranodon*, but the discovery of an egg in association with a putative female provided additional support to the interpretation that
these are sexual morphs, that the differences in pelvic canal dimensions are related to egg laying, and that the cranial crests of males are secondary sexual structures that likely functioned in signalling.

*Darwinopterus* provides a novel perspective on the bizarre, very large, bifurcated cranial crests observed on two adult specimens of *Nyctosaurus* (Bennett, 2003), a pterodactyloid wherein the three previously described specimens lacked crests. Bennett (2003) was reluctant to ascribe the crests to sexual dimorphism because no pterosaurs were then known to exhibit a presence/absence crest dimorphism. He suggested, instead, that the crest appears abruptly late in ontogeny. This interpretation was supported by observations of skeletal immaturity (incomplete fusion of cranial sutures and skeletal structures) in two of the three non-crested individuals, and by the appearance of crests late in ontogeny in some pterodactyloids from Solnhofen (Bennett, 2002, 2003). *Darwinopterus*, as the sister taxon to Pterodactyloidea (Lu et al., 2010), now provides a precedent of discrete crest dimorphism and may make it more plausible to apply a similar interpretation to the specimens of *Nyctosaurus*.

### iii) Dinosauria

Sexual dimorphism has long been a topic of interest in dinosaur research, and dinosaurs may best illustrate the difficulties of studying sexual dimorphism in the fossil record. Many partial reviews of the body of research on sexual dimorphism in dinosaurs are available, and Isles (2009) provided a particularly thorough summary of the subject in his discussion of dinosaur behaviour.

**Thyreophora:** Barden and Maidment (2011) reported sexual dimorphism in the stegosaur *Kentrosaurus aethiopicus*, based upon a shape analysis of a large sample of femora (n = 47; 37 complete) from the Upper Jurassic saurian beds of the Tendaguru Formation, Tanzania. They
found a statistically-significant separation of two groups based on the shape of the proximal end of the femur and the relative size of the greater trochanter (MANOVA, and two-tailed t-test, respectively). The groups were recognised visually and then tested by $k$-means clustering analysis (Barden and Maidment, 2011). That the dimorphism was an ontogenetic signal related to age or allometry was ruled out by limiting the sample to the upper, ‘adult’, end of a relatively complete ontogenetic series, and by finding no significant difference in size between the two groups (two-tailed t-test) (Barden and Maidment, 2011).

**Hadrosauria:** Dodson (1975) suggested that sexual dimorphism was present in in the crests of lambeosaurine hadrosaurs following a morphometric analysis in which he measured up to 48 cranial variables on 36 skulls representing twelve putative species. He calculated allometric coefficients, inspected clustering via bivariate plots with total skull length as the independent variable, and conducted a principal coordinates analysis of 15 crest measurements. Based on his results Dodson (1975) reduced taxonomic diversity to three species arrayed in two genera, namely *Lambeosaurus magnicristatus*, *Lambeosaurus lambei*, and *Corythosaurus casuarius*, and proposed the presence of sexual morphs, differentiated by the form of their cranial crests, for *L. lambei* and *C. casuarius*, and tentatively for *L. magnicristatus*. A study of a complete growth series (consisting of more than 20 individuals) by Evans (2003) found that the two adult morphs of *C. casuarius* were distinguishable by crest shape and supported the hypothesis that they represented sexual dimorphs. The variation between the morphs was largely attributed to differential patterns of growth of the nasals (Evans, 2003; Ryan and Evans, 2005). Sexual dimorphism was subsequently rejected, however, when it the morphs were found to be separated stratigraphically in the Dinosaur Park Formation (Evans et al., 2006). The morphological variation may instead be taxonomic, with the smaller morph comprised of individuals previously
attributed to *C. intermedius* (Evans et al., 2006). Dodson’s (1975) suggestion of sexual dimorphism in *L. magnicristatus* was found to be ‘inconclusive’ (Evans and Reisz, 2007), because the purported sexual difference in crest form was interpreted to be largely attributable to damaged and missing bone. Although Evans and Reisz (2007) did not refute sexual dimorphism in *L. lambei* directly, they cast some doubt on the interpretation.

**Ceratopsia**: Sexual dimorphism was first suggested for the neoceratopsian *Protoceratops andrewsi* by Gregory and Mook (1925) who noticed both long and broad skull morphs. Brown and Schlaikjer (1940) then identified variation in the overall robustness of the skulls throughout ontogeny and noted differences in some elements, including the relative development of the nasal horn, the fronto-parietal depression, and the breadth of the frill. Brown and Schlaikjer’s (1940) proposal of the presence of sexual dimorphism was based strictly on observation, and they admitted that their reasons were ‘tenuous’.

The possibility of sexual dimorphism in this taxon was pursued by Dodson (1976), who recorded 40 variables from 24 skulls of *P. andrewsi*. Dodson (1976) reported two distinct morphs of *P. andrewsi* and proposed they were sexual in nature; ‘male’ specimens were stated to have wider frills and jugal bones, greater skull height, more prominent nasal bosses and greater height at the nasals. The distinction of morphs was based primarily on bivariate plots of four cranial variables (width and height of the frill, height of the nasals, and postorbital width), and on a principal coordinates analysis of the multivariate data. Dodson (1976) identified eight specimens as being juveniles, seven as females, eight as males, and one as being indeterminate. This constitutes one of the better studies of sexual dimorphism in dinosaurs, but without additional supporting evidence (such as a female morph found with medullary bone or gravid with eggs) the conclusions remain far from unequivocal.
Tereschenko (2001) suggested a suite of 19 characters indicative of sex in the postcranial skeleton of *P. andrewsi*, and of protoceratopsids in general. These were determined by comparing specimens that had been assigned to ‘male’ or ‘female’ groups by use of three discriminatory criteria: 1) height of the spinous processes on thoracic vertebrae, 2) abdominal cavity volume, and 3) pelvis width. It should be noted that one of the species included as a protoceratopsid, *Udanoceratops*, is now considered to be a leptoceratopsid (Xu et al., 2002; Makovicky and Norrell, 2006; Chinnery and Horner, 2007; Ryan et al., 2012). Despite Tereschenko’s (2001) assignment of sex to ten specimens, the morphological variation was not documented quantitatively and it is difficult to accept the validity of these supposedly sexually diagnostic characters without some numerical or statistical evidence to support them. Still, the sample of ten *P. andrewsi* specimens accessioned in the collections of the Paleontological Institute of the Russian Academy of Sciences, in conjunction with the large sample at the American Museum of Natural History, represents a population sample that quite likely encompasses any existing sexual variation, and dimorphism may yet be borne out by a well-constructed study.

Lehman (1990) provided one of the most extensive assessments of morphological variation in ceratopsids, having examined material that was collected from a single bonebed in the Campanian-aged Aguja Formation of Texas, representing between ten and fifteen individuals of *Chasmosaurus mariscalensis* (now *Agujaceratops mariscalensis* [Lucas et al., 2006]). From this material, he described two ‘subtly different’ morphs differentiated by the form and orientation of the postorbital horncores. In the purported female morph, the horncores were curved, arose from the anterior margin of the orbit, and were directed upward and anterolaterally. The horns of the male morph were more erect, arose from the dorsal border of the orbit,
and were directed more vertically, with a narrower span when viewed anteriorly (Lehman, 1990). The angle of the horn relative to the frontal plane of the skull was the character that most readily differentiated the morphs, even for juvenile specimens. This discovery spurred a review of morphology and taxonomy in several chasmosaurines, leading Lehman (1990) to synonymise several species and assign sexual morphs to *Chasmosaurus canadensis*, *Pentaceratops sternbergii*, *Anchiceratops ornatus*, *Torosaurus latus*, and *Triceratops horridus*. He even suggested that the only known specimen of *Arrhinoceratops brachyops* exhibited a ‘male’ morphology. Very few of these purported morphs have been further investigated or supported (although see *Anchiceratops* below).

Long before Lehman (1990) reviewed the Chasmosaurinae, Charles Sternberg (1927) proposed gracile/robust sexual dimorphism in the postcranial skeleton of *Chasmosaurus belli*, based on two skeletons recovered from the Dinosaur Park Formation of Alberta. A subsequent review of the material by Mallon and Holmes (2006) found that the variation between the two specimens was more likely interspecific in nature, with the specimens belonging to *C. belli* and *C. russelli*, and that the stratigraphic segregation of the species in the Dinosaur Park Formation supported this notion.

Dodson (1990) documented the taxonomy and morphological variation of the centrosaurine ceratopsids *Monoclonius* and *Centrosaurus*. He suggested that the type of *Centrosaurus nasicornis* (AMNH 5351) is actually a female *Styracosaurus*, based on the tall, straight nasal horn, and that there are two morphs of *Centrosaurus*, a male morph characterised by “C. flexus” (AMNH 5239) and a slightly smaller, more gracile female morph characterised by *C. apertus*, “C. longirostris”, and “C. dawsoni”. “Centrosaurus nasicornis” has since been assigned to *C. apertus* (Ryan et al., 2008), rejecting the suggestion that it represents a female
Styracosaurus (an argument that is supported by the stratigraphic separation of these genera in the Dinosaur Park Formation [Ryan and Evans, 2005]), and although Dodson’s (1990) decision to synonymise all other species of Centrosaurus with C. apertus has since been supported (Ryan and Russell, 2005), his suggestion of sexual dimorphs within C. apertus was seemingly inadequately founded and has not been further supported (Ryan et al., 2001).

Mallon et al. (2011) investigated purported dimorphism in the skull of Anchiceratops, a chasmosaurine ceratopsid from the late Cretaceous of Alberta. The morphological variation in the genus had been attributed to two species (A. ornatus and A. longirostris) but it has also been suspected to represent sexual morphs of a single species. With 26 variables recorded from eight specimens, Mallon et al. (2011) utilised PCA, hierarchical clustering, and k-means clustering analyses to seek evidence of bimodal clustering within the range of variation. Their results did not return evidence of strong clustering and the variation was concluded to be most likely individual and taphonomic in nature. They also supported synonymy of the two species.

Pachycephalosauria: Sexual dimorphism was suggested for Stegoceras validum by Chapman et al. (1981), who reported evidence of dimorphism in skull dome morphology after conducting a principal components analysis on a suite of 15 cranial measurements. Despite their assertion of dimorphism, their results were not well-supported statistically, and their conclusions have been contested in the literature on the grounds that the majority of the specimens are immature or are attributable to other species (Goodwin and Horner, 2004; Schott et al., 2011).

Sauropodomorpha: Weishampel and Chapman (1990) conducted a morphometric analysis employing eleven variables to quantify form in thirty-three Plateosaurus femora from the Trossingen quarry in Germany. They retrieved two clusters, differentiated by the shape of the proximal and distal articular surfaces, as well as by the width of the Mm. caudofemoralis longus
attachment site. They concluded that the range of variation was insufficient to merit the recognition of two species, and instead attributed it to intraspecific variation, one aspect of which could be sexual dimorphism.

Robust and gracile sexual dimorphs were suggested for the Late Triassic prosauropod *Thecodontosaurus antiquus* by Benton et al. (2000). The hypothesis stemmed from the original reviews of the genus, made nearly a hundred years earlier, based upon material that was subsequently destroyed. In those reviews, two species were differentiated solely by ‘slight’ and ‘plump’ limb bones. The only remaining material of the robust species is a scapula and partial femur, and Benton et al. (2000) referred all known material to *T. antiquus*, incorporating whatever morphological variation is evident into the confines of one species, suggesting that the morphs are sexual in nature.

Sexual dimorphism was proposed as a possible explanation when Sander (2000) identified two histological patterns (type ‘A’ and type ‘B’) within a sample of *Barosaurus africanus* limb bones from the Tendaguru Formation of Tanzania. He suggested that a taxonomic difference was unlikely, although it could not be ruled out, and recognised that advocacy for sexual dimorphism was speculative. A subsequent review of African diplodocid material (Remes, 2006, 2007) revealed that there are in fact two diplodocid genera represented in the deposit, supporting the idea that the differences are taxonomic.

**Theropoda**: Sexual dimorphism has been reported several times for the small theropod *Coelophysis*. Raath (1990) invoked sexual dimorphism to explain the presence of purported gracile and robust morphs in a sample of more than 30 individuals of *Syntarsus rhodesiensis* (now *Coelophys rhodesiensis* [Bristowe and Raath, 2004]) from the Chitake River locality in Zimbabwe. Morphological variation in femoral head dimensions and in the prominence of
muscle scars was interpreted as being reflective of intraspecific variation attributable to sexual differences. A plot of maximum femoral head width against lesser trochanter width revealed three clusters – ‘immature’ individuals, ‘gracile’ adults (these two groups being separable by an increase in femoral head width), and ‘robust’ adults. The features of the robust morph are not expressed in smaller individuals, but rather appear only in ‘mature’ specimens, and include an increased width of the lesser trochanter (Raath, 1990). This was interpreted as being reflective of the onset of the robust morphology at or near the attainment of sexual maturity. The gracile morph was identified in four individuals that were of ‘adult’ size, although the mean sizes of the specimens were smaller than those of the robust morph (Raath, 1990). Without a method to assess ontogenetic stage independent of size, it is difficult to rule out that gracile ‘adults’ are not simply large juvenile specimens that have yet to attain sexual maturity, particularly when Raath (1990) states that the variation in muscle scarring of other elements is at least partially a function of age. As well, the case would be strengthened by statistical support, which is lacking. Although morphological variation is evident, it does not demonstrate a “clear and unmistakable instance of sexual dimorphism” (Raath, 1990). Rowe (1989) advocated that material of *Syntarsus kayentakatae* (now *Coelophysis kayentakatae* [Bristowe and Raath, 2004]) supported the hypothesis of a robust morph with hypertrophied muscle attachments and massive femora. The type specimen was identified as exhibiting the ‘robust’ condition, and referred material included two isolated ‘robust’ femoral heads from the type quarry, and one ‘gracile’ subadult housed in the collections of the Museum of Paleontology, University of California, Berkeley (Rowe, 1989).

In contrast to this, Colbert (1990) did not demonstrate dimorphism in femoral dimensions, despite assessing morphological variation and ontogenetic transformations in a sample of *Coelophysis bauri*. It should be noted that despite the claims by other authors that he
did so (Carpenter, 1990; Gay, 2005), Colbert (1990) did not explicitly report a sexual gracile/robust dimorphism in *C. bauri*. Rather he states that sexual dimorphism may be the only logical explanation to account for ‘puzzling’ differences in skull, neck, and forelimb size, and sacral spine fusion observed between two adult specimens, and makes it clear that his suggestion of sexual dimorphism is purely speculative. Additionally, Covey (1993) reported that the results of a principal components analysis of hind limb measurements, as well as an examination of skeletal material, did not reveal dimorphic groups in *C. bauri*, but found rather that hind limb proportions varied with ontogenetic stage.

The question of dimorphism in *Coelophysis* was revisited by Gay (2005), who reviewed *C. bauri* material and concluded that adults exhibit bimodal distributions of the lengths of the skull, humerus, radius, and metacarpal III, in a similar fashion to the situation in *C. rhodesiensis*, and that bimodality was also evident in the ratio of tibia length:femur length. However, none of the data were tested statistically (Gay, 2005), and the bimodality of the distributions is unclear. As a result, the case for sexual dimorphism in *Coelophysis* remains equivocal. Raath’s (1990) and Colbert’s (1990) studies of morphological variation in the genus are thorough, but result in different conclusions with respect to the probability of sexual dimorphism, and the data would benefit from statistical analysis.

A possible sexual difference was suggested for *Allosaurus fragilis* by Smith (1998), who conducted a thorough morphometric study of assigned material. Bimodal distributions were observed for dimensions of the dentary, as well as for weight-bearing structures such as the femoral head. Shapiro-Wilk tests, however, did not reveal these distributions to be significantly different from normal. Smith (1998) did not claim to have demonstrated dimorphism, nor did he attempt to assign sex to any specimens. He recognised that he could not distinguish juveniles by
any criterion other than size. Further study with additional specimens may yield more definitive results.

Sexual dimorphism was first proposed for *Tyrannosaurus rex* by Carpenter (1990), who proposed robust and gracile morphs after comparing six maxillae, six dentaries, two cervical series, and three ischia. Since then, this topic has been broached by more than a dozen authors employing varying lines of inquiry. It was most recently revisited by Larson (2008), who recorded measurements of 28 specimens of *T. rex*, two specimens of *Nanotyrannus*, and one of *Gorgosaurus*. He visually inspected the elements for a gracile or robust morphology, and examined clustering patterns on bivariate plots, interpreting them as evidence of sexual size dimorphs. The data for some elements (such as the femur and humerus) plotted in a way that accorded with the separations made upon visual inspection, and this was reported as being evidence of ‘clear results’ (Larson, 2008). Differences could not be explained by geographic or stratigraphic distribution and so sexual size dimorphism was advanced as the best explanation. The robust morph has been previously advocated (e.g. Carpenter, 1990) to be female, and the discovery of medullary bone in the femur of a robust morph *T. rex* (MOR 1125) (Schweitzer et al., 2008) led Larson (2008) to conclude that the robust morph is female.

iv) Aves

Both sexual dimorphism and sexual size dimorphism have been suggested for the early bird *Confuciusornis sanctus* from the Early Cretaceous of China (Martin et al., 1998; Peters and Peters, 2009). The large collection of specimens of *C. sanctus* yields a bimodal size distribution, and elongate rectrices are present in a subset (20%) of the population independent of size (Chiappe et al., 2008). Peters and Peters (2009) proposed that the body size distribution is
attributable to SSD, but argue that the tail feather size differential is unrelated to sex. They reported a sexual dimorphism ratio \( \left( \frac{M_{\text{larger}}}{M_{\text{smaller}}} - 1 \right) \) of 0.74, employing estimated body masses. The debate over the cause of the bimodal size distribution is unresolved (Chiappe et al., 2008, 2010; Peters and Peters, 2009, 2010), but remains a very interesting case that likely represents some form of sexual dimorphism in early birds.

2.2.7 Mammalia

i) Proboscidea

Sexual size dimorphism has been claimed for American mastodons (\textit{Mammut americanum}), Columbian mammoths (\textit{Mammuthus columbi}) and woolly mammoths (\textit{Mammuthus primigenius}), with male American mastodons reportedly averaging 1.15 to 1.25 times the size of females in linear dimensions, although I was not able to confirm these numbers (see Fisher, 2009; Smith and Fisher, 2011; and references therein). Sexual dimorphism in tusk dimensions is well documented, with females possessing shorter and more slender tusks, as is the case in extant African elephants. Clearly bimodal clustering is evident in plots of tusk circumference at the alveolar margin against age (as determined by cheek tooth eruption patterns) for American mastodons (Fisher, 2009). Plots of tusk circumference against distance from tip reveal differing growth trajectories between the sexes (Fisher, 2009). Sexual dimorphism is evident in the depth of the axial pulp cavity of the tusk, with males exhibiting deeper cavities than females in mastodons and mammoths (Smith, 2003; Fisher, 2009; Smith and Fisher, 2011). A principal components analysis of 21 American mastodon tusks based upon five anatomical variables sorted male and female specimens along the first PC axis by size, but the separation between the smallest males and largest females is not definitive and specimens could not be assigned to sex if
sex was not already known (Smith and Fisher, 2011). The inclusion of five ‘longitudinal’ variables (tusk circumference measured at a series of locations along the tusk, effectively providing ontogenetic data) spread the specimens over the second PC axis by age, and effectively increased the distinction between young males and mature females, suggesting that the PCA of these ten variables could be used to assign sex (Smith and Fisher, 2011). Postcranial sexual dimorphism in the form of the ischia and in the overall shape of the pelvis has been advocated for American mastodons (Fisher, 2009).

ii) Perissodactyla

Sexual dimorphism has been well studied in extinct perissodactyls, despite the comparatively small sample of extant perissodactyls to act as a guide.

Chalicotheriidae: Coombs (1975) reported size dimorphism in limb bones of the chalicothere Moropus from the Miocene Agate Spring quarries of the Harrison Formation, Nebraska. Coombs (1975) studied distributions of linear dimensions recorded from various skeletal elements, in particular the lengths of the radius (n = 17) and tibia (n = 16), and found that probability curves of element length yielded a bimodal distribution. That the groups represented two ontogenetic stages was ruled out by the presence of mature and immature individuals within both groups. Other skeletal differences were attributed to individual variation, or to differing allometric growth between the sexes (Coombs, 1975). Previous authors had considered the two groups to be different species. Coombs (1975) considered the two groups to be different sexes, despite there being no evidence for a difference in pelvic dimensions, and synonymised the smaller Moropus petersoni with M. elatus. She also suggested that sexual dimorphism is likely present in other, or perhaps all, chalicothere species, providing several examples of morphologically similar species.
that differ only in size, as well as examples of observed size classes within known species (Coombs, 1975).

**Brontotheriidae**: Sexual dimorphism in the canines and horns of brontotheres (larger and more robust in ‘males’) was documented by Osborn in 1896 and has subsequently been corroborated (Scott, 1945; Mihlbachler, 2011). Most recently, Mihlbachler (2011) investigated sexual dimorphism in brontothere canines by calculating coefficients of variation (CV, defined as standard deviation/mean x 100) to analyse patterns of size variation, following the logic that, in mammals, only secondary sexual traits typically have CV values greater than 10. He compared the CV’s of upper and lower canine crown diameters with 13 other craniodental variables for 17 brontotheriid and 1 brontotheroid species, and in 12 of the taxa found CV’s that were more than two standard deviations greater than the non-canine craniodental variables. The most likely explanation was deemed to be sexual dimorphism in canine size (Mihlbachler, 2011). Furthermore, Mihlbachler (2011) suggested that canine sexual dimorphism evolved twice within the Brontotheriidae, and that it is closely associated with the evolution of dimorphic frontal horns.

**Rhinocerotidae**: Sexual dimorphism has been very well established for extinct rhinoceroses, due in large part to similarly dimorphic features in extant rhinos such as the tusk-like lower second incisors (Dinerstein, 1991). A review of sexual dimorphism in fossil rhinos was assembled by Chen et al. (2010). Osborn proposed, but did not demonstrate, sexual dimorphism in *Teleoceras fossiger* (1898) and in the genus *Aceratherium* (1903), with males stated to possess larger nasal horn bosses and larger lower ‘canines’ (which were misidentified lower second incisors). This proposal was borne out eight decades later when Voorhies and Stover (1978) reported fetal
remains inside an articulated skeleton of the Miocene rhinocerotid *Teleoceras major*, corroborating the small-tusked morph as female for that genus.

Mead (2000) further studied sexual dimorphism and sexual size dimorphism in *Teleoceras major*. A mass death assemblage in the Ashfall Fossil Beds of Antelope County, Nebraska provided an extremely rare large sample of 35 articulated skeletons (24 female, 11 male), identified as adults by their degree of epiphyseal fusion. Fifty-one measurements were recorded from the specimens and these revealed statistically significant dimorphism in the skull and postcrania (Mead, 2000). The lower second incisor (i2), or tusk, was particularly dimorphic (with a male/female ratio of 1.73), but significant sexual differences were also found for skull and mandible length and transoccipital width. The limb bones also showed significant dimorphism in length and cross-sectional area, with males being larger than females. Furthermore, limb bones were found to grow for a longer duration in males than females, with epiphyseal fusion occurring at a later age (as determined by dental eruption and wear) and larger body size (Mead, 2000). Body mass estimates varied widely depending on which methods and which bones were used to calculate them, and were not statistically supported, but do generally indicate a greater body mass for males, as suggested by skull and limb dimorphism (Mead, 2000). Mihlbachler (2005) later corroborated some of these findings by demonstrating the presence of size dimorphism in some postcranial dimensions and in i2 form in *Teleoceros proterum*, and concluded that male tusks erupted later in ontogeny and continued to grow after female tusks ceased growing. Mihlbachler (2005) also reported significant sexual dimorphism in incisor form in another Miocene rhinocerotid, *Aphelops malacorhinus*, with male tusk dimensions being 60%-100% greater in size, on average, than those of females. This study relied on measurements obtained from a relatively large sample of unsexed adult limb bones and sexed
Mihlbachler (2007) reported sexual dimorphism in the skull of the early Miocene rhinoceros *Menoceras arikarense*, in an assemblage collected from Agate Springs National Monument, Nebraska. Mihlbachler (2007) recorded 66 measurements from the cranium, mandible and postcranium, and assessed dimorphism by comparing CV values for the variables, by using the Shapiro-Wilk test to detect non-normal univariate distributions, and by calculating a coefficient of bimodality to indicate possible bimodal or polymodal distributions. Five cranial variables were identified as having CV’s greater than 10, four of the variables exhibited non-normal distributions (at a p-value of < 0.1), and five variables were identified as being potentially bimodal. The nasal bone was identified as the most dimorphic component of the skull, with molar row length and zygomatic width also showing potential dimorphism. The lower incisors were also found to be highly dimorphic and were identified as sexually diagnostic. Purported males had higher values for the nasal region and skull width, but dental and skull length variables showed less difference between the sexes. After separating the sample into two groups based on nasal thickness and width, t-tests revealed significant differences between the ‘sexes’ for those dimensions, as well as for occipital width, orbital breadth, and zygomatic width (Mihlbachler, 2007). No strong evidence was found for size dimorphism in the postcranial skeleton of *Menoceras*.

Chen et al. (2010) demonstrated sexual dimorphism for the Asian rhinocerotid *Chilotherium wimani* by conducting a morphometric analysis using a suite of cranial measurements taken from 74 adult skulls. Dimorphism in the lower second incisors (i2) (tusks) allowed the assignment of sex to all but one skull *a priori*, permitting the subsequent
identification of several other dimorphic cranial characters such as the width of the mastoid processes and the height of the occipital surface. However, despite statistically significant sexual differences, these additional dimorphic characters likely would not have been detectable in a non-sexed sample as they have male/female ratios of 1.06 and 1.07, respectively.

Deng (2005) proposed sexual dimorphism in the elasmothere rhinocerotid *Iranotherium morgana*, with ‘males’ exhibiting more massive skulls, a larger nasal horn, and larger zygomas bearing hemispherical rugosities that are absent in ‘females’. This was based on the examination of only two skulls plus a mandible from the upper Miocene Liushu Formation in the Linxia Basin, China, and published information about a skull from Maragha, Iran.

Borsuk-Bialynicka (1973) proposed the presence of sexual dimorphism in the Pleistocene woolly rhinoceros *Coelodonta antiquitatis*, based on the recognition of modest bimodality of some cranial dimensions (including width of the occiput, maximum skull length, width at zygomatic arches, orbit-nuchal crest length, and orbit-nares length) in a sample of 15 skulls from Poland. However, the CV’s of these dimensions were generally low (<9). Based on these cranial dimensions, three skulls in the sample were suggested to be male and three to be female (Borsuk-Bialynicka, 1973).

**Indricotheriinae:** Sexual dimorphism has been postulated for indricotheres, although no strong evidence is available. Antoine et al. (2004) suggested the lower canines of *Paraceratherium bugtiense* may be dimorphic in form, although, unlike some rhinocerotids, seemingly not in length. This, however, was based on observations of only two specimens. More tenuously still, Fortelius and Kappelman (1993) suggested that *Indricotherium* exhibited sexual size dimorphism in body mass based on perceived weak bimodality in body mass estimates. Both suggestions would require additional material and work to be substantiated.
**Equidae:** Modern equids are subtly dimorphic in body size (van Asperen, 2010) and in canine form, with adult males possessing small canine teeth that are typically absent or reduced in females (Easley, 2004). Gingerich (1981b) investigated dimorphism in the early equid genus *Hyracotherium*. Using a sample of 24 specimens of *Hyracotherium tapirinum* from the latest Wasatchian, lower Huerfano Formation of Colorado, he found elevated CV’s in dimensions of the canines relative to other craniodental variables, and also reported size dimorphism based on a male/female skull length ratio of 1.15. Sample sizes for this study were extremely low, however, with less than five lower or upper canines from each sex and only two skulls from each sex available for the size estimate. Similar dimorphism was also reported for *H. grangeri* (Gingerich, 1981b). Again, *a priori* knowledge of canine sexual dimorphism in equids was essential to this study; it permitted the tenuous detection of size dimorphism, and provides reasonable grounds for the assignment of sex.

iii) Artiodactyla

As for perissodactyls, sexual dimorphism is rampant within certain groups of artiodactyls. In the fossil record, sexual dimorphism has been reported for numerous species across a wide taxonomic range, and sexual dimorphism in cranial appendages is considered to be plesiomorphic for pectorans (Janis, 1990).

**Tayassuidae:** Extant peccaries are slightly sexually dimorphic in the form of their canine tusks, and dimorphic canines are considered to be primitive for tayassuids (Wright, 1993). Drawing from the extant peccary model, Wright (1993) used canine size to assign sex to skulls of fifteen species of extinct peccary, ranging from the Miocene to recent, and assessed the presence of sexual dimorphism employing bivariate plots, relative frequency histograms, and probability
plots of basal dimensions of the canines and lateral thickness of the zygomatic arch. In several species canine size is clearly bimodal and dimorphism is well-defined, but for others sample sizes are quite small and dimorphism, although quite likely present given the phylogenetic context, would not be readily detectable without *a priori* knowledge of canine dimorphism.  

**Suidae:** In an extensive review of African Plio-Pleistocene suids, Harris and White (1979) reported significant sexual dimorphism in cranial size and upper canine form, as well as additional secondary sexual characters including knobs on the zygoma, differing development of the supracrinal flange and differing degrees of rugosity of the orbital rim, for several species of fossil suid. Material appears to have been sexed by comparison with extant dimorphic characters and the sexes then compared directly as opposed to being resolved statistically.

Geraads (2004) assessed sexual dimorphism in the extant bushpig (*Potamochoerus*) in order to compare it with the fossil suid *Kolpochoerus phacochoeroides* from the Plio-Pleistocene of Morocco. From this comparative model, Geraads (2004) suggested that *K. phacochoeroides* males possessed slightly larger skulls overall than did females, and that dimorphism is most prominent in the size of the canine and supracanine flange. His sample consisted of only two complete male skulls, one partial female skull with a canine and supracanine flange, several mandibles and tooth-rows, and more than 200 complete isolated teeth (Geraads, 2004).

**Anthracotheriidae:** Similar to many other mammalian groups, anthracotheres exhibited marked sexual dimorphism in their teeth. All anthracotheriid subfamilies (Anthracotheriinae, Microbunodontinae, and Bothriodontinae) exhibited sexual dimorphism in the form of their incisors and canines, with males possessing proportionally larger canines and longer sagittal crests (Lihoreau et al. 2004, 2007; Lihoreau and Ducrocq, 2007). Pickford (2006) reported sexual dimorphism in *Libycosaurus*, an anthracothere from the Miocene of northern Africa, with
bivariate plots of lower canines revealing two distinct clusters. Male specimens with large canines possessed deep mandibular symphyseal areas, whereas female mandibles with small canines had shallow symphyseal areas. It seems that dimorphism was largely established by direct comparison of fossil specimens and sex was assigned by inferences from extant ungulates, with males expected to exhibit larger canines. However, see Lihoreau (2003) and Pickford (2009) for examples of the challenges involved in establishing sexual dimorphism in anthracothere.

**Hippopotamidae**: The extant *Hippopotamus amphibius* is sexually dimorphic in the size of the lower canines, with males possessing significantly larger canines than do females (Hooijer, 1950, reproduced by Visser, 2008). Visser (2008) reported similar dimorphism in extinct species of the hipposomatid *Hexaprotodon*. This conclusion was based on the clear segregation of two clusters in a bivariate plot of canine size, whereas bivariate plots of all other dental and cranial characters yielded no distinct clustering. Weston (2003) reported sexual dimorphism in shape, not size, for the extant pygmy hippo, *Hexaprotodon liberiensis*, which may explain why no further cranial dimorphism was detected in the size-based bivariate plots assembled by Visser (2008).

**Protoceratidae**: Sexual dimorphism is the status quo in this clade of artiodactyls, with males possessing elaborate cranial outgrowths and large canines (Prothero and Ludtke, 2007). Sexual dimorphism was first described for *Protoceras celer* in 1892 by Osborn and Wortman, based on a comparison of five skulls from the lower Miocene White River beds. The assignment of sex was largely arbitrary, but likely based on observations of ornamented males in extant artiodactyls. ‘Males’ were recognised as having bony protuberances on the parietals and frontals, vertical plates on the frontals and maxillaries, and large, postero-laterally projecting canines. In contrast ‘females’ exhibit much smaller canines and smaller protuberances that occur only on the
parietals (Osborn and Wortman, 1892). This dimorphism was more firmly established by Patton and Taylor (1973) who studied a larger sample (up to 17 individuals) and found very high CV’s for the length and width of the upper canines in *P. celer* (CV = 44.82 and 27.32, respectively). Recognition of this manifestation of sexual dimorphism, with horns and canines being absent or significantly smaller in females, allowed the subsequent identification of sexual morphs in numerous related species (or, for example, the identification of the only skull of a species as being that of a female [Webb et al., 2003]) with little perceived need to demonstrate or quantify the differences.

**Camelidae**: Hibbard and Riggs (1949) proposed sexual dimorphism in the fossil giant camel *Gigantocamelus spatulus* from the Upper Pliocene Keefe Canyon deposits of Kansas. By comparing skulls and teeth, the ‘male’ morph was suggested to be larger overall, with relatively larger teeth, particularly the laterally-flaring canines. In comparison, the relatively smaller ‘female’ morph possesses smaller canines and upper premolars, and may lack p1 (see Breyer, 1976).

Honey (2007) identified sexual morphs in the fossil camelid genus *Protolabis*. Using sexual differences in the pelves and dentition of extant dromedaries as a guide, Honey (2007) attempted to assign sex to two samples of pelves, one from the Santa Fe group of New Mexico, and the other from the Miocene Barstow Formation of California, in an attempt to test whether the genera *Michenia* and *Protolabis* were valid independent taxa or sexual dimorphs of the same species. Despite identifying all *Michenia* pelves as being female, and most *Protolabis* pelves as being male, Honey concluded that the taxonomic distinction was valid, largely due to the recognition of male and female pelves within *Protolabis*. Sexes were distinguished by the size of the I3 and both canines (larger, more spike-like in males), and by six characteristics of the pelvis,
including the development of the caudal dorsal iliac spine (absent or extremely weakly developed in females) (Honey, 2007).

**Moschidae:** Extant musk deer are sexually dimorphic, with males possessing dagger-like upper canines, and one species, *Moschus chrysogaster*, reported to exhibit female-biased SSD (Prothero, 2007; Sanchez and Morales, 2008). Sanchez and Morales (2008) reported sexual dimorphism for the fossil species *Micromeryx azanzae* from the upper Miocene of Spain. A morphometric analysis revealed two groupings in the dimensions of the molariform teeth, p4 - m3 and M1 - M3, with significant differences being found in the breadth of these teeth. A male skull (identified by its enlarged canines) clustered with the smaller individuals, leading the authors to suggest that males were smaller than females, similar to the situation in *M. chrysogaster*, despite the skull belonging to a juvenile male lacking a fully erupted dentition. Tibiae were also found to separate into two significantly different clusters on the basis of the distal antero-posterior diameter, with the larger size class purported to represent females (Sanchez and Morales, 2008).

**Antilocapridae:** Webb (1973) reported sexual dimorphism in horn morphology for two genera of extinct antilocaprines. Both possess horncores that split into three antero-posteriorly arranged tines (Davis, 2007). In *Hexameryx*, *H. elmorei* was synonymised with *H. simpsoni* because it was concluded that they represent male (*H. elmorei*) and female (*H. simpsoni*) sexual morphs of a single species (Webb, 1973). The sexes were differentiated as a result of bimodal clustering of basal horn dimensions, although there was no associated clustering of molar dimensions (Webb, 1973). Qualitative differences in the relative arrangement of the horn tines and dimensions of the supraorbital foramen further distinguished the two morphs. In *Hexobelomeryx*, the median tine of the horn exhibits two structural variants; sharing a common shaft and supposedly common
sheath with the anterior tine in purported females, and with the posterior tine in purported males (Webb, 1973).

**Palaeomerycidae**: Palaeomerycids bore non-deciduous, unsheathed cranial appendages, similar to, but different from the antlers and horns of cervids and bovids. These are discretely dimorphic in most species, and presumed males bore paired, unbranched supraorbital appendages, and, in several species, also bore a median occipital appendage (Prothero and Liter, 2007). The presumed males also bore large, sabre-like upper canines in several primitive taxa (Prothero and Liter, 2007). One taxon, *Aletomeryx*, appears to have had short cranial appendages in both sexes (Prothero and Liter, 2007).

*Prolibytherium* is an elaborately ornamented pecoran from the lower Miocene of Libya and Egypt (Sanchez et al., 2010) of uncertain phylogenetic position. Prothero and Liter (2007) and Solounias (2007) considered it to be a palaeomerycid, whereas Sanchez et al. (2010) tentatively attributed it to the Climacoceridae, the basal-most clade in the Giraffoidea. Sanchez et al. (2010) proposed sexual dimorphism in the cranial appendages of *P. magnieri* based on the inspection of existing, new, and referred material. The purported male morph carries large, ‘butterfly wing’ cranial structures that are diagnostic for the genus, whereas purported females are thought to have possessed a similar, X-shaped set of four appendages without the shield-like webbing that fills out the wings in males (Sanchez et al., 2010). Both sexes possess a basic strut-like framework, but only in males does bone extend laterally from the struts into broad ‘wings’. Additional fossil material is required to further evaluate this hypothesis of sexual dimorphism.

**Bovidae**: The bovid fossil record is essentially one of dimorphic sexes; hornlessness is considered to be the plesiomorphic condition for female bovids (Janis 1982; Solounias, 2007), with horns in females having arisen independently multiple times (Roberts, 1996; Stankowich
49

and Caro, 2009). Supporting this assertion is *Eotragus*, the earliest definitive bovid, which is known from both horned and hornless skulls dating to the end of the early Miocene (Janis, 1982).

Like many taxa already described, assessments of dimorphism for many bovids depend, at least in part, on an understanding of dimorphism patterns in extant species. For example, Drees (2005) documented sexual dimorphism in *Bison priscus* from a Weichselian-age (Pleistocene) faunal assemblage dredged from the North Sea. Study of extant *Bison bison* and *Bison bonasus* material revealed that the metacarpals are strongly dimorphic, with the greatest difference manifesting in the proximal and mid-shaft transverse diameters. Drees (2005) compiled a suite of seven measurements from eighteen metacarpals and performed a cluster analysis and principal components analysis. The cluster analysis recovered two distinct groups and the PCA separated these groups on the first principal component axis, supporting the hypothesis that the clustering reflected size differences between the two groups (Drees, 2005). Drees (2005) also employed these findings to suggest that the species *Bison schoetensacki* may have been erected for female specimens of *B. priscus*.

*Cervidae*: The same can be said for cervids as for bovids, except that female ‘hornedness’ evolved only once, in *Rangifer* (Roberts, 1996). As a result, the entire cervid fossil record, until proven otherwise, should be considered to be sexually dimorphic, at least with respect to cranial structures (antlers). In ungulates in general, sexual size dimorphism is thought to have arisen as a result of species moving into open habitats, where patchy resource distributions led to clustering and therefore heightened local female densities, increasing the capacity for the evolution of polygynous mating systems (Perez-Barberia et al., 2002). As a result, there is at least theoretical support for an *a priori* expectation of SSD in many ungulates from the Miocene or younger (Perez-Barberia et al., 2002).
iv) Dinocerata
Uintatheres are considered to be dimorphic in body size, relative canine tusk size, and in the size of cranial horns and flanges (Marsh, 1885; Dorr, 1958; Wheeler, 1961). The larger, more robust morph carries relatively larger tusks and horns and is presumed to be male by analogy with sexually dimorphic extant ungulates (Wheeler, 1961). Measurement data have provided support for the suggestion of dimorphism, but these have not yet been statistically supported (Dorr, 1958).

v) Mesonychia
O’Leary et al. (2000) proposed sexual dimorphism in the mesonychian Ankalagon saurognathus, after comparing a previously undescribed partial mandible with the larger holotype specimen. The smaller new specimen was considered to be very close to maturity, based on the state of tooth eruption and low degree of tooth wear. Comparison between the specimens revealed small differences in cheek teeth dimensions (O’Leary et al., 2000). This variation was found to fall within ranges of intraspecific variation in adult dentition for extant carnivorans. However, canine length and width ratios for the Ankalagon specimens revealed high variation and were interpreted to reflect sexual dimorphism (O’Leary et al., 2000). Additionally, the depth of the dentary shows proportional differences between the specimens (O’Leary et al., 2000). Sexual dimorphism can only be tentatively accepted for this species, and awaits corroboration based upon additional material.
vi) Cetacea

**Odontoceti:** A fascinating example of sexual dimorphism in fossil cetaceans is evident in the beaked whales (Ziphiidae). In extant members of the clade, adult males bear large mandibular tusks that are used in male-male combat, whereas female tusks are much smaller and typically do not erupt (Dalebout et al., 2008). A study of the 14 extant species of *Mesoplodon* found that sexual selection on the form of male tusks, and perhaps selection for species recognition cues, has likely played an important role in the radiation of the genus since the Miocene (Dalebout et al., 2008). Males of several species also develop heavily ossified bones in the rostrum (vomer and/or mesethmoid) which grow to fill the mesorostral groove (Bianucci et al., 2008). Similar dimorphism in rostrum form was identified in a large sample of Miocene fossil ziphiid skulls dredged from the sea floor off South Africa, and was recognisable despite the preferential preservation of the more massive male skulls (Bianucci et al., 2008).

Sexual dimorphism in the anterior portion of the mandible was described for a sample of eight specimens of the beaked whale *Messapicetus* from the Miocene Pisco Formation of Peru (Lambert et al., 2010). Purported female specimens possess smaller tusks, as revealed by narrower tusk alveoli (Lambert et al., 2010). Associated with the larger tusks of purported males is an enlarged anteromedian protuberance that projects rostrally between the tusks, from the apex of the dentary, as well as a thickened and dorsally-raised buttress posterior to the tusks that receives the apex of the rostrum when the mouth is closed, similar to the morphology evident in the extant *Ziphius cavirostris* (Lambert et al., 2010). These structures are reduced or absent in purported females (Lambert et al., 2010).
vii) Carnivora

Ursoidea: Kurtén (1969) reported sexual dimorphism in two European populations of the Pleistocene cave bear (Ursus spelaeus), as well as in the Miocene dog-bear Hemicynon teilhardi. Average skull length was found to be 13% larger in male cave bears than in females, and canine width was found to be 25% larger in males. Cheek teeth were less dimorphic, typically being between 5% and 10% larger in males (Kurtén, 1969). How sex was assigned initially was not stated, but the fossil taxa were plotted alongside dimorphism ratios of extant brown bears and polar bears, with the fossil taxa exhibiting strong concordance with the extant data. Patterns of dimorphism were generally similar for Hemicynon, with males being approximately 20% larger in skull and canine size.

Caniformia and Feliformia: Van Valkenburgh and Sacco (2002) investigated sexual dimorphism in the skulls and teeth of the Pleistocene dire wolf, Canis dirus, and the sabertooth cat, Smilodon fatalis. They recorded cranial and dental measurements and inferred the presence of sexual dimorphism from the data, using three different methods: 1) plotting calculated canine CV values onto a regression of sexual dimorphism against CV for extant species, 2) the ‘mean method’, wherein the sample was divided about the mean and the ratio of the subsamples was taken as an estimate of sexual dimorphism, and 3) a finite mixture analysis, which determines the maximum separation between male and female means that could be contained in a unimodal sample (Van Valkenburgh and Sacco, 2002). The shortcomings and strengths of each of these methods as estimators of sexual dimorphism were previously discussed by Plavcan (1994). Both fossil species showed weak dimorphism in skull length and carnassial tooth length, with the larger morph assessed as male by comparison with extant canids and felids. The greatest level of dimorphism was displayed by the canine teeth, with purported male C. dirus canines being 11-
12% larger than those of purported females, and those of male *S. fatalis* being 10-11% larger than those of females.

Following the methods of Van Valkenburgh and Sacco (2002), Anton et al. (2004) and Salesa et al. (2006) reported indices of craniodental sexual dimorphism for the Miocene sabre-toothed cats *Machairodus aphanistus* and *Paramachairodus ogygia*, respectively. The degree of dimorphism documented for *M. aphanistus* is on par with that observed in lions and leopards, the most dimorphic of extant cats. *P. ogygia*, however, falls in the range of dimorphism observed in extant cheetahs and lynx.

Samuels and Binder (2009) estimated sexual size dimorphism in the American lion (*Panthera atrox*) by regressing mandible length against percent canine pulp cavity closure (used as an indicator of relative age). Noting a bimodal distribution, two subsamples were selected above and below the line of best fit, and identified as males and females, respectively. Model testing (Akaike’s Information Criterion (AIC) analysis) revealed that plotting the data as two subsamples with different means explained significantly more of the population variation than plotting it as a coherent sample with a single mean, and resulted in a significant increase in the value of the correlation coefficient, $R^2$. The study used a sexed sample of African lion (*Panthera leo*) specimens, known to be sexually dimorphic, as a proof of concept. Essentially the use of the ‘mean method’ described above in reference to the work of Van Valkenburgh and Sacco (2002), depends heavily on comparison with *P. leo*, and would be highly spurious if the authors did not have such a strong *a priori* assumption as to the cause of the separation in the data. The statistical support gained by dividing a visibly bimodal sample in two and demonstrating a significant difference of means does not contribute to understanding the cause of the separation and should not be taken as evidence that the clusters necessarily reflect sexes; it simply supports
a difference in means. This method of estimation is only reliable when sexual dimorphism is strong, with a ratio greater than 1.20 (Plavcan, 1994).

**Pinnipedinormpha**: Sexual dimorphism has been described for the fossil desmatophocid genera *Allodesmus* and *Desmatophoca* from the Miocene Astoria Formation of Oregon (Deméré and Berta, 2002). Although not demonstrated statistically, purported sexual differences include larger skull size and canine size in males, as well as larger and more rugose sagittal and nuchal crests (Barnes and Hirota, 1994; Deméré and Berta, 2002; and see Mitchell, 1966). In some instances, the discovery of an associated baculum aids in the attribution of sex (Barnes and Hirota, 1994). Similar sexual dimorphism in sagittal and nuchal crest length, as well as a greater rostral width at the canines in males, has been suggested for the coeval pinnipiform *Pteronarctos* (Berta, 1994). Again, however, none of the differences have been demonstrated quantitatively.

viii) Primates

Sexual dimorphism in canine size is common, although not universal, in extant primates, and is known from multiple occurrences in the primate fossil record.

**Strepsirrhini**: Gingerich (1981a) studied sexual dimorphism in the European Eocene primate *Adapis*, employing a sample of eight skulls and 33 dental specimens (which included at least the upper or lower canines and first molar) of *Adapis magnus*, and 12 skulls and 41 dental specimens of *A. parisiensis*. The two species can be differentiated on the basis of M1 size – *A. magnus* is larger and the two species do not have overlapping size ranges (Gingerich, 1981a). Both species were found to exhibit sexual size dimorphism, with clusters of large and small individuals as revealed by both cranial length and breadth. Plots of the cranial measurements reveal intraspecific scaling coefficients greater than the interspecific coefficients, supporting the
hypothesis that the observed variation is indeed intraspecific (Gingerich, 1981a). The ratios of male skull length to female skull length are modest at 1.16 and 1.13 for *A. magnus* and *A. parisiensis*, respectively (Gingerich, 1981a). Male skulls were also found to be relatively broader, with wider zygomatic arches, and to have stronger sagittal and nuchal crests (Gingerich, 1981a). Canine dimorphism is also modest, with multiple methods of estimation yielding male to female canine size ratios of roughly 1.2 and 1.15 for *A. magnus* and *A. parisiensis*, respectively. The degree of canine dimorphism was not particularly greater than the degree of cranial dimorphism, suggesting that the canines themselves may not have been under strong sexual selection, or that cranial length and canine size are correlated. Similar calculations and plots made using measurements taken from extant primates were used as a model to substantiate the methods and conclusions (Gingerich, 1981a).

**Anthropoidea:** Yuerong et al. (1989) studied craniodental material belonging to the early hominoid *Laccopithecus robustus*, from the Miocene of Yunnan Province, China. They reported sexual dimorphism in dimensions of the canine teeth, as well as the upper and lower second molars, based on elevated CV’s and bimodal clustering in bivariate plots of measured variables. Fleagle et al. (1980) reported sexual dimorphism in three species of Oligocene primate from the Jebel el Qatrani Formation in the Fayum Province, Egypt. Fleagle et al. (1980) reported bimodal distributions of dimensions relating to the lower canines and premolars, despite low variability in molar dimensions, for the hominoids *Aegyptopithecus zeuxis* and *Propliopithecus chirobates*, and the parapithecid *Apidium phiomense*, although the plots provided do not clearly demonstrate these distributions. Fleagle et al. (1980) also proposed sexual size dimorphism for *A. zeuxis* and *A. phiomense*, based upon elevated CV’s of mandibular depth that fall within the range of CV’s of extant primate species that exhibit male-biased SSD.
Hominidae: Sexual dimorphism has been reported numerous times for *Australopithecus afarensis* (e.g. Leutenegger and Shell, 1988; McHenry, 1991; Lockwood et al., 1996; Reno et al., 2003, 2005; Lee, 2005; Plavcan et al., 2005; Scott and Stroik, 2006; Gordon et al., 2008). The reason it is so heavily studied is because of the perceived implications that the degree of SSD holds for hypotheses relating to life history and mating strategies in these hominoids. Several methods have been employed, with varying results.

Lockwood et al. (1996) reported sexual dimorphism in *A. afarensis* greater in magnitude than that seen in modern humans and chimpanzees, and that approached the sexual dimorphism observed in gorillas and orangutans. Fossil material consisted of a collection of 17 mandibles, five proximal femora, and three humeri, and they employed bootstrapping to simulate random sampling of comparable samples from the extant taxa. Max/min ratios and CV’s were used as measures of size variation (Lockwood et al., 1996).

Gordon et al. (2008) employed similar, but more resilient, methods to study variation in postcranial dimensions (femur, tibia, humerus, and radius), and found that postcranial dimorphism in *A. afarensis* is similar to that observed in extant gorillas and orangutans, and significantly greater than in modern humans and chimpanzees (Gordon et al., 2008).

As described, these studies employ a comparative method that involves comparing measurements of *A. afarensis* elements with similar measurements of extant hominoids, typically modern humans, chimpanzees, gorillas, and orangutans. Bootstrapping is used as a resampling method to generate multiple random samples of the extant material at sample sizes equivalent to those obtained from the fossil material. The level of dimorphism in *A. afarensis* is then estimated relative to the levels of dimorphism in the extant taxa, and is expressed as being greater than in humans, but less than in gorillas, for example. Unfortunately this method is only applicable to
those vertebrate fossil taxa that have living close relatives that could be used to develop meaningful comparative datasets. Because of this, it could not be used for most dinosaurs including ceratopsids.

2.3 Discussion

This review demonstrates that cases of sexual dimorphism are of widespread occurrence in the vertebrate fossil record, and that it can occur with some degree of frequency. However, it is also clear that many factors affect how confidently we can attribute sexual dimorphism to a fossil species. In studying Tables 2.1 - 2.4, some interesting trends can be observed.

Of the 25 cases that I considered to be the strongest demonstrations of sexual dimorphism, all but two involve some means of recognising sex (the exceptions being *Kentrosaurus* [Barden and Maidment, 2011] and *Pteranodon* [Bennett, 1992]). Several times it is simply a matter of closely related living taxa providing a guide by which sex can be attributed to fossil specimens with reasonable confidence (e.g. claspers in male chondrichthyans, or larger canines in male felids). On other occasions it is the result of an exceptional circumstance, such as an egg-adult association in *Darwinopterus* confirming the female morph, or a collection of mating pairs of *Allaeochelys* turtles confirming both sexes. Either way though, it is clear that without some method of confirming that the two morphs are indeed sexual in nature, it can be very hard to confidently make that claim regardless of how strong the morphological distinction is. As the exceptions, the strength of Bennett’s (1992) and Barden and Maidment’s (2011) conclusions lies in the elimination of stratigraphy, ontogeny and taxonomy as confounding variables, making sex a defensible conclusion - even for *Kentrosaurus*, for which the traits studied are not as obviously sexual as, say, pelvic dimensions.
The results also show that when it comes to confidently labelling dimorphism as sexual in nature, the value of the extant model cannot be overstated. Of the 25 strongest demonstrations of dimorphism, only four were not guided or informed in some way by an understanding of dimorphism in living related taxa (and most often by direct comparison). In contrast, of the 21 cases of sexual dimorphism labelled as having ‘Poor confidence’, only four involved comparisons with extant species to guide the methods or inform the results.

2.3.1 Methods

Although it is useful to identify the strongest examples of sexual dimorphism, it is also worthwhile to look at the studies with the most effective methods. Table 2.5 comprises a list of those studies that employed thorough methods, and that could therefore serve as useful templates for investigating sexual dimorphism in other fossil taxa. These studies present a range of methods for investigating a variety of possible sample types, including large samples with size-based variation (Pteranodon, pachypleurosaurs, Allosaurus), shape analyses and growth studies of specific features (Kentrosaurus and proboscideans), samples with an expectation of sexual dimorphism (tayassuids, rhinocerotids, Bison, carnivores), and resampling methods for bolstering small sample sizes for comparative purposes (Australopithecus). Methods of assessing variation that are effective and common to many of these studies are: examining frequency histograms and bivariate plots, calculating coefficients of variation (CV), testing for deviations from normality with Shapiro-Wilk tests, and conducting principal components analyses (PCA).

These methods are well tailored to assessing an unsexed dataset, and will be tested for their applicability in this thesis. Less frequently, but also successfully, landmark-based geometric morphometrics have been used. Testing observed groupings by cluster analysis (hierarchical or
$k$-means) or discriminant function analysis (DFA) also provides more objective means to support visually detected clustering in multivariate datasets. These methods have been used in some of the more recent, and more effective, studies of sexual dimorphism (e.g. Drees, 2005; Cheng et al., 2009; Barden and Maidment, 2011; Mallon et al., 2011), and some will be utilised in this project when appropriate.

It should also be noted that statistical support of sexual dimorphism appears to be hard come by for fossil taxa. Only ten studies reviewed in this chapter reported significant results for statistical tests related to dimorphism. As statistical support would strengthen any claim of dimorphism, the lack of statistical tests is revealing about how the fossil datasets are often poorly suited to traditional testing methods.

Finally, the paleoanthropological literature reveals techniques that have been developed for estimating the level of sexual dimorphism in extinct species, using repeated sampling methods, such as bootstrapping, and comparisons with phylogenetically relevant, and morphologically similar, dimorphic extant taxa. Although these methods are not applicable to non-avian dinosaurs, they could be employed more readily in studies of sexual dimorphism in many clades with both fossil and extant members.

2.3.2 Ceratopsids

Although sexual dimorphism in ceratopsids has been frequently advocated, this review highlights how few studies have actually tested the idea. Lehman’s (1990) study of variation in *Agujaceratops* may be the most extensive assessment of sexual dimorphism in ceratopsids, but without more rigorous methods the conclusions remain equivocal. Other suggestions of sexual dimorphism have been refuted (e.g. Sternberg, 1927; Dodson, 1990) or remain untested (e.g.
Currie et al., 2008). The most methodologically rigorous study of sexual dimorphism in a species of ceratopsid was conducted by Mallon et al. (2011) for Anchiceratops, and found no evidence for sexual dimorphism.

Although more specimens are being unearthed every year, the samples of most ceratopsid species remain small. Furthermore, species are identified largely by cranial material, which can be highly variable. In contrast, most postcranial material, which may be less prone to individual variation and taphonomic distortion, is dissociated and is not known to encompass sexual variation (Chinnery, 2004; Mallon and Holmes, 2006). Ceratopsids also lack any close extant relatives that could serve as informative guides for studying their cranial morphology. As a result, the ceratopsid fossil record is a challenging one for the study of sexual dimorphism. However, it is not beyond approach, and meaningful conclusions are still tenable. The methods gleaned from the current chapter for assessing the potential for dimorphism without \textit{a priori} groupings should be well suited for use with ceratopsids. In order to verify their usefulness for detecting sexual dimorphism in skeletal material, they will be employed to test for dimorphism in an extant model comprising cranial material from extant ungulates that are known to be dimorphic. The following chapter identifies which species were used as model organisms, and explains why they were chosen for this purpose. The actual testing of these methods and their results is detailed in Chapter 4.

2.4 Conclusions

Evidence of sexual dimorphism is widespread in the vertebrate fossil record, but remains challenging to document for a variety of reasons. The ability to guide or confirm a study of sexual dimorphism by basing it upon related extant taxa is invaluable, and oftentimes provides
the only true test of confidence for the results. For specimens without obvious sexual characters it can be difficult to make a confident claim for sexual dimorphism, and other potential sources of morphological variation must first be ruled out. Although fossil samples are often not readily amenable to simple tests of differences of means, a variety of methods can be effective for discerning elevated variation or bimodality within a sample, and for identifying potential dimorphism. These methods should be well suited to ceratopsid dinosaurs, but they will be tested with an analogous extant model before being applied to dinosaurs.
Table 2.1 Summary table of studies described in Chapter 2 that were attributed a High degree of confidence (“C”) in the conclusion of sexual dimorphism. “High” degree of confidence attributed for: statistical or strong methodological support; extant taxa provide anatomical precedent for dimorphism; exceptional preservational circumstances. Each entry is to be read across two pages and can be followed by the letter and number code provided under “C”. “P” indicates on which page the study is discussed in Chapter 2. “N” indicates sample size in that study. “E” indicates whether an extant taxon was used/is available for comparison (Y = yes) or not (N = no). “Sig. Stats” details any statistical methods that yielded significant results. SSD = sexual size dimorphism; PCA = principal components analysis; DFA = discriminant function analysis; CV = coefficient of variation; AIC = Akaike Information Criterion.
### Table 2.1

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<td>53</td>
<td>Dorsal fin structure and shape</td>
<td>Y</td>
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<td>Lund 1982, 1990</td>
<td>7, 8</td>
<td>Holocephali: <em>Harpagofutator</em></td>
<td>Low</td>
<td>Ethmoid claspers, visceral traces</td>
<td>Y</td>
</tr>
<tr>
<td>H4</td>
<td>Lund 1982</td>
<td>8</td>
<td>Holocephali: <em>Chondrenchelys</em></td>
<td>11</td>
<td>Pectoral fins structure and size</td>
<td>Y</td>
</tr>
<tr>
<td>H5</td>
<td>Lund 1990</td>
<td>8</td>
<td>Holocephali: <em>Echinochimaera</em></td>
<td>High</td>
<td>SSD, supraorbital denticles, dorsal spine, integumentary denticulation</td>
<td>Y</td>
</tr>
<tr>
<td>H6</td>
<td>Pietsch and Lavenberg 1980; Carnevale et al 2008; Carnevale and Pietsch 2009</td>
<td>10,11</td>
<td>Actinopterygii: Ceratioidei</td>
<td>10</td>
<td>SSD</td>
<td>Y</td>
</tr>
<tr>
<td>H7</td>
<td>Joyce et al 2010</td>
<td>11</td>
<td>Cryptodira: <em>Allaeochelys</em></td>
<td>51</td>
<td>Carapace length, tail length, plastral sutures</td>
<td>Y</td>
</tr>
<tr>
<td>H8</td>
<td>Lin and Reippel 1998; Cheng et al 2004, 2009</td>
<td>12</td>
<td>Pachypleurosauria: <em>Keichousaurus</em></td>
<td>70</td>
<td>Humerus, SSD</td>
<td>N</td>
</tr>
<tr>
<td>H9</td>
<td>Bennett 1992</td>
<td>15</td>
<td>Pterosauria: <em>Pteranodon</em></td>
<td>400+</td>
<td>Longbones, metacarpals, crest, pelvis</td>
<td>N</td>
</tr>
<tr>
<td>H10</td>
<td>Lu et al, 2011</td>
<td>15</td>
<td>Pterosauria: <em>Darwinopterus</em></td>
<td>4</td>
<td>Crest, pelvis structure, egg</td>
<td>N</td>
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<tr>
<td>H11</td>
<td>Barden and Maidment 2011</td>
<td>16</td>
<td>Dinosauria: <em>Kentrosaurus</em></td>
<td>49</td>
<td>Femoral head shape</td>
<td>N</td>
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Table 2.1 Continued. Part 2 of 6.

<table>
<thead>
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<th>C</th>
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<th>Conclusions</th>
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<tr>
<td>H1</td>
<td>Visual inspection, sexed by claspers</td>
<td>None</td>
<td>Identified males and females</td>
<td></td>
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<tr>
<td>H2</td>
<td>Visual inspection, sexed by claspers</td>
<td>None</td>
<td>Identified males and females</td>
<td></td>
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<tr>
<td>H3</td>
<td>Visual inspection, sexed by claspers and viscera</td>
<td>None</td>
<td>Identified males and females</td>
<td></td>
</tr>
<tr>
<td>H4</td>
<td>Visual inspection, sexed by claspers</td>
<td>None</td>
<td>Identified 4 males and 2 females</td>
<td></td>
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<tr>
<td>H5</td>
<td>Visual inspection, sexed by claspers</td>
<td>None</td>
<td>Identified males and females</td>
<td></td>
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<tr>
<td>H6</td>
<td>Comparison with extant, assignment to dimorphic species</td>
<td>None</td>
<td>Identified specimens as females and assigned them to an extant species</td>
<td>Specimens are mating pairs, with consistent differences between the individuals in each pair</td>
</tr>
<tr>
<td>H7</td>
<td>Measurement ratios, bivariate plots, comparison of specimens</td>
<td>None</td>
<td>Assigned sex to specimens, propose sexual morphs</td>
<td>Specimens are mating pairs, with consistent differences between the individuals in each pair, Embryos discovered in abdomen of 2 sex 'x' specimens supports sex dim in pachypleurosaurs.</td>
</tr>
<tr>
<td>H8</td>
<td>Frequency histograms, bivariate plots, PCA, DFA</td>
<td>None</td>
<td>Recognised two morphs, identified sexes</td>
<td>Embryos discovered in abdomen of 2 sex 'x' specimens supports sex dim in pachypleurosaurs.</td>
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<tr>
<td>H9</td>
<td>Frequency histograms, comparison of specimens</td>
<td>G-test</td>
<td>Recognised two morphs within each of two species, proposed sexes</td>
<td>Good demonstration of sex dim and of methods</td>
</tr>
<tr>
<td>H10</td>
<td>Comparison of specimens, sexing with egg</td>
<td>None</td>
<td>Proposed two sexual morphs</td>
<td></td>
</tr>
<tr>
<td>H11</td>
<td>Test of means, shape analysis, K-means cluster analysis</td>
<td>MANOVA, two-tailed t-tests</td>
<td>Proposed two morphs</td>
<td>Strong case due to statistical support</td>
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Table 2.1 Continued. Part 3 of 6.

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<tr>
<td>H12</td>
<td>Fisher 2009; Smith and Fisher 2011</td>
<td>26</td>
<td>Proboscidea: <em>Mammut; Mammutus</em></td>
<td>26</td>
<td>SSD, tusk dimensions</td>
<td>Y</td>
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<tr>
<td>H13</td>
<td>Mead 2000</td>
<td>28</td>
<td>Rhinocerotidae: <em>Teleoceras</em></td>
<td>35</td>
<td>Postcrania, skull, teeth, SSD</td>
<td>Y</td>
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<tr>
<td>H14</td>
<td>Mihlbachler 2005</td>
<td>29</td>
<td>Rhinocerotidae: <em>Teleoceras; Aphelops</em></td>
<td>30-70</td>
<td>Limb bones, i2</td>
<td>Y</td>
</tr>
<tr>
<td>H15</td>
<td>Mihlbachler 2007</td>
<td>29</td>
<td>Rhinocerotidae: <em>Menoceras</em></td>
<td>41</td>
<td>Mandible, cranium, post-cranium</td>
<td>Y</td>
</tr>
<tr>
<td>H16</td>
<td>Chen et al 2010</td>
<td>30</td>
<td>Rhinocerotidae: <em>Chiloterium</em></td>
<td>74</td>
<td>Crania and dental dimensions</td>
<td>Y</td>
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<tr>
<td>H17</td>
<td>Wright 1993</td>
<td>32</td>
<td>Tayassuidae</td>
<td></td>
<td>Canine teeth, zygomatic arch</td>
<td>Y</td>
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<tr>
<td>H18</td>
<td>Geraads 2004</td>
<td>33</td>
<td>Suidae: <em>Kolpochoerus</em></td>
<td></td>
<td>Skulls and teeth</td>
<td>Y</td>
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<tr>
<td>H19</td>
<td>Sanchez and Morales 2008</td>
<td>35</td>
<td>Moschidae: <em>Micromeryx</em></td>
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<td>Teeth, tibiae</td>
<td>Y</td>
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<tr>
<td>H20</td>
<td>Drees 2005</td>
<td>37</td>
<td>Bovidae: <em>Bison</em></td>
<td>18</td>
<td>Metacarpals</td>
<td>Y</td>
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Table 2.1 Continued. Part 4 of 6.

<table>
<thead>
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<th>C</th>
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<th>Conclusions</th>
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<tr>
<td>H12</td>
<td>Comparison of linear dimensions, growth curves, PCA. Comparison with patterns in extant elephants.</td>
<td>None</td>
<td>Proposed sexual dimorphs, males larger sex</td>
<td></td>
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<tr>
<td>H13</td>
<td>Identified sex by teeth. Assessed SD with t-tests, CV, sex dim ratio</td>
<td>t-tests</td>
<td>Supported previously recognised sexual morphs with statistics</td>
<td>Enabled by similarities in extant rhinos and a pregnant <em>T. major</em> fossil female</td>
</tr>
<tr>
<td>H14</td>
<td>Tested for non-unimodal variation with Shapiro-Wilk tests, CV's, Bimodality coefficient, bivariate plots</td>
<td>Shapiro-Wilk tests</td>
<td>Supported previously recognised sexual morphs with numerical methods</td>
<td></td>
</tr>
<tr>
<td>H15</td>
<td>Identified variation and groupings using Shapiro-Wilk tests, CV's, Bimodality coefficient, and bivariate plots; then tested between groups with t-tests</td>
<td>t-tests, Shapiro-Wilk tests</td>
<td>Identified i2 as sex diagnostic, proposed sexual morphs distinguished by nasal dimensions, occipital and orbital width, and zygomatic width</td>
<td></td>
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<tr>
<td>H16</td>
<td>Assigned sex by i2, then tested for differences with t-tests. Supported with DFA.</td>
<td>t-tests</td>
<td>Identified males and females, identified dimorphic cranial variables</td>
<td></td>
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<tr>
<td>H17</td>
<td>Frequency histograms, bivariate plots, probability plots; assigned sex by canine size as in extant species</td>
<td>None</td>
<td>Demonstrated variable degrees of sex dim by species, largely in canine size.</td>
<td>Study based on dimorphism in extant tayassuids.</td>
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<tr>
<td>H18</td>
<td>Comparison with extant <em>Potamochoerus</em>. Comparison of measurements, bivariate plots</td>
<td>None</td>
<td>Reported dimorphism in canine and supracanine flange. Proposed male skulls slightly larger than female.</td>
<td>Based on study of sex dim in extant bushpig.</td>
</tr>
<tr>
<td>H19</td>
<td>Bivariate plots, PCA, ANOVA</td>
<td>ANOVA</td>
<td>Proposed sexual morphs, with females larger than males, and males possessing larger canines</td>
<td></td>
</tr>
<tr>
<td>H20</td>
<td>Measurements, PCA, cluster analysis</td>
<td>None</td>
<td>Proposed sexual morphs based on clustering</td>
<td>Study was based on sex dim in the metacarpals of extant <em>Bison</em></td>
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<tr>
<td>H21</td>
<td>Van Valkenburgh and Sacco 2002</td>
<td>41</td>
<td>Carnivora: <em>Canis</em>; <em>Smilodon</em></td>
<td>338; 111</td>
</tr>
<tr>
<td>H22</td>
<td>Anton et al 2004</td>
<td>41</td>
<td>Carnivora: <em>Machairodus</em></td>
<td>16</td>
</tr>
<tr>
<td>H23</td>
<td>Samuels and Binder 2009</td>
<td>42</td>
<td>Carnivora: <em>Panthera</em></td>
<td>13</td>
</tr>
<tr>
<td>H24</td>
<td>Gingerich 1981a</td>
<td>43</td>
<td>Primates: <em>Adapis</em></td>
<td>8-11</td>
</tr>
<tr>
<td>H25</td>
<td>Gordon et al 2008</td>
<td>45</td>
<td>Hominoids: <em>Australopithecus</em></td>
<td>17</td>
</tr>
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Table 2.1 Continued. Part 6 of 6.

<table>
<thead>
<tr>
<th>C</th>
<th>Methods</th>
<th>Sig. Stats</th>
<th>Conclusions</th>
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<tbody>
<tr>
<td>H21</td>
<td>Plotting CV against sex dim, &quot;mean method&quot;, finite mixture analysis. Comparison with 7 extant canids; 11 extant felids</td>
<td>Spearman’s rank correlation coefficient</td>
<td>For both species proposed male and female sexual morphs; males with larger canines</td>
<td></td>
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<tr>
<td>H22</td>
<td>&quot;Mean method&quot;. Comparison with sex dim indices from 11 extant felids</td>
<td>None</td>
<td>Reported sex dim akin to that of extant lions and leopards</td>
<td></td>
</tr>
<tr>
<td>H23</td>
<td>Regression of jaw length vs per cent pulp cavity closure; model fit testing</td>
<td>Spearman’s rank correlation coefficient, ANOVA, AIC</td>
<td>Identified 6 females, 7 males</td>
<td>Used a sexed sample of extant lion specimens as a proof of concept of methods</td>
</tr>
<tr>
<td>H24</td>
<td>Ratios, bivariate plots, allometric scaling coefficients</td>
<td>None</td>
<td>Assigned sex to specimens in two species <em>A. magnus</em> and <em>A. parisiensis</em>; males with larger skulls, canines, crests, and broader zygoma</td>
<td>Compared ratios and scaling coefficients with extant dimorphic and monomorphic primates</td>
</tr>
<tr>
<td>H25</td>
<td>Mean method, with multivariate data set and repeated sampling measures of comparative extant samples and of fossil sample</td>
<td>Yes</td>
<td>Supported post-cranial sex dim similar to that of gorillas and orangutans.</td>
<td>Supports similar findings by Lockwood et al 1996, contrasts the conclusions of Reno et al 2003, 2005; Scott and Stroik 2006</td>
</tr>
</tbody>
</table>
Table 2.2  Summary table of studies described in Chapter 2 that were attributed a Moderate degree of confidence (“C”) in the conclusion of sexual dimorphism. “Moderate” degree of confidence attributed for: some methodological support; extant analogues provide template for some dimorphic patterns; good fossil evidence. Each entry is to be read across two pages and can be followed by the letter and number code provided under “C”. “P” indicates on which page the study is discussed in Chapter 2. “N” indicates sample size in that study. “E” indicates whether an extant taxon was used/is available for comparison (Y = yes) or not (N = no). “Sig. Stats” details any statistical methods that yielded significant results. SSD = sexual size dimorphism; PCA = principal components analysis; DFA = discriminant function analysis; CV = coefficient of variation; AIC = Akaike Information Criterion.
### Table 2.2 Part 1 of 4.

<table>
<thead>
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<tr>
<td>M1</td>
<td>Sander 1989; Reippel 1989</td>
<td>11</td>
<td>Pachypleurosauria: <em>Neusticosaurus</em>; <em>Serpianosaurus</em></td>
<td>340; 35</td>
<td>Humerus, SSD</td>
<td>N</td>
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<tr>
<td>M2</td>
<td>Dodson 1976</td>
<td>18</td>
<td>Ceratopsia: <em>Protoceratops</em></td>
<td>24</td>
<td>Multiple cranial variables</td>
<td>N</td>
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<tr>
<td>M3</td>
<td>Larson 2008</td>
<td>24</td>
<td>Theropoda: <em>T. rex</em></td>
<td></td>
<td>Femora and humerus</td>
<td>N</td>
</tr>
<tr>
<td>M4</td>
<td>Peter and Peters 2009</td>
<td>25</td>
<td>Aves: <em>Confusciusornis</em></td>
<td>90</td>
<td>SSD, elongate tail feathers</td>
<td>Y</td>
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<tr>
<td>M5</td>
<td>Mihlbachler 2011</td>
<td>27</td>
<td>Brontotheriidae</td>
<td>4+</td>
<td>Canine teeth, frontal horns</td>
<td>N</td>
</tr>
<tr>
<td>M6</td>
<td>Deng 2005</td>
<td>31</td>
<td>Rhinocerotidae: <em>Iranotherium</em></td>
<td>4</td>
<td>Skull, mandible</td>
<td>Y</td>
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<tr>
<td>M7</td>
<td>Borsuk-Bialynicka 1973</td>
<td>31</td>
<td>Rhinocerotidae: <em>Coelodonta</em></td>
<td>15</td>
<td>Skulls</td>
<td>Y</td>
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<tr>
<td>M8</td>
<td>Gingerich 1981b</td>
<td>31</td>
<td>Equiidae: <em>Hyracotherium</em></td>
<td>&lt;10</td>
<td>Teeth, skull length</td>
<td>Y</td>
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<tr>
<td>M9</td>
<td>Harris and White 1979</td>
<td>32</td>
<td>Suidae</td>
<td></td>
<td>Skulls and teeth</td>
<td>Y</td>
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<tr>
<td>M10</td>
<td>Lihoreau et al 2004; Lihoreau et al 2007; Lihoreau and Ducrocq 2007; Pickford 2006</td>
<td>33</td>
<td>Anthracotheriidae</td>
<td></td>
<td>Skulls and teeth</td>
<td>N</td>
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<tr>
<td>M11</td>
<td>Visser 2008</td>
<td>34</td>
<td>Hippopotamidae: <em>Hexaprotodon</em></td>
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<td>Canine teeth</td>
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Table 2.2 Continued. Part 2 of 4.

<table>
<thead>
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<th>C</th>
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<th>Sig. Stats</th>
<th>Conclusions</th>
<th>Comments</th>
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<tbody>
<tr>
<td>M1</td>
<td>Measurements, comparison of specimens, frequency histograms</td>
<td>None</td>
<td>Proposed sexual dimorphs, hypothsized sexes</td>
<td></td>
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<tr>
<td>M2</td>
<td>Principal coordinates analysis, bivariate plots</td>
<td>None</td>
<td>Proposed sexual morphs; identified 7 females, 8 males</td>
<td></td>
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<tr>
<td>M3</td>
<td>Bivariate plots, comparison of measurements</td>
<td>None</td>
<td>Proposed robust/gracile sexual morphs</td>
<td>Possible medullary bone in a 'female' adds support</td>
</tr>
<tr>
<td>M4</td>
<td>Growth curves from measurements and body size estimates</td>
<td>None</td>
<td>Proposed SSD in adults, rectrices unrelated to sex</td>
<td>Debated in literature with Chiappe et al (2008, 2010)</td>
</tr>
<tr>
<td>M5</td>
<td>Compared CV's between variables</td>
<td>None</td>
<td>Supported sexual dimorphism in canines and horns</td>
<td>Supported earlier work by Osborn 1896 and Scott 1945</td>
</tr>
<tr>
<td>M6</td>
<td>Measurements, comparison of specimens</td>
<td>None</td>
<td>Proposed sex morphs, with more massive skulls, a larger nasal horn, larger zygomas and zygomatic rugosities in males.</td>
<td></td>
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<tr>
<td>M7</td>
<td>Frequency distributions, CV's</td>
<td>None</td>
<td>Proposed sex dim based on modest bimodality in the sample. Suggested 3 as male, 3 as female.</td>
<td></td>
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<tr>
<td>M8</td>
<td>Measurements, calculating CV's</td>
<td>None</td>
<td>Reported dimorphism in skull length, and a greater difference in canine dimensions</td>
<td></td>
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<tr>
<td>M9</td>
<td>Comparison of specimens, sexed by extant species</td>
<td>None</td>
<td>Reported dimorphism in cranial size, upper canine form, and secondary sex characters in several species</td>
<td></td>
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<tr>
<td>M10</td>
<td>Comparison of specimens, bivariate plots</td>
<td>None</td>
<td>Supported sexual morphs; males possessing larger canines, incisors, and sagittal crests, and deeper mandibular symphyses</td>
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<tr>
<td>M11</td>
<td>Bivariate plot</td>
<td>None</td>
<td>Proposed sexual morphs</td>
<td>Supported by similar results in extant hippos</td>
</tr>
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<td>Taxon</td>
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<tr>
<td>M12</td>
<td>Patton and Taylor 1973</td>
<td>34</td>
<td>Protoceratidae: <em>Protoceras</em></td>
<td>17</td>
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<tr>
<td>M13</td>
<td>Honey 2007</td>
<td>35</td>
<td>Camelidae: <em>Protolabis</em></td>
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<tr>
<td>M14</td>
<td>Bianucci et al 2008</td>
<td>39</td>
<td>Ziphiiidae: <em>Mesoplodon</em></td>
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<tr>
<td>M15</td>
<td>Lambert et al 2010</td>
<td>40</td>
<td>Ziphiiidae: <em>Mesapicetus</em></td>
<td>8</td>
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<tr>
<td>M16</td>
<td>Salesa et al 2006</td>
<td>41</td>
<td>Carnivora: <em>Paramachairodus</em></td>
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<tr>
<td>M17</td>
<td>Fleagle et al 1980</td>
<td>44</td>
<td>Anthropoids: <em>Aegyptopithecus, Propliopithecus, Apidium</em></td>
<td></td>
</tr>
<tr>
<td>M18</td>
<td>Yuerong et al 1989</td>
<td>44</td>
<td>Anthropoids: <em>Laccopithecus</em></td>
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</table>
Table 2.2 Continued. Part 4 of 4.

<table>
<thead>
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<th>C</th>
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<th>Conclusions</th>
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<tr>
<td>M12</td>
<td>Calculated CV's</td>
<td>None</td>
<td>Proposed sexual morphs, with males possessing large canines and ornaments.</td>
<td>Provided numerical support to original idea of sex dim proposed by Osborn and Wortman 1892</td>
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<tr>
<td>M13</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Proposed sexual morphs, with males possessing larger incisors and canines, and pelvic differences.</td>
<td>Used sexual differences in the pelves and dentition of extant dromedaries as a guide</td>
</tr>
<tr>
<td>M14</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Proposed sexual morphs, males with heavily ossified rostral bones as in extant members of the genus</td>
<td></td>
</tr>
<tr>
<td>M15</td>
<td>Comparison of specimens,</td>
<td>None</td>
<td>Proposed sexual morphs, males with larger tusk alveoli and rostral protuberances similar to extant Ziphius cavirostris</td>
<td></td>
</tr>
<tr>
<td></td>
<td>measurements</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M16</td>
<td>&quot;Mean method&quot;. Comparison with SD indices from 11 extant felids</td>
<td>None</td>
<td>Reported sex dim akin to that of extant cheetahs and lynx</td>
<td></td>
</tr>
<tr>
<td>M17</td>
<td>Calculated CV's, bivariate plots</td>
<td>None</td>
<td>Reported sex dim in teeth and mandibular depth, presumed males are larger by comparison with extant primates</td>
<td></td>
</tr>
<tr>
<td>M18</td>
<td>Calculated CV's, bivariate plots</td>
<td>None</td>
<td>Reported sex dim in canine dimensions</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.3 Summary table of studies described in Chapter 2 that were attributed a Low degree of confidence (“C”) in the conclusion of sexual dimorphism. “Low” degree of confidence attributed for: low level of methodological support; but good fossil evidence. Each entry is to be read across two pages and can be followed by the letter and number code provided under “C”. “P” indicates on which page the study is discussed in Chapter 2. “N” indicates sample size in that study. “E” indicates whether an extant taxon was used/is available for comparison (Y = yes) or not (N = no). “Sig. Stats” details any statistical methods that yielded significant results. SSD = sexual size dimorphism; PCA = principal components analysis; DFA = discriminant function analysis; CV = coefficient of variation; AIC = Akaike Information Criterion.
<table>
<thead>
<tr>
<th>C</th>
<th>Author</th>
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<th>Taxon</th>
<th>N</th>
<th>Feature Assessed</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1</td>
<td>Wilson 1984</td>
<td>9</td>
<td>Actinopterygii: <em>Amyzon</em></td>
<td>85</td>
<td>SSD in body depth</td>
<td>N</td>
</tr>
<tr>
<td>L2</td>
<td>Burgin 1990, Lombardo 2003</td>
<td>9,10</td>
<td>Actinopterygii: <em>Peltopleurus</em> (and others)</td>
<td></td>
<td>Anal fin structure, ornamental cranial tubercles</td>
<td>N</td>
</tr>
<tr>
<td>L3</td>
<td>Raath 1990</td>
<td>22</td>
<td>Theropoda: <em>Coelophysis</em></td>
<td>30+</td>
<td>Femoral head, muscle scars, robusticity</td>
<td>N</td>
</tr>
<tr>
<td>L4</td>
<td>Coombs 1975</td>
<td>27</td>
<td>Chalicotheriidae: <em>Moropus</em></td>
<td></td>
<td>Radius and tibia length</td>
<td>N</td>
</tr>
<tr>
<td>L5</td>
<td>Hibbard and Riggs 1949</td>
<td>35</td>
<td>Camelidae: <em>Gigantocamelus</em></td>
<td>21</td>
<td>Skulls and teeth</td>
<td>Y</td>
</tr>
<tr>
<td>L6</td>
<td>Webb 1973</td>
<td>36</td>
<td>Antilocapridae: <em>Hexameryx</em></td>
<td></td>
<td>Horn basal dimensions and tines, supraorbital foramen</td>
<td>N</td>
</tr>
<tr>
<td>L7</td>
<td>Webb 1973</td>
<td>36</td>
<td>Antilocapridae: <em>Hexobelomeryx</em></td>
<td></td>
<td>Horn tines</td>
<td>N</td>
</tr>
<tr>
<td>L8</td>
<td>Sanchez et al 2010</td>
<td>37</td>
<td>Palaeomerycidae: <em>Prolibytherium</em></td>
<td>6</td>
<td>Cranial appendages</td>
<td>N</td>
</tr>
<tr>
<td>L9</td>
<td>Kurten 1969</td>
<td>40</td>
<td>Carnivora: <em>Ursus</em></td>
<td></td>
<td>Skull length, teeth</td>
<td>Y</td>
</tr>
<tr>
<td>L10</td>
<td>Demere and Berta 2002</td>
<td>42</td>
<td>Carnivora: <em>Allodesmus, Desmatophoca</em></td>
<td></td>
<td>Skull, teeth, crests</td>
<td>Y</td>
</tr>
<tr>
<td>L11</td>
<td>Berta 1994</td>
<td>43</td>
<td>Carnivora: <em>Pteronarctos</em></td>
<td></td>
<td>Skull, teeth, crests</td>
<td>Y</td>
</tr>
</tbody>
</table>
Table 2.3 Continued. Part 2 of 2.

<table>
<thead>
<tr>
<th>C</th>
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<th>Sig. Stats</th>
<th>Conclusions</th>
<th>Comments</th>
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<tbody>
<tr>
<td>L1</td>
<td>Size frequency distribution</td>
<td>None</td>
<td>Proposed sex dim, identified female morphs</td>
<td></td>
</tr>
<tr>
<td>L2</td>
<td>Visual inspection</td>
<td>None</td>
<td>Proposed sexual morphs</td>
<td></td>
</tr>
<tr>
<td>L3</td>
<td>Measurements, bivariate plots</td>
<td>None</td>
<td>Proposed robust/gracile sexual morphs, suggested robust morph is female</td>
<td>Supported by Rowe 1989 and Gay 2005, but not supported by Colbert 1990 or Covey 1993</td>
</tr>
<tr>
<td>L4</td>
<td>Probability plots, measurements</td>
<td>None</td>
<td>Proposed sexual dimorphs via synonymy</td>
<td></td>
</tr>
<tr>
<td>L5</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Proposed sexual morphs, with males larger overall and with larger canines.</td>
<td></td>
</tr>
<tr>
<td>L6</td>
<td>Comparison of specimens, bivariate plots</td>
<td>None</td>
<td>Proposed male and female sexual morphs.</td>
<td></td>
</tr>
<tr>
<td>L7</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Proposed male and female sexual morphs.</td>
<td></td>
</tr>
<tr>
<td>L8</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Proposed male and female sexual morphs.</td>
<td></td>
</tr>
<tr>
<td>L9</td>
<td>Measurements, plots of ratios</td>
<td>None</td>
<td>Proposed sexual morphs, males larger and with larger canines. Comparison with extant bears supported the hypothesis</td>
<td></td>
</tr>
<tr>
<td>L10</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Describe sexual differences in skull length, canine size, and size and rugosity of sagittal and nuchal crests</td>
<td></td>
</tr>
<tr>
<td>L11</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Describe sexual differences in rostral width, canine size, and size and rugosity of sagittal and nuchal crests</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.4 Summary table of studies described in Chapter 2 that were attributed a Poor degree of confidence ("C") in the conclusion of sexual dimorphism. “Poor” degree of confidence attributed for: weak, or lack of, methodological support; weak fossil evidence; sexual dimorphism was not concluded; or, was subsequently refuted. Each entry is to be read across two pages and can be followed by the letter and number code provided under “C”. “P” indicates on which page the study is discussed in Chapter 2. “N” indicates sample size in that study. “E” indicates whether an extant taxon was used/is available for comparison (Y = yes) or not (N = no). “Sig. Stats” details any statistical methods that yielded significant results. SSD = sexual size dimorphism; PCA = principal components analysis; DFA = discriminant function analysis; CV = coefficient of variation; AIC = Akaike Information Criterion.
Table 2.4 Part 1 of 4.

<table>
<thead>
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<th>C</th>
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<tbody>
<tr>
<td>P1</td>
<td>Holman 2003</td>
<td>11</td>
<td>Anura: Scotiophryne</td>
<td></td>
<td>Humeral condyle</td>
<td>Y</td>
</tr>
<tr>
<td>P2</td>
<td>Zeigler et al 2002</td>
<td>13</td>
<td>Phytosauria: Pseudopalatus</td>
<td></td>
<td>Snout length, narial crest form</td>
<td>N</td>
</tr>
<tr>
<td>P3</td>
<td>Dodson 1975</td>
<td>17</td>
<td>Hadrosauria: Lambeosaurus and</td>
<td>36</td>
<td>Cranial elements</td>
<td>N</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Corythosaurus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P4</td>
<td>Evans 2003</td>
<td>17</td>
<td>Hadrosauria: Corythosaurus</td>
<td></td>
<td>Crest shape</td>
<td>N</td>
</tr>
<tr>
<td>P5</td>
<td>Tereschenko 2001</td>
<td>19</td>
<td>Ceratopsia: Protoceratops</td>
<td>8</td>
<td>Postcranial characters: pelvis width, abdominal</td>
<td>Y</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>cavity volume, height of spinous processes</td>
<td></td>
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<tr>
<td>P6</td>
<td>Lehman 1990</td>
<td>19</td>
<td>Ceratopsia: Agujaceratops</td>
<td>15</td>
<td>Postorbital horncores</td>
<td>N</td>
</tr>
<tr>
<td>P7</td>
<td>Sternberg 1927</td>
<td>20</td>
<td>Ceratopsia: Chasmosaurus</td>
<td></td>
<td>Postcranial structure</td>
<td>N</td>
</tr>
<tr>
<td>P8</td>
<td>Mallon and Holmes, 2006</td>
<td>20</td>
<td>Ceratopsia: Chasmosaurus</td>
<td>2</td>
<td>Frill, postcrania, humeri</td>
<td></td>
</tr>
<tr>
<td>P9</td>
<td>Dodson 1990</td>
<td>21</td>
<td>Ceratopsia: Centrosaurus</td>
<td></td>
<td>Nasal horncores, robusticity</td>
<td>N</td>
</tr>
<tr>
<td>P10</td>
<td>Mallon et al 2011</td>
<td>21</td>
<td>Ceratopsia: Anchiceratops</td>
<td>8</td>
<td>Multiple cranial variables</td>
<td></td>
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<tr>
<td>P11</td>
<td>Chapman et al. 1981</td>
<td>22</td>
<td>Pachycephalosauria: Stegoceras</td>
<td>29</td>
<td>Cranial dome (fronto-parietal region); braincase</td>
<td>N</td>
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<tr>
<td>P12</td>
<td>Weishampel and Chapman 1990</td>
<td>22</td>
<td>Sauropodomorpha: Plateosaurus</td>
<td>33</td>
<td>Femoral articular surfaces, attachment sites</td>
<td>N</td>
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<tr>
<td>P13</td>
<td>Benton et al 2000</td>
<td>22</td>
<td>Sauropodomorpha: Thecodontosaurus</td>
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<td>Limb bones</td>
<td>N</td>
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</table>
Table 2.4 Continued. Part 2 of 4.

<table>
<thead>
<tr>
<th>C</th>
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<th>Conclusions</th>
<th>Comments</th>
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<tbody>
<tr>
<td>P1</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Proposed sex dim as an explanation</td>
<td></td>
</tr>
<tr>
<td>P2</td>
<td>Linear measurements, comparison of specimens</td>
<td>None</td>
<td>Proposed sexual morphs</td>
<td>Refuted by Nesbitt and Stoker 2008</td>
</tr>
<tr>
<td>P3</td>
<td>Principal coordinates analysis, bivariate plots, allometric coefficients</td>
<td>None</td>
<td>Proposed sexual morphs</td>
<td>Deemed 'inconclusive' by Evans and Reisz 2007</td>
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<tr>
<td>P4</td>
<td>Measurements, allometric growth curves</td>
<td>None</td>
<td>Suggested sexual morphs</td>
<td>Likely invalid on taxonomic grounds</td>
</tr>
<tr>
<td>P5</td>
<td>Comparison of specimens, measurements; compared against observations from extant amniotes</td>
<td>None</td>
<td>Proposed sex diffs, assigned sex to several specimens</td>
<td></td>
</tr>
<tr>
<td>P6</td>
<td>Comparison of specimens, measurements</td>
<td>None</td>
<td>Proposed 'subtly' different sexual morphs in <em>Agujaceratops</em> as well as other chasmosaurines</td>
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<tr>
<td>P7</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Proposed gracile/robust sexual morphs</td>
<td>Refuted by Mallon and Holmes 2006</td>
</tr>
<tr>
<td>P8</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Rejected sex dim, supported two species</td>
<td>Refuted Sternberg 1927</td>
</tr>
<tr>
<td>P9</td>
<td>Comparison of specimens</td>
<td>None</td>
<td>Proposed sexual morphs by synonymy</td>
<td>Not supported by Ryan et al 2001</td>
</tr>
<tr>
<td>P10</td>
<td>PCA, hierarchical clustering, K-means clustering</td>
<td>None</td>
<td>Concluded non-sexual variation, supported synonymy</td>
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<tr>
<td>P11</td>
<td>PCA, bivariate plots</td>
<td>None</td>
<td>Proposed sexual morphs</td>
<td>Later refuted by Goodwin and Horner 2004; Schott et al 2011</td>
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<tr>
<td>P12</td>
<td>PCA, bivariate plots</td>
<td>None</td>
<td>High intraspecific variation may include sexual dimorphism</td>
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<tr>
<td>P13</td>
<td>Review of dated reports of robust and gracile forms</td>
<td>None</td>
<td>Suggested original morphs may be sexual</td>
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Table 2.4 Continued. Part 3 of 4.

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<tr>
<td>P14</td>
<td>Sander 2000</td>
<td>23</td>
<td>Sauropodomorpha: <em>Barosaurus</em></td>
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<td>Limb bones</td>
<td>N</td>
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<tr>
<td>P15</td>
<td>Smith 1998</td>
<td>25</td>
<td>Theropoda: <em>Allosaurus</em></td>
<td>54</td>
<td>Femoral head, dentary dimensions</td>
<td>N</td>
</tr>
<tr>
<td>P16</td>
<td>Carpenter 1990</td>
<td>25</td>
<td>Theropoda: <em>T. rex</em></td>
<td></td>
<td>6 maxillae, 6 dentaries, 2 cervical series, 3 ischia</td>
<td>N</td>
</tr>
<tr>
<td>P17</td>
<td>Antoine et al 2004</td>
<td>31</td>
<td>Indricotheriinae: <em>Paraceratherium</em></td>
<td>2</td>
<td>Lower canines</td>
<td>N</td>
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<tr>
<td>P18</td>
<td>Fortelius and Kappelman 1993</td>
<td>31</td>
<td>Indricotheriinae: <em>Indricotherium</em></td>
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<td>SSD</td>
<td>N</td>
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<tr>
<td>P19</td>
<td>Wheeler 1961; Dorr 1958</td>
<td>38</td>
<td>Uintatheria</td>
<td></td>
<td>SSD, cranial appendages, canines</td>
<td>N</td>
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<tr>
<td>P20</td>
<td>O'Leary et al 2000</td>
<td>39</td>
<td>Mesonychia: <em>Ankalagon</em></td>
<td>2</td>
<td>Mandible, teeth</td>
<td>Y</td>
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<tr>
<td>P21</td>
<td>Kurten 1969</td>
<td>40</td>
<td>Carnivora: <em>Hemicyon</em></td>
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<td>Skull length, teeth</td>
<td>Y</td>
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**Table 2.4 Continued. Part 4 of 4.**

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<tr>
<th>C</th>
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<th>Sig. Stats</th>
<th>Conclusions</th>
<th>Comments</th>
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<tbody>
<tr>
<td>P14</td>
<td>Comparison of 2 histological patterns</td>
<td>None</td>
<td>Proposed sex dim as a possible explanation</td>
<td>Later refuted on taxonomic grounds by Remes (2006, 2007)</td>
</tr>
<tr>
<td>P15</td>
<td>Frequency histograms, Shapiro-Wilk test, PCA, CV's</td>
<td>None</td>
<td>Suggested sex dim as a possible explanation of observed variation.</td>
<td>Good and thorough methods.</td>
</tr>
<tr>
<td>P16</td>
<td>Comparison of specimens, measurements</td>
<td>None</td>
<td>Proposed robust/gracile sexual morphs</td>
<td></td>
</tr>
<tr>
<td>P17</td>
<td>Observation of specimens</td>
<td>None</td>
<td>Suggested the canines may be dimorphic in form</td>
<td></td>
</tr>
<tr>
<td>P18</td>
<td>Body mass estimates</td>
<td>None</td>
<td>Suggested possible SSD in body mass based on perceived weak bimodality in body mass estimates</td>
<td></td>
</tr>
<tr>
<td>P19</td>
<td>Comparison of specimens, measurements</td>
<td>None</td>
<td>Proposed sexual morphs; the larger, more robust morph with larger tusks and horns is presumed to be male.</td>
<td></td>
</tr>
<tr>
<td>P20</td>
<td>Comparison of specimens, comparison of ratios against extant carnivorans</td>
<td>None</td>
<td>Proposed sexual morphs to explain differences in dentary depth and canine size.</td>
<td>Reasonable approach, but cannot be supported with a sample size of 2 without a more definitive character.</td>
</tr>
<tr>
<td>P21</td>
<td>Measurements, plots of ratios</td>
<td>None</td>
<td>Proposed sexual morphs with males larger and with larger canines. Compared with results in extant bears for support.</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.5 List of those studies that incorporate thorough methodologies for investigating sexual dimorphism, regardless of their conclusions. Refer to the legend of Table 2.1 for explanation of acronyms and table arrangement.

<table>
<thead>
<tr>
<th>C</th>
<th>Author</th>
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<th>N</th>
<th>Feature Assessed</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>H8</td>
<td>Lin and Reippel 1998; Cheng et al 2004, 2009</td>
<td>12</td>
<td>Pachypleurosauria: <em>Keichousaurus</em></td>
<td>70</td>
<td>Humerus, SSD</td>
<td>N</td>
</tr>
<tr>
<td>H9</td>
<td>Bennett 1992</td>
<td>15</td>
<td>Pterosauria: <em>Pteranodon</em></td>
<td>400+</td>
<td>Longbones, metacarpals, crest, pelvis</td>
<td>N</td>
</tr>
<tr>
<td>H11</td>
<td>Barden and Maidment 2011</td>
<td>16</td>
<td>Dinosauria: <em>Kentrosaurus</em></td>
<td>49</td>
<td>Femoral head shape</td>
<td>N</td>
</tr>
<tr>
<td>H12</td>
<td>Fisher 2009; Smith and Fisher 2011</td>
<td>26</td>
<td>Proboscidea: <em>Mammut; Mammuthus</em></td>
<td>SSD, tusk dimensions</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td>H13</td>
<td>Mead 2000</td>
<td>28</td>
<td>Rhinocerotidae: <em>Teleoceras</em></td>
<td>35</td>
<td>Postcrania, skull, teeth, SSD</td>
<td>Y</td>
</tr>
<tr>
<td>H14</td>
<td>Mihlbachler 2005</td>
<td>29</td>
<td>Rhinocerotidae: <em>Teleoceras; Aphelops</em></td>
<td>30 - 70</td>
<td>Limb bones, i2</td>
<td>Y</td>
</tr>
<tr>
<td>H15</td>
<td>Mihlbachler 2007</td>
<td>29</td>
<td>Rhinocerotidae: <em>Menoceras</em></td>
<td>41</td>
<td>Mandible, cranium, post-cranium</td>
<td>Y</td>
</tr>
<tr>
<td>H17</td>
<td>Wright 1993</td>
<td>32</td>
<td>Tayassuidae</td>
<td></td>
<td>Canine teeth, zygomatic arch</td>
<td>Y</td>
</tr>
<tr>
<td>H20</td>
<td>Drees 2005</td>
<td>37</td>
<td>Bovidae: <em>Bison</em></td>
<td>18</td>
<td>Metacarpals</td>
<td>Y</td>
</tr>
</tbody>
</table>
Table 2.5 Continued. Page 2 of 4.

<table>
<thead>
<tr>
<th>C</th>
<th>Methods</th>
<th>Sig. Stats</th>
<th>Conclusions</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>H8</td>
<td>Frequency histograms, bivariate plots, PCA, DFA</td>
<td>None</td>
<td>Recognised two morphs, identified sexes</td>
<td>Embryos discovered in abdomen of 2 sex 'x' specimens supports sex dim in pachypleurosaurs.</td>
</tr>
<tr>
<td>H9</td>
<td>Frequency histograms, comparison of specimens</td>
<td>G-test</td>
<td>Recognised two morphs within each of two species, proposed sexes</td>
<td>Good demonstration of sex dim and of methods</td>
</tr>
<tr>
<td>H11</td>
<td>Test of means, shape analysis, K-means cluster analysis</td>
<td>MANOVA, two-tailed t-tests</td>
<td>Proposed two morphs</td>
<td>Strong case due to statistical support</td>
</tr>
<tr>
<td>H12</td>
<td>Comparison of linear dimensions, growth curves, PCA. Comparison with patterns in extant elephants.</td>
<td>None</td>
<td>Proposed sexual dimorphs, males larger sex</td>
<td></td>
</tr>
<tr>
<td>H13</td>
<td>Identified sex by teeth. Assessed SD with t-tests, CV, sex dim ratio</td>
<td>t-tests</td>
<td>Supported previously recognised sexual morphs with statistics</td>
<td>Enabled by similarities in extant rhinos and a pregnant <em>T. major</em> fossil female</td>
</tr>
<tr>
<td>H14</td>
<td>Tested for non-unimodal variation with Shapiro-Wilk tests, CV's, Bimodality coefficient, bivariate plots</td>
<td>Shapiro-Wilk tests</td>
<td>Supported previously recognised sexual morphs with numerical methods</td>
<td></td>
</tr>
<tr>
<td>H15</td>
<td>Identified variation and groupings using Shapiro-Wilk tests, CV's, Bimodality coefficient, and bivariate plots; then tested between groups with t-tests</td>
<td>t-tests, Shapiro-Wilk tests</td>
<td>Identified i2 as sex diagnostic, proposed sexual morphs distinguished by nasal dimensions, occipital and orbital width, and zygomatic width</td>
<td></td>
</tr>
<tr>
<td>H17</td>
<td>Frequency histograms, bivariate plots, probability plots; assigned sex by canine size as in extant species</td>
<td>None</td>
<td>Demonstrated variable degrees of sex dim by species, largely in canine size.</td>
<td>Study based on dimorphism in extant tayassuids.</td>
</tr>
<tr>
<td>H20</td>
<td>Measurements, PCA, cluster analysis</td>
<td>None</td>
<td>Proposed sexual morphs based on clustering</td>
<td>Study was based on sex dim in the metacarpals of extant <em>Bison</em></td>
</tr>
</tbody>
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Table 2.5 Continued. Part 3 of 4.

<table>
<thead>
<tr>
<th>C</th>
<th>Author</th>
<th>P</th>
<th>Taxon</th>
<th>N</th>
<th>Feature Assessed</th>
<th>E</th>
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<tbody>
<tr>
<td>H21</td>
<td>Van Valkenburgh and Sacco 2002</td>
<td>41</td>
<td>Carnivora: <em>Canis; Smilodon</em></td>
<td>338; 111</td>
<td>Skull and teeth</td>
<td>Y</td>
</tr>
<tr>
<td>H22</td>
<td>Anton et al 2004</td>
<td>41</td>
<td>Carnivora: <em>Machairodus</em></td>
<td>16</td>
<td>Skull and teeth</td>
<td>Y</td>
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<tr>
<td>H23</td>
<td>Samuels and Binder 2009</td>
<td>42</td>
<td>Carnivora: <em>Panthera</em></td>
<td>13</td>
<td>Jaw length, teeth dimensions</td>
<td>Y</td>
</tr>
<tr>
<td>H24</td>
<td>Gingerich 1981a</td>
<td>43</td>
<td>Primates: <em>Adapis</em></td>
<td>8-11</td>
<td>Skull, teeth</td>
<td>Y</td>
</tr>
<tr>
<td>H25</td>
<td>Gordon et al 2008</td>
<td>45</td>
<td>Hominoids: <em>Australopithecus</em></td>
<td>17</td>
<td>Humeri, radii, femora, tibiae</td>
<td>Y</td>
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<tr>
<td>M1</td>
<td>Sander 1989; Reippel 1989</td>
<td>11</td>
<td>Pachypleurosauria: <em>Neusticosaurus</em>; <em>Serpianosaurus</em></td>
<td>340; 35</td>
<td>Humerus, SSD</td>
<td>N</td>
</tr>
<tr>
<td>M2</td>
<td>Dodson 1976</td>
<td>18</td>
<td>Ceratopsia: <em>Protoceratops</em></td>
<td>24</td>
<td>Multiple cranial variables</td>
<td>N</td>
</tr>
<tr>
<td>P3</td>
<td>Dodson 1975</td>
<td>17</td>
<td>Hadrosauria: <em>Lambeosaurus</em> and <em>Corythosaurus</em></td>
<td>36</td>
<td>Cranial elements</td>
<td>N</td>
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<tr>
<td>P10</td>
<td>Mallon et al 2011</td>
<td>21</td>
<td>Ceratopsia: <em>Anchiceratops</em></td>
<td>8</td>
<td>Multiple cranial variables</td>
<td>N</td>
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<tr>
<td>P15</td>
<td>Smith 1998</td>
<td>25</td>
<td>Theropoda: <em>Allosaurus</em></td>
<td>54</td>
<td>Femoral head, dentary dimensions</td>
<td>N</td>
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<tr>
<td>C</td>
<td>Methods</td>
<td>Sig. Stats</td>
<td>Conclusions</td>
<td>Comments</td>
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<tr>
<td>H21</td>
<td>Plotting CV against sex dim, &quot;mean method&quot;, finite mixture analysis. Comparison with 7 extant canids; 11 extant felids</td>
<td>Spearman's rank correlation coefficient</td>
<td>For both species proposed male and female sexual morphs; males with larger canines</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>H22</td>
<td>&quot;Mean method&quot;. Comparison with sex dim indices from 11 extant felids</td>
<td>None</td>
<td>Reported sex dim akin to that of extant lions and leopards</td>
<td>Used a sexed sample of extant lion specimens as a proof of concept of methods</td>
<td></td>
<td></td>
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<tr>
<td>H23</td>
<td>Regression of jaw length vs per cent pulp cavity closure; model fit testing</td>
<td>Spearman's rank correlation coefficient, ANOVA, AIC</td>
<td>Identified 6 females, 7 males</td>
<td>Used a sexed sample of extant lion specimens as a proof of concept of methods</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H24</td>
<td>Ratios, bivariate plots, allometric scaling coefficients</td>
<td>None</td>
<td>Assigned sex to specimens in two species <em>A. magnus</em> and <em>A. parisiensis</em>; males with larger skulls, canines, crests, and broader zygoma</td>
<td>Compared ratios and scaling coefficients with extant dimorphic and monomorphic primates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H25</td>
<td>Mean method, with multivariate data set and repeated sampling measures of comparative extant samples and of fossil sample</td>
<td>Yes</td>
<td>Supported post-cranial sex dim similar to that of gorillas and orangutans.</td>
<td>Supports similar findings by Lockwood et al 1996, contrasts the conclusions of Reno et al 2003, 2005; Scott and Stroik 2006</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M1</td>
<td>Measurements, comparison of specimens, frequency histograms</td>
<td>None</td>
<td>Proposed sexual dimorphs, hypothsized sexes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M2</td>
<td>Principal coordinates analysis, bivariate plots</td>
<td>None</td>
<td>Proposed sexual morphs; identified 7 females, 8 males</td>
<td>Deemed 'inconclusive' by Evans and Reisz 2007</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P3</td>
<td>Principal coordinates analysis, bivariate plots, allometric coefficients</td>
<td>None</td>
<td>Proposed sexual morphs</td>
<td>Deemed 'inconclusive' by Evans and Reisz 2007</td>
<td></td>
<td></td>
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<tr>
<td>P10</td>
<td>PCA, heirarchical clustering, K-means clustering</td>
<td>None</td>
<td>Concluded non-sexual variation, supported synonomy</td>
<td>Good and thorough methods.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P15</td>
<td>Frequency histograms, Shapiro-Wilk test, PCA, CV's</td>
<td>None</td>
<td>Suggested sex dim as a possible explanation of observed variation.</td>
<td>Good and thorough methods.</td>
<td></td>
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Chapter 3: Selection of Exemplar Taxa for the Study of Sexual Dimorphism in Ceratopsids

“The necessity of using neozoological data as a frame of reference in paleozoology must be emphasized,” (Kurten, 1969).

3.1 Introduction

In light of Chapter 2, it is clear that studies of sexual dimorphism in the fossil record have been undertaken in a variety of ways, with many approaches employed and a broad range of confidence attributed, or attributable, to the results. It would appear that the simplest method for studying sexual dimorphism in an extinct taxon is to compare it directly with closely related extant taxa and to search for a similar dimorphic condition. Hypotheses of this sort can often be supported using relatively small sample sizes, by direct comparison between individual specimens, or, when appropriate, by repeated sampling measures. When a related extant species is not available, however, the most convincing demonstrations of sexual dimorphism have resulted from thorough studies of morphological variation. It is also clear that when related extant species are unavailable for direct comparison it is still of utmost importance to test methods or validate approaches using the extant biota before drawing conclusions for fossil taxa. To this end, the careful consideration of extant taxa with analogous characteristics may provide exemplar lines of inquiry that can be appropriated for use with fossil taxa. In this case such an approach is adopted for ceratopsid dinosaurs.
3.1.1 The Merit of Models

In order to guide the investigation of dimorphism in ceratopsid horns, it was necessary to develop a research model based on living animals with ostensibly analogous features. The intention of the model is to provide a means for developing and calibrating appropriate methods of investigation, to provide an interpretable dataset similar to the one expected to be obtained for ceratopsids, and to inform the construction of meaningful hypotheses for testing in ceratopsids. Establishing an informative model can therefore be extremely beneficial for the study. Several methods were identified in the previous chapter that may be potentially useful for investigating sexual dimorphism in ceratopsid dinosaur horns, so the next step is to decide which taxa would be most informative as analogous models.

Unfortunately, the closest extant relatives of ceratopsid dinosaurs are birds and crocodilians, and phylogenetic distance and evolutionary time have almost certainly nullified any information relevant to sexual dimorphism that could have been derived from their shared common ancestry. As a result the extant model should be based upon relevant analogy instead of homology, which opens the door to several possible candidates.

3.1.2 The Selection of Bovids and Pronghorn

Three species of horned ruminants were selected as exemplar organisms for this study, for several reasons. After considering several other candidate exemplar taxa, including cervids, chameleons, and horned lizards of the genus *Phrynosoma*, bovids were selected as a focal group for anatomical, functional, and pragmatic reasons, as outlined here.

The horns of bovids have been extensively studied and, with a bony core and a permanent keratinized sheath, they closely approximate the hypothesized anatomy of ceratopsid horns
(Sampson et al., 1997; Hieronymus et al., 2009; Happ, 2010). Chameleon and *Phrynosoma* horns would likely also serve as informative analogues, but fall short in terms of size and sample abundance. The antlers of cervids are unique anatomically and occur only in males (except in *Rangifer*, a derived condition), features that render them less than desirable as models for a clade with non-branching horns seemingly exhibited by both sexes.

Bovids employ their horns for many of the biological roles that ceratopsid horns are hypothesised to have served and, more importantly, have been extensively studied in this regard. This constitutes a body of literature that can inform and guide the questions surrounding horn function, form, and evolution in ceratopsids. Of course, this also risks biasing the perspective of these questions, so an effort must be made to not conflate bovid research with ceratopsid hypotheses.

Finally, pragmatic considerations suggested that bovids would serve as useful ceratopsid analogues – they are abundant, large, and represent a wide range of expression of sexual dimorphism. Having decided upon Bovidae as a focal clade, mountain goats (*Oreamnos americanus*) and North American bison (*Bison bison*) were selected as exemplar species due to their availability in western Canada and abundance in museum collections, their differing expression of horn sexual dimorphism (slight in mountain goats, moderate in bison), their different body sizes, their different breeding habits, and the differing use of their horns. Their horns are also relatively simple as far as bovids go, facilitating measurement and reducing confounding morphological variation. Furthermore, mountain goat horns are known to be sexually dimorphic in shape, making them particularly useful as models for investigating shape variation.
Pronghorn, although not bovids, were then added to the study as an additional exemplar taxon. Dramatically sexually dimorphic in horn form, but subtly if at all sexually dimorphic in cranial dimensions, they provide additional challenges to the study of horn dimorphism. Pronghorn are also abundant in museum collections and are available for study in western Canada, making them a desirable study taxon. Like mountain goats, they are of a convenient size to work with, although their horns are more challenging to measure than those of mountain goats or bison.

3.2 Relevant Characteristics of the Exemplar Taxa

The following discussion provides additional relevant information about sexual dimorphism, growth, and life history, as well as about horn growth, form, and use, in bovids in general, and for each of the three exemplar species.

3.2.1 The Occurrence and Degree of Sexual Dimorphism in Bovids

In general, extant mammals display a pattern of male-biased sexual size dimorphism (SSD), with an average male/female mass ratio of 1.184 (Lindenfors et al., 2007). Also, mammalian species that are subject to greater sexual selection pressure tend to exhibit a greater degree of male-biased SSD, although this is not absolutely so, and several exceptions exist (Lindenfors et al., 2007). This tendency has, however, been well established for ungulates, with the level of polygyny typically being used as a measure of the intensity of sexual selection. More polygynous species exhibit a greater degree of male-biased SSD (Jarman, 1974; Weckerly, 1998; Loison et al., 1999; Perez-Barberia et al., 2002; Bro-Jørgensen, 2007; Lindenfors et al., 2007).
Bovids, in particular, display a wide range of SSD (Loison et al., 1999), with females being heavier than males in the smallest species, and males being considerably heavier (up to twice as heavy) than females in some medium- to large-sized species. The greatest male/female mass differentials occur in medium-sized bovids (approximately 50 – 100 kg), and the mass difference between the sexes tends to decrease toward monomorphism in the largest species (Jarman, 2000). This pattern, with female-biased SSD existing in the smallest bovids and male-biased SSD peaking in mid-size bovids, is related to a correlation between SSD and the level of polygyny, which, in turn, is influenced by a correlation between the level of polygyny and body mass (Loison et al., 1999; Bro-Jorgensen, 2007). There appears to be a body mass threshold for polygyny that mitigates against small bovids expressing a polygynous mating strategy (Jarman, 2000), because no ruminant species under 20-30 kg is polygynous and none over 90 kg is monogamous (Loison et al., 1999). Underlying these observations is a complex interplay between selection pressures and breeding strategies, wherein male body size is under selection to increase in polygynous species due to the significant payoffs in reproductive success conferred on males that dominate contests, whereas female body size is maintained near a species-specific weight due to the lifetime reproductive advantages gained by investment in earlier reproduction over continued growth (amounting to fecundity selection) (Jarman, 2000; Lindenfors et al., 2007). Ontogenetically, these differences in adult body weight typically result from both longer growth periods for males than females, and more rapid growth in males (Jarman, 1983). An interesting alternative occurs in pronghorn, with juvenile males growing at the same rapid rate as juvenile females, but simply maintaining this growth rate for a few months longer (Byers, 1997).

The horns of bovids also exhibit a wide range of sexual dimorphism, from a complete absence of female horns in some species, such as the greater kudu (*Tragelaphus strepsiceros*), to
monomorphism in others, such as the Japanese serow (*Naemorhedus crispus*) (Bro-Jorgensen, 2007). Males of all 135 bovid species possess horns (Lundrigan, 1996), but in only 82 species do females possess horns (Stankowich and Caro, 2009). For those taxa in which both males and females sport horns, the majority are dimorphic with respect to size. The earliest bovids in the fossil record (such as *Eotragus*) were sexually dimorphic, with males already possessing short, straight horns and females lacking horns entirely (Janis, 1982). From these simple origins, male horns are thought to have evolved into their manifold forms today, primarily via sexual selection in the form of male-male competition (Packer, 1983; Lundrigan, 1996; Caro et al., 2003; Bro-Jorgensen, 2007; Stankowich and Caro, 2009). Horn length in male bovids scales positively with body size and breeding group size, and scales negatively with territoriality and female horn size (Bro-Jorgensen, 2007). The evolution of female horns is less well understood, but their horns are suggested to be primarily associated with predator defence and female territoriality (Jarman, 2000; Bro-Jorgensen, 2007; Stankowich and Caro, 2009).

Like many, although certainly not all, sexually selected structures (see Bonduriansky, 2007), bovid horns exhibit positive allometry, even in females. Positive allometric growth of horns in ontogeny is readily apparent, because neonates are born with, at most, incipient horns. With regard to interspecific positive allometry, relative horn size in males follows a distribution similar to the one previously described for SSD, increasing positively before peaking between 50 and 100 kg and decreasing again in the largest species (Jarman, 1983). The overall trend is positive. This similarity of pattern is not surprising, because, as for SSD, there is a correlation between horn size and level of polygyny (Bro-Jorgensen, 2007). Evidence of this can be found in two separate treatments of African antelope. A regression of horn length against shoulder height for 76 species of African antelope yielded an allometric coefficient of 2.2, indicating a marked
increase in relative horn size with increasing body size (Gould, 1974). However, a similar regression conducted for 46 species of African antelope separated by breeding strategy yielded two significantly different slopes, a near isometric plot for monogamous species and a positively allometric slope for polygynous species (Bubenik, 1990). This suggests that positive allometry of horns is not simply a taxonomic feature but is dictated, in large part, by the level of polygyny, and therefore, ultimately, by the intensity of sexual selection.

3.2.2 Exemplar Taxon 1: Oreamnos americanus

*Oreamnos americanus*, the mountain goat, is nested deep within the family Bovidae, but its exact position within the subfamily Caprinae is still debated (Ropiquet and Hassanin, 2004; Hernandez and Vrba, 2005; Campos et al., 2009). Mountain goats are not members of the genus *Capra*, and as a result are not true goats (Cote and Festa-Bianchet, 2004). Four subspecies have been identified in the past (*O. americanus americanus, O. a. kennedyi, O. a. missoulae, and O. a. columbiae*), although none are currently recognized (Côté and Festa-Bianchet, 2003). Another species, *Oreamnos harringtoni*, was considerably smaller than *O. americanus* (Mead and Lawler, 1994) and lived in the American west during the Pleistocene, but became extinct roughly 11,000 years ago (Campos et al., 2009).

A study of a population from Caw Ridge, Alberta indicated that adult body size in mid-summer is about 95-115 kg for males and 60-75 kg for females (Côté and Festa-Bianchet, 2003), revealing substantial sexual size dimorphism in body mass. This dimorphism develops after weaning, with males being about 10% heavier than females by the end of their first year and the disparity continuing to increase into adulthood (Houston et al., 1989). Despite the large discrepancy in body mass, dimorphism in skeletal dimensions is small, adult males being
typically only 5% taller at shoulder height and 7% larger in chest girth (Côté and Festa-Bianchet, 2003). Both sexes lose mass over the winter (Côté and Festa-Bianchet, 2003), so it is likely that the degree of mass dimorphism is less during the winter, as has been reported for the northern chamois (*Rupraca rupicapra*) (Rughetti and Festa-Bianchet, 2011).

The breeding habits of mountain goats are difficult to study, and as a result, are not extensively known (Geist, 1964; Mainguy et al., 2008). Both males and females may mate with multiple partners during a single rut, causing Mainguy et al. (2008) to classify their mating habits as polygamous and not polygynous. As well, both sexes appear to exercise mate choice (Geist, 1964; Mainguy et al., 2008). Females aggressively reject male courtship leading up to, and following, the rut, and gradually become more receptive to males as they near estrous (Geist, 1964; Mainguy et al., 2008). Dominant males employ a tending strategy to form a consort pair and to isolate an estrous female from other males, and will chase off less dominant males, that may attempt to copulate with the tended female, by employing a coursing strategy (Mainguy et al., 2008). Dominant males are most likely to tend ‘experienced’ females of high social rank and greater age, an interesting example of mate choice thought to be correlated with the tendency of older females to produce more offspring and a greater proportion of sons (Mainguy et al., 2008). Sex ratios at birth are 1:1, but differential male mortality means that by three years of age and beyond, male:female ratios fall to 1:2 or 1:3 (Côté and Festa-Bianchet, 2003). Of particular note, older mothers are more likely to produce sons than are younger mothers, with females 3-6 years of age yielding 70% daughters, and females 11 years or older producing 80% sons (Côté and Festa-Bianchet, 2001). Mountain goats are relatively long-lived, but data from Caw Ridge suggests that 25% of yearling females and only 6% of yearling males will survive to an age of 13 years (Côté and Festa-Bianchet, 2003).
Both male and female mountain goats possess horns, and employ them as weapons (Geist, 1964, 1967; Mainguy et al., 2008). Mountain goats do not fight by locking horns, but rather they stab at each other’s flanks in an anti-parallel stance (Geist, 1967). These fights are rare but are highly dangerous, often being fatal to one of the combatants. Males employ intense ritualized displays to resolve most agonistic encounters without resorting to fighting, and seem to display a reluctance to strike with their horns (Geist, 1964, 1967; Mainguy et al., 2008). Female-female aggression is high in mountain goats, and females will employ their horns to threaten or attack conspecifics (Fournier and Festa-Bianchet, 1995); a female killed a male with her horns after they were left together in a small paddock (Geist, 1967).

Horn form in mountain goats is nearly monomorphic. Horn growth in both sexes begins at birth and continues throughout life, although >95% of horn growth is achieved by age 4 (Côté et al., 1998). Males grow a longer first increment (first 18 months) than females, but by age 6 females have caught up and possess slightly longer horns than males when corrected for body size (Côté et al., 1998). Male horns are significantly greater in circumference than are those of females, both absolutely and relative to body size, at all ages (Côté et al., 1998). Along with basal circumference, male and female mountain goats are most readily distinguished in the field by the shape of their horns (Smith, 1988). Male horns have a greater curvature that is continuous over the length of the horn, whereas female horns are straighter and possess a distinct crook 50 to 75 mm from the tip that forms as a result of slowed growth during the first winter (Smith, 1988).

In summary, *O. americanus* is a relatively long-lived, medium-sized polygamous bovid, with moderate SSD in body mass and slight sexual dimorphism in horn form. Sexual selection operates through both male-male competition and female mate choice; males in particular employ ritualized behaviour and limit instances of fighting, although fights do still occur and are
highly dangerous. Females will use their horns aggressively in dominance interactions and defense.

3.2.3 Exemplar Taxon 2: Bison bison

The North American bison, *Bison bison*, is nested deep with the Bovinae, the subfamily of bovids that includes cattle, bison and buffalo. It shares the genus with the European bison, or wisent, *Bison bonasus*, and the sister taxon to the Bison clade is the yak (*Bos grunniens*) (Fernandez and Vrba, 2005; Stankowich and Caro, 2009). Bison are closely related to cattle, and considerable debate has occurred as to whether to include bison within the genus *Bos* (Reynolds et al., 2004). Unless otherwise noted the term ‘bison’ will be used in reference to the North American species, *Bison bison*.

There are two currently recognized subspecies of bison, the plains bison (*Bison bison bison*), and the slightly larger wood bison (*Bison bison athabascae*). They are distinguished by several slight differences in morphology, including dorsal profile, the thickness of hair on the head, presence of chaps on the forelimbs, and length of the tail (van Zyll de Jong et al., 1995; Gates et al., 2010). The recognition of these subspecies is also supported by genetic data, Wilson and Strobeck (1999) found greater genetic distances between wood and plains bison populations than within either subspecies. They reported that the subspecies functioned as separate entities despite genetic evidence for hybridization. Reynolds et al. (2003) and Gates et al. (2010) present reviews of the literature surrounding the validity of the subspecies. All populations of modern North American bison share a most recent common ancestor that existed south of the continental ice sheets between 22 and 15 ky B.P., and belong to a clade that diverged from Beringian bison populations some 83 to 64 ky B.P. (Shapiro et al., 2004).
Bison are gregarious animals that form mobile groups of mixed sex and age-classes, with fluid intra-group movement of individuals (Komers et al., 1992). Bulls typically only join the mixed sex groups during the rut, and live in bachelor groups or alone for the remainder of the year (Komers et al., 1992). During the rut cows outnumber bulls in these mixed-sex groups, and typically only mate once with a single bull during an estrous period, resulting in a polygynous mating strategy with dominant bulls securing the majority of matings (Wolff, 1998). During a three year study of a population of approximately 300 animals, Wolff (1998) reported that 50% of the 6+ year-old bulls bred each year, and that of 28 mature bulls observed, three sired no calves and four bulls sired 10 or more calves over three years. Bulls employ a tending strategy to guard estrous cows, with dominant males tending cows early in the rut before exhausting themselves and leaving the group, creating the opportunity for less dominant males to tend cows that come into estrous later in the rut (Komers et al., 1992; Wolff, 1998). Tending is more successful than the alternate strategy of following tending bulls and attempting to challenge and replace them at opportune moments (Wolff, 1998). Bulls do not select between cows, but cows do appear to differentiate between males and use tactics such as approaching higher ranked bulls or running through groups in attempts to ‘upgrade’ a tending bull for one of more dominant rank (Wolff, 1998).

Bison reach sexual maturity by two or three years of age, but males do not typically participate in the rut, or secure matings, until 5 or 6 years of age, due to competition with older, larger males (Maher and Byers, 1987). Male reproductive effort is at its peak between 8 and 11 years, coinciding with the attainment of full adult size, and begins to decline by the age of 12 (Maher and Byers, 1987). Bison are fairly long-lived, and may reach ages of greater than 20 years in the wild (Berger and Peacock, 1988).
Bison exhibit SSD, with males being somewhat larger and considerably heavier than females. The male:female mass ratio is 1.6 – 1.8 (Kelsall et al., 1978; Berger and Peacock, 1988; Reynolds et al., 2003). As mentioned, wood bison are larger and heavier than plains bison; in populations studied at Elk Island National Park, Alberta, male and female wood bison reached asymptotic mean weights of 880 +/- 15.1 kg, and 540 +/- 5.7 kg at 8 and 7 years of age respectively, whereas male and female plains bison reached asymptotic mean weights of 739 +/- 10 kg, and 440 +/- 2.1 kg, at 8-9 and 6 years of age, respectively (Reynolds et al., 2003). Both sexes also exhibit seasonal weight changes, and considerable inter- and intra-populational variation in weight occurs in bison (Berger and Peacock, 1988). Sexual size dimorphism occurs in the skeleton as well, with males reported to be on average 12.5% larger than females in post-cranial variables (Reynolds et al., 2003). As well, skulls of males are larger and more massive than those of females, with more tubular orbits, larger horncores, and more rapid and complete fusion of the frontal and occipital sutures (Skinner and Kaisen, 1947; Shackleton et al., 1975). The greatest sexual variation, however, occurs in the dimensions of the horncores, which, along with basal skull length and cranial width, provide a reliable means for sexing aged crania (Guthrie, 1966; Shackleton et al., 1975).

As in all other bovids, the horncores of bison arise from the frontal bones, but, as in all Bovini, the frontal bones and their associated sinuses are swept posteriorly relative to the rest of the cranium, resulting in the location of the horncores posterior to the orbits (Solounias, 2007). Both sexes grow relatively short, curved horns that project laterally from the side of the head and point dorsally. Horns of males are more strongly burred at the base and are proportionally stouter; those of females are similar in general form but are smaller and more slender (Meagher, 1986). In older males the keratinous sheath can become quite rugose at the base, and counting
growth rings is not a viable means of estimating age in bison. Horns may also become heavily worn at the tips, sometimes revealing multiple layers of keratin.

Bull bison use their horns in agonistic encounters with other males. Behaviours including threat displays and bellowing are used to assess relative condition and fighting ability, and may resolve encounters before physical contact occurs (Wolff, 1998). If the contest escalates to a fight, which happens relatively frequently (59 bulls were involved in 1088 fights over three years [Wolff, 1998]), males will collide head-on and then twist their heads to bring the horns into contact with their opponent’s head. Occasionally a bull will attempt to gore the flank of a retreating rival or unattentive bull, and broken ribs are common in bulls (Reynolds et al., 2003). Fights are violent and the horns are dangerous; in a three year study Wolff (1998) reported that 21 of 73 mature bulls were injured in some way during fights, including two deaths, two bulls blinded in one eye, five body wounds and five broken legs. Female bison also use their horns in agonistic encounters, employing horn thrusts as one of several aggressive actions (Vervaecke et al., 2005). Horns are important in relation to fighting ability and dominance rank. A top-ranking female that lost both horns in a fight fell to the lowest rank in the female dominance hierarchy the following year (Vervaecke et al., 2005). Bison of all age/sex classes also use their horns in a behaviour known as ‘horning’, wherein they rub their horns, head and shoulders against trees, shrubs, or other objects (Coppedge and Shaw, 1997). The motivation behind the behaviour is not well understood, but is thought to be related to relief from insect harassment, and possibly as an outlet for aggression (Coppedge and Shaw, 1997).

In summary, *Bison bison* is a large, long-lived, polygynous bovid with two recognized subspecies. It has a body mass SSD ratio of 1.6 - 1.8, and some sexual dimorphism in horn form, particularly horn size. During the rut sexual selection operates through both male-male
competition and female mate choice. Both sexes use their horns as weapons in aggressive dominance encounters with conspecifics, and males are particularly combative during the rut.

3.2.3 Exemplar taxon 3: Antilocapra americana

The phylogenetic position of the antilocaprine clade within ruminant artiodactyls is debated; in the past it has been suggested to lie within the superfamily Bovoidea, the superfamily Cervoidea, and as the link between the two (see Janis, 2000; Fernandez and Vrba, 2005). A composite supertree constructed using morphological, ethological, and molecular information retrieved the Antilocapridae as sister group to Giraffidae, together comprising the superfamily Giraffoidea, which was identified as the sister clade to Cervoidea + Bovoidea (Fernandez and Vrba, 2005). Similar findings have been reported elsewhere (Carling et al., 2003), providing support for the hypothesis. Part of the difficulty of placing pronghorn arises from their unique cranial ornaments, their pronghorns, which are discussed further below.

Pronghorn are not antelope, but rather are the sole-remaining members of a once-diverse North American clade, the Antilocapridae. Antilocaprids first appear in the fossil record in the late Hemingfordian North American land mammal age (NALMA) (early Miocene), and reach a peak diversity of fifteen species arrayed in nine genera during the Hemphillian NALMA (late Miocene) (Davis, 2007). Early antilocaprids, often identified as the paraphyletic subfamily “Merycodontinae”, were gracile, cursorial ungulates with smaller body sizes than extant pronghorn (Janis, 1982; Byers, 1997; Davis, 2007). Purported females were hornless, whereas males had branching or palmated horns with a burred pedicel and impressed sulci similar to the antlers of cervids; however, unlike cervids, they did not appear to shed their horns (Janis, 1982; Davis, 2007). “Merycodontids” persisted until the end of the Clarendonian NALMA in the late
Miocene, but gave rise to, and were seemingly replaced by, the Antilocaprinae, the monophyletic subfamily of derived antilocaprids that includes the extant pronghorn (Byers, 1997; Davis, 2007). Antilocaprides are united mainly by features of their horncores, including the loss of burrs from the horncore shaft, the inferred presence of a keratinous sheath, mediolateral flattening of the shaft, and the occurrence of horns in females, as well as by a highly hypsodont dentition, enlarged auditory bullae, and modifications of the distal regions of the limbs (Janis and Manning, 1998).

Pronghorn range over much of western North America, from southern Alberta and Saskatchewan in the north to northern Mexico (including the Baja peninsula) in the south. Today only a single species exists, with five nominal subspecies (A. americana americana, A. a. oregona, A. a. mexicana, A. a. peninsularis, and A. a. sonoriensis), although the validity of the subspecies designations has been questioned (Brown, 2006). Morphological differences between them are slight, with the species being characterised as being “remarkably monotypic” (Brown et al., 2006).

Pronghorn typically give birth to twins (O’Gara, 1969). The sex ratio at birth is near parity, although dominant females give birth to an increased proportion of sons, and at birth the sexes are similar in size and weight (Mitchell, 1971; Byers, 1997). A sample of pronghorn collected in Alberta from 1962 through 1966 yielded mean total body lengths of 1,416 mm for mature males and 1,406 mm for mature females, and mean body weights of 56.4 kg and 50.5 kg (with ranges of 46 – 70 kg and 47 – 56 kg), for males and females, respectively (Mitchell, 1971). Brown et al. (2006) also reported that sexual dimorphism in body size is negligible other than in body mass, with males being heavier than females. Body weight varies seasonally, with males attaining their heaviest weights in late summer before the rut, and losing mass through the fall
and winter. As a result, mature males weigh more than females through most of the year, but not in the winter (Mitchell, 1971). Adult males typically live eight to ten years, whereas females live twelve to fourteen years (Byers, 1997).

Pronghorn organize into large mixed-sex herds during the winter, but with the arrival of spring, males split off to form bachelor herds or to establish territories that they will defend from early spring until after the rut in the late fall (Kitchen and Bromley, 1974). The rut generally occurs in September, but timing varies between populations and more southerly populations have later and longer rutting periods (O’Gara, 1990).

Pronghorn have a polygynous mating system with some unique characteristics. Their mating system operates on the basis of sequestration of females by males and is typically territorial, but can also be manifested as harem defense (Bromley, 1991; Byers, 1997). At three years of age males typically become solitary and site-loyal, returning to the same territory or area every summer for most of their life (Byers, 1997). Dominant bucks establish large territories and actively defend them from intrusion by other males (Kitchen and Bromley, 1974). Young males, along with some non-territorial mature bucks, form bachelor herds that roam on unclaimed areas or at the edges of territories and the movement of which is restricted by territorial males (Kitchen, 1974; Byers, 1997). During the rut these bachelor herds break into smaller groups which then harass territorial males and attempt to drive does from their territories, or to intercept does travelling between territories.

Females seek out male territories, often as a means of escaping harassment by bachelors, and actively switch between territories (Bromley and Kitchen, 1974; Byers, 1997; Min, 1997a). Switching occurs with increasing frequency as females near estrous; a behaviour Byers (1997) suggests is a form of non-comparison-based mate choice. Besides territory sampling, females
also employ two other mating strategies: inciting chases and fights between males and mating with the victor, or forming an isolated pair with a single non-territorial male and remaining with him throughout the rut (Byers et al., 1994). Pronghorn females exert complete control over copulation success because males require the cooperation of females to achieve intromission, and the female can terminate the attempt with a single step forward (Bromley and Kitchen, 1974; Byers, 1997). This provides them with a powerful mechanism for mate choice, and studies suggest that females select vigorous males able to defend territories or harems (Byers et al., 1994; Min, 1997a). Min (1997a) found that females assess the males themselves, not the territories they defend. This supports the suggestion by Byers (1997) that males hold territories to isolate females from other males, and that the value of a territory lies in its usefulness for hiding females, not in its forage resources, as previously suspected (Kitchen, 1974).

As mentioned, sexual differences in size are not apparent at birth, but other sexual differences are visible. Males are born with small horn buds and visible subauricular glands, neither of which are present in females, and by the age of 12 weeks males have 2-4 cm horns (Byers, 1997). Growth is rapid in both sexes during the first 7-8 months of life. After this point female growth slows, whereas male growth continues at juvenile rates until approximately the end of the first year, resulting in a greater body mass in yearling and adult males (Byers, 1997). Relative growth rates also differ between the sexes, with males having proportionately broader heads and longer legs by 4-6 weeks, possibly due to sacrificed fat accumulation as a trade-off for increased skeletal growth (Byers, 1997). By three years of age, males become indistinguishable from older males and participate in the rut. Mating success for males peaks between the ages of three and seven (Byers et al., 1994). Surprisingly, male reproductive success has not been found to be correlated with age, body size, or size of horns (Bromley, 1991; Byers et al., 1994; Min,
Mating success is strongly correlated with the number of females maintained during the rut (Byers et al., 1994), and the ability to maintain territories or harems appears to be directly related to dominance rank and vigour (Kitchen, 1974; Bromley, 1991; Byers et al., 1994). Dominance, in turn, appears to be related to some measures of quality, including cheek patch size, but specific cues have yet to be determined (Kitchen, 1974; Kitchen and Bromley, 1974; Bromley, 1991; Byers et al., 1994; Byers, 1997; Min, 1997b), and generally dominance is associated with the uninformative term ‘confidence’. However there is anecdotal evidence from the use of hunting decoys that bucks can assess the size of a rival’s horns and behave accordingly (O’Gara, 1990).

The horncores of pronghorn arise from the frontal bones directly, without a pedicle, and are typically medio-laterally compressed and blade-like in males. In females the horncores are much shorter and remain elliptical in cross-section.

Pronghorn sheaths consist of keratin (O’Gara and Matson, 1975), and their general form involves a medio-laterally flattened shaft that tapers distally to a sharp, medially to medio-posteriorly directed hook, and a short, anteriorly-directed prong located mid-way up the shaft. Horn shape, inclination and curvature can vary considerably between individuals (O’Gara, 1990). Horn growth in pronghorn is closely linked to the annual testicular cycle (O’Gara et al., 1971). New horn growth begins beneath the existing sheath during the rut in September, just after peak testis size is achieved, and results in the dislodgement and casting of the previous horn sheath in late November or December (O’Gara et al., 1971). The prong and distal hook grow from two separate centres on the horncore, but by March they merge into one sheath structure; elongation of the sheath continues until July, at which point growth ceases (O’Gara and Matson, 1975).
The prongs are capable of catching the horns of rivals, and are used in this manner (Kitchen and Bromley, 1974; O’Gara, 1990; Byers, 1997), whereas the medially-directed hooks are used to swipe at and gore the heads or necks of opponents while fighting, or the rumps of fleeing opponents (Kitchen and Bromley, 1974; Byers, 1997). The hooks are sharp and are capable of inflicting fatal wounds (Kitchen and Bromley, 1974; Byers, 1997). Fights are rare, but violent. Of 15 fights observed by Kitchen and Bromley (1974), 14 occurred during the rut and five resulted in the infliction of injuries. An additional buck was found dead, with puncture wounds attributed to fighting. Byers (1997) observed 82 fights between males in eight years, nearly all of which occurred in the presence of an estrous female. Fourteen injuries were observed, ten of which were fatal (Byers, 1997).

Females grow small horns that can reach a length of 10 cm, but are often nothing more than nubbins of bone with keratin caps (O’Gara, 1990). Females rarely grow rudimentary prongs, and horn sheath asymmetry is considerably more common and pronounced in females than in males (O’Gara, 1990). Despite this, females do occasionally use their horns (or heads) to butt or spar in dominance interactions (Kitchen, 1974), and there is one report of a horned doe attacking a coyote with her head, although hooves are typically used for predator defence (O’Gara, 1990).

In summary, pronghorn are small to medium-sized ruminants with a unique horn morphology and growth cycle. They are gregarious, exceptionally fast, and are the sole extant members of the antilocaprine clade. Males are heavier than females at maturity due to an extended growth trajectory, and grow forked horn sheaths annually that are much larger than the poorly-developed, rudimentary horn sheaths of females. Pronghorn are polygynous and males employ a territorial or harem-defense system to attempt to secure matings. Dominance
relationships are well established and agonistic encounters rely heavily on behaviour and display, whereas fights are rare but highly dangerous.

3.3 Conclusions

Three ruminant species were selected as exemplar taxa to develop an analogous extant model that is intended to guide and inform the study of sexual dimorphism of ceratopsid dinosaur horns. Mountain goats, bison, and pronghorn are North American ruminant artiodactyls that encompass a range of life styles, body sizes, and horn morphologies. They also reveal some associations between horn form, behaviour, and sexual dimorphism.

The horns of mountain goats are simple, stout, and sharp, and are very similar between the sexes. Males are reluctant to use their horns in fights, but both sexes are capable of inflicting deadly wounds with them. The horns of bison are more dimorphic than are those of mountain goats; the horns of male bison are stout and curved, whereas those of females are similar in form but more slender. Males employ their horns in agonistic combat with reasonably high frequency during the rut, and females also use their horns in dominance interactions, although with less frequency and violence than males. Notably, the proportionally stouter horns of males are better suited to withstanding the mechanical stresses of fighting than are the more slender horns of females, and the breakage of both horns by a dominant female supports this difference in functionality. The horns of pronghorn are dramatically sexually dimorphic, and are associated with a difference in behaviour between the sexes. Although females are known to butt at each other, they do not directly fight with their small horns. Males, by contrast, develop large, forked, horn sheaths that they display in dominance contests and, when necessary, employ in violent,
dangerous fights. The prongs and hooks of the male horn sheaths permit a fighting style with both defensive and offensive components.

Although it would be untenable to make suggestions about horn function or evolution in ceratopsids at this point, it is clear from the review of bovids, and from studying these three horned species, that the degree of sexual dimorphism in cranial horns is in part related to how those horns are employed and also to what kind of reproductive strategy is in effect. As a result, a more definitive understanding of sexual differences, or similarities, in horn morphology of ceratopsids may lead to the formulation of hypotheses that address these factors.

The horn dimorphism that was described here for the three exemplar species will be used as a means of assessing the utility of the various investigative methods identified in Chapter 2: frequency histograms, bivariate plots, Shapiro-Wilk tests, the coefficient of variation, the coefficient of bimodality, and, with a multivariate dataset, principal components analysis (PCA) and two types of cluster analyses. As well, the horn sheaths of mountain goats are also dimorphic in shape, with the horns of females possessing a distinctive crook in the distal portion, providing a foundation for testing methods of investigating shape dimorphism. The task of demonstrating sexual dimorphism in horn form is explored in the following chapter.
Chapter 4: Sexual Dimorphism in Bovids

“With problematic data, it is easier to interpret results if the behavior and biases of the morphometric techniques are well-known,” (Weishampel and Chapman, 1990).

4.1 Introduction
In the previous chapter, information was provided about three species of ruminant artiodactyls. They were reported to exhibit varying degrees of sexual dimorphism of horn morphology, as well as of body size and mass. However, when we move from studying the living animals to studying their skeletons, and when the sex of the specimens becomes uncertain, some of this information is lost, and demonstrating sexual dimorphism becomes more challenging. Because these are factors that are evident and reflective of the ceratopsid fossil record, this chapter documents a proof of principle study intended to test methods of demonstrating sexual dimorphism based upon skull material.

In the previous chapter, it was stated that mountain goats exhibit moderate levels of sexual dimorphism in body mass, and have slight, but detectable, dimorphism in the postcranial skeleton. The horns of female mountain goats are slightly longer, for a given body size, than those of males, but the horns of males are greater in basal circumference, both absolutely and relative to body size. The horns of males also curve continuously, whereas those of females are straighter and end in a distal ‘crook’. Bison exhibit greater sexual dimorphism in body mass than do mountain goats, and a slightly greater degree of dimorphism in the dimensions of the postcranial skeleton. Skulls of male bison are larger than those of females, with proportionally larger horns and horncores as well. Pronghorn are considered to be monomorphic in body size,
although adult males weigh significantly more than adult females. Their horns and horncores are strongly sexually dimorphic, with males developing large forked horns and females growing little more than nubbins of bone and caps of keratin.

So, with this information in hand, it was attempted, for each of the three exemplar species, to demonstrate these dimorphic horn characteristics from samples of their skulls. This was done using tests of equality of means and an index of sexual dimorphism. The results were then used to investigate the following methods, identified in Chapter 2: frequency histograms, bivariate plots, Shapiro-Wilk tests, the coefficient of variation, the coefficient of bimodality, and, with a multivariate dataset, principal components analysis (PCA) and two types of cluster analyses. Following the discussion in Chapter 3 of shape dimorphism in mountain goat horns, eigenshape analysis was also explored as a method of investigating dimorphism in horn shape for mountain goats and bison.

4.1.1 Objectives

To effectively carry out this proof of principle study, its objectives are as follows:

1) To sex, age, and measure a representative sample of skulls from each of the three exemplar taxa.
2) To assess the degree of sexual dimorphism in multiple dimensions of the horn sheaths and horncores of the exemplar taxa.
3) To assess several known methods of investigating sexual dimorphism in the context of their ability to reveal dimorphic patterns in an unsexed sample of skulls.
4) To test the effectiveness of Eigenshape methods for investigating dimorphism in horn shape.

Objectives 1-3 build directly upon each other, and will be addressed in a sequential and consecutive order. The fourth objective is somewhat more independent and will be addressed in a separate section of this chapter.
4.2 Materials and Methods

4.2.1 Material

Skeletal material for the three ruminant species was accessed in the collections of the following institutions: The Royal Alberta Museum, Edmonton (RAM); The University of Alberta Museum of Zoology (UAMZ), Edmonton; The Royal Ontario Museum, Toronto (ROM); The Canadian Museum of Nature, Ottawa (CMN); The American Museum of Natural History, New York (AMNH); The Yale Peabody Museum, New Haven, CT (YPM); and The Smithsonian Museum of Natural History, Washington, D.C. (USNM).

Material consisted of crania and associated horn sheaths. The skulls represent a combination of field collected, donated, and harvested specimens ranging from material collected over a century ago to very recently acquired material. Accession information was recorded when available, but sex, age, locality, and subspecies assignments were of variable completeness and reliability. Although post-cranial dimensions such as cross-sectional area of the femur can provide useful data related to body size, they would have contributed little information relevant to the interpretation of the ceratopsid fossil record (post cranial material is rarely associated with skulls in ceratopsids) and were not recorded. Most crania lacked associated mandibles. Although the majority of specimens included associated horn sheaths, some did not, particularly for pronghorn. Some mountain goat and bison specimens had horn sheaths that were firmly attached to the skull, preventing measurement of the horncores. Total sample sizes of crania for each species are: Oreamnos, n = 43; Bison, n = 50; Antilocapra, n = 65.
4.2.2 Measurements

Measurements were selected to best capture the varied morphologies of the horns and horn sheaths of the exemplar taxa, and to include some measure of body size. Measurements were made with Mitutoyo dial calipers, accurate to 0.05 mm and recorded to the nearest 0.1 mm, and with flexible measuring tape, recorded to the nearest 1 mm. Measurements were made three times and averaged, although circumstances occasionally required additional, or necessitated fewer, repetitions.

For all three species I recorded medio-lateral width and dorsoventral height of the foramen magnum with the calipers inserted into the foramen magnum perpendicular to the plane of the opening. This was intended to approximate a measure of body size similar to the use of the dimensions of the occipital condyle in ceratopsids (Anderson, 1999).

For all three species I recorded the antero-posterior length of the second upper molar (M2) at the alveolar margin. M2 length shows a high correlation with body mass for all ungulates ($r^2 = 0.933 – 0.944$) (Janis, 1990), and so was chosen as an indicator of body size. Because I was measuring specimens from a wide range of ages (and therefore a wide range of relative tooth wear) I decided to measure molar length at the alveolar margin. This was done in order to have a consistent reference point and to reduce complications from wear at the occlusal surface, as Janis (1990) reported that molar length decreases with progressive wear. However, the decision to measure length at the alveolar margin differed from the methods reported by Janis (1990) and Damuth (1990), which were to measure length of the occlusal surface, and maximum length, respectively, and I later realised that the alveolar margin does not provide a consistent reference point because the hypsodont tooth moves relative to the bone as it continues to erupt. This
change in measurement technique may have weakened the correlation with body mass, diminishing the value of M² length as an indicator of body mass. To investigate this, I tested the correlation between M² length at the alveolar margin and M² length at the occlusal margin for six specimens of each species. This was done using the program ImageJ (version 1.45s) to record relative measurements from laterally-oriented photographs of the toothrow, and then plotting the measurements in a reduced major axis regression. For Oreamnos, Bison, and Antilocapra, the squared correlation coefficients were \( r^2 = 0.876 \), \( r^2 = 0.915 \), and \( r^2 = 0.883 \), respectively. This suggests that the M² measurements recorded from the alveolar margin may be slightly less informative than intended, but should still provide useful information relating to body size.

The remainder of the measurements were of selected dimensions of the horns and horncores and were specific to each taxon, as outlined below and in Tables 4.1 – 4.3.

*Oreamnos americanus*: Figure 4.1 illustrates horn dimensions measured for mountain goats. The height of the horn sheath was measured along its anterior and posterior surfaces, from base to tip, with tape [following the curve from A to C, and B to C, respectively, in Fig. 4.1]. The chord of the sheath was also measured with tape, from the posterior basal rim of the horn sheath to its tip [straight line from B to C, in Fig. 4.1]; ‘chord’ was not measured for the horncore. For the basal dimensions of the sheath, the antero-posterior length and medio-lateral width were measured with calipers [length from A to B; width measured medio-laterally at the midpoint of A-B, in Fig. 4.1], and the basal circumference was measured with tape [around the sheath through points A and B, in Fig. 4.1]. Similar height and base measurements were recorded for the horncore, with the horncore ‘base’ being identified as the proximal rim of the burr [demarcated by D and
E, in Fig. 4.1]. All basal measurements were made perpendicular to the longitudinal axis of the horn or horncore.

*Bison bison:* Figures 4.2 and 4.3 illustrate horn dimensions measured for bison. Directions and orientations refer to the skull as it rests on its maxillary toothrows. Horn sheath length was measured for both the dorsal and ventral surfaces of the sheaths. This was done with measuring tape, from the dorsal and ventral points on the proximal rim of the sheath, following the curve of the surface of the horn, to the distal tip [following the curve from A to B, and C to B, in Fig. 4.2]. Dorsal and ventral horncore lengths were measured in a similar fashion to the horn sheaths [following the curve from A to B, and C to B, in Fig. 4.3], with the dorsal and ventral margins of the burr rim used as the proximal starting points. For both the horn sheaths and horncores, ‘chord’ was measured with tape as the distance from the dorsal sheath base, or horncore burr, to the tip [straight line from A to B, in Figs. 4.2 and 4.3]. Basal measurements included the height, width, and circumference of the horn sheath and horncore [height from D to E; width measured antero-posteriorly at the midpoint of D-E; circumference along the line connecting points D and E, in Figs. 4.2 and 4.3], with height and width considered relative to the orientation of the horns as the skull rests on its maxillary toothrows. Height and circumference were measured perpendicular to the longitudinal axis of the horn or horncore, and width was measured in the same plane. If the sheath was particularly rugose, or the burr knobby, care was taken to avoid bumps or protrusions that would increase the measurements. Basal height and width were measured with calipers whereas circumference was measured with tape.
Antilocapra americana: Figure 4.4 illustrates the horncore dimensions measured for pronghorn. The bony horncores of pronghorn range from nubbin-like buds to tall, medio-laterally flattened blades that diverge distally in a V-shape. This range of morphology, as well as the horncores’ smooth confluence with the bones of the skull roof (there are no pedicels or burrs), makes them challenging to measure. Horncore height was measured with tape as a straight line from the dorsal rim of the orbit to the distal tip [A to B, in Fig. 4.4], as per O’Gara and Matson (1975). For female specimens with very short horns, height and basal length were measured from digital photographs taken in lateral view, with a scale bar in the approximate plane of the horn. This was done using ImageJ v1.45s. A lack of photographs in anterior view with a reliable scale in the plane of the horns prevented this method from being used to measure horncore width.

For larger horncores, basal length was measured by placing the open calipers around the horncore and resting them on the dorsal rim of the orbit. This was used to establish a consistent location for the measurement on all specimens. The open calipers were then pressed against the lateral face of the horncore and tilted so as to become perpendicular to the longitudinal axis. The calipers were then closed and length measured [D to E, in Fig. 4.4]. Basal width was then measured medio-laterally at this same location [midpoint of D-E, in Fig. 4.4]. Because of the challenges of measuring basal circumference in a consistent location on smaller horncores, this dimension was not recorded at all. Height to the prong was measured only on male horncores. It was recorded as the distance from the dorsal rim of the orbit to the angle on the anterior edge of the horncore that demarcates the point of prong origination [A to C, in Fig. 4.4]. This was measured only for interest.

The horn sheaths of pronghorn are shed annually. Because of this, many specimens lack associated sheaths. For those specimens that possessed sheaths, they were measured while in
place on the horncore in order to facilitate comparison between horncore height and sheath height by maintaining a consistent starting point – the dorsal rim of the orbit. A small number of female specimens possessed sheaths that were no more than caps perched atop the horncore apices. These were not measured. Figure 4.5 illustrates horn sheath dimensions measured for pronghorn. Sheath height was measured along the curve of the lateral surface from the dorsal rim of the orbit to the distal tip of the sheath [A to B along the surface of the sheath, Fig. 4.5]. Height to the prong was measured as the shortest line from the dorsal rim of the orbit to the anterior tip of the prong [A to C, Fig. 4.5]. Prong length was measured along its dorsal surface from the notch to the tip [D to C along the surface of the prong, Fig. 4.5]. Basal length, width and circumference were measured at the base of the sheath, perpendicular to the longitudinal axis [length from E to F; width measured medio-laterally at the midpoint of the line between E and F; circumference around the sheath through points E and F, Fig. 4.5]. If the basal rim was tattered or broken, measurements were taken either slightly distally at the most proximal intact portion of the sheath, or not at all.

4.2.3 Ageing

Age classes were assigned to the specimens based upon photographs and observations that were recorded at the time the specimens were examined. Each taxon required its own ageing criteria. It was not the intention to assign a highly specific age to each individual, but rather to recognise coarse ontogenetic stages for each species and to distinguish adult specimens of both sexes from younger individuals. Assigning very specific ages, although likely possible (and labour intensive), would reduce the subsamples to impractical sizes, and would not reflect the currently limited ability to assess ontogenetic stages in ceratopsid specimens. Details of how age was assigned for each individual specimen are provided in Appendix A.
Oreamnos americanus: Ageing of mountain goats is somewhat more straightforward than it is for bison or pronghorn as long as the horn sheaths are preserved and in good shape, as was the case for most of the sample studied here. Kids are born in the early summer (mid-May to early June) and horn growth starts at birth (Côté and Festa-Bianchet, 2003). Growth occurs throughout the spring, summer and fall, and ceases during the winter, leading to the formation of annuli that demarcate annual growth (Côté and Festa-Bianchet, 2003). No annulus is formed during the first winter though, so an individual goat’s age can be estimated by counting the annuli on the sheath and adding one (Brandborg, 1955). Horn growth rate is greatest during the first years of life, and approximately 93% of total horn growth is achieved by age 3 (Côté et al, 1998), making it difficult to accurately distinguish annuli in, and therefore estimate age for, very old individuals. When dealing with skulls that no longer have preserved sheaths, ageing is more difficult.

Tooth replacement is not typically used to age mountain goats, but has been documented in the literature and was observed in this study. The third molars begin to erupt during the third year of life (that is, in two year old animals), with the upper molars erupting slightly later than those in the dentary, and are fully erupted in three year old goats (Brandborg, 1955). Tooth wear and loss can become severe in older individuals, but has not been documented as a proxy for ageing (Côté and Festa-Bianchet, 2003).

Field studies typically split mountain goat populations into kids (0-12 months), yearlings (13-24 months), two-year olds, and adults; three-year olds are not distinguishable from older individuals (Smith, 1988; Côté and Festa-Bianchet, 2003). Assigning the term ‘adult’ to mountain goats is somewhat subjective. In terms of sexual versus somatic maturity, body mass in both sexes continues to increase at a relatively constant rate until at least 6 years of age, but male
goats are fertile by two to three years of age, and the age of primiparity for females can be three years in native populations and as low as two years in introduced populations (Côté and Festa-Bianchet, 2003). As a result, goats older than three years are typically identified as adults, and this is the ageing criterion that I applied, with any goat under three years identified as subadult.

_Bison bison_: Ageing of bison skeletal material, particularly skulls, has been developed for the study of paleontological and archaeological bison finds. Using a relative ageing system based on horn and cranial bone growth following Skinner and Kaisen (1947) and Shackleton et al. (1975), I divided the sample into ‘Adolescent’, ‘Early Maturity’, and ‘Fully Mature’ age classes.

Several features of the cranium were used to assess relative age. The most important was the degree of fusion of the parieto-frontal sutures and the frontal-frontal suture (Shackleton et al., 1975), but protrusion and rugosity of the orbit, prominence of the horncore burr, development of grooving on the horncore, and occlusion of the third upper molar (M₃), were also assessed. Reference descriptors for each class are provided below, as modified from Skinner and Kaisen (1947) and Shackleton et al. (1975). See Figure 4.6 for representative male specimens.

Adolescent (Figure 4.6A): Parieto-frontal and frontal-frontal sutures unfused; orbits only slightly prominent, nearly confluent at anterior rim, rims mostly smooth; horncores generally slender, burr step slight to moderate, surface may have incipient longitudinal grooves; frontal, lacrimal, and nasal sutures unfused; M₃ not in occlusion to unworn on posterior half.

Early maturity (Figure 4.6B): Parieto-frontal suture knitted to fused, and frontal-frontal suture unfused to knitting posteriorly; orbits tubular to prominently so, rims slightly rugose; horncores
larger in circumference, burr step prominent and well defined, longitudinal ridges becoming more prominent; frontal, lacrimal, and nasal sutures unfused; M³ in full occlusion.

Fully mature (Figure 4.6C): Parieto-frontal suture fused and may be visible or obscured, frontal-frontal suture fused, at least posteriorly; orbits protruding and tubular, rims rugose; horncores with distinct burrs and longitudinal ridges; frontal, lacrimal, and nasal sutures starting to fuse.

Unfortunately, this ageing system was developed for male specimens. Although female bison follow a similar growth trajectory and proceed through similar horn and bone growth stages, they do so at a slower pace and do not reach equivalent end points (Shackleton et al., 1975). The pattern of sutural fusion in females is less consistent than it is in males, and does not begin to occur until at least 5.5 years of age (Shackleton et al., 1975). As a result I was concerned that many adult female bison may not be identified as fully mature when assessed using a male-specific ageing scheme. Despite this, after studying the data it became clear that sexual differences were readily detectable within the age classes and that the size differences between the mature age classes were slight. As a result the ‘Early Maturity’ and ‘Fully Mature’ specimens were treated as a single ‘Adult’ age class to bolster sample size.

*Antilocapra americana*: Age classes were assigned to the pronghorn specimens based largely on the eruption of M³ and the premolars. Although the published eruption sequences focus on the mandibular dentition (Dow and Wright, 1962; Lubinski, 2001), the maxillary teeth erupt at approximately the same time as their mandibular counterparts (Dow and Wright, 1962), allowing them to be used to estimate age in specimens lacking mandibles.
Any specimens with M\(^3\) (or M\(^2\) for that matter) still below the alveolar margin were identified as ‘fawns’, as M\(^3\) begins to erupt at the end of the first year (Dow and Wright, 1962; Lubinski, 2001). Specimens with M\(^3\) in the process of erupting, but not yet in full occlusion with wear on all cusps, were identifiable as yearlings because M\(^3\) emerges over the course of the second year of life, but does not come fully into wear until early in the third year of life (Dow and Wright, 1962; Lubinski, 2001). The permanent premolars (P\(^2\)-P\(^4\)) erupt during the third year of life and only come into full occlusion after three years (Dow and Wright, 1962; Lubinski, 2001). As a result, any specimens with M\(^3\) in full occlusion and the permanent premolars in the process of replacing the deciduous premolars were identified as two-year olds and classified with yearlings as ‘subadults’. Those individuals with a full adult dentition were identified as ‘adults’.

Unfortunately, the deciduous premolars are not easily distinguished from the adult premolars. As a result there is a brief window of perceived overlap in tooth eruption between adults and two-year olds that have yet to shed their premolars. Also, several specimens had premolars that were heavily damaged or absent, without clear evidence of whether they had been shed or simply lost. In these instances individuals were identified as ‘subadult’ or ‘adult’ based on general tooth wear and using my personal judgement (tooth wear was not extensively studied, but M\(^3\) shows limited wear in two-year olds, thereby providing a discriminatory criterion [Dow and Wright, 1962]).

4.2.4 Analysis of Data

Having assigned age-classes to each species, the adult specimens were organised into datasets that comprised all of the measurements just described in 4.2.2 (referred to as the non-scaled dataset). Full non-scaled datasets for mountain goats, bison, and pronghorn are provided in
Appendix B. A second dataset was then created for each species to account for the influence of body size (referred to as the scaled dataset). This was done by dividing the mean value for each trait by the average M² length for that individual (or, if only one molar was measured on a specimen, its mean length was used). Some specimens lacked teeth and were therefore unusable, slightly reducing the sample size for some analyses.

For each species and both datasets, Student’s t-tests (unpaired, two-tailed) were used to investigate differences between male and female means and were considered significant at p = 0.05. The F-test was used to assess the difference in variance between the male and female samples, and was considered significant at p = 0.1. If the variance was found to be significantly different, Welch’s t-test was used in lieu of Student’s t-test. The results of these t-tests, along with the sexual dimorphism index (SDI) (see below), provided a baseline metric of sexual dimorphism that was be used to assess the methods under investigation.

The sexual dimorphism index was calculated for each variable (SDI = \[\frac{\text{Mean}_{\text{Male}}}{\text{Mean}_{\text{Female}}} - 1\]) as per Fairbairn (2007). However, I chose to maintain a positive value for male-biased sexual dimorphism instead of assigning it a negative value, as suggested by Fairbairn (2007). The SDI provides an intuitive measure of the difference in size between the sexes, for instance, an SDI of 0.2 would indicate that males are 20% larger for that given trait.

The ability to predict the presence of sexual dimorphism in the adult age classes was tested using three common methods. For each trait the coefficient of variation, \(CV = \frac{\text{standard deviation}}{\text{mean} \times 100}\); coefficient of normality, \(W\) (calculated using the Shapiro-Wilk test of normality); and a coefficient of bimodality, \(b = \frac{((\text{skew})^2 + 1)}{((\text{kurtosis}) + 3)}\), were calculated. A CV of 10 or more is greater than that typically expected for a normally distributed morphological trait, and may indicate a dimorphic trait. A sample that fails the Shapiro-Wilk test
of normality (at p < 0.1) may reflect a bimodal or polymodal distribution and, therefore, may indicate a dimorphic trait. Finally, the coefficient of bimodality is an additional method of detecting non-normality in a distribution, and values of $b$ greater than 0.55 may indicate a bimodal or polymodal distribution (Mihlbachler, 2007). I refer to these three tests as ‘predictor values’.

Frequency histograms were created and inspected for each trait, as well as bivariate plots of each variable against $M^2$ length. Bivariate plots of specific variables were also made to illustrate meaningful morphological variation; for instance basal horncore width against length. Principal components analysis (PCA) was employed as a multivariate method of assessing the sources of morphological variation in each dataset. PCA’s were run for each taxon, utilizing the non-scaled datasets only. The scaled datasets were not used because they comprise unit-less ratio data, would need to be inspected for spurious correlations, and because there was no equivalent scaled dataset created from the ceratopsid data. Missing data were estimated by the iterative imputation function, wherein missing values are initially replaced with the column mean and then progressively updated as successive iterations of the PCA return better estimates until consensus is reached (Ilin and Raiko, 2010). This method of treating missing data is preferable to mean value estimation, which is prone to reducing variance in the dataset, or pairwise deletion, which can potentially bias the sources of variance in the analysis (Strauss et al., 2003). A variance-covariance matrix was used in each case, because all variables have the same units (mm).

Two types of cluster analysis were conducted to explore the results of each PCA. A hierarchical clustering algorithm, Unweighted Pair Group Method with Arithmetic Mean (UPGMA), was used to create a dendrogram wherein clusters are joined based on the average
Euclidean distance between all members in the two groups, and ‘branch’ length is indicative of the level of similarity between the groups. If the specimens in the dataset are dimorphic the dendrogram is expected to yield a basal dichotomy that separates the two morphs – however, clusters will always be formed regardless of the separation in the data, so dendrograms must be interpreted with caution (Hammer and Harper, 2006). One thousand bootstrap repetitions were applied in order to assess the stability of the groupings. The second cluster analysis employed is k-means clustering, a non-hierarchical method that seeks to create a user-specified number of clusters by iteratively assigning specimens to the cluster with the closest overall mean until consensus is reached (Hammer and Harper, 2006). All PCA’s and cluster analyses were conducted using PAST v. 2.11.

4.3 Results

4.3.1 Mountain goats

i) Equality of Means and Sexual Dimorphism Index

Results are provided in Table 4.4 for non-scaled data, and Table 4.5 for scaled data. Analysis of the results indicates that the horn sheaths of adult mountain goats are not dimorphic in length, but are dimorphic in their basal dimensions (length, width, and circumference), with those of males being larger. This is in agreement with the published literature (Cote and Festa-Bianchet, 2003). However, females were not found to have longer sheaths for a given body size. As well, the horncores were found to be dimorphic in all measured dimensions, with those of males being significantly larger than those of females, as indicated by Student’s t-tests or Welch’s t-tests (considered significant at p < 0.05).
The sexual dimorphism index (SDI) was considered to indicate dimorphism at a value of 0.1 or greater. For the non-scaled dataset (not scaled to body size), this index identified dimorphism in all of the same variables that were identified by statistical tests of equal means, as well as one additional variable, foramen magnum height (FMH), which was narrowly non-significant (Welch test; \( p = 0.06 \)). For the scaled dataset, the SDI again closely matched the results of the \( t \)-tests, failing to identify dimorphism in only one significant variable. The SDI appears to be an informative metric of sexual dimorphism in mountain goats.

ii) Visual Inspection of Plots

Frequency histograms were created using non-scaled measurement data, and so were compared against the results from the non-scaled dataset. Of the 16 traits that were identified as having non-equal means with \( t \)-tests, bimodal distributions were apparent in histograms of 14 of them. Left core basal length (LCBL) was one such variable, and is shown in Figure 4.7 as a representative example of the bimodal distributions that were observed in the frequency histograms.

Bivariate scatter plots were prepared by plotting traits against \( M^2 \) length, and so were compared against the scaled dataset. Of the 16 traits that were identified as having non-equal means with \( t \)-tests, bivariate scatters revealed dimorphic clustering in 12 of them. A clear signal of dimorphism was not detectable in measures of horn length, but was readily detectable in the basal dimensions of the sheaths and cores. An example of a dimorphic distribution can be seen in a plot of right horn basal width (RHBW) against right \( M^2 \) length (RM2L). It is shown in Figure 4.8, as a representative plot. The remainder of the plots are not figured in this chapter, because there is a very large number of them, and because the intention was less about actually
visualising the mammal data, and was more about assessing the usefulness of these plots for investigating dimorphism. This aspect is further discussed below.

iii) Predictor Variables

The ability to predict the presence of this dimorphism is mixed. For the non-scaled dataset, the CV and $b$ values predicted all 16 dimorphic traits, with one extra trait identified as being possibly dimorphic, the nearly-significant foramen magnum height (FMH). The normality test (W) correctly predicted ten dimorphic traits, misidentified FMH, and failed to identify six.

When body size was taken into account, the predictor variables were less informative. Of 16 dimorphic traits, the CV identified twelve, missed four, and misidentified four additional ones. The $b$ value correctly identified eleven traits and missed five. The normality test correctly identified ten traits and missed six. The performance of the predictor variables as indicators of dimorphism for both datasets of all three taxa is summarised in Table 4.6.

iv) PCA and Cluster Analysis

A PCA was conducted with all 26 measured variables in the non-scaled adult mountain goat dataset. Any specimens with 50% or more missing data were removed from the analysis, leaving 16 females, 11 males, and six unsexed specimens. Conducting a PCA with fewer specimens than variables is not particularly problematic because it simply limits the number of informative (non-zero) principal components (PC’s) that can be recovered (Hammer and Harper, 2006). In the analyses conducted here, with only two or three readily interpretable PC’s, the impact of including more variables than specimens is not a concern. There is also some precedent for this in paleontological studies (for example, Mallon et al., 2011). For mountain goats, the first two PC’s accounted for 94.4% of the variation in the dataset (62.93% and 31.43%, respectively), and loadings are provided in Table 4.7. Male and female specimens were separated across both axes.
The scatter plot of PC1 and PC2, and the resultant dendrogram of an accompanying hierarchical cluster analysis, are displayed in Figures 4.9, and 4.10, respectively, as representative results. Similar results were obtained for bison and pronghorn, and are not figured. Interpretation of the mountain goat PCA revealed that horn sheath length and basal circumference, as well as horncore basal circumference, increased most rapidly with increasing horn size, and that males have somewhat larger horns and horncores than do females. The analysis also suggested that males have proportionally stouter horn sheaths than do females, with greater circumference for a given horn length, as well as larger horncores with proportionally greater circumference. Of note, $M^2$ length and the dimensions of the foramen magnum contributed virtually nothing to the variance in the dataset.

A hierarchical cluster analysis of the scores from the PCA returned two major clusters differentiated by sex, and a third cluster of 3 males and 1 unsexed individual that grouped on their own (Figure 4.10). Although the two major groupings visible in the PCA are differentiated, the ‘distance’ between the sex-based clusters is small. The $k$-means cluster analysis did not return a consistent clustering of the sexes, with only 5 of 20 iterations successfully separating males and females.

v) Summary

Mountain goats were found to be dimorphic in the basal dimensions of their horn sheaths, but not in sheath length, as has been previously reported. They were also found to be dimorphic in all measures of their horncores relative to body size, with male horncores being approximately 10% longer overall and nearly 30% wider at the base. Although it is not identified as such, similar sexual dimorphism in horncores can be recognised in measurements of the extinct mountain goat, *Oreamnos harringtoni* (Mead and Lawler, 1994). I do not know that horncore dimorphism
in mountain goats has otherwise been reported; horn measurements in mountain goats are typically of the sheaths so there are relatively few data available for horn core dimensions.

4.3.2 Bison

i) Equality of Means and Sexual Dimorphism Index

Results are provided in Table 4.8 for non-scaled data, and Table 4.9 for scaled data. Testing for equality of means in the bison dataset is interesting. As expected from the literature, males are absolutely larger than females in all aspects of their horns, so of the 28 variables in the non-scaled dataset only the \( M^2 \) lengths and foramen magnum width (FMW) were non-significant. Along with this came a big difference in variance, with several more traits failing the F-test of equal variance between the sexes than was seen in mountain goats. This necessitated more extensive use of Welch’s \( t \)-test.

More informative are the results for the traits when they are scaled to body size. Significant differences between male and female means were detected for the basal sheath dimensions (width, height, and circumference), as well as for all horncore traits, indicating that male bison have relatively larger horncores and relatively stouter sheaths.

For the non-scaled measurement data the SDI identified as dimorphic all the same horn and horncore traits as the \( t \)-tests, but did not identify foramen magnum height (FMH) as dimorphic. For the relative size data the SDI identified all the same traits as the \( t \)-tests, but also identified the dorsal lengths and chords of the horn sheaths as being dimorphic.
ii) Visual Inspection of Plots

Frequency histograms revealed bimodal distributions in 17 of the 25 traits that were identified as having non-equal means with $t$-tests. Several additional plots were potentially bimodal but inconclusive overall.

Eighteen traits were identified as having non-equal means with $t$-tests, and bivariate scatter plots of measured traits against $M^2$ length revealed dimorphic clustering in 16 of them. Only the ventral lengths of the horncores did not provide a clear signal of dimorphism.

iii) Predictor Variables

For the non-scaled measurement data, of 25 significant traits the CV identified all but FMH as being possibly dimorphic. The $b$ value correctly identified 16 traits as being possibly dimorphic and missed nine. The normality test correctly identified 13, missed 12, and misidentified one additional trait as possibly dimorphic.

When body size was taken into account the predictor variables became less informative. The CV identified all 26 possible traits as being potentially dimorphic, although only 18 were identified as being significant by the $t$-tests. The $b$ value correctly identified seven traits and missed 11, whereas the normality test correctly identified a single trait as being possibly dimorphic and missed 17.

iv) PCA and Cluster Analysis

A PCA was conducted for all 28 measured variables in the non-scaled dataset. Any specimens with 50% or more missing data were removed from the dataset, leaving six females and ten males. The first two PC’s accounted for 93.4% of the variation in the dataset (80.73% and 12.71%, respectively). Males and females separated well along the first axis, forming two distinct clusters with two male outliers. Interpretation of the PCA revealed that males have larger
horns overall than do females, with horn sheaths and cores that are proportionally greater in basal circumference and ventral length.

Hierarchical cluster analysis recovered both sexes as distinct clusters with a reasonable separation ‘distance’, and 20 of 20 $k$-means iterations returned the same clustering pattern. One of the anomalous male outliers, YPM 3405, was clustered consistently with the female specimens, however.

v) Summary

Male bison were found to have significantly larger horns in all dimensions than females in an absolute sense, as expected. When body size was taken into account, male bison were found to have relatively larger horn sheath bases than females, being 50-60% larger in width, height, and circumference. Horn sheaths were not found to be relatively longer in males, although this could be due to greater wear of the distal tips, effectively reducing measurements of length. Males were also found to have relatively larger horncores in all dimensions measured, as was previously reported (Shackleton et al., 1975). Of note, male bison were not found to have significantly larger $M^2$ molars than females, which was somewhat surprising given the expectation of larger overall skull size. As well, four specimens, two of each sex, are identified in the dataset as wood bison, *Bison bison athabascae*. Twelve are identified as plains bison, *B. b. bison*, and the remainder are not classified to subspecies, although I expect that most of them are plains bison. No effort was made to separate the specimens by subspecies due to the small number of plains bison. Although both male and female wood bison tended to be larger than their counterparts from the plains, any effect on the dataset was effectively swamped by the greater difference between the sexes. If a greater proportion of plains bison were included, their greater size would become more apparent in the results and would need to be addressed.
4.3.3 Pronghorn

i) Equality of Means and Sexual Dimorphism Index

Results are provided in Table 4.10 for non-scaled data, and Table 4.11 for scaled data. Due to the known dramatic dimorphism in pronghorn horns, testing for a difference in means was largely redundant. In both the non-scaled and body-size corrected datasets, all horncore traits with sufficient female specimens to permit testing were egregiously significant (e.g. LCHT, \( p = 5.78 \times 10^{-12} \)). The only surprising result was that foramen magnum height (FMH) was found to have a significant difference in means, with that of females being larger than that of males. This was true of the non-scaled and scaled data. Sample sizes of female horn sheaths were too low to permit testing of those variables.

For both datasets the SDI identified as dimorphic all the same traits as the \( t \)-tests. Some horncore traits were nearly 400% larger in males than females. The SDI also identified FMH as being 10% larger in females, with a value of -0.10. Not surprisingly, all horn sheath traits had very high SDI scores, but these were calculated with female sample sizes of only one or two, and are not considered to be representative.

ii) Visual Inspection of Plots

Of the non-scaled measurements of pronghorn, eight traits were found to have significant differences in means between the sexes. Of these, the seven horncore traits had bimodal frequency distributions and only foramen magnum height did not.

For the scaled data, eight traits were identified as having non-equal means with \( t \)-tests, and bivariate scatter plots of measured traits against \( M^2 \) length revealed dimorphic clustering in seven of them. Again, only FMH did not provide a distinct separation of clusters.
iii)  Predictor Variables

For the non-scaled dataset there were 11 traits with sufficient samples of female specimens to allow testing for a difference in means. Of these, eight were significant and the CV and $b$ scores identified seven of them correctly, missed one, and misidentified one and two additional traits, respectively. The normality test correctly identified all eight, but also identified another two traits that were not significant as possibly being dimorphic.

For the scaled dataset there were nine traits with sufficient sample sizes to conduct $t$-tests, and of these eight were found to be significant. The CV identified all nine traits as possibly being dimorphic, with most coefficients being well above 10. The $b$ value and normality test both correctly identified five traits and missed three.

iv)  PCA and Cluster

A PCA was conducted using 15 female and 15 male adult pronghorn specimens, employing ten non-scaled variables related to the dimensions of the horncores, $M^2$, and foramen magnum. The first principal component alone accounted for 93.9% of the variation in the dataset, with PC2 capturing another 5.6%. Males and females separated well over the first axis, forming two tight clusters with two male outliers. By and large the greatest sources of variance are the heights of the horncores, and these variables account for the major difference between the sexes in the PCA.

Unsurprisingly, the hierarchical and $k$-means cluster analyses recovered very strong clusters, with a deep basal dichotomy in the former, and 20 of 20 iterations recovering separate male and female clusters in the latter.
Pronghorn, not surprisingly, were clearly dimorphic in their horncore dimensions. Horn sheaths were so rarely preserved for female specimens in museum collections that no meaningful tests could be performed, but sheaths are also clearly dimorphic. The only surprising result was that female pronghorn were found to have a significantly larger foramen magnum height than males. For this dimension, one male outlier was notably smaller than the rest of the sample, but this likely did not affect the overall trend because without this outlier the male mean was still well below the female mean.

4.4 Eigenshape Analysis

Shape has been proposed to be an important component of the morphological variation in ceratopsid horns, having been hypothesized to relate to sex (e.g. *Agujaceratops* [Lehman, 1990]) and to ontogeny (e.g. *Triceratops* [Horner and Goodwin, 2006]). These hypotheses have not been explicitly tested however, and the importance of shape as a source of morphological variation in ceratopsid horns remains relatively unexplored. One method that may be useful in this regard is eigenshape analysis.

Eigenshape analysis is an outline-based morphometric method used to compare the digitised outlines of shapes. The variation is depicted in principal component space, allowing the determination of which segments of the outline account for the greatest variation in shape, and also allowing the visualisation of transformations of the outline. Improvements to the algorithm allow it to be applied to open curves, such as that described by the surface of a horn, providing an advantage over alternate methods of outline analysis (McLeod, 1999).
As stated in Chapter 3 (section 3.2.2), the horn sheaths of mountain goats are known to be sexually dimorphic in shape. This provided an avenue by which to explore the effectiveness of eigenshape analyses for detecting shape variation related to sex. The horn cores of mountain goats and bison were also investigated.

4.4.1 Eigenshape Analysis – Methods

Because the horns of mountain goats diverge slightly from the sagittal plane, the specimens were photographed in lateral view and tilted away from the camera in order to bring the selected horn core or sheath into full profile. The specimen was tilted so that the midline of the horn was vertical and perpendicular to the camera lens. Bison specimens were photographed from the posterior, with the skull resting on the maxillary toothrows, in order to consistently capture the ventral curvature of the horncores. The camera was placed at a consistent distance from the skulls.

The anterior surfaces of the mountain goat horn sheaths and horncores were traced from digital photographs using the program tpsDig v2.16. This was done by placing a series of coordinate points along the anterior surface to capture its shape. The first point of each outline was placed at the anterior basal lip of the sheath, or anterior basal rim of the burr for horncores, and then as many points as necessary were placed sequentially along the profile of the anterior horn surface to capture its outline. The curve was then ‘resampled’ to comprise 35 equally spaced coordinate points. This allows each horn outline to be captured by an equivalent number of coordinate points, permitting comparison between the outlines. See Figures 5.6 and 5.7 in Chapter 5 for an illustration of the traced and resampled horncore curves for a Triceratops prorsus specimen. Left sheaths and horncores were used, but in order to maximise sample size
the mirror images of a small number of specimens were included when only the right core or sheath was available or was in better condition. The coordinate data were then analyzed with PAST v.2.11. Sample sizes were 13 males, 16 females, and two unsexed specimens for the horn sheath study, and four males, five females, and two unsexed specimens for the horncore study. Similar methods were used for bison specimens, except that the ventral curve of the left horncore was traced, with the first point placed at the ventral lip of the burr, and the curve was resampled with 25 equally spaced coordinate points instead of 35. A smaller number of coordinate points was used for bison because the program reduces the coordinates to the minimum number of points that capture the shape variation, and the mountain goat analyses revealed that fewer points were necessary. The bison sample comprised ten males, eight females, and two unsexed specimens.

4.4.2 Eigenshape Analysis – Results

The results of the eigenshape study are mixed. For the horn sheaths of mountain goats, which were predicted to reveal a dimorphic pattern, males and females do separate moderately well over the first axis, but the signal is diffused by the six unsexed specimens, and by one odd male and one odd female. The first axis accounts for 58.32% of the variance, and when moving from negative to positive along that axis (from male to female, generally), we see a straightening of the main portion of the curve with a progressive deflection of the distal segment (1/6th), as illustrated in Figure 4.11. This is similar to the sexual shape distinction that has been described for mountain goats (Smith, 1988). Clustering is not apparent overall and is not supported by hierarchical cluster analysis. When only sexed specimens are used, and the two odd specimens are removed, males and females segregate clearly over the first axis and hierarchical cluster
analysis recovers two prominent clusters, with only one specimen (of 27) clustering with the opposite sex. Together these results suggest that the horn shape distinction in mountain goats is valid overall, but perhaps not as distinctive or diagnostic as previously thought. This also illustrates how individual variation will always be problematic for morphological studies in the fossil record, and assigning sex to specimens runs the risk of returning false positives.

Mountain goat horncores also appear to be separable by sex, although the sample size is quite low (n = 11) and clustering is not apparent. The first axis captures 70% of the variation, and moving from negative to positive along this axis (male to female, generally) we see a progressive straightening of the distal 1/3rd of the horncore.

For bison the sexes do not appear to separate well according to horncore shape, and clustering by sex is not apparent. There is considerable overlap along the first axis, which accounts for 69.9% of the total variation, although there is a general trend when moving from negative to positive of moving from female space to male space. This can be visualised by a tightening of the curl of the horn as it points more dorsally.

4.5 Discussion

By recording appropriate measurements of a sample of skulls for each exemplar species, it was possible to demonstrate those aspects of horn and horncore morphology that were previously described as being sexually dimorphic. Mountain goats were found to be dimorphic in the basal dimensions of their horn sheaths, and in the relative size of their horncores. As expected, bison were found to be dimorphic in all dimensions of their horncores and sheaths despite a lack of dimorphism in M₂ length. Horn sheath lengths were not found to be dimorphic, however, once body size was taken into account. Pronghorn were found to have strongly dimorphic horncores
as expected, but limited samples of female specimens prevented the use of tests for many variables. With these results, and regarding the $t$-tests and the SDI as indicators of dimorphism, it was possible to evaluate the effectiveness of the other methods that were tested here. These are discussed in turn (including eigenshape analysis) below.

4.5.1 Discussion of Methods

Visual inspection of frequency histograms and bivariate scatter plots is an effective method of detecting a dimorphic signal within a sample. Only 18 of 81 traits that were found to differ statistically were not readily identified from plots. Several of the horn dimensions were sufficiently dimorphic that a clear delineation between clusters could be visually recognised on scatter plots, or bimodality was clearly displayed in frequency histograms. Unfortunately this method is somewhat labour intensive as it requires creating and then visually inspecting each plot and histogram.

The effectiveness of the predictor variables for detecting a dimorphic signal was mixed. In many instances they failed to predict the presence of dimorphism, or identified traits that were not dimorphic. This is not surprising since none is a direct test of dimorphism, but suggests considerable caution against interpreting them as indicators of dimorphism in unsexed samples. They also all performed less well with the scaled data than with the non-scaled data, as can be seen in Table 4.4. The coefficient of variation (CV) was the most successful of the three, as it was the best by far at predicting sexual dimorphism and missed very few dimorphic traits. However, it was also the most prone to misidentifying non-dimorphic traits. The bimodality coefficient ($b$) performed reasonably well, but failed to identify dimorphism nearly half as many times as it succeeded. One of the strengths of this coefficient is the low rate of misidentification.
The coefficient of normality (W) was the least reliable of the three predictor variables, and appeared to be most effective only when the non-normality of the sample was great (i.e. when dimorphism was strongly apparent). Like the bimodality coefficient, however, it rarely misidentified variables as dimorphic when they were not. This study suggests that calculating the CV and $b$ scores for measured traits would be useful as a preliminary survey of potential dimorphism, and any traits that return elevated scores (CV $\geq 10$; $b \geq 0.55$) should be further investigated.

Interpreting the output from the PCA’s revealed patterns of variation in the datasets similar to what was revealed by the $t$-tests, plots, and predictor variables. With the non-scaled data, the sexes were separated over the first PC axis (or PC1 and PC2 for mountain goats) and the loadings were indicative of which variables contributed the most to that separation. This provided directly interpretable morphological information, such as males having stouter sheaths and greater horncore circumference in mountain goats and bison, or taller horncores in pronghorn. Of course with an unsexed sample these differences would not be directly interpretable as being related to sex, but the morphological information is still valid and the bimodal nature of the distributions is evident. This supports the use of PCA as a tool for studying sexual dimorphism by exploring the sources of variation in a multivariate dataset and for quickly establishing which variables may be of interest. This result is better than anticipated, as I was sceptical of the feasibility of extracting interpretable morphological signals from a PCA of a large multivariate dataset. I think that it would be unwise, however, to draw conclusions of sexual dimorphism directly from the results of a PCA without following up on the variables and groupings that were identified by the scatter and loadings.
The cluster analyses did not prove to be as informative as initially hoped. Although they provide a somewhat more objective method of assessing clustering in the PCA, the interpretation of the hierarchical dendrograms remains essentially subjective, and both methods only seem to provide definitive signals of dimorphism when the clusters are already readily apparent in the scatter plot. As a result, cluster analyses seem to be better suited to facilitating the interpretation of the PCA, less in the context of directly seeking dimorphism and more as a means of identifying which groups to contrast and seek differences between. The combination of recognising clusters from these methods and detecting morphological variation from PCA is a powerful tool.

The results of the eigenshape analysis indicate that this method is capable of recovering sexual shape dimorphism when it is present, and confirms it as an effective tool for visualising shape variation in animal horns regardless of the presence of dimorphism. Again the use of cluster analysis to guide the interpretation of the results can be beneficial. This method is worth applying to the horns of ceratopsid dinosaurs and could reveal significant shape variation even in instances with limited morphological variation.

4.6 Conclusions
This proof of concept study has demonstrated multiple approaches to assessing sexual dimorphism in cranial horns, and the single greatest conclusion is likely that a combination of several methods may be the best approach. When working with a dataset of morphological variables, calculating the CV and \( b \) coefficients provides a quick way to flag those variables that may be dimorphic and merit further attention. The coefficient of normality (\( W \)) was less informative and will not be carried forward. Following this up by creating frequency histograms
and bivariate plots for those variables of interest and inspecting them for bimodality appears to be a reliable method of assessing dimorphism. Exploring the multivariate dataset with a PCA is an effective method for detecting potentially dimorphic variables as well as for interpreting the morphological relationships between specimens. The use of cluster analysis can aid in the interpretation of these results, although should not be considered a test of dimorphism in its own right. Hierarchical cluster analysis and $k$-means cluster analysis provided generally similar results, so the much more labour intensive $k$-means analysis will not be carried forward. Eigenshape analysis was found to be an effective method of capturing shape variation and can demonstrate sexual shape dimorphism if it is present in a sample. Based on these results, the methods summarised here are applied in the following chapter to the horns of two species of ceratopsid dinosaur in order to substantiate the presence or absence of sexual dimorphism.
Figure 4.1 Left horncore and in-situ longitudinal section of left horn sheath of a typical mountain goat specimen. Letters indicate reference points for measurements, as follows: A) anterior proximal rim of sheath, B) posterior proximal rim of sheath, C) distal tip of sheath, D) anterior proximal lip of burr, E) posterior proximal lip of burr, F) distal tip of horncore. Dot indicates where medio-lateral width was measured.
**Figure 4.2** Skull and horn sheaths of a typical bison specimen, posterior view. Letters indicate reference points for measurements, as follows: A) dorsal rim of sheath, B) distal tip of sheath, C) ventral rim of sheath, D) proximal-most point on ventral surface of sheath, E) point on the dorsal sheath surface that forms with (D) a line perpendicular to the longitudinal axis of the horn. Basal circumference and width were measured in the same plane as D-E, with width measured antero-posteriorly at the midpoint of the line between D and E.
**Figure 4.3** Skull and horncores of a typical bison specimen, posterior view. Letters indicate reference points for measurements, as follows: A) dorsal rim of burr, B) distal tip of horncore, C) ventral rim of burr, D) proximal-most point on ventral surface of horncore, E) point on the dorsal horncore surface that forms with (D) a line perpendicular to the longitudinal axis of the horncore. Basal circumference and width were measured in the same plane as D-E, with width measured antero-posteriorly at the midpoint of the line between D and E.
**Figure 4.4** Right horncore measurements for a typical male pronghorn, right lateral view. Letters indicate reference points for measurements, as follows: A) dorsal rim of orbit, B) distal tip of horncore, C) angle of prong formation, D) posterior horncore base, E) anterior horncore base. Medio-lateral width was measured at the midpoint of the line between D and E, and basal circumference was measured around the base in the plane of D and E.
Figure 4.5 Right horn sheath measurements for a typical male pronghorn, right lateral view. Letters indicate reference points for measurements, as follows: A) dorsal rim of orbit, B) distal tip of horn sheath, C) distal tip of prong, D) prong notch, E) posterior horn sheath base, F) anterior horn sheath base. The measurement of height to sheath tip is not figured, but is measured from A to B along the curving lateral and dorsal surfaces of the sheath. Medio-lateral width was measured at the midpoint of the line between E and F, and basal circumference was measured around the base in the plane of E and F.
Figure 4.6 Three male bison skulls representative of the three age classes used in this study, (reproduced from Shackleton et al. [1975]), dorsal view. A) Adolescent – Note completely unfused sutures, non-protruding orbits with smooth rims, and modest definition of horncore burr. B) Early Maturity – Note partial knitting of parieto-frontal sutures and completely open frontal-frontal suture. Orbits are protruding, tubular and slightly rugose. This specimen would fall at the young end of this age class. C) Fully Mature – Note complete fusion of the parieto-frontal sutures, and fusion of the posterior portion of the frontal-frontal suture. Orbits strongly protruding and rugose, and burr strongly defined.
Figure 4.7 Frequency histogram of the measured variable Left Core Basal Length (LCBL) in mountain goats, demonstrating a bimodal distribution. Such distributions were observed in 13 other variables for mountain goats. Scale on the x-axis is in millimetres (mm).
**Figure 4.8** Bivariate scatter plot of right horn basal width (RHBW) against right M$^2$ length (RM2L), showing bimodal clustering indicative of a dimorphic pattern in mountain goats. Axes are in millimetres. Open squares indicate males, closed squares indicate females, dots are individuals of indeterminate sex.
**Figure 4.9.** Results of a PCA of the non-scaled mountain goat data. Principal Components (PC’s) 1 and 2 are figured, accounting for 94.4% of the variation in the dataset. Open squares indicate males, closed squares indicate females, dots are individuals of indeterminate sex. Clustering of the sexes is clearly evident.
**Figure 4.10** Dendrogram of a hierarchical cluster analysis (UPGMA) of the scores from the PCA of the non-scaled mountain goat data (Fig. 4.9). Blue indicates male specimens, magenta indicates female specimens, and black indicates specimens of indeterminate sex. Strong clustering of the sexes corroborates the separation visible in Figure 4.9, but the ‘distance’ between the clusters is not high. Numbers at branch nodes indicate percentage support of 1000 bootstrap iterations. The three major clusters observable in Fig. 4.9 are demarcated by the first two branching nodes in this dendrogram.
**Figure 4.11** Illustration of the shape change in anterior horn sheath profile for mountain goat specimens over the first axis, as determined by eigenshape analysis. From left to right the outlines correspond to scores of +0.3, 0.0, and -0.3, on the first axis, and represent the minimum values that capture all specimens. The female and male symbols indicate a general transition in outline profile from female-dominated to male-dominated shape space.
Table 4.1 Horn dimension measurement codes and descriptions for mountain goats. Only left measures are given.

<table>
<thead>
<tr>
<th>Code</th>
<th>Dimension</th>
<th>Description</th>
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</thead>
<tbody>
<tr>
<td>LHAL</td>
<td>Left Horn Anterior Length</td>
<td>Height from base to tip along the anterior/posterior surface of the horn sheath.</td>
</tr>
<tr>
<td>LHPL</td>
<td>Left Horn Posterior Length</td>
<td></td>
</tr>
<tr>
<td>LHC</td>
<td>Left Horn Chord</td>
<td>Sheath height in a straight-line from the posterior basal rim to tip.</td>
</tr>
<tr>
<td>LHBL</td>
<td>Left Horn Basal Length</td>
<td>Antero-posterior length / medio-lateral width / circumference, measured at the basal rim of the sheath perpendicular to the longitudinal axis.</td>
</tr>
<tr>
<td>LHBW</td>
<td>Left Horn Basal Width</td>
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</tr>
<tr>
<td>LHBC</td>
<td>Left Horn Basal Circumference</td>
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<td>LCAL</td>
<td>Left Core Anterior Length</td>
<td>Height from burr to tip along the anterior/posterior surface of the horncore.</td>
</tr>
<tr>
<td>LCPL</td>
<td>Left Core Posterior Length</td>
<td></td>
</tr>
<tr>
<td>LCBL</td>
<td>Left Core Basal Length</td>
<td>Antero-posterior length / medio-lateral width / circumference, measured at the burr perpendicular to the longitudinal axis of the horncore.</td>
</tr>
<tr>
<td>LCBW</td>
<td>Left Core Basal Width</td>
<td></td>
</tr>
<tr>
<td>LCBC</td>
<td>Left Core Basal Circumference</td>
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Table 4.2 Horn dimension measurement codes and descriptions for bison. Only left measures are given.

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<td>LHDL</td>
<td>Left Horn Dorsal Length</td>
<td>Length from base to tip as measured along the dorsal/ventral surface of the horn sheath.</td>
</tr>
<tr>
<td>LHVL</td>
<td>Left Horn Ventral Length</td>
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<tr>
<td>LHC</td>
<td>Left Horn Chord</td>
<td>Shortest straight-line length from the dorsal basal rim to sheath tip.</td>
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<td>LHBH,</td>
<td>Left Horn Basal Height</td>
<td>Dorso-ventral height / antero-posterior width / circumference, measured at the basal rim of the sheath perpendicular to the longitudinal axis.</td>
</tr>
<tr>
<td>LHBW</td>
<td>Left Horn Basal Width</td>
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</tr>
<tr>
<td>LHBC</td>
<td>Left Horn Basal Circumference</td>
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<tr>
<td>LCDL</td>
<td>Left Core Dorsal Length</td>
<td>Length from burr rim to tip as measured along the dorsal/ventral surface of the horncore.</td>
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<td>Left Core Ventral Length</td>
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<tr>
<td>LCBH</td>
<td>Left Core Basal Height</td>
<td>Dorso-ventral height / antero-posterior width / circumference, measured at the burr rim perpendicular to the longitudinal axis.</td>
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<td>LCBW</td>
<td>Left Core Basal Width</td>
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<td>LCBC</td>
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Table 4.3 Horn dimension measurement codes and descriptions for pronghorn. Only left measures are given.

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<th>Description</th>
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<td>LSHT</td>
<td>Left Sheath Height to Tip</td>
<td>Height from dorsal rim of orbit to distal sheath tip, measured along lateral surface of sheath.</td>
</tr>
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<td>LSHP</td>
<td>Left Sheath Height to Prong</td>
<td>Straight-line height from dorsal rim of orbit to distal tip of prong.</td>
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<tr>
<td>LSPL</td>
<td>Left Sheath Prong Length</td>
<td>Prong length from notch to tip along dorsal surface.</td>
</tr>
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<td>LSBL</td>
<td>Left Sheath Basal Length</td>
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</tr>
<tr>
<td>LSBW</td>
<td>Left Sheath Basal Width</td>
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</tr>
<tr>
<td>LSBC</td>
<td>Left Sheath Basal Circumference</td>
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<td>LCHT</td>
<td>Left Core Height to Tip</td>
<td>Straight-line height from dorsal rim of orbit to distal core tip.</td>
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<tr>
<td>LCHP</td>
<td>Left Core Height to Prong</td>
<td>Straight-line height from dorsal rim of orbit to angle of prong formation. Not discernible on some males. *See text for details.</td>
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<td>LCBL</td>
<td>Left Core Basal Length</td>
<td>Antero-posterior length / latero-medial width, measured at the horncore base perpendicular to the longitudinal axis.</td>
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<td>LCBW</td>
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Table 4.4 Tests of equality of means between the sexes for measured variables in mountain goats. N indicates total sample size, ‘male x’ and ‘female x’ refer to male and female means, respectively. F-test of equal variance was considered significant at p = 0.1. t- and Welch tests were considered significant at p = 0.05. F-scores, t-scores, and Welch-scores are provided. SDI is the sexual dimorphism index. Significant p-values for t-tests and Welch-tests are **bolded**. SDI scores ≥ 0.1 are **bolded**.

<table>
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<th>Variable</th>
<th>N</th>
<th>Mean</th>
<th>n male</th>
<th>n female</th>
<th>male x</th>
<th>female x</th>
<th>F (variance)</th>
<th>F (p)</th>
<th>t</th>
<th>t (p)</th>
<th>Welch</th>
<th>Welch (p)</th>
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<th>female x</th>
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<th>F (p)</th>
<th>t</th>
<th>t (p)</th>
<th>Welch</th>
<th>Welch (p)</th>
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Table 4.5 Tests of equality of means between the sexes in mountain goats for measured variables scaled to body size. Legend as in Table 4.4

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<th>female x</th>
<th>F</th>
<th>F (p)</th>
<th>t</th>
<th>t (p)</th>
<th>Welch</th>
<th>Welch (p)</th>
<th>SDI</th>
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<th>female x</th>
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Table 4.6 Summary of performance of the predictor variables. CV = coefficient of variation; $b =$ bimodality coefficient; W = coefficient of normality. Indicated for each predictor variable is the number of dimorphic traits it identified (ID’d), the number of non-dimorphic traits it misidentified as dimorphic (Mis-ID’d), and the number of dimorphic traits it failed to identify (Missed). These are arranged by taxon and by dataset (scaled and non-scaled). ‘n’ indicates the total number of morphological variables in the dataset, and ‘Dim.’ indicates the number that were identified as dimorphic by the $t$-tests.

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<th>W</th>
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Table 4.7 Variable loadings for first two principal components (PC) of mountain goat PCA.

Measurement codes as described in Table 4.1.

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Table 4.8 Tests of equality of means between the sexes for measured variables in bison. N indicates total sample size, ‘male x’ and ‘female x’ refer to male and female means, respectively. F-test of equal variance was considered significant at p = 0.1. t- and Welch tests were considered significant at p = 0.05. F-scores, t-scores, and Welch-scores are provided. SDI is the sexual dimorphism index.

Significant p-values for t-tests and Welch-tests are **bolded**. SDI scores ≥ 0.1 are **bolded**.

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<th>female x</th>
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<th>F (p)</th>
<th>t</th>
<th>t (p)</th>
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Chapter 5: Investigating Sexual Dimorphism in Ceratopsid Horncores

“The variations of ceratopsian skulls due to age, sex, or the individual are such that no two ever seem to agree,” (Lull, 1933).

5.1 Introduction

With a model for investigating sexual dimorphism in horns established in Chapter 3, and the methods tested in Chapter 4, we can now turn our attention to investigating sexual dimorphism in the horns of ceratopsid dinosaurs.

To this end, the ceratopsid species *Triceratops horridus* and *Centrosaurus apertus* have been selected for study. Together, they represent the two subfamilies of the Ceratopsidae, providing an opportunity to examine both clades and both major patterns of cranial horn development in ceratopsids (that is, greater expression of the postorbital horns, or greater expression of the nasal horns). They are the two most abundant ceratopsid species available for study and provide the largest available samples of horncores, which is important given the nature of the methods of investigation. They are also almost certainly the two most scientifically well-known ceratopsids, meaning that the question of horn dimorphism can be more strongly framed and that any results may be more readily contextualised.

5.1.1 Distribution and Abundance

*Triceratops* is known from the latest Cretaceous (Maastrichtian) of Western North America, having been recovered from deposits in Wyoming, Colorado, North Dakota, South Dakota, Montana, Alberta, and Saskatchewan. It lived during the final 2 million years of the Cretaceous
period (Sampson et al., 2010); in fact, the youngest fossil of a non-avian dinosaur is a horncore that may belong to *Triceratops* (Lyson et al., 2011). *Triceratops* appears to have been a highly abundant genus, comprising some 40% of all skeletons recovered from the Hell Creek Formation of Montana, and 69% of all skeletons from the Upper Hell Creek alone (Horner et al., 2011). Despite this abundance, and in stark contrast to *Centrosaurus apertus*, *Triceratops* is known almost exclusively from individual specimens, as only a single *Triceratops* ‘bonebed’, comprising three juvenile specimens, has been reported (Matthews et al., 2009).

*Centrosaurus apertus* is known from the late Cretaceous (Campanian) of Alberta and Saskatchewan. It is restricted stratigraphically to the lower 28 metres of the Dinosaur Park Formation (DPF) (Mallon et al., 2012). The species spans a temporal range of approximately 700,000 years, based on a sedimentation rate of 4.1 cm/1000 years for the DPF exposures in Dinosaur Provincial Park (Eberth, 2005). In Dinosaur Provincial Park, *C. apertus* shares a megaherbivore assemblage zone (MAZ) with *Corythosaurus* and *Chasmosaurus russelli* that comprises the lower 28m of the DPF, the MAZ-1 of Mallon et al. (2012). A turnover pulse in the palaeoenvironment may have seen *C. apertus* rapidly replaced by *Styracosaurus albertensis*, which occupies a second megafaunal assemblage in the ensuing 23 m of the Dinosaur Park Formation (Ryan and Evans, 2005; Mallon et al., 2012).

Most famously, *Centrosaurus* is known from highly abundant monodominant bonebeds in the Dinosaur Provincial Park area. At least 20 bonebeds have been documented within Dinosaur Provincial Park, and of these, 17 are dominated by *C. apertus* material (Eberth and Getty, 2005). For example, 4m² samples from Bonebeds 30, 91, and 41a revealed taxonomic compositions with 91%, 96%, and 89%, respectively, of identifiable elements belonging to ceratopsids, with *Centrosaurus apertus* being the only identifiable centrosaurine taxon (Eberth
and Getty, 2005). As well, a census of Bonebed 43, from which more than 1500 dinosaur elements have been catalogued, estimated a composition of 93% ceratopsid material, with all but a single partially articulated *Chasmosaurus* skull being attributed to *C. apertus* (Ryan et al., 2001). Furthermore, 14 centrosaurine bonebeds near Hilda, Alberta have been hypothesized to comprise a single ‘mega-bonebed’ with a minimum area of 2.3 km² and a death assemblage numbering in the thousands (Eberth et al., 2010). Such high fossil abundances have allowed detailed study of *C. apertus*, and earned it more attention than might otherwise be expected given its relatively limited stratigraphic and geographic distribution.

5.1.2 *Horns and Horncores*

Centrosaurine nasal horncores are seemingly highly morphologically variable, both between and within taxa (Sampson et al., 1997). Despite this variability displayed by adult individuals, juveniles of all centrosaurine species share a seemingly common morphology and pass through very similar stages with respect to nasal horncore and frill growth (Sampson et al., 1997; Ryan et al., 2001; Currie et al., 2008; Brown et al., 2009; see figured nasals in McDonald, 2011) (although fusion of the nasals may occur later in ontogeny in the basal centrosaurine *Albertaceratops* than in other species [Ryan, 2007]). Only with the attainment of maturity do generic traits, such as curving horncores and parietal spikes become fully expressed (Sampson et al., 1997). The paired postorbital horncores are small or completely resorbed to bosses in most derived centrosaurines, and are long (approximately 25-50 cm) and curved only in the basal centrosaurines *Albertaceratops*, *Diabloceratops*, and *Xenoceratops* (Sampson et al., 1997; Ryan, 2007; Kirkland and DeBlieux, 2010; Ryan et al., 2012). Little is known about postorbital ontogeny in these taxa.
This is quite different from the situation in chasmosaurines, in which the nasal horncores are generally small and the postorbital horns are similar between most taxa, with only *Chasmosaurus*, *Vagaceratops*, and *Utahceratops* not developing elongate postorbitals (Sampson et al., 2010) (although *Kosmoceratops* has odd, laterally protruding postorbitals [Sampson et al., 2010]). As well, the postorbital horncores seem to be expressed even in the earliest growth stages (Horner and Goodwin, 2006). Postorbital ontogeny in *Triceratops* will be discussed further below.

The difference in horn form and timing of development between these two lineages could be related to a difference in function, and therefore selection regime, and may be mirrored by differences in the expression of sexual dimorphism. An assessment of horncore morphology and sexual dimorphism may help to resolve some of these outstanding questions.

Although no horn sheath has ever been recovered for a ceratopsian, anecdotal accounts (see Hatcher et al., 1907) and some anatomical and histological evidence suggest that in both lineages the horncores supported a sheath structure (Ryan, 2003; Hieronymus et al., 2009; Happ, 2010). The size and appearance of the sheaths, and how they would affect the mechanical properties of the horns, can only be speculated upon at this time, but they would undoubtedly have some impact on the suitability of the horns for fulfilling certain functions. Most artistic reconstructions include a horn sheath that somewhat augments the size of the horns.

5.2 Materials and Methods

5.2.1 Material

Ceratopsid material was accessed in the collections and exhibits of the following institutions: The Royal Tyrrell Museum of Palaeontology (RTMP), Drumheller, AB; The University of
Articulated (and partially articulated) skulls were examined for each species, as well as disarticulated nasal horncores of *Centrosaurus* and disarticulated postorbital horncores of *Triceratops*. Taxonomic and stratigraphic information for each specimen was recorded from the collections and obtained from the literature. Total sample sizes for each species are: articulated and partially articulated skulls: *Centrosaurus*, n = 10; *Triceratops*, n = 12; isolated horncores: *Centrosaurus*, n = 20; *Triceratops*, n = 9. An additional eight isolated occipital condyles were measured for both taxa.

### 5.2.2 Taxonomy

*Centrosaurus*: Several of the isolated horncore specimens that were examined for this study were not identified to genus or species in the accession data. In order to maximise the possible sample size, these problematic individuals were investigated for further clues as to their taxonomic affinity. Three RTMP specimens and four ROM specimens were attributable to *C. apertus* by their stratigraphic location within Dinosaur Provincial Park, and by their affiliations with the Hilda bonebed (Eberth et al., 2010) and bonebed 43 (Ryan et al., 2001), respectively. One
additional RTMP specimen was attributable to *C. apertus* by its stratigraphic position within MAZ-1 (Mallon et al., 2012) of Dinosaur Provincial Park. Details are provided in Appendix E.

Any specimens attributed to *Centrosaurus* ‘flexus’, ‘dawsoni’, ‘nasicornis’ or ‘longirostris’, were identified as *C. apertus*, following Ryan and Russell (2005). Ryan and Russell (2005) assign ‘*Monoclonius*’ to *Centrosaurus*; unfortunately an exquisite nasal (AMNH 3989) attributed to ‘*Monoclonius crassus*’ was collected from the Judith River Formation of Montana, and because *C. apertus* is currently unknown from Montana, cannot be confidently assigned to *Centrosaurus*. The same applies to USNM 12745, a nasal horncore attributed to ‘*Monoclonius dawsoni*’ that was collected from the Two Medicine Formation of Montana. In contrast, the complete skull of ‘*Monoclonius lowei*’ (CMN 8790) was recovered from Alberta (Sternberg, 1938; 1940), but from the uppermost Dinosaur Park Formation (Ryan and Russell, 2006), again rendering it not attributable to *Centrosaurus*. One horncore attributed to *Centrosaurus* ‘*recurvicornis*’ (*nomen dubium*) (CMN 190) was attributed herein to *Centrosaurus* sp. With the removal of *Coronosaurus brinkmani* from *Centrosaurus* leaving it as a monospecific genus (Ryan et al., 2012), and due to the restricted stratigraphic distribution of *C. apertus* (Mallon et al., 2012), any specimens from Dinosaur Provincial Park attributed to *Centrosaurus* sp. are herein considered to be *C. apertus*.

*Triceratops*: As outlined in Chapter 2, *Triceratops* taxonomy is somewhat problematic, although a single genus containing two species, *T. horridus* and *T. prorsus*, is the currently accepted model (Forster, 1996; Scannella and Fowler, 2009; Sampson et al., 2010; Scannella and Horner, 2010; Farke, 2011; Longrich and Field, 2012). *T. horridus*, however, has been hypothesised to undergo significant cranial transformations late in ontogeny, progressing rapidly from the
traditional ‘adult’ state (Horner and Goodwin, 2006) through a transitional form suggested to be represented by *Nedoceratops hatcheri* (Scannella and Horner, 2011), and attaining a mature form represented by *Torosaurus latus* (Scannella and Horner, 2010). This has been debated in the literature (Farke, 2011; Longrich and Field, 2012) and remains unresolved; so, for the purposes of this thesis, *Triceratops*, *Torosaurus*, and *Nedoceratops* are considered to be distinct genera, and the postorbital horncores of *Nedoceratops* and *Torosaurus* are not considered to represent advanced stages beyond the previously hypothesised ontogenetic trajectory of *Triceratops* postorbitals (Horner and Goodwin, 2006). The revised diagnosis of *Triceratops* (and *T. horridus*) provided by Scannella and Horner (2010) is, therefore, rejected, and I revert to that of Forster (1996); the specific diagnosis for *T. prorsus* remains as defined by Forster (1996). The only character of the *T. prorsus* diagnosis related to the postorbital horncores states that they are relatively short with a horn length/basal skull length ratio of 0.61 or less. Because of this, and to increase the sample of *Triceratops* specimens, both species of *Triceratops* were included in the study and evidence of distinctions in horncore morphology was sought.

Specimens identified as *T. elatus*, *T. flabellatus*, *T. obtusus*, or *T. serratus* were assigned to *T. horridus* following Forster (1996). *Triceratops alticornis* and *T. sulcatus* were deemed *nomina dubia* by Forster (1996). They have been retained here as *Triceratops* sp.

### 5.2.3 Ontogeny

*Centrosaurus*: As previously mentioned, ontogenetic transformations in centrosaurines are considerable. Attempts to demarcate ontogenetic stages have typically yielded three coarse categories: ‘juvenile’, ‘subadult’, and ‘adult’, although the criteria for defining each stage vary somewhat between authors (Sampson et al., 1997; Ryan et al., 2001; Tumarkin-Deratzian, 2003;
Brown et al., 2009). Sampson et al., (1997) also suggest a fourth stage, ‘old adult’, and Brown et al. (2009) also illustrated a nine-step progression of textural pattern change on the parietal.

This project was primarily concerned with the nasal horncores of Centrosaurus, so some measure of the ontogenetic stages of nasal horncore development needed to be established. Sampson et al. (1997) considered the fusion of the nasals to occur prior to the development of the adult condition, but suggested that full expression of the diagnostic morphologies, including the form of the nasal horncore, did not occur until after the attainment of full adult size.

Ryan et al. (2001) stated that as adult size was attained in Centrosaurus, the nasals fused along the midline and expanded, often becoming procurved, and that this was probably coincident with the onset of sexual maturity. In adult specimens the line of fusion of the horn is obliterated and only remains visible on the ventral roof of the narial passage. Ryan et al. (2001) also suggested that the transitional sub-adult stage was probably brief, with the nasals, parietals, and supra-orbital horns rapidly attaining their adult morphology and bone texture.

Brown et al. (2009) thoroughly studied the pattern of surficial texture change that occurred during growth of the centrosaurine parietal and described a consistent pattern of textural change associated with progressive growth of the frill. They suggested that for most specimens, growth to adult, or near-adult, size was largely completed, with the associated transition in bone texture, before the onset of development of the parietal ornamentation (Brown et al., 2009). Although Brown et al. (2009) do not comment on the development of the nasal horncore, they identify the problematic specimen CMN 8790 (“Monoclonius lowei”) as having attained adult size and displaying adult bone texture, but lacking developed parietal ornamentation. The nasal of this specimen is completely unfused (Sampson et al., 1997; personal observation, 2010), supporting the idea that the ontogenetic transformation of the nasals occurs
late in ontogeny, after, or coincident with, the attainment of adult size and development of the parietal ornamentation.

Unfortunately, no one has commented on the exterior surficial bone texture of the nasal horncores directly. However, Ryan et al. (2001) reported long-grained texture on the medial surface of the unfused juvenile nasal horncore, an observation that I too have made. Brown et al. (2009) provide photographs of representative samples of the bone textures, and I have not observed anything other than ‘adult’ texture on large, fused nasal horncores, although this was not explicitly tested.

Collectively, these reports and observations suggest that fusion of the nasal horncores most likely occurred once the individual had attained, or nearly attained, adult size, and subsequent enlargement (and probably curvature) of the horn occurred in the adult stage. As a result, any fully-fused, isolated, nasal horncores should be attributable to the ‘adult’ ontogenetic stage, but no further refinement of relative age can be supported at this time.

Several of the complete or partial skulls examined for this study were assessed for ontogenetic stage by Sampson et al. (1997), Ryan et al. (2001), and Brown et al. (2009). Their conclusions are listed in Table 5.1, and were adopted here. Only three of the skulls examined for this study had not been previously assessed for ontogenetic stage: AMNH 5377, a broken, partial *C. apertus* skull with a detached nasal horncore; RTMP 1997.065.0001, a partial *C. apertus* skull on display in the RTMP; and ROM 43214, an incompletely prepared, broken, partial *C. apertus* skull with a detached nasal horncore. Both AMNH 5377 and ROM 43214 are large, fused skulls, with fully fused nasal horncores, and these features identify them as ‘adult’ specimens. RTMP 1997.065.0001 has a fully fused nasal horncore and well-developed parietal ornamentation,
identifying it as ‘adult’ by the criteria of Sampson et al. (1997), Ryan et al. (2001), and Brown et al. (2009).

*Triceratops*: Horner and Goodwin (2006) identified four cranial ontogenetic stages in *Triceratops*: baby, juvenile, subadult, and adult; each characterised by progressive transformations in a suite of cranial structures. The postorbital horncores are described as being straight in the baby stage, but adopt a prominent posterior curvature in the juvenile stage. The horns then straighten in the subadult stage before becoming procurved in the adult stage (Horner and Goodwin, 2006). The processes by which these transformations occur are not explained, but the stages are reasonably well documented (Horner and Goodwin, 2006). Internal excavation of the horncores begins in the juvenile stage and progresses into the adult stage (Horner and Goodwin, 2006). Additional ontogenetic trends include: the smoothing of the posterior margin of the frill (from scalloped to wavy to smooth), the fusion and flattening of epoccipitals along the frill margin, the fusion of the paired nasals along their medial surfaces, the enlargement of the epinasal (horn) and its fusion to the underlying nasals, and the progressive exclusion of the supraoccipital from the foramen magnum (Horner and Goodwin, 2006, 2008).

Longrich and Field (2012) describe a generally similar ontogenetic progression for *Torosaurus* and *Triceratops*, with three developmental phases: juvenile, subadult and adult. All major growth and corresponding shape changes are achieved by the subadult phase, with enlargement of the parietals, smoothing of the frill margin, and enlargement and anterior reorientation of the postorbitals all occurring in the juvenile phase. The subadult and adult phases are characterised by the cessation of growth and progressive fusion of the skull, and the fusion of the dermal epi-ossifications and snout, respectively (Longrich and Field, 2012).
Forster (1996) reported that the postorbital horncores of *Triceratops* exhibit a range of orientations, grading from approximately 30º to 50º from the vertical, and that the horncores display variation in curvature and angle of splay. Of note, Forster (1996) reported that no pattern was discernible in the variation in curvature.

As best as possible, the complete and partial skulls that were examined for this thesis were assigned to ontogenetic stages following the criteria of Horner and Goodwin (2006) and Longrich and Field (2012). This was based on the fusion of the facial sutures, fusion of the epoccipitals, and orientation of the postorbital horncores. Table 5.2 provides these ontogenetic assignments. Some of the specimens were aged by Longrich and Field (2012), although their conclusions were not necessarily followed. Of the nine isolated postorbital horncores that contributed measurements to the analyses, six were tentatively identified as ‘adult’ because of their strong anterior curvature (USNM 12098, 4286, 6525, 7085, 7086, and 8054), following Goodwin and Horner (2006). One specimen (USNM 2416) was tentatively identified as ‘subadult’ because it exhibited slight dorsal deflection in curvature, again following Goodwin and Horner (2006). Two specimens (USNM 8027 and USNM 398270) were deemed inconclusive. These ontogenetic assignments were abandoned for the eigenshape analysis because curvature was the trait being explored in that analysis.

5.2.4 Measurements

Measurements were made with large Mitutoyo ‘Digimatic’ digital calipers, accurate to 0.1 mm and recorded to the nearest 0.1 mm, and with flexible measuring tape, recorded to the nearest 1 mm. Measurements were made three times and averaged, although circumstances occasionally
required additional, or necessitated fewer, repetitions. Descriptions of measurements are
provided below and in Tables 5.3 – 5.5, and are illustrated in Figures 5.1 and 5.2.

On each skull, whenever possible, the following measurements were recorded: basal skull
length, from the anterior edge of the rostral bone to the posterior edge of the occipital condyle
[from D to E, in Fig. 5.1; and E to F, in Fig. 5.2]; length of the left and right toothrows, from the
posterior edge of the posterior alveolus to the anterior edge of the anterior alveolus [from F to G
in Fig. 5.1; and G to H in Fig. 5.2 and 5.2]; and the maximum horizontal width and vertical
height of the occipital condyle, as well as its maximum circumference in a vertical plane. Left
and right toothrow lengths were combined into an ‘average toothrow length’ variable.

*Centrosaurus*: Figure 5.1 illustrates skull and nasal horncore measurements for *Centrosaurus*
specimens. The height of the horncore was measured along its anterior and posterior surfaces,
from its base on the nasal bones to its tip, with measuring tape [following the curve from A to C,
and B to C, in Fig. 5.1]. An average height was calculated as the mean of these values. If the
horncore was curved, the chord of the horncore was measured in a straight line from base to tip
[straight line from A or B (depending on curvature), to C, in Fig. 5.1]. For the basal dimensions
of the horncore, the antero-posterior length and medio-lateral width were measured with calipers
[length from A to B; width measured at the midpoint of A-B, in Fig. 5.1], and the basal
circumference was measured with tape [around the horncore in the plane of A and B, in Fig. 5.1].
For nasal horncores that were broken distally, only basal dimensions were recorded. For
disarticulated nasal horncores the anterior direction was established by examining the fossae on
the ventral surface of the nasal bone.
*Triceratops*: Figure 5.2 illustrates skull and horn measurements that were recorded for *Triceratops* specimens. Postorbital horncore length was measured along its ventral and dorsal surfaces, from the proximal contact with the orbital rim to the distal tip for the ventral length [following the curve from A to C, in Fig. 5.2], and from the midpoint of the dorsal base of the postorbital to the distal tip for the dorsal length [following the curve from B to C, in Fig. 5.2]. Dorsal length was later dropped from the analysis (see below). The basal dimensions of the horncores were measured perpendicular to the long axis of the horncore immediately distal to the orbital rim; the dorso-ventral height and medio-lateral width were measured with calipers [height from A to D; width measured at the midpoint of A-D, in Fig. 5.2], and the basal circumference was measured with tape [around the horncore through the plane of A and D, in Fig. 5.2]. For these metrics, both horncores were measured whenever possible, and any breakage or deformation was noted. For use in the analyses, left and right horncore measurements were averaged, or if only one horncore was intact, it was used for that specimen. For those few specimens that had both horncores intact, a comparative plot of left, right, and average ventral horncore lengths revealed relatively minor asymmetry in the horncores (Figure 5.3), so averaging the horncore measurements was considered to be an acceptable approximation.

Width between the horncores was measured in two locations: at the base, measured between the midpoints of the ventral horncore surfaces at the junction with the orbital rim [from A to A’, in Fig. 5.2], and at the distal tips [from C to C’, in Fig. 5.2].

When measuring disarticulated postorbital horncores, it was necessary to first identify the ventral and dorsal surfaces of the horncore, and then to determine whether a clear indication of the proximal base was apparent on the ventral surface that would allow the measurements to be made in the correct locations. If this point could be established (typically indicated by the
deflection of the ventral surface at the junction with the orbital rim), ventral length and the basal dimensions were measured as previously described.

As more specimens of *Triceratops* were examined it quickly became clear that point B, the dorsal midpoint of the base of the postorbital horncore, was not reliably identifiable between specimens because the posterior margin of the postorbital fuses with the parietal and squamosal during ontogeny, leaving a smooth, unbroken transition from the dorsal surface of the horncore onto the slope of the frill. As a result, the ‘dorsal length’ (DL) measurement could not be meaningfully compared between specimens, and was dropped from the dataset.

Anderson (1999) used occipital condyle area as a metric of body size in *Triceratops*, with area approximated as condyle width x height, after finding evidence that area was an effective predictor of body size in *Basilicus vittatus* and *Alligator mississippiensis*. For this study, occipital condyle width, height, and circumference were measured with the intention of using circumference as an indicator of body size instead of ‘area’. To test this, ‘area’ was calculated as per Anderson (1999), and regressed against occipital condyle circumference in a reduced major axis regression. They were found to be very highly correlated ($r^2 = 0.989$), so circumference was maintained as an indicator of body size instead of ‘area’.

5.2.5 Analysis of Data

Following the methods utilised in Chapter 4, non-scaled datasets were compiled for both taxa. The *Centrosaurus* measurement data are provided in Table 5.6; *Triceratops* measurement data are provided in Table 5.7. For both taxa, coefficients of variation (CV) and coefficients of bimodality ($b$) were calculated for each variable, as described in Chapter 4. Frequency histograms were created and inspected for each trait, as were bivariate plots.
Principal components analysis (PCA) was employed to explore patterns of variation in the datasets. As in Chapter 4, missing data were estimated by the iterative imputation function. A variance-covariance matrix was used because all variables were in the same units (mm). Hierarchical cluster analysis using the UPGMA algorithm aided in the interpretation of the results of the PCA as well as some of the bivariate scatter plots. Based on the performance of the cluster analyses in the exemplar model, k-means cluster analysis was dropped from the data analysis as it was not found to contribute useful information beyond that offered by the hierarchical clusters.

Eigenshape analysis was employed to investigate variation in the curvature of the postorbital horncores of Triceratops. Methods were similar to those described in Chapter 4, with each horncore photographed in lateral view to best capture the curvature of the ventral surface. Again, the outline was traced from digital photographs using tpsDig v2.16, with the first point of each outline placed at the point on the ventral surface that indicated the junction with the orbital rim. The outline of the ventral surface was then traced by placing coordinate points along the ventral surface to its distal tip, as shown in Figure 5.4. The curve was then resampled to comprise 25 equally spaced coordinate points, as shown in Figure 5.5. The sample for this analysis consisted of the horncores of eight complete or partial skulls and eight isolated postorbital horncores, representing five specimens of T. horridus, four specimens of T. prorsus, and seven identified as Triceratops sp.
5.3 Results

5.3.1 Centrosaurus

i) Predictor Variables

The predictor variables identified several traits for investigation. These results are provided in Table 5.8. The coefficient of variation revealed elevated levels of variation (CV ≥ 10) in all measures of the height of the nasal horn (posterior, anterior, average, and chord heights), as well as the width and length at the base of the horn, and the height and circumference of the occipital condyle. Basal horncore circumference, basal skull length, and occipital condyle width were also high, but slightly less than 10. Toothrow length showed low levels of variation.

Only one trait returned an elevated bimodality score ($b \geq 0.55$), and that was right toothrow length (RTL). Too few specimens were available to calculate $b$ for the left toothrow length (LTL), but average toothrow length (ATL) only narrowly missed the cut-off ($b = 0.54$). This is somewhat surprising as these variables had low CV scores, and this highlights the differences between how these coefficients are calculated.

ii) Visual Inspection of Plots

Frequency histograms were generated for each variable, except left and right toothrow lengths, for which average toothrow length was used instead. None of the histograms showed good evidence of bimodality. Of the 12 variables, five exhibited a slight left skew. This was particularly notable for the occipital condyle circumference (OCC) (Figure 5.6) and average toothrow length, suggesting smaller individuals are more common than larger individuals. Negative skew was also observed in anterior horncore height, which is contrasted by a slight positive skew in the histogram of posterior horncore height. This is attributable to a stronger curvature in procuring horns, providing smaller anterior height values, and greater posterior
height values. As well, the somewhat odd distribution of average horncore height, with a spike in the frequency of mid-range values, is due to the fact that most curved specimens will produce ‘average’ average heights as a result of their necessarily different anterior and posterior heights (i.e. one ‘high’ height and one ‘low’ height).

Bivariate scatter plots were generated using the *Centrosaurus* dataset. Specimens were colour coded according to the curvature of the nasal horncore in order to determine whether any additional morphological change was associated with the variation in curvature. Basal skull length (BSL) was the most abundant ‘body size’ variable for *Centrosaurus* (n = 9), so it was utilised in the bivariate plots instead of OCC (eight occipital condyles were isolated specimens, leaving only six that could provide comparative information). Even so, a large proportion of specimens lacked a measurement for BSL, so several other combinations of variables were plotted in order to further explore the morphology. In general, plotting variables against BSL revealed little discernible pattern other than a loose positive association attributable to size. Some interesting variation related to horn curvature was observed in other plots, however.

Plotting occipital condyle height (OCH) by width (OCW) revealed a generally linear pattern of growth (Figure 5.7), wherein specimens with procurved horns represent five of the six largest individuals. Unfortunately, only one adult specimen with a recurved horn could be plotted (ROM 767), and no specimens with straight horncores could be plotted, so it is difficult to compare between the groups (Figure 5.8). ROM 767 plots at the small end of the distribution. AMNH 5351 has a tall, slightly recurved horncore and, extrapolating from its OCW value, it too would have plotted in the lower third.

Plotting basal horncore width (BW) against basal horncore length (BL) also revealed differences between specimens with different horn curvatures (Figure 5.9). Horncores with
posterior, straight, and anterior curvature overlap with respect to their basal lengths, but appear to segregate in that order as basal width increases. A similar distribution was observed in the plot of average horncore height (AvgH) against BW - recurved specimens display a greater range of heights, but procured specimens appear to have greater basal horncore widths (Figure 5.10). To investigate this further, t-tests were conducted to test for a difference in basal horncore widths between specimens with procured, recurved, and straight horncores. Notably, procured nasal horncores were found to have a significantly greater basal width than recurved horncores ($t = -2.63$, $p = 0.018$). Neither was significantly different from straight horncores. Basal length and circumference were also tested, but were not found to differ significantly between the groups.

Plotting anterior horncore height (AH) against posterior horncore height (PH) revealed a distinction between recurved and procured horncores, with straight horns plotting roughly in the middle (Figure 5.11). This is not surprising, because as the horncore curves one side must increase in length relative to the other, but the pattern of the distribution indicates that procured horns tend to curve more strongly than do recurved horns, and that recurved horns may reach greater heights. One straight horncore specimen (TMP 1992.36.224) plots in the midst of the procured horncores because, although it is not curved, it leans anteriorly, resulting in a greater relative posterior height.

Finally, a plot of BW against BL appears to contain two size clusters separated by a gap (Figure 5.12). Hierarchical cluster analysis modestly supports this clustering, as illustrated in Figure 5.13. An unrelated gap is apparent in a plot of AvgH against BL, with no specimens plotting between 128mm and 144mm lengths. Unfortunately, this appears to be simply a sampling artifact, as six horncore specimens in the dataset have basal length values that fall in that gap. These specimens were not plotted because they could not be measured for height.
iii) PCA and Cluster

Two PCA’s were conducted to explore patterns of variation in the *Centrosaurus* dataset. The first iteration used only partial or complete skulls of *C. apertus*, totalling nine specimens. Seven variables were included in the analysis, and the dataset is shown in Table 5.9. The first three principal components captured 95.78% of the variation (53.87%, 34.33%, and 7.58%, respectively). The plot of PC1 and PC2 is provided in Figure 5.14, and the loadings are provided in Table 5.10. Interpretation of the scatter plot and loadings revealed the first axis to be largely a size axis, not surprisingly, and dominated by basal skull length. Basal horncore circumference increased most strongly with skull size, but notably, average horncore height showed essentially no change. The second axis was dominated by average horn height, which seemed to be influenced little by skull size, and was accompanied by weak positive loadings for basal horncore length and circumference, as well as occipital condyle circumference. The results were likely influenced somewhat by AMNH 5351, which plots alone high on the second axis, and has the tallest horn in the dataset. The third axis revealed variation in the basal horncore dimensions.

A hierarchical cluster analysis of the scores from the first PCA simply grouped the specimens as they appeared in the PC1 x PC2 scatter plot, and did not reveal any additional information.

The second iteration of the PCA explored variation in the horncores directly, including only four horncore variables. The inclusion of isolated horncores bolstered the sample size to 21. The dataset is shown in Table 5.11, and the scatterplot is provided in Figure 5.15. The first principal component captured 76.83% of the variation and reflected change in horncore size. It was most strongly influenced by average horncore height, but basal circumference loaded strongly as well, reflecting a gradual increase in circumference with height. The specimens were
fairly well distributed over the second axis, which captured 19.42% of the variation. This axis reflected a change in horncore proportions, with a decrease in height as basal circumference (and width and length) increased. Notably, moving from negative to positive along the second axis results in a general progression from space occupied by posteriorly curved horncores into space occupied by straight and anteriorly curved horncores. That procurved or straight horncores appear to be more ‘stout’ (shorter height with greater basal dimensions) than recurved specimens, supports the observations made from the bivariate scatters. Loadings of the first two PC’s are provided in Table 5.12.

A hierarchical cluster analysis of the scores from the second PCA recovered a series of nested groupings that did not provide further useful information.

iv) Summary

The curvature of the nasal horncores is a strong source of morphological variation in *Centrosaurus*. Procurred horncores have significantly greater basal widths than do recurved horncores, and tend to curve more strongly. Five of the six largest specimens, as assessed by occipital condyle circumference, exhibit procurved nasal horncores. Evidence of bimodal clustering was weakly present in a bivariate plot of basal horncore width against length.

5.3.2 Triceratops

i) Predictor Variables

The predictor variables identified many traits for investigation. These results are provided in Table 5.13. All 14 horncore-related variables and all three occipital condyle variables returned elevated coefficients of variation (CV ≥ 10). So too did right toothrow length, although average
toothrow length scored under ten (CV = 9.81). Elevated bimodality coefficients (b ≥ 0.55) were recovered only for basal horncore height (left, right, and average).

ii) Visual Inspection of Plots

Frequency histograms were generated for each variable, although only the averaged measures were used for those variables with left and right sides. A bimodal pattern was apparent for occipital condyle circumference (OCC) and occipital condyle width (OCW), with no specimens plotting between 85 mm and 94 mm in the latter (Figure 5.16). The two T. prorsus specimens that were included plot below the gap in the distribution, and the five T. horridus specimens appear to show a general progression from subadult to adult with increasing size, with two of the three subadult specimens plotting below the gap. Average basal horncore circumference (BCA) and height (BHA) both had negatively skewed distributions, whereas average basal horncore width (BWA) was close to normal. Horncore spread at base (HSB) showed a strongly positively skewed distribution, indicative of two specimens with abnormally low values due to medio-lateral compression of the skulls.

Bivariate scatter plots were generated using the Triceratops dataset. Species assignments were identified in the scatter with different symbols (open squares for T. horridus, ‘plus signs’ for T. prorsus, and dots for Triceratops sp.), and subadult and adult specimens were identified with an ‘S’ or ‘A’ at the end of the specimen number, respectively (e.g. ROM 55380S). Occipital condyle circumference (OCC) was used as an indicator of body size. Average basal horncore height (BHA) and circumference (BCA) showed a positive trend, both increasing with body size, and suggested a subadult to adult growth trend in T. horridus (Figures 5.17 and 5.18). In contrast, average basal horncore width (BWA) showed little increase with body size (Figure 5.19), suggesting that the majority of the growth in the horncore base occurs in height (that is,
the dorso-ventral/antero-posterior basal dimension). Plotting the average ventral horncore length (VLA) against horn spread at tips (HST) revealed a positive association between the variables, and a progression from *T. prorsus* to *T. horridus* (Figure 5.20). This suggests that horncore spread is a function of length and that *T. prorsus* simply does not grow horncores as long as those of *T. horridus*. Furthermore, their horncores appear to be ‘stouter’, as plotting VLA against any of BWA, BHA, or BCA indicates that *T. prorsus* have shorter horncore lengths with greater basal circumference (Figure 5.21). A growth trajectory from subadult to adult is also visible for *T. horridus*, as length and circumference steadily increase. Plotting OCW against OCC revealed the gap that was identified in the histograms, with the *T. prorsus* specimens clustering with the smaller *T. horridus* specimens, suggesting that *T. horridus* attained larger overall body sizes than did *T. prorsus*.

iii) PCA and Cluster

Two PCA’s were conducted to explore patterns of variation in *Triceratops*. The first iteration used only partial or complete skulls of *Triceratops*, and included seven specimens and nine variables. The dataset for the PCA is shown in Table 5.14, and the PC scatters in Figures 5.22 and 5.23. The first three axes accounted for 42.2%, 38.46%, and 13.95% of the total variation, respectively, and the loadings are provided in Table 5.15. The first axis revealed patterns of relative growth, with average basal horncore circumference and basal skull length varying the most with size. The second axis revealed a positive association between average horncore length and the spread at the horncore tips, as was found with the bivariate scatters, and again showed some separation of the species. Surprisingly, those two variables loaded in opposition on the third axis, revealing the loose nature of the correlation between them.
A hierarchical cluster analysis of the PCA scores somewhat supported the species groupings that were observed on PC2, but the signal is somewhat muted by the overlap of the species on PC1.

The second iteration of the PCA involved only four horncore variables in an effort to explore their relationships more thoroughly. Seventeen specimens were included. The dataset is shown in Table 5.16, and the PC scatters in Figures 5.24 and 5.25. The first and second axes accounted for 67.25% and 31.51% of the total variation, respectively. On the first axis, the four variables had sub-equal positive loadings, indicating that basal circumference increased most rapidly with increasing horncore length, followed by height and width. This is not surprising, but supports the observation from the bivariate plots that basal height increases more rapidly than width. This was applicable to both species, but some separation along the first axis appeared attributable to ontogeny, as three of the four subadult specimens scored negatively on PC1 and most of the adult specimens scored positively. The second axis, however, showed some separation of the species, with *T. prorsus* specimens scoring higher on PC2. The loadings (Table 5.17) reveal a proportional change with horncore length decreasing as basal circumference increases, supporting the previous observation of ‘stouter’ horncores in *T. prorsus*.

A hierarchical cluster analysis supported the perceived separation of two clusters on the first axis, with three subadult *T. horridus* specimens clustering with two *T. prorsus* specimens and the other cluster being dominated by adult specimens with positive PC1 scores (Figure 5.26).

iv) Eigenshape Analysis

Eigenshape analysis revealed some patterns in the degree and angle of ventral horncore curvature. The first three axes accounted for 69.46%, 20.28%, and 10.26% of the shape variation, respectively. No consistent differences were apparent between the two species,
suggesting that curvature generally varies similarly in both, although *T. prorsus* appeared to score slightly higher on the second axis. Unfortunately, too few specimens were identifiable to ontogenetic stage to permit meaningful investigation of the proposed ontogenetic changes in horncore curvature (the isolated horncores could not be aged except by curvature, which was rejected as circular logic). Shape variation along the first axis, however, from positive to negative, reflected a transition from a slightly procurved horncore with a posterodorsally deflected distal portion to one with a prominent, continuous anterior curvature. Variation on the second axis was largely related to the angle of procurvature of the horncore in its proximal 1/5th, with a progression from a nearly straight, to an anteriorly deflected, proximal section as one moves from negative to positive along the axis. The scatter plot of the first two axes is presented in Figure 5.27

v) Summary

There is considerable morphological variation in body size and in the horncores of *Triceratops*. Perceived bimodality in occipital condyle width is surprising and may indicate an ontogenetic signal in the dataset. Basal horncore dimensions were found to increase with horncore length, although it appears that most of the basal growth occurs in dorso-ventral/antero-posterior ‘height’, whereas horncore width does not vary greatly. There is also some evidence of an increase in horn length from the subadult to adult stages in *T. horridus*. Differences between the species were apparent, as *T. prorsus* appears to attain smaller overall body sizes and exhibits ‘stouter’ postorbital horncores with shorter lengths and greater basal dimensions than does *T. horridus*. The largest source of variation in ventral horncore outline shape is attributable to the development of a smooth anterior curvature from a deflected distal tip, although it could not be assessed with respect to ontogeny.
5.4 Discussion

5.4.1 Centrosaurus

This study revealed some interesting morphological variation in *Centrosaurus* *apertus*. From the mammalian model it was clear that in species with subtly sexually dimorphic horns, the basal horn dimensions are the most likely to exhibit this dimorphism. Therefore the most probable source of horncore dimorphism in *Centrosaurus* was expected to be the basal dimensions, and the slight bimodal clustering observed in the bivariate plot of basal horncore width against basal horncore length (Figure 5.12) was tantalizing. This is particularly interesting because it does not appear to be directly related to horn curvature, which dominated so much of the other observed variation, as one straight specimen and one recurved specimen plot in the larger cluster alongside four procurved specimens. The pattern is slightly similar to some of the bimodal distributions observed in the bivariate plots of mountain goat horns, but the scatter is much less constrained in *Centrosaurus*, and the gap is not as well defined. It is tempting to consider this pattern as evidence for two adult size clusters, with a common ‘adult’ size class and a rarer larger class, but such a conclusion is difficult to support without a better understanding of horncore ontogeny in *Centrosaurus*. Furthermore, that the gap is real morphologically is called into question somewhat given the demonstrably false gap that was apparent in the plots of average horncore height against basal horncore length.

A great deal of variation in the dataset is associated with the curvature of the nasal horncores, and merits further discussion. Ryan et al. (2001) reported that the greatest variation in adult nasal horncores was exhibited in their robustness (compressed versus ovoid in cross section) and in the degree of procurvature, but that those features were not correlated. In this study, however, horncores that curved anteriorly were found to have significantly greater basal
widths than horncores that curved posteriorly, suggesting that robusticity and procurvature may in fact be correlated to some degree (see Figure 5.9). Specimens with procured nasal horncores were also found to have the largest occipital condyles, suggesting that they may have larger overall body sizes than specimens with straight or recurved horncores. These results have interesting implications for what is understood about ontogeny in *Centrosaurus*.

Horncore growth and curvature in *Centrosaurus* is thought to only really begin at or near the attainment of adult size (Sampson et al., 1997; Ryan et al., 2001; Brown et al., 2009). It is unclear, however, what adult size is, exactly, and whether adulthood is thought to coincide with a cessation of overall body growth or not. Also, it has been previously suggested that procured nasal horncores may be associated with maturity in *Centrosaurus* (Sampson et al., 1997; Ryan et al., 2001). If this is true, are specimens with recurved horncores, such as ROM 767 and AMNH 5351, which are considered ‘adult’ but are generally small specimens (judging by their occipital condyles, toothrow lengths, and basal skull lengths), expected to continue to grow and to have their fully fused, erect, nasal horncores ‘mature’ into a procurred state? From the information that was gathered for this study it is not possible to comment on maturity, as all specimens were considered to be ‘adult’, so only body size can be addressed here. With respect to body size and curvature, there are two possibilities: the first is that curvature is not related to body size, so curvature should be random with respect to body size, and the second is that curvature is associated with body size and should therefore not be random. The results here support the latter, because specimens with procured horncores had the largest occipital condyles and demonstrably greater horncore widths. This then leads to a second set of possibilities: either procuring nasals are indeed more ‘mature’, and adult individuals with recurved or straight nasal horncores continue to grow in size and their horncores increase in width and curl anteriorly as
they grow, or, procuring horncores are not more ‘mature’, and specimens with straight or recurved horncores simply attain maturity at smaller body sizes. Unfortunately, neither possibility can be favoured over the other by the evidence gathered here. If the latter were correct, however, it would be suggestive of dimorphism in *Centrosaurus* associated with horncore curvature, and sex would need to be seriously considered as a factor.

5.4.2 *Triceratops*

This study found evidence in support of the distinction between *Triceratops horridus* and *Triceratops prorsus*. Bivariate plots and PCA indicated that *T. prorsus* exhibits stouter postorbital horncores than does *T. horridus*, with shorter ventral lengths and greater basal dimensions. Notably, shorter relative postorbital horns was one of the characters listed in the species diagnosis of *T. prorsus* (Forster, 1996), although no mention was made of a difference in basal horncore dimensions. Despite these differences in horncore form, eigenshape analysis did not reveal substantial differences in the shape of the ventral horncore curvature, although *T. prorsus* specimens may possibly exhibit a sharper angle of anterior curvature in the proximal portion of the horncore than do *T. horridus* specimens. Although interesting, and a small endorsement of the two species model, differences between the species accounted for much of the variation in the dataset, and ontogenetic variation seemed to account for the rest. As a result, the sample in which evidence of dimorphic patterns might have been found, became rather small, and no such patterns were discerned amidst the taxonomic and ontogenetic variation. Still, several interesting morphological trends were revealed, including some informative ontogenetic signals.
The bimodal distributions of occipital condyle circumference and width indicated a size distinction between subadult and adult specimens of *T. horridus*, and between adult specimens of *T. prorsus* and *T. horridus*. This suggests that occipital condyle size may be indicative of relative growth in *T. horridus*, and that *T. horridus* attains larger body sizes than does *T. prorsus*. With only two specimens of *T. prorsus* providing occipital condyle measurements, however, this species difference cannot be regarded as truly informative, and would be in opposition to the conclusions of Anderson (1999). There was some evidence of an ontogenetic trajectory in horncore growth in *T. horridus*, as horncore length and basal circumference appeared to increase from subadult to adult specimens (Fig. 5.28). Although this seems obvious and uninteresting, it has some implications for the ontogenetic stages proposed by Longrich and Field (2012). They stated that the postorbitals become ‘long, massive, and procurved’ in the first stage of growth, and are at full size in the ‘subadult’ stage. However, the *T. horridus* specimens of interest here were all identified as subadults by Longrich and Field (2012), and yet they create what appears to be direct growth trajectory into space occupied by the largest *T. horridus* specimens. It cannot be said that those specimens had not already stopped growing, but the pattern is at least suggestive of growth continuing in the ‘subadult’ stage, contrary to Longrich and Field (2012).

Also, with respect to ontogeny, the largest source of variation in ventral horncore outline shape was found to be similar to the ontogenetic trajectory that has been proposed to occur in *Triceratops* horncores (Goodwin and Horner, 2006). This relates to the progression of the horncores from a recurved and near-vertical orientation in subadults to an anteriorly curved orientation in adults (Goodwin and Horner, 2006), and is roughly approximated in the progression of shape variation observed along the first axis of the eigenshape scatter. Unfortunately, this pattern could not be thoroughly evaluated as not enough specimens could be
staged by other ontogenetic criteria. These results are still informative though, and they indicate that the eigenshape method effectively recognises variation in horncore curvature and would provide an effective test of this hypothesised ontogenetic pattern if a growth series were staged based on other ontogenetic indicators.

5.5 Conclusions

This study did not find sufficient evidence to reject the null hypothesis of monomorphism in either *Centrosaurus apertus*, or *Triceratops horridus*. Possible bimodal clustering in basal horncore width and length, and some evidence of larger size in specimens with procurved nasal horncores, indicate that further investigation into dimorphism in *Centrosaurus* is merited. Moreover, these findings suggest that there is still considerable variation in cranial morphology that has not been documented in *Centrosaurus*, especially with respect to ontogeny. The relationships between maturity, body size, and horncore growth, need to be explored, as it remains unclear what happens after an individual attains ‘adult size’. A better understanding of how the procurved horncores develop, in terms of regional bone growth patterns, would likely shed light on many of these questions.

The species distinction in *Triceratops* was found to have morphological merit, but the inclusion of both species, as well as subadult specimens, did not permit a thorough examination of sexual dimorphism in *T. horridus*, or in *Triceratops*, more generally. Some of the findings from this study suggest that the ontogenetic stages in *Triceratops* are still not fully resolved, so even if only *T. horridus* specimens were examined for evidence of dimorphism, considerable ontogenetic variation could still hamper the search. With the ongoing debate about the hypothesised *Triceratops* to *Torosaurus* transformation drawing attention to the ontogenetic
trajectory of *Triceratops*, it is hopeful that continued scrutiny will resolve some of these problems.

Until a better understanding of cranial ontogeny in ceratopsid dinosaurs is developed, it is unlikely that the presence or absence of sexual dimorphism in these dinosaurs can be further resolved. Stratigraphic control and taxonomic resolution have been fairly thoroughly established for *Centrosaurus* and *Triceratops* in recent years, and ontogeny now appears to be under the microscope. Once this becomes more thoroughly understood, revisiting the question of sexual dimorphism should be relatively straightforward and highly informative.
**Figure 5.1** *Centrosaurus* skull (USNM 8897) in left lateral view. Letters indicate reference points for measurements, as follows: A) anterior base of nasal horncore, B) posterior base of nasal horncore, C) distal tip of nasal horncore, D) anterior-most point of rostral bone, E) posterior-most point of occipital condyle, F) anterior rim of anterior-most alveolus in maxillary toothrow, G) posterior rim of posterior-most alveolus in maxillary toothrow. Basal horncore dimensions (width, length, circumference) are measured in the plane of A-B, with medio-lateral width measured at the midpoint of the line between A and B.
Figure 5.2 Triceratops skull measurements. Letters indicate reference points for measurements, as follows: A) anterior base of postorbital horncore at junction with orbital rim, B) posterior base of postorbital horncore at estimated midpoint of base, C) distal tip of postorbital horncore, D) point on dorsal margin of horncore that shares a plane with A that is perpendicular to the longitudinal axis of the horncore, E) anterior-most point of rostral bone, F) posterior-most point of occipital condyle, G) anterior rim of anterior-most alveolus in maxillary toothrow, H) posterior rim of posterior-most alveolus in maxillary toothrow. Basal horncore dimensions (width, height, circumference) are measured in the plane of A-D. a) RTMP 035 (AMNH 5116) in left lateral view; b) in anterior view; c) USNM 1205 in palatal view, anterior to left.
Figure 5.3 Line plot of left (black), right (red), and average (blue) ventral horncore lengths for six *Triceratops* specimens. Labels along the x-axis are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7. Asymmetry in horncore length appears to be neither consistent, nor great, supporting the use of the average value.
Figure 5.4 *Triceratops prorsus* specimen SMNH P1163.4. Ventral horncore surface has been traced by the placement of numerous coordinate points along its outline. This represents the first step in eigenshape analysis. Screen capture from tpsDig v2.16.
Figure 5.5 *Triceratops prorsus* specimen SMNH P1163.4. The outline traced in Figure 5.4 has been resampled by tpsDig v2.16 to comprise 25 equally spaced coordinate points. This represents the second step of capturing shape variation in eigenshape analysis. Screen capture from tpsDig v2.16.
Figure 5.6 Frequency histogram of occipital condyle circumference (OCC) for *Centrosaurus*. Red line indicates an approximation of the distribution curve, and can be compared against the black line, which indicates a theoretical normal distribution. Note the left (positive) skew of the distribution.
Figure 5.7 Bivariate scatter of occipital condyle height against occipital condyle width for *Centrosaurus*. Axes are in millimetres. Labels are specimen numbers and specimen data can be found in Table 5.6.
Figure 5.8 Bivariate scatter of occipital condyle height against occipital condyle width for *Centrosaurus*. Axes are in millimetres. Labels are specimen numbers and specimen data can be found in Table 5.6. Open circles and open squares indicate specimens with procurved, and recurved, nasal horncores respectively.
Figure 5.9 Bivariate scatter of basal horncore width against basal horncore length for *Centrosaurus*. Axes are in millimetres. Open circles and open squares indicate specimens with procurved, and recurved nasal horncores, respectively. Black dots indicate specimens with a straight nasal horncore.
Figure 5.10 Bivariate scatter of average horncore height against basal horncore width for *Centrosaurus*. Axes are in millimetres. Open circles and open squares indicate specimens with procurred, and recurved, nasal horncores respectively. Black dots indicate specimens with a straight nasal horncore. Labels are specimen numbers. Specimen data can be found in Table 5.6.
**Figure 5.11** Bivariate scatter of anterior horncore height against posterior horncore height for *Centrosaurus*. Axes are in millimetres. Open circles and open squares indicate specimens with procurred, and recurved, nasal horncores respectively. Black dots indicate specimens with a straight nasal horncore.
Figure 5.12 Bivariate scatter of basal horncore width against basal horncore length for *Centrosaurus*. Axes are in millimetres. Open circles and open squares indicate specimens with procurred, and recurved, nasal horncores respectively. Black dots indicate specimens with a straight nasal horncore.
**Figure 5.13** Dendrogram of hierarchical cluster analysis (UPGMA) of basal horncore width and basal horncore length for *Centrosaurus*. Specimens are colour-coded by horncore curvature: purple = procurved, blue = recurved, black = straight. Numbers at branch nodes indicate percentage support of 1000 bootstrap iterations.
Figure 5.14 Results of the first *Centrosaurus* PCA, showing PC1 and PC2, which collectively account for 88.2% of the variance. Loadings are provided in Table 5.10.
Figure 5.15 Results of the second *Centrosaurus* PCA, showing PC1 and PC2, which collectively account for 96.25% of the variance. Loadings are provided in Table 5.12.
**Figure 5.16** Bivariate scatter of occipital condyle height against occipital condyle width for *Triceratops*. Axes are in millimetres. Open squares indicate *T. horridus* specimens, ‘plus signs’ indicate *T. prorsus* specimens, black dots indicate specimens assigned to *T. sp*. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
Figure 5.17 Bivariate scatter of average basal horncore height against occipital condyle circumference for *Triceratops*. Axes are in millimetres. Open squares indicate *T. horridus* specimens, ‘plus signs’ indicate *T. prorsus* specimens, black dots indicate specimens assigned to *T. sp*. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
**Figure 5.18** Bivariate scatter of average basal horncore circumference against occipital condyle circumference for *Triceratops*. Axes are in millimetres. Open squares indicate *T. horridus* specimens, ‘plus signs’ indicate *T. prorsus* specimens, black dots indicate specimens assigned to *T. sp*. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
**Figure 5.19** Bivariate scatter of average basal horncore width against occipital condyle circumference for *Triceratops*. Axes are in millimetres. Open squares indicate *T. horridus* specimens, ‘plus signs’ indicate *T. prorsus* specimens, dots indicate specimens assigned to *T.* sp. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
**Figure 5.20** Bivariate scatter of horn spread at tips against average ventral length for *Triceratops*. Axes are in millimetres. Blue squares indicate *T. horridus* specimens, red ‘plus signs’ indicate *T. prorsus* specimens, and the black dot indicates a specimen assigned to *T. sp.*
Figure 5.21 Bivariate scatter of average ventral horncore length against average basal horncore width for *Triceratops*. Axes are in millimetres. Blue squares indicate *T. horridus* specimens, red ‘plus signs’ indicate *T. prorsus* specimens, black dots indicate specimens assigned to *T. sp.*
**Figure 5.22** Scatter plot of Principal Components 1 and 2 for the first *Triceratops* PCA. Blue squares indicate *T. horridus* specimens, red ‘plus signs’ indicate *T. prorsus* specimens. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
**Figure 5.23** Scatter plot of Principal Components 2 and 3 for the first *Triceratops* PCA. Blue squares indicate *T. horridus* specimens, red ‘plus signs’ indicate *T. prorsus* specimens. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
Figure 5.24 Scatter plot of Principal Components 1 and 2 for the second *Triceratops* PCA. Blue squares indicate *T. horridus* specimens, red ‘plus signs’ indicate *T. prorsus* specimens, dots indicate specimens assigned to *T.* sp. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
Figure 5.25 Scatter plot of Principal Components 2 and 3 for the second *Triceratops* PCA. Blue squares indicate *T. horridus* specimens, red ‘plus signs’ indicate *T. prorsus* specimens, dots indicate specimens assigned to *T*. sp. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
Figure 5.26 Dendrogram of hierarchical cluster analysis (UPGMA) of PCA scores from the second Triceratops PCA (Fig. 5.22). Specimens are colour-coded by taxon: red = *T. prorsus*, blue = *T. horridus*, black = *T. sp*. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7. Numbers at branch nodes indicate percentage support of 1000 bootstrap iterations.
Figure 5.27 Scatter plot of the first and second axes for the *Triceratops* eigenshape analysis. Blue squares indicate *T. horridus* specimens, red ‘plus signs’ indicate *T. prorsus* specimens, black dots indicate specimens assigned to *T*. sp. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
Figure 5.28 Bivariate scatter of average ventral horncore length against average basal horncore circumference for *Triceratops*. Axes are in millimetres. Open squares indicate *T. horridus* specimens, ‘plus signs’ indicate *T. prorsus* specimens, black dots indicate specimens assigned to *T. sp*. Labels are specimen numbers plus a letter indicative of ontogenetic stage: S = subadult, A = Adult. Specimen data can be found in Table 5.7.
Table 5.1 Ontogenetic stages assigned to *Centrosaurus* specimens by Brown et al. (2009), Ryan et al. (2001), and Sampson et al. (1997). Conclusion identifies the ontogenetic stage that was accepted.

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Table 5.2: Ontogenetic assignment of *Triceratops* specimens. Results listed under “Longrich and Field, 2012” are adopted from that paper, unless marked with (*), in which case they were aged by Borkovic following the criteria of Longrich and Field (2012). Results listed under “Horner and Goodwin, 2006” were aged by Borkovic following the criteria of Horner and Goodwin (2006). “Conclusion” indicates the ontogenetic stage that was accepted. NA indicates criteria were not applicable to isolated horncores.
Table 5.3 Skull dimension measurement codes and descriptions for both *Centrosaurus* and *Triceratops*. Only left measures are given, when applicable. Additional information provided in the text and Figures 5.1 and 5.2.

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<td>Basal Skull Length</td>
<td>Skull length as measured from the anterior-most edge of the rostral bone to the posterior-most edge of the occipital condyle.</td>
</tr>
<tr>
<td>LTL</td>
<td>Left Toothrow Length</td>
<td>Length of left maxillary toothrow as measured from the anterior rim of the anterior-most alveolus to the posterior rim of posterior-most alveolus.</td>
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<tr>
<td>ATL</td>
<td>Average Toothrow Length</td>
<td>Average of left and right toothrow lengths.</td>
</tr>
<tr>
<td>OCW</td>
<td>Occipital Condyle Width</td>
<td>Greatest width / height / circumference of the occipital condyle as measured in a vertical transverse plane through the center of the condyle.</td>
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<tr>
<td>OCH</td>
<td>Occipital Condyle Height</td>
<td></td>
</tr>
<tr>
<td>OCC</td>
<td>Occipital Condyle Circumference</td>
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Table 5.4 Horncore dimension measurement codes and descriptions for *Centrosaurus*. Additional information provided in the text and Figure 5.1.

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<td>Height from base to tip along the anterior/posterior surface of the horncore.</td>
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<td>Posterior horncore Height</td>
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<tr>
<td>AvgH</td>
<td>Average horncore Height</td>
<td>Average of anterior and posterior horncore heights.</td>
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<tr>
<td>CH</td>
<td>Chord of horncore</td>
<td>Straight line chord, from base (anterior or posterior) to tip on curved specimens.</td>
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<td>BL,</td>
<td>Basal horncore Length</td>
<td>Antero-posterior length / medio-lateral width / circumference, measured at the base of the horncore perpendicular to its longitudinal axis.</td>
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Table 5.5 Horncore dimension measurement codes and descriptions for *Triceratops*. Additional information provided in the text and Figure 5.2.

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<td>Length as measured along the ventral surface of the horncore from the orbital rim to the distal tip.</td>
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<td>Ventral Length Average</td>
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<td>LHBH</td>
<td>Left Horncore Basal Height</td>
<td>Dorso-ventral height / medio-lateral width / circumference, measured at the base of the horncore perpendicular to its longitudinal axis.</td>
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<td>Horncore Spread at Base</td>
<td>Width between the midpoints of the anterior bases of the horncores.</td>
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<td>Horncore Spread at Tip</td>
<td>Width between the tips of the horncores.</td>
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Table 5.6 Measurement data for *Centrosaurus apertus* specimens used in this study. All measurements in millimetres (mm). “Curve” indicates direction of curvature of nasal horncore, ant = anterior, post = posterior, NA indicates that a horncore was not available for measurement. Measurement codes are as described in section 5.2.4 Measurements and in Tables 5.3 and 5.4.

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Table 5.7 Measurement data for *Triceratops* specimens used in this study. Stage indicates ontogenetic stage of the specimen, as assigned in Table 5.2, where applicable. All measurements in millimetres (mm). Measurement codes are as described in section 5.2.4 *Measurements* and in Tables 5.3 and 5.5.

| Institution | Specimen | Genus       | Species   | Stage | VLL | VLR | VLA | BWL | BWR | BWA | BHL | BHR | BHA |
|-------------|----------|-------------|-----------|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| AMNH        | 5116     | *Triceratops* | *horridus* | Adult | 774 | 750 | 762 | 159 | 156 | 157 | 177 | 178 | 177 |
| ROM         | 55380    | *Triceratops* | *horridus* | Subadult | 508 | 481 | 495 | 106 | 82  | 94  | 158 | 166 | 162 |
| USNM        | 1201     | *Triceratops* | *horridus* | Adult | 692 | NA  | 692 | 144 | NA  | 144 | 258 | NA  | 258 |
| USNM        | 2416     | *Triceratops* | *horridus* | Subadult | NA  | 395 | 395 | NA  | 113 | 113 | NA  | 156 | 156 |
| USNM        | 4720     | *Triceratops* | *horridus* | Adult | 519 | 544 | 531 | NA  | NA  | NA  | NA  | NA  | NA  |
| YPM         | 1821     | *Triceratops* | *horridus* | Subadult | 710 | NA  | 710 | 154 | NA  | 154 | 218 | NA  | 218 |
| YPM         | 1823     | *Triceratops* | *horridus* | Subadult | 530 | NA  | 530 | 136 | 135 | 135 | 172 | 163 | 167 |
| CMNH        | 1219     | *Triceratops* | *prorsus*  | Adult | 425 | 454 | 440 | 157 | 142 | 150 | 231 | 240 | 236 |
| EM          | P15.1    | *Triceratops* | *prorsus*  | Adult | NA  | 590 | 590 | NA  | 154 | 154 | NA  | 234 | 234 |
| SMNH        | 1163.4   | *Triceratops* | *prorsus*  | Adult | 626 | 627 | 626 | 187 | 184 | 186 | 273 | 261 | 267 |
| USNM        | 1205     | *Triceratops* | *prorsus*  | Adult | NA  | NA  | NA  | 137 | NA  | 137 | 175 | NA  | 175 |
| YPM         | 1822     | *Triceratops* | *prorsus*  | Adult | NA  | 503 | 503 | 138 | 133 | 135 | 177 | 167 | 172 |
| USNM        | 1208     | *Triceratops* | sp.        | Adult | 678 | 744 | 711 | 176 | 178 | 177 | 180 | 188 | 184 |
| USNM        | 4286     | *Triceratops* | sp.        | Adult | NA  | NA  | NA  | 155 | 157 | 156 | 196 | 202 | 199 |
| USNM        | 4739     | *Triceratops* | Inconc.    | NA    | 635 | 635 | NA  | 130 | 130 | NA  | 184 | 184 |
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Table 5.8 Predictor variable results for measured traits for *Centrosaurus*. Measurement codes are as described in section 5.2.4 *Measurements* and in Tables 5.3 and 5.4. n = sample size; CV = coefficient of variation; b = bimodality coefficient. Elevated scores are indicated in bold.

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Table 5.9 Dataset for the first *Centrosaurus* PCA. All measurements in millimetres (mm), ‘?’ indicates missing data. Measurement codes are as described in section 5.2.4 *Measurements* and in Tables 5.3 and 5.4.

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Table 5.13 Predictor variable results for measured traits for *Triceratops*. Measurement codes are as described in section 5.2.4 *Measurements* and in Tables 5.3 and 5.5. n = sample size; CV = coefficient of variation; $b$ = bimodality coefficient. Elevated scores are indicated in bold.

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Table 5.14 Dataset for the first *Triceratops* PCA. All measurements in millimetres (mm), ‘?’ indicates missing data. Measurement codes are as described in section 5.2.4 Measurements and in Tables 5.3 and 5.5.

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<th>ATL</th>
</tr>
</thead>
<tbody>
<tr>
<td>ROM</td>
<td>55380</td>
<td>495</td>
<td>94</td>
<td>162</td>
<td>423</td>
<td>269</td>
<td>342</td>
<td>525</td>
<td>1110</td>
<td>351</td>
</tr>
<tr>
<td>YPM</td>
<td>1823</td>
<td>530</td>
<td>135</td>
<td>167</td>
<td>465</td>
<td>266</td>
<td>335</td>
<td>632</td>
<td>1038</td>
<td>380</td>
</tr>
<tr>
<td>YPM</td>
<td>1821</td>
<td>710</td>
<td>154</td>
<td>218</td>
<td>543</td>
<td>295</td>
<td>318</td>
<td>442</td>
<td>1133</td>
<td>377</td>
</tr>
<tr>
<td>AMNH</td>
<td>5116</td>
<td>762</td>
<td>157</td>
<td>177</td>
<td>532</td>
<td>?</td>
<td>337</td>
<td>730</td>
<td>1050</td>
<td>340</td>
</tr>
<tr>
<td>CMNH</td>
<td>1219</td>
<td>440</td>
<td>150</td>
<td>236</td>
<td>630</td>
<td>336</td>
<td>228</td>
<td>473</td>
<td>1160</td>
<td>428</td>
</tr>
<tr>
<td>YPM</td>
<td>1822</td>
<td>503</td>
<td>135</td>
<td>172</td>
<td>490</td>
<td>272</td>
<td>318</td>
<td>336</td>
<td>933</td>
<td>390</td>
</tr>
<tr>
<td>SMNH</td>
<td>1163.4</td>
<td>627</td>
<td>186</td>
<td>267</td>
<td>730</td>
<td>?</td>
<td>267</td>
<td>520</td>
<td>?</td>
<td>456</td>
</tr>
</tbody>
</table>

Table 5.15 Variable loadings for the first three principal components of the first *Triceratops* PCA. Measurement codes are as described in section 5.2.4 Measurements and in Tables 5.3 and 5.5.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>VLA</td>
<td>0.1919</td>
<td>0.6238</td>
<td>0.7176</td>
</tr>
<tr>
<td>BWA</td>
<td>0.1372</td>
<td>0.0337</td>
<td>0.0947</td>
</tr>
<tr>
<td>BHA</td>
<td>0.2428</td>
<td>-0.0615</td>
<td>0.042</td>
</tr>
<tr>
<td>BCA</td>
<td>0.6211</td>
<td>-0.0852</td>
<td>0.0693</td>
</tr>
<tr>
<td>HSB</td>
<td>-0.1891</td>
<td>0.1442</td>
<td>0.092</td>
</tr>
<tr>
<td>HST</td>
<td>0.0325</td>
<td>0.7384</td>
<td>-0.6306</td>
</tr>
<tr>
<td>OCC</td>
<td>0.2215</td>
<td>-0.1029</td>
<td>-0.0323</td>
</tr>
<tr>
<td>BSL</td>
<td>0.6145</td>
<td>-0.0036</td>
<td>-0.2465</td>
</tr>
<tr>
<td>ATL</td>
<td>0.1904</td>
<td>-0.1483</td>
<td>-0.0390</td>
</tr>
</tbody>
</table>
Table 5.16 Dataset for the second *Triceratops* PCA. All measurements in millimetres (mm), ‘?’ indicates missing data. Measurement codes are as described in section 5.2.4 *Measurements* and in Tables 5.3 and 5.5.

<table>
<thead>
<tr>
<th>Institution</th>
<th>Specimen</th>
<th>VLA</th>
<th>BWA</th>
<th>BHA</th>
<th>BCA</th>
</tr>
</thead>
<tbody>
<tr>
<td>ROM</td>
<td>55380</td>
<td>494.5</td>
<td>94.1</td>
<td>162.0</td>
<td>422.5</td>
</tr>
<tr>
<td>USNM</td>
<td>2416</td>
<td>395.0</td>
<td>113.4</td>
<td>156.1</td>
<td>441.0</td>
</tr>
<tr>
<td>USNM</td>
<td>8027</td>
<td>?</td>
<td>124.4</td>
<td>165.4</td>
<td>466.3</td>
</tr>
<tr>
<td>USNM</td>
<td>4739</td>
<td>635.0</td>
<td>130.5</td>
<td>184.3</td>
<td>504.0</td>
</tr>
<tr>
<td>YPM</td>
<td>1823</td>
<td>530.0</td>
<td>135.2</td>
<td>167.3</td>
<td>464.8</td>
</tr>
<tr>
<td>YPM</td>
<td>1822</td>
<td>503.3</td>
<td>135.4</td>
<td>171.7</td>
<td>489.6</td>
</tr>
<tr>
<td>YPM</td>
<td>1205</td>
<td>?</td>
<td>137.3</td>
<td>175.0</td>
<td>519.7</td>
</tr>
<tr>
<td>USNM</td>
<td>6525</td>
<td>?</td>
<td>143.6</td>
<td>169.7</td>
<td>504.3</td>
</tr>
<tr>
<td>USNM</td>
<td>1201</td>
<td>692.3</td>
<td>143.7</td>
<td>258.0</td>
<td>682.0</td>
</tr>
<tr>
<td>CMNH</td>
<td>1219</td>
<td>439.7</td>
<td>149.5</td>
<td>235.9</td>
<td>630.2</td>
</tr>
<tr>
<td>YPM</td>
<td>1821</td>
<td>710.3</td>
<td>153.7</td>
<td>217.6</td>
<td>542.7</td>
</tr>
<tr>
<td>EM</td>
<td>P15.1</td>
<td>590.0</td>
<td>153.8</td>
<td>234.0</td>
<td>635.3</td>
</tr>
<tr>
<td>USNM</td>
<td>4286</td>
<td>?</td>
<td>155.9</td>
<td>199.1</td>
<td>553.3</td>
</tr>
<tr>
<td>AMNH</td>
<td>5116</td>
<td>762.0</td>
<td>157.1</td>
<td>177.4</td>
<td>531.5</td>
</tr>
<tr>
<td>USNM</td>
<td>1208</td>
<td>711.3</td>
<td>176.9</td>
<td>184.1</td>
<td>589.7</td>
</tr>
<tr>
<td>SMNH</td>
<td>1163.4</td>
<td>626.5</td>
<td>185.6</td>
<td>267.1</td>
<td>730.4</td>
</tr>
<tr>
<td>USNM</td>
<td>8054</td>
<td>640.0</td>
<td>?</td>
<td>183.3</td>
<td>515.3</td>
</tr>
</tbody>
</table>

Table 5.17 Variable loadings for the first two principal components of the second *Triceratops* PCA. Measurement codes are as described in section 5.2.4 *Measurements* and in Tables 5.3 and 5.5.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>VLA</td>
<td>0.7854</td>
<td>-0.6128</td>
</tr>
<tr>
<td>BWA</td>
<td>0.1545</td>
<td>0.0707</td>
</tr>
<tr>
<td>BHA</td>
<td>0.1987</td>
<td>0.3153</td>
</tr>
<tr>
<td>BCA</td>
<td>0.5655</td>
<td>0.7211</td>
</tr>
</tbody>
</table>
Chapter 6: Synthesis and Retrospective

This thesis was undertaken with the intention of exploring the perceived absence of sexual dimorphism in ceratopsid dinosaurs, and in particular, in their cranial horns. Considerable morphological variation was found in the horncores and skulls of *Triceratops* and *Centrosaurus apertus*, although none could be confidently attributed to sexual dimorphism. The results, therefore, do not provide reason to reject monomorphism in these species, but they also do not provide a very strong endorsement of monomorphism either. Rather, the variation that is present suggests that there is still much about these animals that we do not understand, particularly with regard to how they matured.

Although ontogeny in *Triceratops* has lately been a focal point of study and debate, the growth of the nasal horncores in *Centrosaurus* is no less confusing, nor better understood. Although sexual dimorphism could not be supported in *Centrosaurus*, some evidence was found of an association between anteriorly curving nasal horncores, greater horncore widths, and larger size, so the potential for sexual dimorphism is far from being eliminated. Before this can be explored much further though, the link between maturity and size in *Centrosaurus* needs to be investigated, and adopting size variables other than the usual basal skull length may be of use. Also, whether the development of procurving horncores is a result of a growth trajectory or a remodelling process remains largely unresolved.

The review of the paleontological literature in Chapter 2 provided methods with which to explore sexual dimorphism in ceratopsid horns, but it also provided some warning about sources of variation that can hamper studies of sexual dimorphism and that need to be mitigated when investigating sexual variation. A great deal of effort was put into testing those methods and
developing an extant model to guide the study of ceratopsid horn morphology, and this was highly informative, as well as interesting, and was essential for the drawing of confident conclusions from the ceratopsid studies. However, paying greater heed to those warnings of complicating factors would also have been of use. Geography, stratigraphy, taxonomy, and ontogeny are potential sources of morphological variation that must be taken into account when investigating sexual dimorphism, and they were certainly taken into consideration for this study, as was detailed in Chapter 5. Despite these efforts, taxonomy and ontogeny turned out to have considerable effects on the results. *Triceratops prorsus* was included along with *T. horridus* in an effort to bolster sample size, to explore the distinctions between the two species, and also in the hope that if a similar pattern of sexual dimorphism existed between them, as is true of many bovid species, it may be more apparent with both species included. Instead though, the taxonomic signal became the most prominent one, and may have obscured weaker sources of variation. Similarly, the assignment of several of the *T. horridus* specimens to the subadult stage limited the sample of adult specimens and created a large range of ontogenetic variation. The same can be said for *Centrosaurus*, and although all the specimens that were used in the analyses were considered to be ‘adult’, this clearly reflects an incomplete picture of the growth trajectory in that species.

As a result, if this study were to be repeated, those factors would need to be more thoroughly mitigated. Furthermore, *Triceratops horridus* may be the species of choice for studying sexual dimorphism in ceratopsids. Excluding *T. prorsus* would provide fairly strong taxonomic control, and recent sampling efforts in Montana have yielded a large sample of *Triceratops* specimens with strong stratigraphic and geographic control (Horner et al., 2011). Ontogeny would need to be rigorously assessed, but *Triceratops* ontogeny may still be the most
well understood of any ceratopsid, despite the ongoing debates. It is regrettable that access to those specimens in Montana could not be granted during the course of this study.

Finally, the perceived lack of sexual dimorphism in these ceratopsid species has interesting implications with respect to ceratopsid evolution and selection. Ceratopsids evolved the largest skulls, in absolute size, of any terrestrial animal (Sereno et al., 2007), and there is a progressive enlargement of the cranium in relative and absolute size in the ceratopsian phylogeny. This strongly suggests some form of selection was operating on the skull region, and it has been suggested to have been sexual selection (Sereno et al., 2007). Furthermore, the diverse array of cranial structures that appeared during the late Cretaceous ceratopsid radiation (Sampson et al., 2010) suggests that selection on the cranial region continued throughout that time. This makes the monomorphic condition all the more surprising; but, if monomorphism is indeed present, this might suggest that developmental processes constrained intersexual variation, even while overall variation was high. There is clearly still much to be learned about the evolution and life history of these dinosaurs, and every new morphological insight is a step in the right direction.


Appendix A: Details of age assignments for all mammal specimens

A1: Mountain goats. Age indicates age in years as estimated by the author. Age Class indicates assignment to ontogenetic stage. Ageing criteria and staging are explained in Chapter 4 section 4.2.3 Ageing.

<table>
<thead>
<tr>
<th>Institution</th>
<th>Specimen</th>
<th>Taxon</th>
<th>Age Class</th>
<th>Age</th>
<th>Age Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>35286</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3</td>
<td>2 annuli with third segment just beginning. Sutures tight but unfused. M3 in occlusion.</td>
</tr>
<tr>
<td>AMNH</td>
<td>35334</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>4</td>
<td>3 annuli, sutures closed but not fused.</td>
</tr>
<tr>
<td>AMNH</td>
<td>35545</td>
<td>Oreamnos</td>
<td>Subadult</td>
<td>2.5-3</td>
<td>1 distinct annuli, but 2 full growth segments. M3 erupted but may not have been fully in occlusion. Sutures firmly closed but not tight.</td>
</tr>
<tr>
<td>AMNH</td>
<td>41381</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>6 or 7</td>
<td>5 annuli, 6th segment forming. Sutures tight and fusing.</td>
</tr>
<tr>
<td>AMNH</td>
<td>70573</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>5</td>
<td>4 annuli. Sutures tight, not fused.</td>
</tr>
<tr>
<td>AMNH</td>
<td>121474</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>6+</td>
<td>5 or so annuli. P/F sutures fused, F/F tight, not fused.</td>
</tr>
<tr>
<td>AMNH</td>
<td>122670</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3</td>
<td>2 annuli, third segment forming. Sutures tight but not fused. Young adult female</td>
</tr>
<tr>
<td>AMNH</td>
<td>122671</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>4</td>
<td>3 annuli, fourth small. Sutures closed but not tight/fused. Young adult male</td>
</tr>
<tr>
<td>AMNH</td>
<td>125413</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3-3.5</td>
<td>2 annuli, third segment formed, sutures closed, but not tight.</td>
</tr>
<tr>
<td>AMNH</td>
<td>127759</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>5 or 6</td>
<td>4 or 5 annuli, sutures tight, beginning to fuse.</td>
</tr>
<tr>
<td>AMNH</td>
<td>128461</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>6</td>
<td>At least 5 annuli Sutures fused.</td>
</tr>
<tr>
<td>AMNH</td>
<td>130223</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>5 or 6</td>
<td>4 or 5 annuli, sutures fusing</td>
</tr>
<tr>
<td>NMC</td>
<td>1291</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3</td>
<td>2 annuli, third segment forming, sutures closed, but not tight.</td>
</tr>
<tr>
<td>NMC</td>
<td>1900</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>4</td>
<td>3 annuli. Horns slender. Sutures fused.</td>
</tr>
<tr>
<td>NMC</td>
<td>1903</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3 or 4</td>
<td>2 or 3 annuli, photos unclear. Sutures tight but visible. Horns large like males, but crooked like females. ID'd as male</td>
</tr>
<tr>
<td>NMC</td>
<td>1904</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>5</td>
<td>4 annuli. Sutures tight but visible.</td>
</tr>
<tr>
<td>NMC</td>
<td>10408</td>
<td>Oreamnos</td>
<td>Subadult</td>
<td>2.5-3</td>
<td>1 annulus, 2 growth segments. Horns very slender. Skull dirty, sutures unclear.</td>
</tr>
<tr>
<td>NMC</td>
<td>10445</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>4</td>
<td>3 annuli, died at beginning of 4th year. Sutures visible but tight.</td>
</tr>
<tr>
<td>NMC</td>
<td>10446</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>4+</td>
<td>Sutures tight. Horn rings unclear. I estimated at 4-5 years when in hand. No reason to suspect younger.</td>
</tr>
</tbody>
</table>
Appendix A1 - Continued.

<table>
<thead>
<tr>
<th>Institution</th>
<th>Specimen</th>
<th>Taxon</th>
<th>Age Class</th>
<th>Age</th>
<th>Age Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>NMC</td>
<td>13757 Oreamnos Adult 3+</td>
<td>No horns. Sutures tight but not fused. M3 in occlusion. If M3's in occlusion, then at least 3 years old.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NMC</td>
<td>75079 Oreamnos Adult 6</td>
<td>4.5 years according to tag. 5 annuli. P/F, F/F sutures very tight but not fused.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NMNH</td>
<td>175583 Oreamnos Adult 3</td>
<td>Two annuli, third segment forming. Sutures tight but not fused.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RAM</td>
<td>Z01.1.1 Oreamnos Subadult 2</td>
<td>1 annulus, M3 not erupted. Sutures not fused</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RAM</td>
<td>Z72.64.1 Oreamnos Adult 3</td>
<td>2 annuli, third segment forming. Sutures tight but not fused.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RAM</td>
<td>Z73.26.1 Oreamnos Adult ?</td>
<td>Unclear, may be two or three growth segments. Sutures tight but not fused. Labelled as adult</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RAM</td>
<td>Z80.58.1 Oreamnos Adult 3</td>
<td>2 annuli, just turned 3, just making adult category. Sutures tight but very clear.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RAM</td>
<td>Z92.24.2 Oreamnos Subadult 2</td>
<td>1 annulus, second segment large. M3 not fully erupted.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ROM</td>
<td>23428 Oreamnos Adult 3+</td>
<td>No horns. M3 fully erupted.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ROM</td>
<td>231191 Oreamnos Adult 3</td>
<td>2 annuli, M3 fully erupted. Sutures visible, not fusing.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>UAMZ</td>
<td>2692 Oreamnos Adult 5+</td>
<td>One sheath heavily worn with 5 annuli. Sutures mostly fused, teeth worn.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>UAMZ</td>
<td>2693 Oreamnos Adult 4</td>
<td>3 annuli, sutures mostly fused</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix A1 – Continued.

<table>
<thead>
<tr>
<th>Institution</th>
<th>Specimen</th>
<th>Taxon</th>
<th>Age Class</th>
<th>Age</th>
<th>Age Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>UAMZ</td>
<td>3688</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3+</td>
<td>2 annuli at least. Sutures visible, not fusing.</td>
</tr>
<tr>
<td>UAMZ</td>
<td>5477</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>4</td>
<td>3 annuli. P/F sutures beginning to fuse.</td>
</tr>
<tr>
<td>UAMZ</td>
<td>5478</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3</td>
<td>2 annuli with well-formed third segment.</td>
</tr>
<tr>
<td>UAMZ</td>
<td>5479</td>
<td>Oreamnos</td>
<td>Subadult</td>
<td>2</td>
<td>1 poorly formed annulus. Horns very thin and elongate. Nearly adult.</td>
</tr>
<tr>
<td>UAMZ</td>
<td>5665</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>4+</td>
<td>At least 3 annuli, maybe 4. Horns robust. Sutures fused.</td>
</tr>
<tr>
<td>UAMZ</td>
<td>5666</td>
<td>Oreamnos</td>
<td>Subadult</td>
<td>2</td>
<td>1 annulus, second segment well formed. Died during third summer. Horns robust. Sutures visible. M3 only beginning to erupt.</td>
</tr>
<tr>
<td>UAMZ</td>
<td>5668</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3</td>
<td>2 annuli, third segment forming. Labelled as adult.</td>
</tr>
<tr>
<td>UAMZ</td>
<td>5669</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3</td>
<td>2 annuli, three growth segments. M3 in occlusion.</td>
</tr>
<tr>
<td>UAMZ</td>
<td>5671</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3</td>
<td>2 annuli, third segment forming. Labelled as adult. M3 in occlusion.</td>
</tr>
<tr>
<td>YPM</td>
<td>14604</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3</td>
<td>2 annuli. Third segment well formed. Sutures tightly fused, M3 in occlusion.</td>
</tr>
<tr>
<td>YPM</td>
<td>14605</td>
<td>Oreamnos</td>
<td>Adult</td>
<td>3</td>
<td>2 annuli. Third segment well formed. Sutures tightly fused, M3 in occlusion.</td>
</tr>
</tbody>
</table>
Appendix A. Details of age assignments for all mammal specimens. A2: Bison. Age Class indicates assignment to ontogenetic stage, as estimated by the author. Criteria are explained in Chapter 4 section 4.2.3 Ageing.

<table>
<thead>
<tr>
<th>Institution</th>
<th>Specimen</th>
<th>Taxon</th>
<th>Sex</th>
<th>Age Class</th>
<th>Age diagnosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>3757</td>
<td>Bison</td>
<td>male</td>
<td>A</td>
<td>P/F open, F/F open. Orbits slightly protruded, very slightly rugose. Burr step moderate, well defined. No grooving.</td>
</tr>
<tr>
<td>AMNH</td>
<td>19380</td>
<td>Bison</td>
<td>female</td>
<td>FM</td>
<td>P/F fused, mostly gone, F/F fused, beginning to disappear posteriorly. Orbits moderately protruded, slightly rugose. Longitudinal grooves forming.</td>
</tr>
<tr>
<td>AMNH</td>
<td>24200</td>
<td>Bison</td>
<td>NA</td>
<td>FM</td>
<td>P/F fused, F/F fused but visible along length. Orbits somewhat protruded, slightly rugose. Burr step prominent ventrally, longitudinal grooves well developed.</td>
</tr>
<tr>
<td>AMNH</td>
<td>35372</td>
<td>Bison</td>
<td>NA</td>
<td>A</td>
<td>P/F unfused, F/F fused halfway to anterior but still visible. Orbits non-protruded, smooth. Burr small.</td>
</tr>
<tr>
<td>AMNH</td>
<td>35707</td>
<td>Bison</td>
<td>female</td>
<td>EM</td>
<td>P/F fused, F/F mostly fused, beginning to disappear. Orbits somewhat protruded, mostly smooth. Burr small. Longitudinal grooves beginning to form.</td>
</tr>
<tr>
<td>AMNH</td>
<td>70376</td>
<td>Bison</td>
<td>NA</td>
<td>A</td>
<td>P/F unfused, F/F unfused. Orbits slightly protruded, smooth. Burr slight, no grooves. M3 in occlusion. Horns suggested 2.5 years?</td>
</tr>
<tr>
<td>AMNH</td>
<td>73615</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>Sutures completely gone. Orbits very strongly protruded and rugose. Burr step massive.</td>
</tr>
<tr>
<td>AMNH</td>
<td>77739</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F fully fused, F/F fully fused halfway to anterior. Orbits strongly protruded, moderately rugose. Burr step prominent, longitudinal grooves prominent.</td>
</tr>
<tr>
<td>AMNH</td>
<td>77740</td>
<td>Bison</td>
<td>NA</td>
<td>FM</td>
<td>P/F fully fused, F/F fully fused halfway to anterior. Orbits somewhat protruded, heavily worn. Burr step strong, abrupt.</td>
</tr>
</tbody>
</table>
Appendix A2 – Continued.

<table>
<thead>
<tr>
<th>Institution</th>
<th>Specimen</th>
<th>Genus</th>
<th>Sex</th>
<th>Age Class</th>
<th>Age diagnosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>77866</td>
<td>Bison</td>
<td>male</td>
<td>EM</td>
<td>P/F unfused, F/F open along length. Orbits protruded and moderately rugose. Burr well defined. Longitudinal grooves forming.</td>
</tr>
<tr>
<td>AMNH</td>
<td>80247</td>
<td>Bison</td>
<td>female</td>
<td>FM</td>
<td>P/F fused but visible. F/F fused, gone in posterior quarter. Orbits slightly protruded, slightly rugose. Burr step small, longitudinal grooves present.</td>
</tr>
<tr>
<td>AMNH</td>
<td>86950</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F gone, F/F fused posteriorly, open anteriorly. Orbits strongly protruded, rugose. Burr step moderate, longitudinal grooves well developed.</td>
</tr>
<tr>
<td>AMNH</td>
<td>98954</td>
<td>Bison</td>
<td>female</td>
<td>EM</td>
<td>P/F open. F/F tight but open. Orbits slightly protruded, smooth. Burr step moderate, longitudinal grooves slight. Just barely makes the EM category, the level of horn develop is what makes it non-adolescent.</td>
</tr>
<tr>
<td>AMNH</td>
<td>98957</td>
<td>Bison</td>
<td>female</td>
<td>EM</td>
<td>P/F knitted, fusing. F/F fused, fading but visible. Orbits slightly protruded, slightly rugose. Burr step moderate, longitudinal grooves moderate. M3s in occlusion</td>
</tr>
<tr>
<td>AMNH</td>
<td>100140</td>
<td>Bison</td>
<td>male</td>
<td>A</td>
<td>P/F open, F/F tight but open. Orbits non-protruded, smooth. Burr moderate, no grooving.</td>
</tr>
<tr>
<td>NMC</td>
<td>45416</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F suture fully fused, F/F fused halfway to anterior. Orbits strongly protruded and rugose. Burr prominent and step-like</td>
</tr>
<tr>
<td>NMC</td>
<td>48089</td>
<td>Bison</td>
<td>male</td>
<td>A</td>
<td>P/F sutures only beginning to knit. F/F open. Orbits slightly protruded and smooth. Burr rim present, small step.</td>
</tr>
<tr>
<td>NMC</td>
<td>51416</td>
<td>Bison</td>
<td>female</td>
<td>FM</td>
<td>P/F fused, F/F only beginning to fuse. Orbits protruded and rugose. Burr rim very slight.</td>
</tr>
<tr>
<td>RAM</td>
<td>88.26.1</td>
<td>Bison</td>
<td>female</td>
<td>EM</td>
<td>P/F fused, but highly visible. F/F fused, gone in posterior fourth. Orbits only slightly protruded, very slightly rugose. Burr essentially smooth.</td>
</tr>
<tr>
<td>Institution</td>
<td>Specimen</td>
<td>Genus</td>
<td>Sex</td>
<td>Age Class</td>
<td>Age diagnosis</td>
</tr>
<tr>
<td>-------------</td>
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<td>------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>RAM 89.10.2</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>P/F suture full fused, F/F fully fused halfway to anterior. Orbits strongly protruded, very rugose. Burrs prominent, large step.</td>
</tr>
<tr>
<td>RAM 89.10.3</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>P/F fully fused, F/F fully fused one-third to anterior. Orbits somewhat protruded, becoming rugose. Burr step small.</td>
</tr>
<tr>
<td>RAM 89.10.4</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>P/F fully fused, F/F fully fused in posterior quarter. Orbits strongly protruded, rugose. Burr lip small, longitudinal grooves forming.</td>
</tr>
<tr>
<td>RAM 89.10.5</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>P/F fused but visible, F/F fused halfway to anterior. Orbits protruded, becoming rugose. Burr lip moderate, longitudinal grooves forming.</td>
</tr>
<tr>
<td>RAM 90.2.2</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>P/F fused but visible, F/F fused but clear for anterior four-fifths. Orbits protruded, becoming rugose. Burr step slight. Longitudinal grooves beginning to form.</td>
</tr>
<tr>
<td>ROM 16215</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>Fused up like crazy. Orbits strongly protruded and rugose.</td>
</tr>
<tr>
<td>ROM 20126</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>P/F fused, F/F fused only beginning to fuse. Orbits protruded, beginning to rugose. Burr rim present, step moderate.</td>
</tr>
<tr>
<td>ROM 850601001</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>P/F fully fused, F/F fully fused halfway to anterior. Orbits strongly protruded, rugose. Burrs prominent on ventral.</td>
</tr>
<tr>
<td>ROM 2702110002</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>'Very fused' in notes. No photos somehow. 'Adult' in ROM data</td>
</tr>
<tr>
<td>ROM 2705020205</td>
<td><em>Bison</em></td>
<td>male</td>
<td>FM</td>
<td></td>
<td>P/F fused, F/F fused. Orbits protruded and very rugose.</td>
</tr>
<tr>
<td>Institution</td>
<td>Specimen</td>
<td>Genus</td>
<td>Sex</td>
<td>Age Class</td>
<td>Age diagnosis</td>
</tr>
<tr>
<td>-------------</td>
<td>------------</td>
<td>-------</td>
<td>-----</td>
<td>-----------</td>
<td>-----------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>ROM</td>
<td>3211080020</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F fully fused, F/F fully fused halfway to anterior. Orbits protruded, slightly rugose.</td>
</tr>
<tr>
<td>ROM</td>
<td>3211080021</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F fully fused, F/F fully fused three-quarters to anterior. Orbits strongly protruded, rugose.</td>
</tr>
<tr>
<td>ROM</td>
<td>3211080022</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F fully fused, F/F fully fused halfway to anterior. Orbits protruded, rugose.</td>
</tr>
<tr>
<td>ROM</td>
<td>3211080023</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F fully fused, F/F fully fused two-thirds to anterior. Orbits strongly protruded, rugose. Burrs prominent, step large.</td>
</tr>
<tr>
<td>ROM</td>
<td>3304060007</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F fully fused, F/F fully fused one-third to anterior. Orbits strongly protruded, becoming rugose.</td>
</tr>
<tr>
<td>ROM</td>
<td>1109260005b</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F fully fused, F/F fused half way anterior. Orbits strongly protruding, rugose.</td>
</tr>
<tr>
<td>ROM</td>
<td>3306200004</td>
<td>Bison</td>
<td>female</td>
<td>FM</td>
<td>P/F fully fused, F/F fused one-third to anterior. Orbits non-protruding, mostly smooth. Burrs slight, longitudinal ridges very well-developed.</td>
</tr>
<tr>
<td>YPM</td>
<td>1462</td>
<td>Bison</td>
<td>NA</td>
<td>A</td>
<td>P/F tight but unfused, F/F tight posteriorly but unfused. Orbits non-protruded, mostly smooth. Burr step moderate, grooving slight.</td>
</tr>
<tr>
<td>YPM</td>
<td>3401</td>
<td>Bison</td>
<td>female</td>
<td>EM</td>
<td>P/F largely fused but visible, P/ASO fused but visible, F/F fused, beginning to disappear at posterior. Orbits slightly protruded, slightly rugose around rim. Burr step distinct but small, grooves slight.</td>
</tr>
<tr>
<td>YPM</td>
<td>3412</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F fully fused, F/F fully fused halfway to anterior. Orbits strongly protruded, moderately rugose. Burr step prominent, longitudinal grooves prominent.</td>
</tr>
<tr>
<td>YPM</td>
<td>3415</td>
<td>Bison</td>
<td>male</td>
<td>FM</td>
<td>P/F fully fused, F/F fully fused halfway to anterior. Orbits strongly protruded, moderately rugose. Burr step sharp longitudinal grooves slight, long</td>
</tr>
</tbody>
</table>
Appendix A. Details of age assignments for all mammal specimens. A3: Pronghorn. Age indicates assignment to ontogenetic stage, as estimated by the author. Criteria are explained in Chapter 4 section 4.2.3 Ageing.

<table>
<thead>
<tr>
<th>Institution</th>
<th>Specimen</th>
<th>Taxon</th>
<th>Sex</th>
<th>Age</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>1968</td>
<td>Antilocapra</td>
<td>NA</td>
<td>subadult</td>
<td>young in notes. M3 fully erupted, but appears very sharp. Premolars mostly missing, probably shed.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11147</td>
<td>Antilocapra</td>
<td>Female</td>
<td>adult</td>
<td>adult in notes. M3 fully erupted, doesn’t seem fresh. F/F tight. All PMs</td>
</tr>
<tr>
<td>AMNH</td>
<td>11145</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>adult in notes. M3 fully erupted, doesn’t seem fresh. F/F tight. All PMs</td>
</tr>
<tr>
<td>AMNH</td>
<td>1977</td>
<td>Antilocapra</td>
<td>NA</td>
<td>subadult</td>
<td>adult in notes. M3 fully erupted, very sharp. F/F tight. PMs mostly missing, probably shed.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11095</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>adult in notes. M3 appears worn. F/F gone. PMs broken.</td>
</tr>
<tr>
<td>AMNH</td>
<td>120947</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>adult in notes. M3 somewhat worn. Right P2 gone, but P3, P4 worn. F/F gone.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11102</td>
<td>Antilocapra</td>
<td>Male</td>
<td>fawn</td>
<td>M2 erupting.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11098</td>
<td>Antilocapra</td>
<td>Male</td>
<td>fawn</td>
<td>M3 unerupted. F/F suture already tight, snout narrow.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11099</td>
<td>Antilocapra</td>
<td>Female</td>
<td>subadult</td>
<td>M3 erupting. F/F tight but clearly visible. Snout tapers to narrow.</td>
</tr>
<tr>
<td>AMNH</td>
<td>329</td>
<td>Antilocapra</td>
<td>Female</td>
<td>subadult</td>
<td>M3 very sharp. PMs coming in. Sutures tight but clearly visible.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11104</td>
<td>Antilocapra</td>
<td>Male</td>
<td>subadult</td>
<td>M3 erupting. F/F tight gone. Snout tapers somewhat.</td>
</tr>
<tr>
<td>AMNH</td>
<td>142361</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>M3s appear sharp, but also heavily damaged. Premolars worn. F/F gone.</td>
</tr>
<tr>
<td>AMNH</td>
<td>142362</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>No teeth, no sutures. Adult in notes. Appears unlikely to be 2 yr old.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11101</td>
<td>Antilocapra</td>
<td>Male</td>
<td>fawn</td>
<td>M3 unerupted. F/F suture already tight, snout narrow.</td>
</tr>
<tr>
<td>AMNH</td>
<td>10419</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>adult in notes. M3 appears worn. F/F gone. PMs broken.</td>
</tr>
</tbody>
</table>
Appendix A3 – Continued.

<table>
<thead>
<tr>
<th>Institution</th>
<th>Specimen</th>
<th>Taxon</th>
<th>Sex</th>
<th>Age</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>100354</td>
<td>Antilocapra</td>
<td>Male</td>
<td>subadult</td>
<td>adult in notes. Left M3 sharp. PMs erupting. F/F gone.</td>
</tr>
<tr>
<td>AMNH</td>
<td>15586</td>
<td>Antilocapra</td>
<td>Female</td>
<td>adult</td>
<td>teeth appear heavily worn, but also PMs seem short. F/F gone.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11105</td>
<td>Antilocapra</td>
<td>Male</td>
<td>subadult</td>
<td>juvenile on tag. M3 sharp, posterior seems unworn. F/F partially gone. PMs all there.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11096</td>
<td>Antilocapra</td>
<td>Female</td>
<td>adult</td>
<td>adult in notes. M3 slightly worn. F/F partially gone. PMs all there.</td>
</tr>
<tr>
<td>AMNH</td>
<td>11100</td>
<td>Antilocapra</td>
<td>Male</td>
<td>fawn</td>
<td>M3 at alveolar margin.</td>
</tr>
<tr>
<td>AMNH</td>
<td>21529</td>
<td>Antilocapra</td>
<td>Male</td>
<td>subadult</td>
<td>adult in notes. M3 sharp. PMs broken off but one may be erupting. F/F not fully gone</td>
</tr>
<tr>
<td>AMNH</td>
<td>245097</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>adult in notes. M3 sharp but mangled PMs still in sockets. F/F mostly gone</td>
</tr>
<tr>
<td>AMNH</td>
<td>41384</td>
<td>Antilocapra</td>
<td>Female</td>
<td>fawn</td>
<td>M3 unerupted. Sutures not closing, snout narrow.</td>
</tr>
<tr>
<td>AMNH</td>
<td>34952</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>M3 heavily worn/damaged. Teeth destroyed, F/F gone</td>
</tr>
<tr>
<td>AMNH</td>
<td>15585</td>
<td>Antilocapra</td>
<td>NA</td>
<td>subadult</td>
<td>young in notes. M3 fully erupted, but appears very sharp. Right P2 missing, likely shed. Left P2 shows little wear</td>
</tr>
<tr>
<td>AMNH</td>
<td>130197</td>
<td>Antilocapra</td>
<td>Male</td>
<td>subadult</td>
<td>adult in notes. M3 just in occlusion, very sharp. F/F not fully gone.</td>
</tr>
<tr>
<td>YPM</td>
<td>9743</td>
<td>Antilocapra</td>
<td>NA</td>
<td>subadult</td>
<td>M2 erupting</td>
</tr>
<tr>
<td>YPM</td>
<td>2687</td>
<td>Antilocapra</td>
<td>Male</td>
<td>subadult</td>
<td>M3 erupting</td>
</tr>
<tr>
<td>YPM</td>
<td>1513</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>M3 heavily worn. F/F gone</td>
</tr>
<tr>
<td>YPM</td>
<td>3898</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>adult in notes. M3 fully erupted, but toothrow largely destroyed. F/F gone</td>
</tr>
<tr>
<td>YPM</td>
<td>2935</td>
<td>Antilocapra</td>
<td>Male</td>
<td>adult</td>
<td>adult in notes. M3 erupted. Toothrow largely wrecked, yet PMs still in sockets. F/F gone</td>
</tr>
<tr>
<td>Institution</td>
<td>Specimen</td>
<td>Taxon</td>
<td>Sex</td>
<td>Age</td>
<td>Comments</td>
</tr>
<tr>
<td>-------------</td>
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<td>---------</td>
<td>--------------------------------------------------------------------------</td>
</tr>
<tr>
<td>YPM</td>
<td>3362</td>
<td><em>Antilocapra</em></td>
<td>Male</td>
<td>subadult</td>
<td>isolated core and sheath - cannot be defined as subadult or adult, therefore going with subadult</td>
</tr>
<tr>
<td>YPM</td>
<td>3370</td>
<td><em>Antilocapra</em></td>
<td>Male</td>
<td>subadult</td>
<td>isolated core and sheath - cannot be defined as subadult or adult, therefore going with subadult</td>
</tr>
<tr>
<td>YPM</td>
<td>15003</td>
<td><em>Antilocapra</em></td>
<td>Male</td>
<td>subadult</td>
<td>F/F fused, sheaths weathered. Indeterminate age, therefore going with subadult.</td>
</tr>
<tr>
<td>YPM</td>
<td>2989</td>
<td><em>Antilocapra</em></td>
<td>Male</td>
<td>subadult</td>
<td>M3 very sharp, posterior un worn. P2 P3 not erupted, cranial sutures fused</td>
</tr>
<tr>
<td>YPM</td>
<td>6679</td>
<td><em>Antilocapra</em></td>
<td>Female</td>
<td>adult</td>
<td>adult in notes. M3 well worn, PMs erupted, but some lost. F/F gone</td>
</tr>
<tr>
<td>YPM</td>
<td>2915</td>
<td><em>Antilocapra</em></td>
<td>Female</td>
<td>subadult</td>
<td>M3 in occlusion, but PMs erupting. F/F tight, skull narrows to snout. Male on tag.</td>
</tr>
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Appendix A3 – Continued.

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Appendix B: Mountain goat non-scaled measurement data

All measurements in millimetres (mm). Measurement codes are explained in Table 4.1, and section 4.2.2 Measurements. NA indicates information was not available. Age Class indicates ontogenetic stage, as explained in section 4.2.3 Ageing, and as assigned in Appendix A.

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CMN | 1904 | NA | NA | NA | NA | NA | NA | NA | NA | NA | 15.3 | 15.7
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ROM | 231191 | 32.6 | 114.3 | 99.3 | 92.7 | 37.4 | 31.5 | 114.7 | 24.4 | 18.3 | 19.6 | 19.1
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RAM | Z80.58.2 | NA | NA | NA | NA | NA | NA | NA | 28.6 | 21.7 | NA | 18.5
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Appendix C: Bison non-scaled measurement data

All measurements in millimetres (mm). Measurement codes are explained in Table 4.2, and in section 4.2.2 Measurements. NA indicates information was not available. Age Class indicates ontogenetic stage, as explained in section 4.2.3 Ageing, and as assigned in Appendix A.

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**Appendix D: Pronghorn non-scaled measurement data**

All measurements in millimetres (mm). Measurement codes are explained in Table 4.3, and in section 4.2.2 *Measurements*. NA indicates information was not available. Age Class indicates ontogenetic stage, as explained in section 4.2.3 *Ageing*, and as assigned in Appendix A.

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## Appendix E: Taxonomic assignment of problematic centrosaurine nasal horncores

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