Title

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Publication Date

2017

Interpretation of Homoplasies in *Oreopithecus* and Their Relevance for Elucidating the Chimpanzee-Human Last Common Ancestor

By

Joshua Carlson

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

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Professor Paul Renne

Summer 2017

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Abstract

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A new species of hominid, *Ardipithecus ramidus*, was published in 1994 and 1995. The discovery team initially diagnosed and assigned the 4.4-million-year-old *Ardipithecus ramidus* to the hominid branch of the hominoid family tree based on the limited available dental, cranial, and postcranial characters exclusively shared with later hominids (i.e., all species derived in the human direction after the last common ancestor shared with chimpanzees; equivalent to "hominin"). A subsequent and limited parsimony-based cladistics analysis in 2006 again aligned *Ardipithecus* with later *Australopithecus* based on shared, derived characters of the dentition, as did other independent efforts based on the 1994 publication.

A more comprehensive exposition of the species followed in 2009 when a suite of 11 research papers comprising ~600 manuscript pages of description, data, and analysis was published in *Science*. The additional anatomy revealed in these publications employed the numerous additional shared derived characters observable on newly recovered fossils. These characters are spread across developmentally separate parts of the body. The combined evidence for phylogenetic placement reinforced the team's earlier inference that *Ardipithecus ramidus* was a hominid exclusively related to *Australopithecus* and *Homo*. By illuminating the 4-6 Ma time period, the *Ardipithecus* fossils allowed practitioners to contextualize both the chronologically younger *Australopithecus afarensis*, despite the latter's many derivations, and the Late Miocene common ancestor that we humans once shared with chimpanzees (CLCA).

After the 2009 publication of *Ardipithecus* several analysts doubted its hominid phylogenetic status based on arguments invoking the Late Miocene (8.3 - 6.7 Ma) Tusco-Sardinian hominoid *Oreopithecus*. These claims were based on several anatomical characters of its dentition, cranium, and postcranium that were argued to have been evolved in parallel with *Ardipithecus*. Such parallel acquisitions (homoplasies, or traits evolved in parallel from a last common ancestor that did not share the trait) in *Oreopithecus* potentially confound the recognition of phylogenetically primitive hominids, and might falsify claims of derived characters argued to exclusively link *Ardipithecus* with later hominids.

Since its discovery in 1872, *Oreopithecus* has inspired 145 years of field and laboratory research, hundreds of primary publications, and countless mentions in scientific and popular literature. This taxon has been proposed by some, since its discovery, as a mysterious member of the family Hominidae or as a distant relative ape taxon that evolved several features claimed to be hominid-like. Despite the extremely distorted and damaged condition of the fossils, many of

these features were originally alleged to be synapomorphic between *Oreopithecus* and later hominids, but with the better resolution of the phylogenetic position of *Oreopithecus*, these are today widely promulgated as homoplasies.

This dissertation aims to evaluate whether features are actually shared between *Oreopithecus* and hominids, and if so, whether they are homoplastic (evolved in parallel), synapomorphic (shared derived), or symplesiomorphic (the shared primitive condition). Such a comprehensive examination and evaluation of claims of hominid homoplasy in *Oreopithecus*, conducted with original fossils in comparison with original *Ardipithecus* fossils, has not been undertaken until now.

The objectives of this dissertation are to determine whether the claimed morphological features in *Oreopithecus* are present/observable and if so, whether the alleged characters can be diagnosed as hominid homoplasies. The following three research questions are addressed:
(1) Is the claimed morphological feature present/observable, or can it be reasonably inferred on the basis of the actual fossil evidence?
(2) If the claimed morphological feature is verified as present/observable, has the feature been accurately diagnosed in hominids (*Australopithecus, Ardipithecus*, and others)?
(3) Can allegedly shared characters that remain after testing per (1) and (2) be diagnosed as symplesiomorphic, synapomorphic, autapomorphic (uniquely derived), or)?

Key character complexes and their subdivided characters claimed to be hominid synapomorphies or homoplasies in *Oreopithecus* were examined and evaluated by comparing *Ardipithecus*, *Australopithecus*, *Homo sapiens*, extant hominoids, and fossil hominoids. Claims of hominid homoplasy in five (5) of the character complexes and eighteen (18) of their subdivided characters of *Oreopithecus* skeletal anatomy were falsified because relevant *Oreopithecus* anatomy is absent or has been misinterpreted. Claims of homoplasy in two (2) character complexes were falsified because the similarities in *Oreopithecus* and *Ardipithecus* anatomy are probably the primitive condition for the two taxa. The claim of homoplasy in one (1) subdivided character (vertical implantation of upper and lower incisors) of the character complex of an anteroposteriorly short face in *Oreopithecus* could not be falsified and represents a probable homoplasy. Of the six (6) singular characters claimed as hominid homoplasies in *Oreopithecus*, two (2) are revealed to have been based on *Oreopithecus* anatomy that is absent or has been misinterpreted and four (4) represent possible homoplasies but further fossils and outgroup analysis will be required to confirm them.

The results of this study form a foundation for future comparative work to test the potential hominid homoplasies in *Oreopithecus* when further fossils suffering from comparatively less distortion of relevant anatomy become available. In the meantime, future studies illuminating the underlying developmental genetic relationship of potentially homoplastic morphological characters in Hominoidea is warranted.

I dedicate this dissertation to my family.

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Acknowledgements

I thank my dissertation committee for their gracious guidance in this project, from our earliest discussions to its completion. I wish to especially thank my advisor and dissertation chair Tim White for his support and mentorship through the duration of my graduate career. Leslea Hlusko deserves special thanks as well for her encouragement and support during the drafting process and broadly, across my time as a graduate student. Paul Renne contributed valuable time and consideration in reading my drafted work and I wish to thank him for helping me improve this dissertation.

Other scientists contributed valuable time in helping me develop this project from conceptualization to production. I wish to thank Gen Suwa, Berhane Asfaw, C. Owen Lovejoy, and Henry Gilbert for helpful discussions. I also wish to thank Anthony Barnosky, William Clemens, Katherine Milton, Todd Dawson, Cesur Pehlevan, Sabrina Sholts, Jackson Njau, Oliver Rizk, Theresa Grieco, Yonatan Sahle, Antoine Souron, Michel Brunet, Faysal Bibi, and David Degusta for their help and guidance at different times.

This work depended on access to museum collections and I am extremely grateful to the curators and collections managers at the different institutions I visited. I humbly thank Alemu Admasu as well as the National Museum of Ethiopia and the Authority for Research and Conservation of Cultural Heritage, and the Middle Awash Project (Tim White, Berhane Asfaw, Yonas Beyene, and Giday Woldegabriel) for access to *Ardipithecus* fossils. Thanks also to curator Loïc Costeur and collections manager Martin Schneider at Naturhistorisches Museum Basel for access to *Oreopithecus* fossils. I also thank Elisabetta Cioppi and Lorenzo Rook of Museo di Storia Naturale Università di Firenze for access to *Oreopithecus* fossils. Finally, I thank Tim White for access to the cast collection and the modern human teaching collection at the Human Evolution Research Center.

Many thanks to the Human Evolution Research Center, the HERC-Desmond Clark Graduate Student Support Grant, and the Department of Integrative Biology for financial support for this dissertation research.

My experience with this project specifically and my graduate career generally was greatly enhanced by the supportive research environment at the Human Evolution Research Center. Thanks to former postdoctoral researchers Cesur Pehlevan, Sabrina Sholts, Jackson Njau, Yonatan Sahle, Antoine Souron, and Michaela Huffman and former graduate students Kyle Brudvik and Benjamin Mersey. Thanks also to the many undergraduate researchers that provided support, expecially Kathryn Rieck, Edgar Yap, Elizabeth Duran, Lina Nilsson, Kim Rhoten, Nandar Yuki, Colleen Young, Ondine Legris, Eva Herbst, Noah Cho, Neev Batavia, Paolo Rigo, Kalynn Graham, Emma Thatcher, Nick Shepetuk, and John Francis. Finally, several members of the HERC-affiliated Hlusko lab, past and present, deserve thanks. These include Sarah Amugongo, Oliver Rizk, Theresa Grieco, Whitney Reiner, Tesla Monson, and Marianne Brasil.

I wish to also thank my family, whose support, love, and especially patience drove the completion of this dissertation.

Chapter 1: Introduction

1.1 Background to the Dissertation

1.1.1 The discovery of *Ardipithecus*

In 1994, a new species of the family Hominidae (see section 1.1.4 for familial definitions used in this work) was published (White *et al*. 1994, 1995). The fossils that represent *Ardipithecus ramidus* were recovered from the Afar Rift of Ethiopia, in sediments dating to 4.4 million years ago (Ma) (Woldegabriel *et al*. 1994). In 2009, a more detailed, comprehensive treatment was given to this species when a suite of 11 research papers comprising ~600 pages of description, data, and analysis was published in *Science* (Louchart *et al*. 2009, White *et al*. 2009a, 2009b; Woldegabriel *et al*. 2009; Suwa *et al*. 2009a, 2009b; Lovejoy *et al*. 2009a, 2009b, 2009c, 2009d, Lovejoy 2009).

Much attention was focused on what was revealed about the phylogenetic placement of *Ardipithecus ramidus*, but the contextual evidence encompassing these fossils also provided a wealth of insight into behavior and habitat. Because of the unique depositional setting bracketed by two securely dated volcanic ash horizons of radioisotopically indistinguishable age (Renne *et al*. 1999), the vertebrate and invertebrate fossils recovered with *Ardipithecus ramidus* in the Middle Awash paleoanthropological study area opened a new window on the African Pliocene by revealing taxa ranging from *Ardipithecus* to *Celtis* seeds, tragelaphine bovids to lizards, and phytoliths to peacocks.

1.1.2 Implications of *Ardipithecus*

Chimpanzees still lack a useful fossil record (largely due to their tropical refugia; see McBrearty and Jablonski 2005), but were long conceptualized as a close approximation of the last common ancestor of humans and chimpanzees ("CLCA" is used here as the "Human and Chimpanzee Last Common Ancestor," as defined in White *et al*. 2009a). By the time their genetic proximity to humans had been revealed, this concept of chimpanzees as proxies for human ancestors only deepened, and indeed came to dominate human evolutionary studies for decades (e.g., Washburn 1967, Stern and Susman 1983, Pilbeam 1996). However, a good hominid fossil record older than 4 million years did not exist before the discovery of *Ardipithecus*.

The discovery of *Ardipithecus* therefore allowed practitioners to contextualize the chronologically younger *Australopithecus afarensis*, despite the latter's many derivations. By illuminating the 4-6 Ma time period, the *Ardipithecus* fossils may now actually force a paradigm shift in the way that practitioners of human evolutionary studies conceive of the Late Miocene common ancestor that we humans once shared with chimpanzees.

Phylogenetically, the *Ardipithecus* discovery team had initially diagnosed and assigned *Ardipithecus ramidus* (White *et al*. 1994) to the hominid branch of the hominoid family tree based on the limited available derived dental, cranial, and postcranial characters shared exclusively with later hominids (defined herein as including *Homo* and *Australopithecus*). A subsequent, limited parsimony-based cladistic analysis aligned *Ardipithecus* with later *Australopithecus* based on shared, derived characters of the dentition (White *et al*. 2006). The additional anatomy revealed in the Middle Awash research team's 2009 publications added many additional shared derived characters from developmentally separate parts of the body to this body of evidence for phylogenetic placement, and the combined evidence reinforced the team's earlier inference that *Ardipithecus ramidus* was a hominid exclusively related to *Australopithecus* and *Homo*:

> *"Parsimony-based cladistic analyses are useful in deciphering relationships within the hominid family tree, despite their shortcomings (72, 73). The distribution of characters identified in Table 1 clearly shows that* Ar. ramidus *is derived relative to all known Late Miocene fossils attributed to the hominid clade."* (White *et al*. 2009, p. 81).

The limitations of parsimony-based cladistic methods of phylogeny inference for resolving relationships have been long and widely recognized, particularly among hominoid primates. Trinkhaus (1990) noted that the parsimony method's positive attributes include its forcing of explicit definition of morphological characters, its provision of a "heuristic device for preliminary sorting of the hominid fossil record" (8), and its generation of testable hypotheses about hominid phylogeny. To that end, Strait and Grine (2004) concluded that the hypothesis of *Ardipithecus ramidus* being "…the ancestor or near the ancestry of all other hominids…" (White *et al*. 1994) was: "…supported in a general sense insofar as *Ar. ramidus* branches off near the base of the hominid tree, if not necessarily at the basal node." (p. 438), that "…the relationships of *Ar. ramidus*, *A. anamensis*, and *Pr. afarensis* obtained here (Fig. 10) are equivalent to those proposed by Asfaw *et al*. (1999a)" (p. 439) and that "…cladistic analysis reveals that *S. tchadensis*, *Ar. ramidus* and *A. anamensis* are the basal members of the hominid clade" (p. 441).

Despite those conclusions, the parsimony cladistic methodology employed in that study and elsewhere (Strait and Grine 1999) includes characters for which variability and integration are not well understood or appreciated. Misapplication of formal cladistic methods – particularly formal parsimony approaches to such traits – can be misleading because of "…arbitrary boundaries of presence or absence criteria, variability within species, limited sample sizes, and possible correlation between features." (Asfaw *et al*. 1999b, p. 1209). Accurate, biologically relevant, and independent character definition is crucial in order to refine interpretations of early hominid phylogeny:

> *Current interpretations of human evolution can be refined in two fundamental ways: by expanding the fossil record and by elucidating the biological basis of characters that are candidates for inclusion in phylogenetic analyses by rigorous anatomical study.* (Asfaw *et al*. 1999b, p. 1209).

As a pathway around such formidable obstacles, McCollum notes that patterns of integration among craniodental developmental modules may reveal such character redundancy:

> *"...the number of craniodental characters commonly used to infer early hominid phylogeny (often 50 to 70) far exceeds the number of modules ultimately responsible for adult skull form. Many of these characters are therefore redundant, and their inclusion in cladistic studies is a fundamental violation of the method."* (McCollum 1999, p. 1209).

1.1.3 Character definitions

This dissertation is not the appropriate place to rehearse issues that compromise the effective use of phylogenetic systematics among hominoid primates. As noted in the previous section, the parsimony approach in cladistic methodology is often inadequate for resolving relationships among hominoid taxa (Trinkhaus 1990, Asfaw *et al*. 1999b, McCollum 1999, White *et al*. 2009a). The choice of unambiguous characters to be employed in such analyses depends on their biological independence. Beyond character definition, choice, and independence, issues of character weighting and operational taxonomic unit (OTU) identification can contribute to the failure of the parsimony approach in providing adequate tests of hypotheses about the relationships among hominoid taxa. Characters evolved in parallel have long been known as a potential source of error in phylogenetic inference. Such characters that are shared by two sister taxa but absent in the last common ancestor of those taxa are today often referred to as "homoplasies," and this term has a history that goes back to the 1800s (Lankester 1870, as cited by Wood and Harrison, 2011).

In this systematic context, the history of discovery and interpretation of *Oreopithecus* is far more complicated than that of *Ardipithecus* (White 2009a, 2009b). *Oreopithecus* biology was fundamentally injected into paleoanthropological considerations during the Modern Synthesis of evolutionary biology, during which practitioners such as LeGros Clark, E. Mayr, and G.G. Simpson were using idiosyncratic weighting, unparsed character complexes, and "total morphological patterns" to infer relationships among taxa (White 2009b). However, as noted in Chapter 2, the most comprehensive assessment of *Oreopithecus* (Hurzeler 1968) actually presaged the adoption of a more explicitly cladistic approach in paleoanthropology.

In contrast, by the time *Ardipithecus* was discovered and announced in the early 1990s, the debates between evolutionary systematists and Hennigian phylogeneticists and taxonomists had already taken place. One positive result of these discussions was that character definition became more rigorous. Today, strict, formalized cladistic parsimony approaches dominate paleoanthropology (Strait *et al*. 2015, Dembo *et al*. 2016) and have extended to studies including *Oreopithecus* (Finarelli and Clyde 2004). These studies routinely attempt to subdivide character complexes by parsing anatomical regions, elements, and joints into "characters." Such efforts aim to achieve greater statistical robusticity in the parsimony assessments, but as many have noted, such atomization has the potential to generate error because of issues related to character definition, weighting, independence, and biology.

The vocabulary associated with cladistic methodology has now also become ubiquitous in paleoanthropology. The focus of this dissertation involves one such term. For consistency, I will use the terminology associated with standard Hennegian cladistics interchangeably throughout this dissertation according to the following equivalencies. Here, "synapomorphic" means "shared derived," "symplesiomorphic" means "shared primitive," "autapomorphic" means "uniquely derived," and "homoplastic" means "evolved in parallel from a last common ancestor that did not share the trait." For a detailed consideration of homoplasy, see section 1.2 below.

During the long publication history of *Oreopithecus* (detailed below in Section 1.4), this taxon's known anatomy has been inconsistently parsed to character complexes that were often further subdivided into individual "characters." This required my adoption of a hybrid approach to character assessment in *Oreopithecus.* I approached the subject of claimed homoplasies of *Oreopithecus* by considering both "character complexes" and the "characters" onto which they have sometimes been parsed. My focus is on alleged homoplasies that have been proposed since the taxon was created. To reiterate, is important to note that earlier authors worked within the framework of the Modern Synthesis and focused on character complexes, whereas more recent workers operating under a more Hennigian framework have more often attempted to divide such complexes into discrete "characters."

In the work that follows, I have attempted to comprehensively assess all claims of homoplasy, both involving individual characters and character complexes, that have been claimed to be homoplastic between *Oreopithecus* and later hominids. Many of these were originally alleged to be synapomorphic between *Oreopithecus* and later hominids, but with the better resolution of the phylogenetic position of *Oreopithecus*, these are today widely promulgated as homoplasies. I evaluate whether each character complex and/or its component analogous characters allegedly shared between *Ardipithecus* and *Oreopithecus* is indeed homoplastic, symplesiomorphic, or synapomorphic. In many cases I have found that fossils themselves are not adequate to make the distinction. I return to the attendant issues in my concluding chapter.

1.1.4 Classificatory definitions

Before undertaking a comprehensive consideration of claims for homoplasy in *Oreopithecus* and *Ardipithecus*, some taxonomic considerations are in order. The term "hominid" is used in this dissertation following traditional usage that dates to Simpson (1945) and even Darwin (1871), and continues among major researchers today (Berger *et al*. 1993; Brunet *et al*. 2002, 2005; Lordkipanidze *et al*. 2013; Bermúdez de Castro *et al*. 1997; Hlusko *et al*. 2013). White (2002) follows this practice in defining Hominidae:

> *"Fortunately, there is a phylogenetic means of classifying fossil forms at the family level that is consistent with traditional taxonomic practice. This defines Hominidae as the sister group of the African apes (Panidae (or Panidae and Gorillidae)). Hominids thus comprise all species derived in the human direction after the last common ancestor of African ape(s) (the chimpanzees based on molecular data) and humans. By this definition, Hominidae currently has one extant genus (*Homo*) and two extinct ones (*Ardipithecus *and* Australopithecus*).*" (p. 407).

Haile Selassie *et al.* follow this practice as follows:

> *"…to refer to the family Hominidae, which includes modern humans and all taxa phylogenetically closer to humans than to* Pan *(common chimpanzee and bonobo)—that is, all taxa that postdate the cladogenetic split between the lineage leading to modern humans and the lineage that led to extant chimpanzees."* (Haile-Selassie *et al*. 2009, p. 159).

Alternative taxonomic schema subsume extant African apes in a family Hominidae (Groves 1989, Boyle and Wood 2017). Such grouping requires the term "hominin" to refer to members of the tribe Hominini, and is most usually equivalent to the way "hominid" is used in this dissertation.

The genus *Ardipithecus* in this dissertation is restricted to the species lineage containing the younger *Ardipithecus ramidus* and its temporally older (5.7 Ma) chronospecies, *Ardipithecus kadabba* (Haile-Selassie *et al*. 2004, 2009). The genera *Sahelanthropus* (Brunet *et al*. 2002, 2005) and *Orrorin* (Senut *et al*. 2001; Pickford *et al*. 2002) are reserved as separate genera in this dissertation, but additional evidence may reveal both *Sahelanthropus* and *Orrorin* to be junior subjective synonyms of *Ardipithecus* (Haile-Selassie *et al*. 2004, White 2009b).

1.1.5 Positional and locomotor terminology

When describing the positional orientations and locomotor repertoires of extant and fossil primates, investigators have opted to use specific terminology to describe postures and "modes" of locomotion (White *et al*. 2015). These words carry implicit assumptions about evolutionary trajectory and adaptational regimes, and have often been used inconsistently by workers during the last several decades. As such, definitions of locomotion-related terms used in this dissertation is warranted for precision, clarity, and to avoid confusion.

Positional terms are limited to "orthograde/y," signifying an upright trunk posture, and "pronograde/y," signifying a horizontal trunk posture. These terms are often combined with a "mode" of locomotion. "Quadrupedalism" is defined as movement with all four appendages in contact with a substrate. "Palmigrade/y" is a form of quadrupedalism in which the palms of the hands are in direct contact with a substrate. "Plantigrade/y" refers to the foot. "Suspension" involves below-branch hanging, whereas "brachiation" involves swinging below branches. Climbing is complicated and can include the vertical climbing, clinging, and leaping practiced by some prosimians, as well as complex quadrumanous ascent practiced among great apes. Vertical climbing is used in this dissertation "for ascent or descent of supports angled at ≥ 45°…" from the horizontal (Hunt *et al*. 1996: 366).

Extant hominoids routinely practice some combination of these locomotor "modes" depending on the environmental context in which they find themselves. Chimpanzees, for example, knuckle-walk or walk bipedally with bent knees and hips while on the ground. To enter the canopy, they vertically climb. Once in the canopy, they suspend and occasionally brachiate.

It is important to note that extant hominoids are relict species of a once vast hominoid adaptive radiation during the Miocene (Begun *et al*. 1997b, Harrison 2010, Tuttle 2014, Begun 2015, Andrews 2015). Many of the diverse extinct taxa comprising this radiation did not locomote in exactly the same ways as that their living ape counterparts. On the other hand, some postural and locomotor "modes" have evidently recurred throughout the Miocene, as evidenced by anatomical similarities to living apes that appear to have been evolved in parallel. Adaptations for suspension among the living great apes are also seen in some fossil apes, but not in *Ardipithecus* or later hominids. Such suspensory adaptations are discussed throughout this dissertation in the context of *Oreopithecus* and great ape anatomy.

1.1.6 The phylogenetic position of *Ardipithecus*

Whether interpreted as a phylogenetic hominid or a sister taxon to *Australopithecus*, *Ardipithecus* fossils have important implications for not only elucidating hominid origins, but also for understanding the evolution of lineages of extinct Miocene apes, as well as the extant great apes. For example, living chimpanzees and bonobos are now considered to be separately evolving, rarely introgressing their species lineages (de Manuel *et al*. 2016). Their still-unknown common ancestor separated from the hominid clade approximately 7 million years ago, so we humans are therefore removed from either of these closest living relatives by a cumulative ~14 Ma (~7 Ma along each lineage) subsequent to the CLCA.

Our closest living relatives, chimpanzees and gorillas, are knuckle-walkers. Because *Australopithecus* fossils exhibit no clear anatomical signals of this type of locomotion (*contra* Begun 1992, Richmond and Strait 2000, Richmond *et al*. 2001, Begun 2004). Prior to the discovery of *Ardipithecus*, parsimony considerations had led some workers to the prediction that the ancestor of chimpanzees, gorillas, and humans were also knuckle-walkers, and the conclusion that the behavior and morphology associated with this form of locomotion had been lost sometime early in the hominid clade, between our split from the CLCA and the appearance of *Australopithecus*.

Ardipithecus is from securely dated sediments postdating our estimated split from the chimpanzee lineage (Steiper and Young 2006, Langergraber *et al*. 2012, Pozzi *et al*. 2014, Moorjani *et al*. 2016). It manifests no trace of morphology specifically related to knuckle-walking (Matarazzo 2008, Wunderlich and Jungers 2009, Williams 2010). Consequently, being so much closer to the CLCA, *Ardipithecus* offered a new and different perspective on the CLCA. Furthermore, the reckoning forced by *Ardipithecus* biology also extends to Miocene hominoid taxa with fossil records, some of them with long publication histories. One of the best represented and earliest studied is *Oreopithecus*.

1.1.7 The significance of *Oreopithecus* for inferring the geometry of the hominid family tree

As introduced above, when the initial 1992-1993 Middle Awash discoveries were published in *Nature* in September of 1994, the authors concluded that *Ardipithecus* was a hominid:

> *"…characters such as the modified C/P3 complex, an anterior foramen magnum, and proximal ulnar morphology (shared with later* Australopithecus *species) suggest that the Aramis fossils belong to the hominid clade."* (White *et al*. 1994, p. 312).

This conclusion was met with prominent agreement and widespread endorsement, and as Bernard Wood described the newly named Middle Awash fossils in an accompanying commentary:

> *"They represent the remains of a species that lies so close to the divergence between the lineages leading to the African apes and modern humans that its attribution to the human line is metaphorically and literally - by the skin of its teeth.*" (Wood 1994, p. 280).

Others implicitly accepted *Ardipithecus* by including it in their discussion of hominids (Carroll 2003) or in their cladistic analyses as a sister taxon of all later hominids (Strait and Grine 2004). Additional fossils were also subsequently attributed to the taxon (Semaw *et al*. 2005). Then, after a protracted interval of annually repeated fieldwork and years of laboratory curation and analysis, in 2009 the *Ardipithecus* discovery team published a great many additional fossils of *Ardipithecus ramidus*, noting their importance as a new data set that tested and extended many hypotheses about hominid origins and early evolution, including the phylogenetic inference that this taxon was a hominid:

> *"The expanded* Ar. ramidus *sample allows more detailed consideration of early hominid phylogenetics. The placement of* Ardipithecus *relative to later hominids can be approached by using modern and Miocene apes as the outgroup. An earlier cladistics study of this kind concluded that* Ar. ramidus *was the sister taxon of all later hominids (71). A more recent assessment of* Ar. ramidus *dental characters came to the same conclusion (7). In these analyses, a suite of derived features and character complexes exclusively aligning* Ar.ramidus *with Australopithecus was identified, but these were based on comparatively limited anatomical elements. The* Ar. ramidus *characters reported here, combined with those from Gona (36), allow a more complete analysis that clarifies the relationships among early hominid taxa.*" (White *et al*. 2009a, p. 81).

Surprisingly, however, the greatly expanded constellation of characters sampled across the entire skeleton of *Ardipithecus ramidus* led some authors to reverse their earlier assessments and question the hominid status of *Ardipithecus*. Several of them turned to the Miocene hominoid *Oreopithecus* to make the argument that the shared derived characters and character complexes advanced by the discovery team as evidence of a unique evolutionary relationship with *Australopithecus* were actually evolutionary parallelisms ("homoplasies" in Hennigian parlance), and were therefore unreliable indicators of affinity.

Subsequent to the 2009 publication of the greatly enlarged *Ardipithecus ramidus* hypodigm, one of the first authors to adopt such a position was Terry Harrison, whose brief review of the matter identified *Ar. ramidus* as a "purported hominin," albeit noting that the Ethiopian fossils were of "critical importance for understanding human evolution" (Harrison 2010, p. 532). Harrison had long published on *Oreopithecus* and depicted its phylogenetic relationships as do virtually all modern workers – as a highly derived, insular, non-hominid Miocene ape. About *Ardipithecus*, his review posed the question:

> *"Are they truly members of the hominin lineage, or simply apes among the tangled branches that constitute the basal hominine bush?*" (Harrison 2010, p. 532).

Esteban Sarmiento, another worker with a long interest in *Oreopithecus* (Sarmiento 1987, 1998, 2007; Sarmiento and Marcus 2000; Sarmiento *et al*. 2002) also commented in *Science* (28th May, 2010), specifically referring to *Oreopithecus* and concluding that:

> *"Molecular and anatomical studies rather suggest that Ar. ramidus predates the human/African ape divergence.*" (Sarmiento 2010, p. 1105).

The most explicit and detailed claims that *Ardipithecus* characters could have evolved in parallel with their homologs in later hominids would next appear in a "Research Review" by Wood and Harrison, in *Nature* (17th February, 2011). In what purported to be a needed basic primer for the paleoanthropologists who found fossils (and readers of their publications), they reminded colleagues that:

> *"…homoplasy needs to be taken into account when generating hypotheses about the relationships among the taxa in the higher primate part of the tree of life."* (Wood and Harrison 2011, p. 348).

That homoplasy might confound efforts at phylogeny inference was hardly surprising to paleobiologists or, more narrowly, paleoanthropologists. After all, senior colleagues had been using the history of *Ramapithecus* to teach generations of undergraduate students the time-worn lesson about how fragmentary fossils can mislead the unwary if homoplasy is mistaken for synapomorphy. Indeed, Pilbeam had concluded (in *Scientific American* a decade before *Ardipithecus* was created), that his long-standing inferences of hominid status and deep species divergence had been based on a failure to adequately recognize homoplasy:

> *"The resemblances led many, including me, to argue that* Ramapithecus *was in fact an early hominid, that the hominids had diverged from the hominoids of Africa at least 15 million years ago and therefore that the divergence date of four million years ago, based on the molecular data, was wildly incorrect."* (Pilbeam 1984, p. 93).

A quarter century later, apparently stimulated by the more comprehensive presentation of *Ardipithecus*, Wood and Harrison returned *Oreopithecus* to center stage as a "cautionary tale" to remind readers about the potential that homoplasy has to confound inferences of affinity. I quote at length here because the explicit hypothesis being promulgated by Wood and Harrison is based on the facts and assertions about *Oreopithecus* that they superficially summarize. These set out a series of hypotheses that this dissertation will test.

> *"What is instructive about* Oreopithecus *with respect to developing hypotheses about the relationships of* Ar. ramidus *is that it is a species of hominoid that is well-enough known anatomically (that is, almost every bone in the skeleton is represented) to be certain that it is not a member of the hominin clade, yet it shares many anatomical similarities with later hominins, including some that are generally considered to be uniquely associated with bipedal behaviour."*

Wood and Harrison go on to review the characters and character complexes that they consider to be possibly homoplastic between the two taxa:

> "*The incidence of a prominent metaconid, absence or small size of a diastema in the upper tooth row, a vertically oriented mandibular symphysis, a mental foramen situated high on the mandibular corpus, a short orthognathic face, an anteriorly placed zygomatic process of the maxilla, anterior projecting nasal apophyses and a deep pit on the palmar associated with bipedal behaviour include an anteriorly situated foramen magnum, short and broad iliac blades, infero-superiorly short pubic symphysis, a well-developed anterior inferior iliac spine, a large ischial spine, medial and lateral condyles of the distal femur similar in size, possibly associated with a bicondylar angle. The impressive suite of shared these features are most parsimoniously interpreted as either homoplasies or retained primitive hominid features."*

Having asserted rampant homoplasy, they summarize by casting *Oreopithecus* as a potentially fatal flaw for all published assessments of hominid status for Late Miocene and early Pliocene African fossils:

> "Oreopithecus *is a classic example of how a late Miocene hominid can independently acquire a suite of structural– functional complexes of the dentition, cranium, hand, hip and hindlimb that closely parallel the specialized features uniquely associated with the hominin lineage, and thereby encourage researchers to generate erroneous assumptions about evolutionary relationships.*
> Oreopithecus *highlights the dangers inherent in uncritically assuming that shared similarities are a secure indication of relationship or that extant primates are an adequate guide to the potential behavioural diversity of extinct taxa.*
> *The object lesson that* Oreopithecus *provides is critical to the debate about interpreting the relationships of the earliest purported hominins. It demonstrates how features considered to be hominin specializations can be shown to have been acquired independently in a non-hominin lineage in association with inferred behaviours that are functionally related to, but not necessarily narrowly restricted to, terrestrial bipedalism"*. (Wood and Harrison 2011, p. 350-351).

In Chapter 2, I more fully consider Wood and Harrison's "cautionary tale" usage of alleged *Oreopithecus* homoplasies. Here, it is only necessary to note that it contains a curious abandonment of earlier claims by Harrison (1987, 1991; Harrison and Rook 1997), in that many of the very same characters and character complexes invoked here as "homoplastic" had been previously identified as uniquely evolved or primitively shared (i.e. were "autapomorphies" or "symplesiomorphies" in *Oreopithecus,* see Chapter 2 and Appendix 2*).*

The present dissertation is intended to closely and comprehensively examine the evidence – the facts and the assertions about *Oreopithecus* – that shape current debate on hominid origins and early evolution. But before proceeding with that, I shall provide an overview of the fundamental issue of evolutionary parallelism, or homoplasy. Building on this, I apply these observations and principles specifically to the hominoid clade. Finally, I review the history of discovery and context for both *Oreopithecus* and *Ardipithecus* to provide the broader foundation for the analytical chapters that follow.

1.2 Brief introduction to the concept of homoplasy

Since the 2009 *Science* publications about *Ardipithecus* (White *et al*. 2009a, 2015; Suwa *et al*. 2009a, 2009b; Lovejoy *et al*. 2009a, 2009b, 2009c, 2009d), investigators resistant to the interpretations and conclusions published therein have questioned its interpretation as a hominid (*sensu* this dissertation, see above). In part, such efforts were founded on emphasizing alleged instances of parallel acquisition (homoplasy) of hominid-like characteristics in distantly related fossil ape taxa. In fact, the *Ardipithecus* discovery team had persistently and explicitly addressed the question of potential homoplasy in Miocene hominoid taxa such as *Dryopithecus*, *Ouranopithecus*, *Gigantopithecus*, and *Oreopithecus* (White *et al*. 1994, Suwa *et al*. 2009a, 2009b; Lovejoy *et al*. 2009a, 2009b, 2009c).

Such claims of homoplasy (Sarmiento 2010; Wood 2010, Wood and Harrison 2011) have already inspired some critical assessment (Lovejoy and McCollum 2010, Russo and Shapiro 2013, White *et al*. 2015), but regarding *Oreopithecus*, a comprehensive examination of these claims has not been undertaken until now. Before such an examination can begin, it is important to better clarify what homoplasy is. An exhaustive review of the immense literature that addresses the diagnosis and utility of homoplasy in phylogenetic reconstruction is beyond the scope of this study, but a concise overview is useful for what follows.

Even before Darwin, convergent and parallel evolutionary acquisition of characters was understood. Darwin himself noted:

> *"I am inclined to believe that in nearly the same way as two men have sometimes independently hit on the very same invention, so natural selection, working for the good of each being and taking advantage of analogous variations, has sometimes modified in very nearly the same manner two parts in two organic beings, which owe but little of their structure in common to inheritance from the same ancestor."* (Darwin 1859, p. 267).

Proponents of the Modern Synthesis likewise appreciated convergent and parallel evolutionary acquisition of characters. Simpson defined parallelism as:

> *"The independent occurrence of similar changes in groups from a common ancestry and because they had a common ancestry...parallelism should be used only when community of ancestry is pertinent to the phenomenon."* (Simpson 1961, p. 103).

By contrast,

> *"Convergence, strictly defined, involves adaptation to ecologically similar situations by two groups of distinct ancestries, at least one of which did not have the adaptation common to the convergent descendants."* (Simpson 1961, p. 91).

In contemporary evolutionary biology, "homoplasy" is defined as:

> "*...similarity that is the result not of simple ancestry, but of either reversal to an ancestral trait in a lineage or of independent evolution (convergence, similarity resulting from different developmental genetic mechanisms; or parallelism, similarity resulting from the same developmental genetic mechanisms).*" (Wake *et al*. 2011, p. 1032).

Such evolution most often results from similar adaptive responses to similar selection operating on phenotypes related to life history. Modification of phenotypic traits in the form of evolutionary loss, reduction, or the development of new morphologies is deeply constrained by developmental genetic mechanisms and evolutionary history; it is precisely these constraints that limit morphological space and dictate the likelihood of homoplasy (Wake and Larson 1987, Wake 1991, Wake *et al*. 2011).

Hennig (1966) addressed the issue of identifying homoplasy in a phylogenetic analysis, advocating the *a posteriori* identification of homoplasies by including possible parallel characters in a comparative context with other characters in the same species and with other taxa. Wake and others have argued for a hierarchical approach based on the consideration of potential homoplasies at the level of a gene, tissue, or organ. Others have noted the great difficulty in discriminating between convergence, parallelism, and evolutionary loss/reversals (Nelson 1994, Hall 2003, 2007; Wake 2008, Wake *et al*. 2011).

Importantly in paleobiology, the inference of the genetic basis of similarity and therefore the identification of the type of homoplasy is notoriously difficult when dealing with fossils that preserve no genetic material and that suffer from varying degrees of depositional distortion that hinder reliable observations of phenotype. An accurate characterization of the morphological trait in question is a fundamental first step. In the hominoid clade, the words "homoplasy" and "parallelism" are synonymous and will be used that manner throughout this dissertation.

1.3 Homoplasy in Hominoidea

Homoplasy in hominoid evolution is particularly difficult to assess due to the few extant taxa and their limited fossil records. Without adequate documentation of morphological evolutionary history for these lineages, and without adequate fossil records of ancestors and/or outgroups, reliable interpretations of parallel acquisition or loss are difficult (Larson 1998). Resolving the stratophenetic relationships of fossil and extant species lineages depends on the accurate, character-by-character understanding of homoplasy. More fossils and better appreciation of inter- and intraspecific variation are both necessary in such an endeavor, as Schultz noted long ago:

> *"It is the intra-populational variability of the anthropoids, however, which appears so impressively great to all students with access to large series of these primates.'* (Schultz 1951).

Indeed, this variation in hominoids can be considerable across idiosyncratic, geographic, ontogenetic, sexual, and temporal axes (White 2009b).

All of the extant apes demonstrate anatomical adaptations associated with suspensory locomotor behaviors in their postcranial skeletons (see Section 1.1.5 above for a fuller account of locomotor terminology). These include high (100%+) intermembral indices (expressed as a percentage and defined as humerus length plus radius length divided by femur length plus tibia length multiplied by 100), elongated non-pollical digits, short thumbs, lateral orientation of the shoulder joint, invagination of the spinal column into the anteroposteriorly broad thoracic space, and stiff lower backs featuring some lumbar entrapment within the bi-iliac space (*contra* Whitcome 2012, Ward *et al*. 2017). African apes employ specializations of the metacarpals and wrists to allow for terrestrial knuckle-walking. Many, if not all of these specializations are interpreted by the *Ardipithecus* discovery team to have developed in chimpanzees and gorillas as the result of parallel acquisitions after diverging from an inferred more primitive ancestor that was likely a palmigrade, above-branch, quadrupedal ape (White *et al*. 2009a, Lovejoy *et al*. 2009a, 2009b, 2009d). Others disagree (Harrison 2010, Sarmiento 2010; Wood and Harrison 2011).

As hominoid paleontologists moved past their mistakes based on incomplete appreciation of homoplasy and faulty restorations of limited craniodental remains in the 1970s, (Simons 1960, Simons and Pilbeam 1965, Washburn and Ciochon 1974, Pilbeam 1979, Andrews and Cronin 1982, Lewin 1997), the hominoid fossil record and knowledge of hominoid comparative anatomy and variation improved. In the course of these investigations of newer fossil material, researchers noted multiple instances of anatomical similarities between and among taxa and in the course of their phylogenetic studies began to more frequently identify instances of homoplasy (Lockwood and Fleagle 1999, Begun *et al*. 1997a, Begun and Kordos 1997, Begun 2007).

Begun advocated for parallelism as an explanation for similarities he observed in extant hominoid phalanges relative to fossil forms *Dryopithecus* and *Sivapithecus* (1993). Moyà-Solà and Kohler likewise cite parallelism as an explanation for postcranial similarities observed between *Dryopithecus* and *Pongo* (1996). Other mid-Miocene taxa manifest other similarities; *Nacholapithecus* demonstrates spinal invagination into the thoracic space and large forelimbs (Ishida *et al*. 2004, Nakatsukasa *et al*. 2007), as does *Pierolapithecus* (Moyà-Solà *et al*. 2004). *Sivapithecus* shares similarities of the face with extant *Pongo* (Pilbeam *et al*. 1990). Late Miocene examples of parallelism abound, and some of it continues to be mistaken for synapomorphy. *Ouranopithecus* evinces relatively reduced canines (de Bonis and Melentis 1977, de Bonis *et al*. 1990, de Bonis and Koufos 2004, Koufos and de Bonis 2005) whereas *Hispanopithecus* (Almécija *et al*. 2007) exhibits morphology of the hand and wrist that is suggestive of both above branch and below branch competence. Parallel acquisition of these "characters" will, of course, confound phylogenetic analysis, something that has long been recognized (Kimbel and Martin 1993, Martin and Andrews 1993, Shea *et al*. 1993).

Indeed, by the 1990s, these and many other instances of potential and asserted parallelisms had already led to the general conclusion that homoplasy was pervasive across Hominoidea (Larson 1998, Begun 2007). However, none of these taxa has yielded ancient DNA with which to either understand the underlying developmental mechanisms of these homoplasies, or to test hypotheses of homoplasy. Nor are the fossil samples on which the taxa have been based sufficiently large enough to adequately assess sexual, geographic, idiosyncratic, or evolutionary variation in various characters.

Other vertebrates that are currently undergoing adaptive radiations may be instructive in this regard (Shapiro *et al*. 2004, Colosimo *et al.* 2005, Miller *et al*. 2007). Similar selective pressures acting on shared genetic toolkits within Hominoidea might be responsible for the similarities associated broadly with adaptive suites, such as modifications for suspensory behaviors observed on fragmentary fossil remains. But homoplasies should not be inferred without reliable "readings" of relevant anatomy (Reno *et al*. 2005). Doing this for *Oreopithecus* is a central goal of this dissertation. Only careful, detailed examination of the actual fossil evidence for true anatomy of the once-living organism will reveal whether assertions of homoplasy are paleontologically and biologically well-founded in the first place. These goals, and the research questions and methods that address them, are presented in Chapter 2.

1.4 *Oreopithecus*

Often described as "enigmatic" despite the fact that it is one of the best known extinct fossil apes, *Oreopithecus* lived during the Late Miocene on an insular, island archipelago in what is today Tuscany, Italy and Sardinia. Interpreted by nearly all paleoanthropologists as a smallbrained, large-bodied ape (males were similar in size to female chimpanzees) and unconstrained by direct competitors or large carnivores, *Oreopithecus* had teeth specialized for folivory and several adaptions in its postcranial skeleton thought to correspond to vertical climbing and suspensory below-branch locomotion (a detailed discussion of these and other positional and locomotor forms is provided in section 1.1.5).

Oreopithecus has been proposed by some, since its discovery, as a mysterious member of the family Hominidae or as a distant relative ape taxon that evolved several features claimed to be hominid-like. Paleontologist, zoologist, and Chair of Comparative Anatomy at the Paris Museum of Natural History Paul Gervais named an "anthropomorphous ape" *Oreopithecus bambolii* in 1872. This introduced the scientific community to a primate that has since inspired 145 years of field and laboratory research (Gervais 1872a, 1872b), hundreds of primary publications, and countless mentions in scientific and popular literature. Discovered in lignite (a dark brown or black coal often with traces of plant structure, formed from compressed peat) at Monte Bamboli in modern day Tuscany, Italy, Gervais designated as the holotype a nearly complete mandible of a juvenile with partially erupted lower third molars (IGF 4335), (Figure 1.1).

Subsequent investigations of other coal mines in the Grosetto Province during the next 50 years led to the discovery of 3 more localities, Casteani, Montemassi, and Ribolla, which, along with the original locality, yielded a few dozen primarily dental, maxillodental, or mandibulodental specimens (Gervais 1872a, Gervais 1872b, Ristori 1890, Schwalbe 1915, Hürzeler 1949; see Figure 1.2). Postcranial remains from these localities are relatively few, comprising a single proximal radius fragment with an associated proximal ulna fragment (IGF 4336) (Hürzeler 1949).

Interpretations of the initial sample varied, and some investigators argued for relationships with hylobatids (Rütimeyer 1876). Others noted a similarity with humans, namely a bicuspid lower third premolar (Forsyth Major 1880). Some attributed the fossils to cercopithecids (Schlosser 1887, Ristori 1890), whereas Schwalbe argued for a distinct family, Oreopithecidae (1915).

Johannes Hürzeler, a Swiss paleontologist and Professor of Zoology at the University of Basel, began studying *Oreopithecus* in the late 1940s. He attempted to compile and illustrate the then known specimens from Basel (Naturhistorisches Museum) and Florence (Instituto di Geologia di Firenze = IGF, today the Museo di Storia Naturale, Sezione di Geologia e Paleontologia dell'Università di Firenze). Hürzeler published two monographs documenting the predominantly dental material he gathered, first concluding that the teeth could not belong to a cercopithecoid (1949) and later presenting what would become his central thesis with regard to this taxon – that *Oreopithecus* represented a primitive hominid based on relative canine size and postcanine tooth proportions (1954).

The latter interpretation generated interest and high-level controversy, with Von Koenigswald (1955) dismissing *Oreopithecus* as a specialized hominoid and others regarding it as a possible platyrrhine (Remane 1955), a cercopithecoid (Heberer 1952), or agreeing with earlier assertions that it be sequestered in its own family (Butler and Mills 1959).

Meanwhile, a team led by Hürzeler removed a block of lignite from the collapsing Baccinellocoal mine in 1958. It contained a highly compressed juvenile male skeleton (IGF 11778) of *Oreopithecus*. This became the basis for a series of papers that began with a preliminary report and culminated with a comprehensive review (Hürzeler 1958, 1959, 1960, 1968). In these, Hürzeler reasserted claims of hominid affinity and argued that *Oreopithecus* was either a hominid or a very close relative based on around 20 characters or character complexes that he interpreted as uniquely shared with later *Australopithecus* and *Homo* (see Chapter 2 for an accounting). Additional blocks of lignite were extracted from Baccinello and several more fossils representing additional individuals were recovered. Several of these lignite blocks today remain intact, their contents not yet revealed, at the Naturhistoriches Museum Basel.

Interest in the new fossil material from Baccinello increased as the sample was enlarged by fieldwork and laboratory preparation. Most prominently, Schultz (1960) examined the IGF 11778 skeleton and other potentially informative specimens. He noted adaptations for a suspensory locomotor repertoire in comparison with extant catarrhines, in a primate whose body mass he approximated to that of *Pan*.

Straus (1963), in an attempt to place *Oreopithecus* phylogenetically, confirmed some of Hürzeler's observations and assertions of hominid similarity in the Baccinello material, particularly the forward positioning of the zygomatic root and vertical implantation of the incisors (and overall short face), short and broad ilia, but disagreed with others such as the significance of lower molar length proportions, and femoral shaft obliquity. He could neither confirm nor falsify still others based on the preservation of the fossils.

Overburden pressures within the lignite beds had seriously distorted the fossils, and as this dissertation will demonstrate, this fact has led to a great deal of confusion and misinformation about the original shape of individual skeletal elements. Indeed, Straus was himself perhaps misled by this distortion, evident in his own confusion about where to phylogenetically place *Oreopithecus* (1963). Others at the time and in the two decades that followed also struggled with how to interpret *Oreopithecus* anatomy in a phylogenetic context (Simpson 1963, Knussman 1967, Szalay and Delson 1979) or with Hürzeler's descriptions and interpretation of the anatomy itself (Coon 1962, Szalay and Berzi 1973, Delson 1979).

Oreopithecus experienced a reappraisal during the mid 1980's in conjunction with a workshop in 1984, a symposium in 1985 (to which Hürzeler was not invited), and a series of articles published in the *Journal of Human Evolution* in 1987 and 1988 detailing the work that resulted from these meetings. Of course, this more modern work was done in the context of the belated adoption of Hennigian principles of phylogeny inference and classification within paleoanthropology (see White 2009a).

These 1980s publications attempted to address the paleontological context and biology of *Oreopithecus* more comprehensively than had been done previously, specifically addressing some of the original work and subsequent reaction to it. Whereas Delson (1987) exhaustively outlined the scholarly history of the taxon, Azzaroli *et al*. (1987) detailed the chronology and fauna of the five known *Oreopithecus*-bearing localities, approximating the fauna and paleogeography it occupied to be approximately 8.5 Ma old.

Harrison (1987) concluded, based primarily on his analysis of postcrania, that *Oreopithecus* belonged in the superfamily Hominoidea. However, because it lacked observable shared derived characters (synapomorphies) with extant hominoids, and in agreement with Schwalbe (1915), he concluded that it was best placed in its own family. Jungers (1988) revised Schultz's (1960) body mass estimate to approximately 32kg for *Oreopithecus* based on multiple regression analysis on better-preserved elements of the knee and wrist compared with extant hominoids.

Szalay and Langdon (1987) examined the *Oreopithecus* foot and noted anatomical similarities with *Proconsul* and *Pan* as well as inferred mechanical similarities with *Pan.* They speculated the latter to have been independently derived based on the then available fossil evidence for other Miocene hominoid taxa (in turn, sparse save for *Proconsul*). Separately, Sarmiento largely concurred with these major points (that at least postcranially, *Oreopithecus* was a hominoid), and went a step further by speculating that *Oreopithecus* might represent a possible ancestor to large-bodied extant hominoids in general (Sarmiento 1987).

The Miocene fossil record in Europe improved throughout the 1990's at the same time that the early hominid fossil record was greatly expanded elsewhere, particularly in Africa. These again spurred interest in the *Oreopithecus* material housed in Basel and Florence. With the discovery of new *Dryopithecus (Hispanopithecus)* postcranial material from the Can Llobateres site at Sabadell, Spain (Moyà-Solà and Köhler 1993, 1995, 1996) and earlier *Pierolapithecus* postcranial material from the nearby Barranc de Can Vila site (Moyà-Solà *et al*. 2004), this research group secured a preparation and study loan of the *Oreopithecus* fossils housed at Naturhistorisches Museum Basel.

In the course of their study, some of the similarities that Hürzeler (1958, 1968) and Straus (1963) observed between *Oreopithecus* and Hominidae were resurrected and co-opted in support of a new hypothesis – that the orthograde *bauplan* that some had interpreted as adapted for climbing and suspensory behaviors (Harrison 1987) was instead an adaptation for bipedal locomotion in an insular setting (Köhler and Moyà-Solà 1997, 2003; Moyà-Solà and Köhler 1997, Moyà-Solà *et al*. 1997, Rook *et al*. 1999, 2004).

This insular setting was defined by the endemic faunas outlined by Lorenz (1968) and repeatedly by Hürzeler and colleagues (Hürzeler 1975, 1982, 1983, Hürzeler and Engesser, 1976). The associated faunal assemblage demonstrates the hallmarks of the "Island Rule" (Van Valen 1973), with gigantism evident in rodent species and dwarfism in bovids. An endemic faunal assemblage is found in the two oldest named layers, V1 and V2 (the *Oreopithecus*-bearing layers) at Baccinello, and comparable faunal assemblages at Casteani, Montemassi, Ribolla. Azzaroli *et al*. (1987) interpreted the paleogeography to be that of an island archipelago connected by on at least one occasion a "filter bridge" allowing dispersal of African mammals into the area. This implicit origin for *Oreopithecus* has been debated based on a putative European *Dryopithecus* ancestor for *Oreopithecus* (Moyà-Solà and Köhler 1997, Bernor *et al*. 2001), but it seems clear that the fossil-bearing localities evince an insular environment dominated by swamps.

A fauna similar to the one contained at Baccinello V1 and V2 was discovered in the early 1990s at a new site, Fiume Santo in Sardinia, and has since yielded 20 isolated teeth and one fragmentary right mandible (P3-P4) of *Oreopithecus* (Cordy and Ginesu 1994, Cordy and Ginesu 1995, Abbazzi *et al*. 2008). The dates for *Oreopithecus*-bearing sediments have been refined in recent years based on ^{40}Ar/^{39}Ar dating of the Passonaio ash layer, which is located between the two *Oreopithecus*-bearing layers at Baccinello:

> *The age spectra (Figure 2) reveal well-defined plateaux with indistinguishable ages ranging from 7.50±0.10 to 7.61±0.09 Ma (1 σ errors). The weighted (by inverse variance) mean of these six ages (7.55±0.03 Ma) is taken as the age of the ash layer, and thus a constraint on the age of* Oreopithecus *faunas* (Rook *et al*. 2000, p. 579-580)

Since the publication of those radioisotopic dates and because the Passonaio tephra passes between the two layers, a magnetostratigraphic study attempted to refine the dates for the *Oreopithecus*-bearing V1 and V2 layers at Baccinello:

> *The oldest* Oreopithecus *bearing sediments in BCB (V1) are found in upper C4r, and so are likely to have an age between 8.3 and 8.1 Ma. The youngest* Oreopithecus *remains (from the so-called V2 assemblages) are from sediments attributed to C3Ar, and have an age between 7.1 and 6.7 Ma*. (Rook *et al*. 2011).

1.5 *Ardipithecus*

In his most famous book, *On the Origin of Species*, Darwin deferred the question of human evolution by stating "Light will be thrown on the origin of man and his history." (1859, p. 576). Lacking any human fossil record, Darwin and his contemporaries largely relied on extant ape morphology to speculate about human origins (White 2010). The following decades witnessed the recovery of older and older hominids from the caves of Europe and South Africa (Boule 1911, 1912, 1913; Gorjanovic-Kramberger 1900, 1906; Schoetensack 1908; Broom and Schepers 1946; Broom 1937, 1950; Broom and Robinson 1950, among many others), to the river banks of Java (Dubois 1894, 1896a, 1896b), and to the sediments of the African Rifts (Leakey *et al*. 1964, Tobias 1967, Leakey and Hay 1979, Taieb *et al*. 1972, Taieb 1974, Taieb 1975, Johanson and Coppens 1976).

The 1970s and 1980s extended the *Australopithecus* record more deeply, and in particular, *Australopithecus afarensis* (a 3.75-3.0 Ma hominid) was shown to have had already evolved many of the anatomies that were by then universally recognized as "hominid" (Bush *et al*. 1982; Johanson *et al*. 1978; Johanson *et al*. 1982a, 1982b, 1982c; Kimbel *et al*. 1982; Latimer *et al*. 1982; Lovejoy *et al*. 1982a, 1982b, 1982c; Lovejoy 2005a, 2005b; Ward *et al*. 1982, White and Johanson 1982, Lovejoy *et al*. 2002; Protsch 1981, White 1977, 1980a, 1980b). *Australopithecus* was an obligate bipedal walker with derivations of the pelvis, knee and foot, with a small brain, and with feminized male canines. Despite claims to the contrary, it showed no specific characters unequivocally tied to knuckle-walking. Paleoanthropologists struggled with these observations, but the chimpanzee as "living missing link" model held (Wrangham and Pilbeam 2001; Fleagle 1988, 1998, 2013).

Australopithecus ramidus was first described in 1994 on the basis of cranial, dental, and postcranial fossils (White *et al*. 1994) and was subsequently reassigned to the new genus *Ardipithecus* in 1995 on the basis of the taxon's primitively small postcanine teeth relative to *Australopithecus* (White *et al*. 1995). Subsequent field seasons throughout the 1990s (and continuing today) at Aramis and nearby localities in the Middle Awash study area (Afar Region, Ethiopia) then yielded additional thousands of plant, invertebrate, and vertebrate fossils. Of these, 110+ specimens are attributed to *Ardipithecus*, including a partial female skeleton and the remains of numerous additional individuals (White *et al*. 2009a, 2015). The environmental context was revealed by multiple independent lines of evidence, including isotopic work done with dental enamel of the diverse fauna; the fauna and flora in aggregate were typical of a woodland environment (Louchart *et al*. 2009, Suwa and Ambrose 2014, White 2014, White *et al*. 2009b, 2015).

This conclusion, when combined with the independent anatomical and isotopic evidence from *Ardipithecus*, effectively falsified the "Savanna Hypothesis," an 18th century evolutionary scenario holding that the selective context for hominid emergence and the evolution of bipedal walking was a dry grassy habitat (see Lamarck 1809, Suwa and Ambrose 2014, White 2014, White *et al*. 2015 *contra* Domínguez-Rodrigo 2014, Cerling *et al*. 2015, Cerling *et al*. 2015).

The anatomical evidence supportive of hominid attribution includes a number of craniodental characteristics that align *Ardipithecus* between earlier *Sahelanthropus* and *Orrorin,* and with temporally younger *Australopithecus* (Brunet *et al*. 2002, 2005; White *et al*. 2006; 2009a; Suwa *et al*. 2009a, 2009b). Dentally, *Ardipithecus* showed no signs of the dietary specializations characteristic of extant African apes in that its molar enamel was thicker than the frugivorous chimpanzee and its tooth attrition not consistent with that observed for the herbivorous gorilla (White *et al*. 2009a, Suwa *et al*. 2009b). Like *Australopithecus*, *Ardipithecus* lacks an upper canine/lower third premolar honing complex, suggesting a reduction or elimination of male-male aggression typical of many anthropoid primates (Lovejoy 2009). Across the variation observed in the *Ardipithecus* sample, canine sexual dimorphism is effectively comparatively minor when compared to earlier or extant apes (White *et al*. 2009a, Suwa *et al*. 2009b).

The *Ardipithecus* postcranium is cumulatively primitive (e.g. not derived) relative to both later hominids and extant and some mid- to late-Miocene hominoid apes. Its body proportions are like those of *Proconsul* and extant arboreal quadrupeds, with neither the forelimb elongation and hindlimb shortening seen in extant apes, nor the obverse condition derived in *Homo*. The thorax and shoulder are inferred to be like those of a primitive ape, with the shoulder reorganized and enhanced distal forelimb manipulation. The elbow was fully extensible, but unlike habitually suspensory apes, its thumb was relatively elongate relative to the other digits (White *et al*. 2009; Lovejoy *et al*. 2009a).

Ardipithecus manifested none of the hand morphology associated with knuckle-walking or consistent below-branch suspension typical of extant and several fossil apes. It lacked the metacarpal head doming and modifications of the wrist that buttress the chimpanzee and gorilla hand during knuckle-walking. It also lacked the "locking" mechanism of the central carpal joint seen in extant and some fossil ape taxa that supports the hand during suspension (White *et al*. 2009; Lovejoy *et al.* 2009a). Primitive foot morphology includes a divergent hallux and a retention of propulsive and leverage characteristics of the midfoot lost in the apes and seemingly co-opted in *Ardipithecus* for habitual terrestrial bipedality (White *et al*. 2009, 2015; Lovejoy *et al*. 2009a, 2009c).

Whereas the lower pelvis in *Ardipithecus* reveals a primitive hominoid retention of a long ischium associated with vertical climbing, its upper pelvis demonstrates a suite of derived, interrelated characters shared exclusively with *Australopithecus* and *Homo*. The pubic symphysis is short, the ilia are mediolaterally broad and superoinferiorly short, and the anterior inferior iliac spine, which anchors the iliofemoral ligament and rectus femoris muscles that flexes and stabilizes the hip during bipedal walking is relatively large and apparently arose developmentally from a separate apophysis (White *et al*. 2009, 2015; Lovejoy *et al*. 2009b, Zirkle 2015).

The biology of *Ardipithecus* has important implications for the evolution of hominids, extant apes, and fossil apes. Among these is the robust confirmation of the fact that no matter what its phylogenetic placement relative to other hominids and apes, considerable parallelism has been characteristic of the hominoid clade. *Oreopithecus* is a prime example of this phenomenon. This dissertation examines whether this homoplasy so confounds phylogenetic inference that placement of even well-documented fossil taxa lies beyond our grasp [as Wood, Harrison, and others have contended subsequent to the 2009 *Science* publications on *Ardipithecus* (see above)].

1.6 Organization of the Dissertation

The framework that this dissertation will employ is as follows. Chapter 2 details the goals, research questions, and methodology employed and a presentation of summaries of each of the major hominid-like morphological characters claimed for *Oreopithecus*. I categorize these into the major anatomical regions (craniodental, axial, and appendicular skeletons), noting where characters are subdivided as disarticulated parts belonging to a larger character complex. In successive chapters I provide a detailed comparison of each individual character within each character complex between *Oreopithecus Ardipithecus*, using all available fossils for these element-by-element comparisons. For example, Chapter 3 evaluates character complexes and their subdivided characters pertaining to the craniodental skeleton of *Oreopithecus* in comparison with *Ardipithecus*, extant apes, and all available fossil apes. Chapter 4, assesses the axial skeleton in the same manner, primarily focusing the lower vertebral column and pelvic anatomical complexes and their individual characters that have been claimed as homoplastic between *Oreopithecus* and *Ardipithecus*. Chapter 5 presents a similar consideration of the appendicular skeleton (hands and feet). In the final chapter I review these results and interpret their meaning for hypotheses about hominoid and hominid evolution.

Figure 1.1 *Oreopithecus bambolii* holotype IGF 4335 (Gervais 1872).

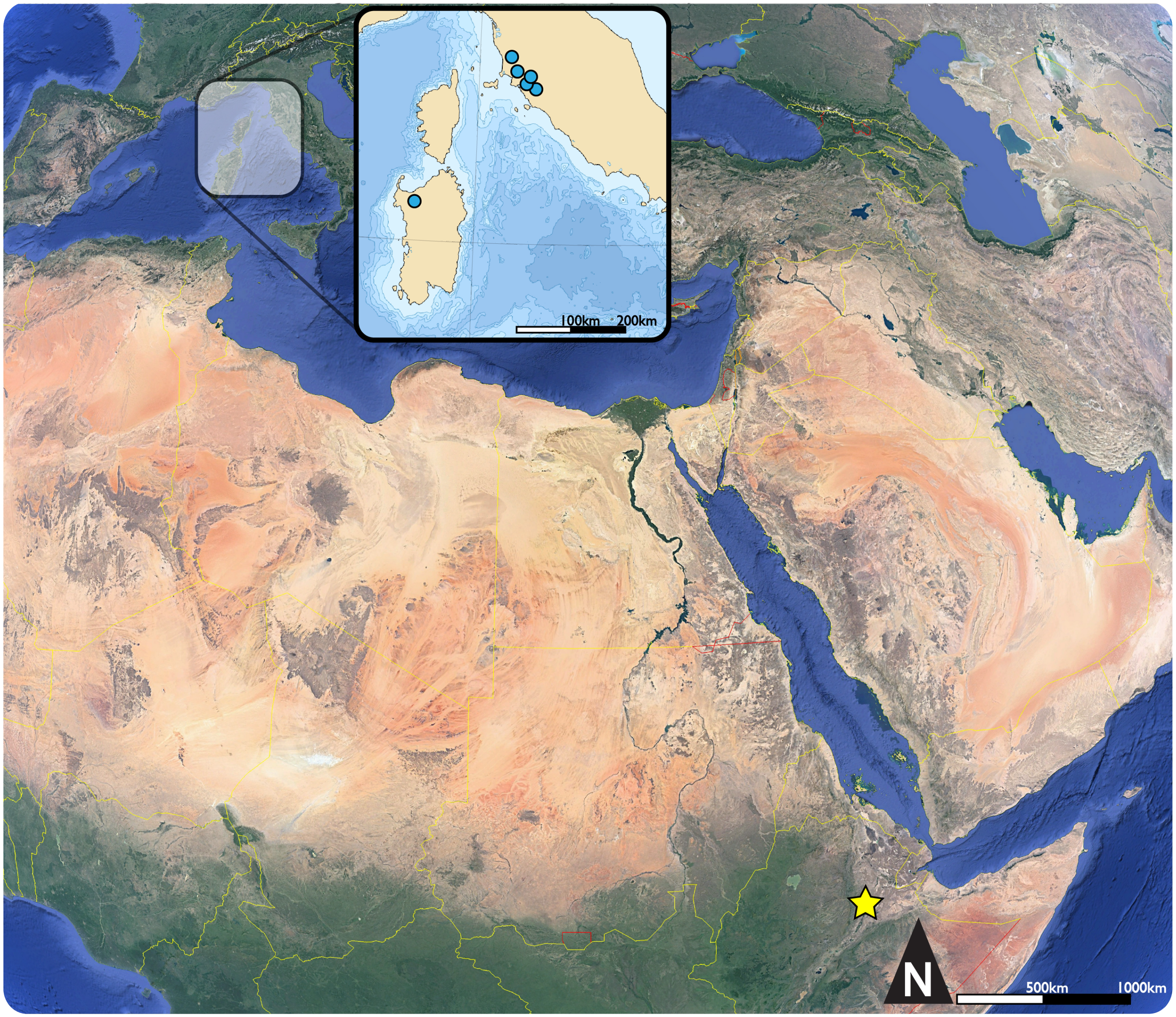

Figure 1.2 Map of Tusco-Sardinian *Oreopithecus* and Ethiopian *Ardipithecus* localities (indicated by a star symbol). Inset map illustrates the location of Oreopithecus bearing localities, indicated by blue dot symbols. Base image from Google Earth.

Chapter 2: The Hominid-like Characteristics of *Oreopithecus*

2.1 Introduction

In this chapter, I first continue to build on the rationale of the work presented in Chapter 1 by presenting explicit hypotheses to be tested. I then describe the materials and methods used in my investigation. Finally, I present a comprehensive list of *Oreopithecus* characters that have been proposed as hominid-like, hominid parallelisms (homoplasies) during the 145+ years of research concerning this extinct taxon.

2.2 Materials

This dissertation examines *Oreopithecus* anatomy by employing direct and indirect comparisons of the original fossil material for that taxon with available *Oreopithecus* fossils and casts, with *Ardipithecus* original fossils and casts, with extant hominoid skeletal remains, and casts of other Miocene hominoids. Where original fossils or casts were not available, published descriptions were utilized in their stead.

Over the 145 years since it was first discovered, ~415 *Oreopithecus* specimens have been accessioned at as many as 11 different institutions or museums and 8 private collections (Harrison 1991, Rook 1993, Rook *et al*. 1996, Carnieri and Malegni 2003, Abbazzi *et al*. 2008). More *Oreopithecus* specimens are likely to be added because there are current investigations in Grossetto Province in Tuscany and at the Sardinian locality of Fiume Santo that occasionally yield sparse new dental material (Rook 1993, Carnieri and Mallegni 2003, Abbazzi *et al*. 2008).

Because of various accession protocols over the years, *Oreopithecus* specimens carry either a museum-specific prefix (e.g. BNHM=British Natural History Museum or IGF=Instituto di Geologia di Firenze, now the Museo di Storia Naturale, Sezione di Geologia e Paleontologia dell'Università di Firenze) or a locality designation. In the latter case, BAC or BA, depending on the publication, both refer to Baccinello, FS refers to Fiume Santo, and IR refers to the formal inventory register of Fiume Santo material according to the "Inventario Regionale della Soprintendenza," (for more explication see Abbazzi *et al*. 2008). Specimens collected from the Baccinello locality have often been published with a "field number" in lieu of separate accession numbers ever since the earliest publications describing and interpreting them (Hürzeler 1958, Hürzeler 1968, Straus 1963). This practice continues today (Lovejoy and McCollum 2010, Russo and Shapiro 2013), most likely to maintain consistency across publications.

I have chosen to use the "BAC" specimen prefix and both the accession number and field number for specimens originating from the Bacinello locality. I have done this for comprehensive clarity and for future work examining these fossils when new data and/or analytic procedures become available. For example, the *Oreopithecus* specimen preserving a pubic symphysis at the midline will be referred to as BAC 71/44, where BAC refers to Bacinello, 71 is the museum accession number, and 44 is the field number. All *Oreopithecus* specimens from the six *Oreopithecus*-bearing Tusco-Sardinian localities are listed comprehensively in Appendix 1. These include as much identification, repository, and citation information as was available. Published identifications and repository locations were confirmed, updated, or corrected as needed.

2.2.1 *Oreopithecus bambolii*

Original *Oreopithecus* specimens in two collections were accessed in October 2013 in order to make direct comparisons with ~95% of the *Oreopithecus* hypodigm. The Naturhistorisches Museum of Basel, Switzerland where the bulk of the *Oreopithecus* material recovered from Baccinello is accessioned provided additional human, *Pongo*, *Gorilla*, and *Hylobates* comparative material. They also provided access to crucially important, unique first generation casts of the IGF 11778 skeleton before the lignite block containing it was sent to Florence, where the skeleton was prepared and removed from the block. I also studied original fossils at the Museo di Storia Naturale, Sezione di Geologia e Paleontologia dell'Università di Firenze, Italy (formerly the Instituto di Geologia di Firenze = IGF), where the holotype mandible (IGF 4335) and juvenile male skeleton (IGF 11778) are housed.

At both institutions, full access to the *Oreopithecus* material was afforded with the notable exception of the IGF 11778 pelvis, which was (and is presumably still) being prepared for "reconstruction" and publication by a research team from Institut Català de Paleontologia Miguel Crusafont (ICP), Sabadell, Spain working in conjunction with Professor Lorenzo Rook at the Università di Firenze. Furthermore, my request to view published radiographs of this specimen (Rook *et al*. 1999) was not honored, as they were being kept in an archive in Rome and were as such not available during my visit. A study cast was made available in the place of the missing pelvis during the stay in Florence, and a similar cast was available as part of the collection at the Human Evolution Research Center (HERC), Berkeley.

Three other published specimens were not in the Naturhistorisches Museum of Basel, Switzerland collection when I visited. These specimens, BAC 76/49, a partial os coxa and associated proximal femur, and two partial ischia, BAC 182/50 (associated with a sacrum) and BAC 208 were missing and unaccounted for at the time of my visit. These specimens are discussed in more detail in Chapter 4.

2.2.2 *Ardipithecus ramidus*

Selected highest-quality research casts of *Ardipithecus* were transported to Basel and Florence in order to make direct, relevant comparisons, and the original *Ardipithecus* fossils curated in the National Museum of Ethiopia were also examined.

2.2.3 *Homo sapiens*

Homo sapiens skeletal material documenting a range of inter- and inter-populational variation from archaeological and medical contexts were accessed at the Human Evolution Research Center (HERC) and the Phoebe Apperson Hearst Museum of Anthropology at the University of California at Berkeley.

2.2.4 Extant apes

Where appropriate, a sample of wild-shot and captive extant large-bodied ape skeletal remains and casts were studied and employed in comparisons at the Human Evolution Research Center (HERC), Berkeley. In addition, a wild-shot gorilla, orangutan, and gibbon were examined at the Naturhistorisches Museum of Basel, Switzerland.

2.2.5 Fossil apes

In addition to a sample of *Oreopithecus* casts, relevant casts of fossil apes sampling *Proconsul*, *Dryopithecus*, *Ouranopithecus*, *Sivapithecus, Gigantopithecus,* and other Miocene taxa were examined for comparative purposes at the Human Evolution Research Center (HERC), Berkeley. A cast of the *Hispanopithecus* (IPS 18800, Almècija *et al*. 2007) was examined at the Museo di Storia Naturale, Sezione di Geologia e Paleontologia dell'Università di Firenze, Italy.

2.2.6 Published descriptions

Where specimens or casts were unavailable, published descriptions of relevant comparative material were employed.

2.3 Methods

In accordance with the research questions outlined in Section 2.4, the description and investigation of hominid-like similarities outlined in Section 2.5 and treated in detail in Chapters 3-5 are explicitly comparative per the approach favored by White *et al*. (2000). For example, when investigators have claimed that the pubic symphyseal face of *Oreopithecus* is superoinferiorly short (Schultz 1960, Köhler and Moyà-Solà 1997), effort has been made to establish the comparative context. For example, in the case of whether the pubic symphyseal face of *Oreopithecus* is superoinferiorly short relative to *Ardipithecus* or *Proconsul* or *Pan*, etc. All comparisons of *Oreopithecus* anatomy were made with the original fossils with four exceptions (see the Comparative Materials section 2.2.1).

Attempts have been made to account for the considerable multi-dimensional distortion that typifies the preservation of the *Oreopithecus* fossils. Depositional distortion is well known for its ability to confound morphological interpretation and lead to erroneous taxonomic classification and phylogenetic claims (e.g., White 2003 and references therein). Most of the distortion in the *Oreopithecus* collections involves the flattening of specimens to the degree that it is doubtful that restoration via either physical means or computed tomography is possible or ethical. I describe and compare relevant specimens for cases in which bony morphology is relatively undistorted and interpretable for *Oreopithecus* specimens, and I assess distortion to the extent possible upon macroscopic and microscopic examination.

Direct, explicit comparisons of *Oreopithecus* with *Ardipithecus*, extant hominoids, or fossil hominoids were guided by the research background presented in Chapter 1 and Section 2.4 below. The considerable distortion and small sample sizes for most skeletal elements of *Oreopithecus* rendered evaluation of the claims outlined above in Section 2.5 and treated in depth in Chapters 3-5, difficult for many specimens. For example, claims about hominid similarity of pelvic anatomy in *Oreopithecus* have been made mostly on the basis of a single severely distorted, subadult specimen. For those reasons, the current dissertation must rest on investigator assessment of exactly what morphology can reliably be discerned from distorted or inaccurately restored *Oreopithecus* specimens. This severely limits assessment of the cranial and axial body parts of *Oreopithecus*. When evaluating claims made on the basis of better-preserved dental, manual, and pedal elements, I employ both qualitative (outlined above) and quantitative methods.

2.4 Research questions

This dissertation addresses claims of hominid-like characteristics in *Oreopithecus*. I employ an explicitly comparative, descriptive approach to assess each morphological claim of homoplasy (or symplesiomorphy, synapomorphy, or autapomorphy) from a qualitative standpoint, and include quantitative assessment where this was possible or relevant to the claim of hominid similarity. Such a process represents the essential, indeed axiomatic, first step in any direct comparisons among the specimens that comprise paleontological taxa (White *et al*. 2000, Lovejoy *et al*. 2002). In the course of these explicitly comparative, and largely qualitative tests of the claimed hominid-like characteristics of *Oreopithecus*, I will address the following three fundamental questions (which some may prefer to express as hypotheses):

(1) Is the claimed morphological feature present/observable, or can it be reasonably inferred on the basis of the actual fossil evidence?

The anatomy/morphological feature that is claimed to be hominid-like should be directly and reasonably observable on the specimen/group of specimens that form the basis of the claim.

Hypothesis 1: The claimed hominid-like character of *Oreopithecus* is based on morphology that can be accurately observed and/or reasonably "inferred" from the actual fossils.

(2) If the claimed morphological feature is verified as present/observable, has the feature been accurately diagnosed in hominids (*Australopithecus, Ardipithecus*, and others)?

This constitutes an explicit portion of each of the seven (7) character complexes composed of twenty-six (26) subdivided characters and six (6) other singular characters of morphological hominid similarity claimed between *Oreopithecus* and later hominids, which are summarized below in Section 2.5. After direct comparisons between *Oreopithecus* and *Ardipithecus,* and among extant and fossil apes, is the "readable" morphological feature a homolog or an analog of what has been observed on the same skeletal element among later hominids?

Hypothesis 2: The claimed hominid-like anatomical characteristics (synapomorphies, syplesiomorphies, autapomorphies, or homoplasies) of *Oreopithecus* are actually shared with their hominid counterparts.

(3) Can allegedly shared characters that remain after testing per (1) and (2) be diagnosed as symplesiomorphic (shared primitive), synapomorphic (shared derived), autapomorphic (uniquely derived) or homoplastic (evolved in parallel)?

Work on vertebrates with shorter generations and therefore shorter chronology of speciation/cladogenesis than hominoids (Shapiro *et al*. 2004, Colosimo *et al*. 2005, Miller *et al*. 2007) reveals that parallel evolution (homoplasy) is (and evidently has been) a frequent phenomenon in vertebrate evolution. A core issue is really one of scale, and the distinction between a deep homology and a homoplasy blurs. For example, what constitutes a deep homology with multiple evolutionary trait reversals in related taxa, as opposed to a convergence? Are there other reasonable explanations to the evolution of similar traits in related taxa, such as epigenetic and environmental influences acting on a genetic predisposition for evolving a particular bony trait that was once lost in a lineage but later regained in similar form? What sort of additional evidence or analytical procedure would allow a test of these hypotheses? Such considerations are more fully considered in the concluding chapter of this dissertation.

Hypothesis 3: *Oreopithecus* hominid-like characteristics truly present and shared with *Ardipithecus* are best considered to be parallel acquisitions (homoplasies per authors such as Harrison, Wood, and others, see Chapter 1 and below), as opposed to symplesiomorphies, synapomorphies, or autapomorphies.

2.5 The claimed hominid-like characteristics of *Oreopithecus*

As noted in the historical section of Chapter 1, a multitude of features, or "characters" have been invoked with which to assess the phylogenetic placement of *Oreopithecus* and *Ardipithecus.* For the former, several of these have been claimed to be true homologies, synapomorphies, or evolutionarily parallel acquisitions (homoplasies) since the early 1950s. Many of the latter have recently been employed to challenge the inference that *Ardipithecus* is a taxon in the hominid clade (Wood 2010, Sarmiento 2010, Harrison 2010, Wood and Harrison 2011).

2.5.1 Character definitions

As discussed in section 1.1.3, the long publication history of *Oreopithecus* has led to the identification of both singular characters and character complexes (involving a set of potentially interrelated characters) that have been interpreted as hominid synapomorphies, symplesiomorphies, or homoplasies by investigators of *Oreopithecus*. My consideration of both aggregated character complexes or the characters by which these have been maximally or partially parsed for parsimony-based cladistic methods is necessitated by the history of investigations into *Oreopithecus* across a period in which paleoanthropologists used both evolutionary and Hennigian systematic approaches.

The identification of character complexes by evolutionary systematists was the prevailing tool for phylogenetic inference at the time of the description and interpretation of the bulk of *Oreopithecus* fossils from Baccinello in the late 1950s. Preceding those discoveries, Le Gros Clark (1936) advocated for caution when identifying singular characters:

> *"...the systematic position of the animal can only be established by complete anatomical survey, and the systematist is liable to fall into serious error if he confines his attention to one part of the body only."* (1936, p. 4).

Le Gros Clark later called his approach the identification of the "total morphological pattern" (1950). In his defense of Broom and Robinson's interpretations of *Australopithecus* dentition he wrote:

> *"...conclusions regarding the hominid nature of the dentition must ultimately be based on the total pattern determined by all these features in a particular combination...So far as I am aware no similar combination of* all *of these*

> *hominid features together has been found in the dentition of any of the anthropoid apes."* (1950, p. 894).

It may have been such practice that led early investigators of *Oreopithecus* [such as Hürzeler (1958), Schultz (1960), and Straus (1963)] to combine character complexes as well as singular characters in to examine whether *Oreopithecus* belonged to the hominid clade.

By the time of the revival of *Oreopithecus* research in 1980s and 1990s, parsimony-based cladistic methodology had taken root in paleoanthropology. This methodology requires a more explicit parsing, weighting, and scoring of characters. Modern practitioners describing and interpreting newly discovered fossil material in a phylogenetic context must today reckon with cladistic methodology and its terminology, even if the elucidation of the biology of the fossil form is best considered in terms of functionally integrated suites of characters.

The *Ardipithecus* discovery team, for example, addressed both approaches by enumerating "the assembly of shared derived characters" in their Table 1. They concluded that whether considered individually or as complexes as characters, *Ardipithecus* was uniquely linked phylogenetically with later hominids (White *et al*. 2009a, p. 82). In their table, character complexes were listed with their nested constituent characters. This table provides foundational support for evaluation of claims of hominid homoplasy in *Oreopithecus* in this dissertation. Only *Oreopithecus* characters/complexes that have been published as hominid synapomorphies or homoplasies will be evaluated in the sense of White *et al.*'s Table 1 (2009a, p. 82).

This dissertation focuses on the key characters claimed to be homoplasies in *Oreopithecus* (see Appendix 2) in arguments regarding the placement of *Ardipithecus* as a phylogenetic hominid (in the sense of the nomenclature outlined in Chapter 1). Some of these have similarly been claimed to undermine the hominid status of *Sahelanthropus* and *Orrorin*. In the remainder of this chapter, I define each of the key characters/character complexes by examining how they have been used by historical workers ranging from evolutionary systematists to Hennegian parsimony phylogeneticists. The key characters/character complexes have been outlined and deployed in analyses authored by Aquatic Ape Hypothesis aficionados (Williams 2008) to more serious scholars. Appendix 2 outlines these character complexes (and their subdivided characters where applicable) with respect to how the previous workers have attempted to employ them in phylogenetic analysis. Subsequent chapters will assess these characters via direct comparisons among the taxa and materials outlined above.

2.5.2 Craniodental

While noting what he (and others) had interpreted as hominid dental similarities (often synapomorphies) in earlier descriptions (Hürzeler 1949, 1951, 1954; Remane 1955), Hürzeler made extensive claims for craniodental similarity between Oreopithecus and *Ardipithecus* on the basis of a series of characters listed in his preliminary report of the IGF 11778 skeleton (1958). The sample from Baccinello had greatly increased a previously largely dental sample from five known localities. Having established *Oreopithecus* as a hominoid, Hürzeler rejected earlier phylogenetic suggestions (Schwalbe 1915) of placing *Oreopithecus* in its own family, Oreopithecidae. Instead, he endeavored to align the taxon exclusively with the younger hominids *Australopithecus* and *Homo* on the basis of 9 craniodental characters that he interpreted to be features shared exclusively with Hominidae.

In the ensuing decades, many of these claimed derived characters were revealed to be catarrhine or hominoid symplesiomorphies (Szalay and Delson 1978, Harrison 1987, Harrison and Rook 1997). Three of the characters have persisted as hypothesized hominid homoplasies, and another was recently proposed as such (Wood and Harrison 2011) despite earlier cautions (Straus 1963). These four character complexes/characters are considered in detail below.

2.5.2.a. Short Face

The claim for a short face in *Oreopithecus* is based on a character complex comprising two characters culled from the literature: incisor verticality and position of the zygomatic root above the upper tooth row.

For Hürzeler, the observation of a short face logically followed from an earlier claim he made about "orthodentism," the vertical implantation of the upper and lower incisors. He had inferred this for *Oreopithecus* from incisor attrition patterns contrasted to the procumbent incisors and attendant lingual wear of extant hominoids and *Proconsul*. Additionally, he noted a relatively anterior origin of the zygomatic root, arising midway between the upper fourth premolar (UP4) and first molar (UM1), and the nearly vertical mandibular and maxillary symphyses. Hürzeler included these characters in his list of 19 characters shared with Hominidae (1968), and though he does not use the vocabulary, his phylogenetic placement of *Oreopithecus* with hominids allows the interpretation of his listed characters as synapomorphies (see Appendix 2). Based on a plaster reconstruction of the severely distorted IGF 11778 skull (See Figure 3.1A-B), he later qualified this, noting that the face was anteroposteriorly short relative to a large braincase (Hürzeler 1958, 1960), in turn suggesting a low degree of facial prognathism.

Straus assessed a cranial capacity for *Oreopithecus* consistent with what Schultz observed for orangutans and chimpanzees (Straus and Schon 1960; Schultz 1941). Straus noted that the face was "…strikingly short." (1963, p. 149). Investigators have continued to interpret the face as short based on incisor verticality and zygomatic origin position (Harrison 1987, 1991; Harrison and Rook 1997, Moyà-Solà and Köhler 1997). Harrison initially interpreted these characters as autapomorphic in his examination and evaluation of the *Oreopithecus* fossils (Harrison 1987, Harrison and Rook 1997). However, after the publication of *Ardipithecus* in 2009, he interpreted these characters as homoplasies or sympleisiomorphies (Wood and Harrison 2011, see Appendix 2). Some have deduced that the facial reduction is the result of paedomorphic neoteny (Moyà-Solà and Köhler 1997, Alba *et al.* 1999, 2001a) but such interpretations have not escaped skepticism from others (Berzi 1973, Szalay and Berzi 1973, Clarke 1997).

2.5.2.b. Reduced size and sexual dimorphism of the canines

This "character" as presented below is actually two character complexes consisting of multiple subdivided characters each. Reduced canine size relative to the postcanine dentition in hominids involves "feminization" of the male canine (White *et al.* 2009a, Suwa *et al.* 2009b). Reduced canine size thus involves the characters of upper and lower canine size relative to postcanine dentition, and the following "feminization" characters of the upper and lower canines: shoulder height, shoulder flare, lingual marginal ridge, main mesial lingual ridge, and crown height of the upper canine; and mesial shoulder height, lingual marginal ridge, distal crest, and distal tubercule of the lower canine. So, reduced canine size is a character complex involving eleven (11) characters when maximally parsed.

Reduced sexual dimorphism is similarly a character complex composed of characters that practitioners of parsimony-based cladistic methodology would treat as two: the degree of sexual dimorphism of canine size and the relative size of the female canine.

Hürzeler claimed, based on an earlier observation by Vallois (1954), that the canines of *Oreopithecus* were reduced relative to *Proconsul*. Hürzeler claimed that *Oreopithecus* exhibited less sexual dimorphism than the extant great apes and that it exhibited more sexual dimorphism than Pleistocene hominids (Hürzeler 1958, 1968). Schultz noted an unusual absence of large canines in the *Oreopithecus* sample (Schultz 1960). Straus described both upper and lower canines as relatively small (Straus 1963). Moyà-Solà and Köhler note small canines, and Alba *et al*. attribute this and low sexual dimorphism of the canines to be a consequence of paedomorphic shortening of the face from a larger faced, and presumably more dimorphic *Dryopithecus* ancestor (Moyà-Solà and Köhler 1997; Alba *et al*. 1999, 2001a, 2001b). Other investigators have disagreed; noting marked sexual dimorphism and large canines relative to postcanine teeth in *Oreopithecus* (Harrison 1987, 1991). However, Harrison has subsequently asserted that *Oreopithecus* canines were relatively small, and that this character represents a potential hominid homoplasy (Wood and Harrison 2011).

2.5.2.c. Lack of a functional UC/LP3 honing complex

As in the above "character," a functional upper canine/lower third premolar honing complex is a character complex consisting of multiple characters that have been conflated. However, in this case, most recent workers have not subdivided the complex. For this study, this character complex consists of the following characters of the upper canine and lower third premolar: the presence of a distolabial honing edge of the upper canine, a mesiobuccal honing facet on the lower third premolar, basal crown size/shape of the lower third premolar, the absence of a lower third premolar metaconid, and the absence of a mesial marginal ridge.

Hürzeler described *Oreopithecus* canines as short, and the lower third premolars as homomorphic and mesiodistally long. He observed the presence of two cusps on the latter, in a decidedly non-sectorial arrangement (Hürzeler 1954, 1958, 1960). Straus also made brief mention of this complex (Straus 1963). Harrison and Rook noted a very short mesial honing facet and a lack of enamel extension onto the mesial root on the lower third premolar, in contrast to cercopithecids. This is a character they interpret as symplesiomorphic in hominoids (Harrison and Rook 1997). Despite this, Sarmiento (2010) and Harrison and Wood (2011) have subsequently both independently claimed that *Oreopithecus* lacked an upper canine-lower third premolar honing complex (see Appendix 2). This interpretation led them to conclude that the lack of a functional UC/LP3 honing complex was unreliable as a diagnostic hominid trait due to its claimed parallel acquisition in *Oreopithecus* (Wood and Harrison 2011).

2.5.2.d. Foramen magnum

The positioning of the foramen magnum in hominoids is a complicated character involving basicranial length (Kimbel *et al*. 2014, White *et al*. 2015). In this dissertation, it is treated as a singular character for reasons owing to preservation of relevant elements (see below and Chapter 3).

Some 250 years of research (Daubenton 1764, Russo and Kirk 2017) has focused on the importance of the anterior placement of the of the foramen magnum and the length of the basicranium (Suwa *et al*. 2009a, Kimbel *et al*. 2014, White *et al*. 2015), both for the inference of locomotor repertoire in Hominidae and/or for its utility in reflecting encephalization (Biegert 1957) or the effects that neocortex size has on its placement (Ruth *et al*. 2010, 2016). With respect to *Oreopithecus*, Hürzeler never mentioned the foramen magnum and Straus noted that its position in *Oreopithecus* "…remains uncertain." (1963, p. 149). Despite this, and the considerable depositional distortion on *Oreopithecus* specimens currently available, Wood and Harrison claim an anterior placement of the foramen magnum in *Oreopithecus*, and imply that the presence of this character in *Oreopithecus* effectively invalidates foramen magnum positioning as a phylogenetically informative hominid trait in *Ardipithecus* (2011). They cite Hürzeler (1958) as the basis of this claim, though there is no mention of the foramen magnum in that report. Neither do they identify what features they used to 'position' the foramen itself. This claim was repeated recently by Nelson and Rook in a paper dealing with habitat change as a potential correlate of *Oreopithecus* extinction (2016).

2.5.3 Axial Skeleton

Whereas many past and present practitioners disagree on aspects of *Oreopithecus* cranial and canine anatomy, most agree that in addition to possessing a highly derived post-canine dentition adapted to folivory (and therefore unlike that of any other known ape), the *Oreopithecus* general *bauplan* exhibited adaptations for below-branch, suspensory locomotion. The characters used to support this interpretation include relatively elongate forearms, a great-ape like elbow, a wide thorax, and a shortened (relative to *Proconsul*) lower back (Straus 1963, Harrison 1987, Harrison and Rook 1997, Pilbeam 2004). Contemporary arguments about the anatomy of the lower back and pelvis are ongoing, and are summarized below because many of the characters are claimed hominid homoplasies.

2.5.3.a Lordotic lumbar spine consisting of 5 lumbar elements

Most practitioners treat this "character" separately, listing lumbar vertebrae count and, if fossil evidence allows, lordosis of the lumbar column. In this dissertation, these characters are considered two separate characters. Lordosis of the lumbar spinal column is improbable with less than 5 lumbar vertebrae, particularly if one or more caudal lumbar vertebrae are entrapped in the bi-iliac space. This S-shaped feature of the lower lumbar vertebral column has long been appreciated for its role in weight transmission, force absorption, and orthogonal orientation of the trunk during upright walking (Weber & Weber 1836, Virchow 1911, Straus 1929, Robinson 1972, Gracovetsky 1986, Latimer and Ward 1993, Haeusler *et al*. 2002).

Schultz (1960) noted the presence of 5 lumbar vertebrae in *Oreopithecus*, as did others (Straus 1963, Harrison 1987, 1991; Köhler and Moyà-Solà 1997, Rook *et al*. 1999, McCollum *et al*. 2009). Köhler and Moyà-Solà claimed a hominid-like pattern of vertebral wedging as "…direct evidence of lordosis…considered a uniquely hominid condition," thereby identifying it as a homoplasy (Köhler and Moyà-Solà 1997, p. 11747). Further examinations of *Oreopithecus* lumbar vertebrae have since cast doubts on both the functional and fossil evidentiary bases of that claim (McCollum and Lovejoy 2010, Russo and Shapiro 2013).

2.5.3.b Short and broad iliac blades

This morphological character complex consists of two characters, the height of the iliac isthmus and the relative breadth of the ilia themselves. Superoinferiorly short and broad ilia (both the iliac isthmus as defined in White *et al*. 2015, and the ilium itself) are thought to have developed early in hominid evolution. This appears to be part and parcel of the sagittal reorientation of the iliac blades to enhance the positioning of the anterior gluteal muscles (gluteus minimus and gluteus medius) as abductors during upright walking (Lovejoy *et al*. 1999, Lovejoy 2005, Lovejoy *et al*. 2009b, Lovejoy and McCollum 2010). This important, diagnostic morphological complex has been claimed as present on the IGF 11778 os coxa specimen (Hürzeler 1958, 1968; Straus 1963; Simons 1967; Harrison and Rook 1997; Köhler and Moyà-Solà 1997, 2003; Moyà-Solà *et al*. 1999, 2008; Rook *et al*. 1999; Wood and Harrison 2011). Interpretations of the phylogenetic significance of this character in *Oreopithecus* have varied, with some investigators interpreting it as a hominid synapomorphy (Hürzeler 1968), a hominoid symplesiomorphy (Harrison 1987, 1991; Harrison and Rook 1997), or a potential homoplasy shared with hominids (Köhler and Moyà-Solà 1997, Rook *et al*. 1999, Wood and Harrison 2011).

2.5.3.c Well-developed anterior inferior iliac spine

This character is often treated as a singular character in published character lists and parisimony-based cladistic analyses (White *et al*. 2009a, Lovejoy *et al*. 2009b). It is likewise treated as a singular character in this dissertation.

In humans, the anterior inferior iliac spine is a bony projection in the lower anterior border of the iliac blade just superior and anterior to the acetabulum. It serves as the attachment origin site of the of the rectus femorus muscle, a flexor of the thigh and an extensor of the knee, and attachment site for the iliofemoral ligament, a hip stabilizer. Its presence on a fossil os coxae is one inferential indicator of orthograde posture and bipedal locomotion.

Straus (1963) claimed its presence on the IGF 11778 os coxa specimen and several other investigators have included this as a hominid-like feature in their claims of *Oreopithecus* hominid similarity and/or interpretations of *Oreopithecus* bipedal locomotion (Kummer 1965, Köhler and Moyà-Solà 1997, Köhler and Moyà-Solà 2003, Moyà-Solà *et al*. 1999, Moyà-Solà *et al*. 2008, Rook *et al*. 1999, Wood and Harrison 2011). Phylogenetic interpretations of this character in *Oreopithecus* have either been that it represents a hominid synapomorphy (Straus 1963, Hürzeler 1968, Harrison 1987, 1991) or a hominid homoplasy (Köhler and Moyà-Solà 1997, Rook *et al*. 1999, Wood and Harrison 2011) – see Appendix 2. The claim for its presence on the *Oreopithecus* specimen and for the interpretations that have followed have been the subject of recent re-examinations (Lovejoy and McCollum 2010, Zirkle 2015).

2.5.3.d Superoinferiorly short pubic symphysis

Despite the fact that this character is likely functionally linked to overall pelvic shortening and broadening (Lovejoy *et al*. 1999, 2009b) and is therefore not a truly independent character, the superoinferior length of the pubic symphysis relative to the ilia is treated as singular character in this dissertation.

Relative to the living great apes whose elongate pelves appear to be related to *bauplan* modifications emphasizing forelimb superiority and fixation/stabilization of their lower axial skeleton in a suspensory locomotor context, *Australopithecus* and *Homo* share superoinferiorly short pubic symphyseal faces. Hürzeler asserted a short pubic symphyseal face in *Oreopithecus* and listed it as the 15th of 19 characters that he believed *Oreopithecus* shared exclusively with hominids (e.g., synapomorphies). (Hürzeler 1968). Köhler and Moyà-Solà (1997) also note the close resemblance of the *Oreopithecus* pubic symphysis to that of *Australopithecus afarensis*, but curiously claim that this resemblance of shortness was "…previously unrecognized," (1997, p. 11747) despite citing the Hürzeler (1968) paper where the claim seems to originate in the same sentence. The Spanish research group further explored this region of the pelvis in *Oreopithecus*, concluding that the ischiopubic ramus was similar to that of modern humans in showing evidence of bony crests for the attachment of perineal ligaments and musculature (Moyà-Solà *et al*. 2008). Other investigators were cautious in interpreting a short pubic symphysis in *Oreopithecus*, noting that superoinferior pubic symphyseal length varied considerably in catarrhine taxa (Harrison 1987). His interpretation was subsequently altered after the publication of *Ardipithecus* in 2009 to be a homoplastically acquired character in *Oreopithecus* and Hominidae.

2.5.3.e Large ischial spine

The relative size of the ischial spine is treated as a singular character in this dissertation. The ischial spine serves as the attachment site for the sacrospinous ligament. Its function is to prevent rotation of the ilium during bipedal walking. Straus (1963) was the first to claim that the presence of a large ischial spine in *Oreopithecus* was similar to the hominid condition. This claim has been repeated and/or examined may times and has generally been interpreted as a hominid homoplasy in *Oreopithecus* (Simons 1967; Köhler and Moyà-Solà 1999, 2003; Moyà-Solà *et al*. 1999, 2008; Rook *et al*. 1999; Wood and Harrison 2011).

2.5.4 Appendicular Skeleton

Due to their greater robusticity, many postcranial appendicular skeletal elements of *Oreopithecus* – particularly those of the hand and foot – have largely escaped the extreme depositional crushing that obscures and alters morphology in cranial and axial elements of *Oreopithecus*. These elements received little attention in the earliest phases of description and interpretation of *Oreopithecus*, and it was not until the 1980s and early 1990s that they received more detailed study (Susman 1985, Harrison 1987, Harrison 1991, Szalay and Langdon 1987, Sarmiento 1987). The late 1990s saw further examinations of *Oreopithecus* hand and foot fossil recovered from Baccinello by the research team charged with their preparation (Köhler and Moyà-Solà 1997, Moyà-Solà *et al*. 1999), and by those critical of that work (Susman 2004, 2005). Several of these appendicular elements feature characters that have been claimed to be homoplastic with analogous ones in later hominid fossils.

2.5.4.a Hand: Human-like precision grip

This character complex involves several constituent characters that parsimony-based cladistic analyses have parsed as separate characters. A human-like precision grip is therefore parsed into the following characters for this dissertation, per the published literature: a long thumb relative to the other fingers, a short overall "hand length" relative to extant great apes, a mobile capitate-third metacarpal articulation, and a distinct deep pit on the terminal pollical phalanx for insertion of the flexor pollicis longus.

In an effort to highlight the claimed hominid-like features of the *Oreopithecus* skeleton, Moyà-Solà *et al*. (1999) argued that *Oreopithecus* was capable of a human, rather than ape-like, "precision grip." Based on comparisons with the hands of *Hispanopithecus*, *Australopithecus, Homo, Papio, Theropithecus*, *Proconsul*, and *Pan*, these researchers note the allometrically small hand proportions of *Oreopithecus*. They further note that its ray 1/ray 2 proportions and long first proximal phalanges are broadly comparable to both hominids and extant baboons. They also note deep (deeper than any other hominoid except hominids) pits on all *Oreopithecus* ray 1 distal phalanges (n=5) for the insertion of the flexor pollicis longus muscle, contending that this allows "precision pinching" as in hominids (Moyà-Solà *et al*. 1999:313, Almécija *et al*. 2014). Finally, these researchers note an *Oreopithecus* capitate/metacarpal 2 articulation that demonstrates hominid-like transverse orientation. They claim both features as "convergences" (technically, parallelisms; see Chapter 1 definitions) with hominids that, along with claimed bipedalism, are alleged to have developed in a similar selective context (Moyà-Solà *et al*. 1999). Susman (2004, 2005) offered a comprehensive assessment of these claims on methodological grounds, claiming faulty *a priori* assumptions in the Moyà-Solà *et al*. (1999) paper regarding thumb length and incorrect identification of hand elements, criticism that has been echoed elsewhere (Nakatsukasa *et* al. 2016). The argument about the correct identification of the pollical phalanx and therefore the validity of the claim of a long thumb length in *Oreopithecus* is further complicated by observations made recently that Miocene apes appeared to have generally longer thumbs than their extant counterparts (Almécija *et al*. 2012*)*.

2.5.4.b Foot: A grasping organ deployed in bipedal locomotion

Straus (1963) offered a cursory report on a few pedal elements from Baccinello, but Szalay and Langdon (1988) offered the first extensive treatment of the *Oreopithecus* foot, based on fossils extracted from a lignite block containing left and right elements of what they presumed to be the same animal (BAC 83/36 and BAC 79/37). They concluded that the foot was convergent (again technically, parallelisms; see Chapter 1 definitions) on foot function in extant apes, but morphologically dissimilar to great apes in some aspects. The differences they identifed involve tarsal proportions and directionality of the calcaneal lever arm, and are largely in agreement with subsequent observations made by Sarmiento (1987) and Szalay and Langdon (1988).

Other authors have claimed that Oreopithecus shared pedal features with extant and extinct apes, such as increased grasping ability with a fully abducted hallux, a short, mobile tarsus, and moderately long and curved pedal phalanges (Harrison 1991, Harrison and Rook, 1997).

No investigators have explicitly itemized the *Oreopithecus* pedal characters that they interpret as derived and shared (synapomorphies) or acquired in parallel (homoplasies) with hominids. Köhler and Moyà-Solà present a different interpretation of the *Oreopithecus* foot, claiming a foot that is ill-suited for vertical climbing and more suited for bipedal posture and (slow) locomotion. They characterize the *Oreopithecus* foot as having proportions relative to body mass that approximate that seen in *Homo*. However, they interpret these proportions and overall morphological pattern as autapomorphic. They maintain that the *Oreopithecus* foot functioned as "…an especially well-designed platform for stable postural harvesting, as the tripod formed by the deviated metatarsals and the widely-abducted hallux provides a large area of support…" (1997, p. 11750). This dissertation will examine and evaluate the *Oreopithecus* foot as interpreted by Köhler and Moyà-Solà (1997) in comparison with *Ardipithecus*, fossil apes, and extant apes.

In this chapter, I have presented the comparative materials and outlined the methodology employed in successive chapters. Furthermore, I have presented the goals and research questions that drive the methods presented here and the analysis that follows in Chapters 3-5. I have also considered the definition of characters and provided the analytical rationale for why I will consider both character complexes, and the single characters that they have been subdivided into within the published literature. Finally, I have introduced these by anatomical zone, in keeping with the organization of the three chapters to follow. In Chapter 3, I will present the evidence for claims of *Oreopithecus* craniodental hominid synapomorphies and homoplasies and evaluate those claims in comparison with *Ardipithecus* as well as other living and fossil apes.

Chapter 3: Claimed Craniodental Hominid-like Characteristics of *Oreopithecus*

3.0 Introduction

Most attention has been paid to the postcranial remains of *Oreopithecus* in recent decades and today most investigators interpret its craniodental anatomy as derived or autapomorphic in response to an insular environment (Harrison 1987, 1991; Harrison and Rook 1997, Köhler and Moyà-Solà 1997, Rook *et al*. 1999, Alba *et al*. 2001a, 2001b). However, four key potential hominid craniodental features interpreted as synapomorphies or homoplasies between *Oreopithecus* and later hominids have persisted. This chapter includes an examination and evaluation of each of the claimed hominid-like character complexes, their consitituent characters, or singular characters of *Oreopithecus* craniodental anatomy summarized in Chapter 2 (Sections 2.5.2.a-d) in a comparative context. Appendix 2 provides a summary of the literature on each of these.

3.1 Short face

As noted in Chapter 2, the first of the four craniodental characters claimed as hominid synapomorphies or homoplasies in *Oreopithecus* is the comparatively short face. This is treated as a "character" in the published literature, but is actually a character complex that I have parsed into two characters for the purpose of the comparative analysis that follows. These characters are the vertical implantation of the incisors in the maxilla and mandible, and the position of the zygomatic root above the maxillary tooth row.

Because of the depositional context of compressed lignite forming each of the *Oreopithecus*-bearing layers of the 6 Maremma and Sardinian localities, *Oreopithecus* fossils suffer from varying degrees of severe distortion and/or absolute crushing (along either anteroposterior, superoinferior, oblique, or a combination of axes). Much, if not all, of the relevant cranial anatomy has been altered by such forces. The majority of the earliest reconstructions were illustrations based on a plaster cast that was based on comparisons with extant hominoids and large cercopithecids (Hürzeler 1958, Straus 1963). These illustrations were often either uncritically reprinted or slightly altered in subsequent publications (Simons 1960, Pilbeam 1972). These illustrated reconstructions were in turn sometimes subsequently more extensively altered to suit an alternative view on some aspect of cranial anatomy (e.g., disagreements about the angle of the nuchal plane, see Szalay and Berzi 1973).

For decades (and indeed even today) *Oreopithecus* was the best-known Miocene hominoid from this period (~8Ma) and at least dentally, it is highly derived relative to any other known hominoid. Potential sister or immediate ancestor taxa were relatively unknown, or known only from craniodental or mandibular material lacking associated postcrania with which to establish a phylogenetic relationship with *Oreopithecus*.

As the Miocene hominoid fossil record improved during the 1990s and 2000s, cranial restorations based on potentially relevant European Miocene taxa became possible. Harrison and Rook offered an illustrated reconstruction, presumably based on a more robust Miocene fossil record, though they neither explicitly detail which *Oreopithecus* specimens were used, nor the comparative taxa they employed to generate their illustration (Harrison and Rook 1997). Moyà-Solà and Köhler and Alba *et al*. offered a reconstruction based on their comparative work with *Dryopithecus* (*Hispanopithecus*, on which this research group is still currently working) (Moyà-

Solà and Köhler 1997, Alba *et al*. 2001). The *Oreopithecus* specimens they employed include the specimens listed in below in addition to four others that were unavailable in Basel or Florence.

Clarke subsequently offered a reconstruction using the original fossil based on his experience with taxa including *Pongo*, sub-fossil lemurs, and *Paranthropus* (Clarke 1997). Clarke and the Spanish research group reject each other's reconstruction, with Alba *et al*. dismissing the Clarke reconstruction on the basis of its longer length than the fossil (IGF 11778), and Clarke rejecting the Moyà-Solà and Köhler reconstruction because the face was too short (Clarke 1997, Alba *et al*. 2001a; Figure 3.2B). Rather than discussing the relative merits of restoration and reconstruction from such a pancaked specimen, I will focus on the anatomy preserved on actual fossils.

Available *Oreopithecus* specimens that bear on the evaluation of the characters outlined above (that constitute the claim for a short face) include the cranium IGF 11778 (Figure 3.1 and 3.2) and the partial crania BAC 60 (43), BAC 61 (119), and BAC 101 (60).

3.1.1 Vertically implanted upper and lower incisors

The published claims for a short face in *Oreopithecus* include the character of vertically implanted incisors. Hürzeler observed that *Oreopithecus* incisors were very nearly vertically implanted (Hürzeler 1958). Harrison and Rook noted that the upper incisors were slightly procumbent in an abbreviated premaxilla and the lower incisors were nearly vertically implanted (Harrison and Rook 1997). Clarke described the incisors as retracted, in line with the canines, where the opposite is expected based on the relative size of the canines (Clarke 1997). My observations confirm the above observations. The maxillary incisors are very slightly procumbent in male *Oreopithecus* specimens and nearly vertical in female specimens. The mandibular incisors of the male specimen IGF 11778 specimen are nearly vertically implanted. In modern apes, incisor verticality increases with age and wear, and can become pronounced in elderly individuals, but in *Oreopithecus*, incisor verticality is present in both young and old individuals.

3.1.1.1 Comparison with *Ardipithecus*

A female *Ardipithecus* maxilla (ARA-VP-6/500-115) and the upper and lower dentition of another, male individual (ARA-VP-1/300) are difficult to judge with respect to verticality of incisor implantation in the distorted maxilla and isolated dental sets. Mandibular specimen ARA-VP-1/401 has an intact incisor row. From what can be discerned, maxillary implantation is similar to *Oreopithecus*, and a comparison between the single known *Ardipithecus* individual in which mandibular incisor implantation is best observed shows incisors that are nearly vertical relative to the best *Oreopithecus* specimen, IGF 11778.

3.1.1.2 Comparison with fossil and modern hominoids

In *Pan* and *Gorilla*, incisors are generally procumbent, projecting anteriorly. This likely reflects dietary adaptations (*Pan* is largely frugivorous) combined with large, tusk-like male canines. In *Ouranopithecus*, upper and lower incisors are slightly procumbent and positioned somewhat anteriorly to the canines. In *Gigantopithecus*, lower incisors are more vertical and in line with the canines. On the basis of these comparisons, the vertical implantation of upper and lower incisors is a potential hominid homoplasy in *Oreopithecus*. A fuller discussion follows at the end of section 1 and in the concluding section of this chapter.

3.1.2 Position of the zygomatic root

The published claims for a short face in Oreopithecus include the relatively anterior position of the origin of the zygomatic root relative to the position along the maxillary tooth row. Hürzeler noted the position of the zygomatic root as occurring midway between the upper fourth premolar and upper first molar. Hürzeler – in accord with Dart's characterization of *Australopithecus* (1925) and Gregory's observation (1951) – recognized the relatively progressive reduction of lower facial prognathism as a trend in hominid evolution, and, interpreting the lower face of *Oreopithecus* to be weakly prognathic, he aligned the taxon with Hominidae (Dart 1925, Gregory 1951, Hürzeler 1968).

Harrison confirmed Hürzeler's observations in a broader comparative study of 23 extant primate groups (Hürzeler 1958, Harrison 1987). Moyà-Solà and Köhler positioned the zygomatic root above the fourth premolar whereas Clarke placed it at the rear of the first molar (Moyà-Solà and Köhler 1997, Clarke 1997). In their study of two specimens preserving zygomatic and maxillary morphology, Alba *et al*. placed the zygomatic root above the distal portion of the upper fourth premolar in one specimen (BAC 61/119, interpreted as female) and above the anterior/mesial portion of the upper first molar in the other specimen (the male 11778 specimen) (Alba *et al*. 2001a).

None of the above investigators define how they identify the position of the zygomatic root. Based on the data and observations of the above investigators, the position of the zygomatic root is the bony region of the maxilla immediately inferior to and including the zygomatic process of the maxilla, in which in some hominids form a "notch" in the sense of Weidenreich's "incisura malaris," Sergi's "incurvatio inframalaris frontalis," or Tobias' "inframalar incurvation" (Weidenreich 1943, Sergi 1947, Tobias 1967). Hylander noted infraspecific variation in the position of this feature in *Homo sapiens*, which he called "the anterior root of the zygoma" (Hylander 1977). Others have noted interspecific variation of this feature in multiple hominid taxa (Pope 1991).

Even with the above definitions, the determination of where to place the origin of a line on continuous bone surface drawn perpendicular to the tooth row is difficult. Standardization of this observation is lacking in the published literature and issues involving orientation of specimens lead to different observations.

Nevertheless, my observations find that the zygomatic root in *Oreopithecus* occurs above the distal upper fourth premolar in BAC 61/119 and IGF 11778 (see Figure 3.3).

3.1.2.1 Comparison with *Ardipithecus*

The zygomatic zoot occurs in an *Ardipithecus* maxilla (ARA-VP-6/500-115) above the upper first molar, more posterior than *Australopithecus* but less posterior than *Pan* or male *Gorilla* (Suwa *et al*. 2009b). This is comparable to the placement of the zygomatic root in *Oreopithecus*.

3.1.2.2 Comparison with fossil and modern hominoids

In *Pan* and *Gorilla*, the position of the zygomatic root is highly variable, occurring anywhere from above the middle of the first upper molar to the anterior portion of the third upper molar. However, in both taxa the highest frequency of zygomatic root position is above the anterior/mesial portion of the second upper molar (Harrison 1987). In European fossil hominoid genera *Pierolapithecus*, *Ouranopithecus,* and *Dryopithecus* the zygomatic root occurs above the distal portion of the upper first upper molar or between the first and second upper molars. A comparison of the position of the zygomatic root in *Oreopithecus*, *Dryopithecus*, *Pan*, *Gorilla*, and *Ardipithecus* is presented in Figure 3.3.

3.1.3 Discussion and summary

The evaluation of the character complex "short face" in *Oreopithecus* and the two characters that comprise this character complex is hindered by small to inadequate sample sizes and considerable postmortem distortion. Harrison explains the position of the zygomatic root and attendant reduced lower facial prognathism in the context of a postcanine dentition derived for extreme folivory. He interprets the overall short face as autapomorphic (Harrison 1987, 1991), in contrast to his earlier speculation as to the phylogenetic interpretation of this character complex when he wrote:

> *"Vogel (1966, 1968) and Delson and Andrews (1975) have argued that the relatively short face in the recent colobines and and gibbons may represent the primitive catarrhine pattern. This suggestion is certainly supported by the comparative data, although there is some indication that the primitive catarrhine facial morphotype is relatively undifferentiated from the primitive anthropoid condition. The relatively short face in the small-bodied apes, as demonstrated by the relative position of the orbits, conforms to this inferred primitive catarrhine facial pattern. The relatively longer faces in the large East African fossil apes, assigned to* Proconsul*, may represent a derived condition, as in the long-faced cercopithecines and the Great Apes. However, as the relative length of the face appears to be positively correlated with body size (Vogel, 1968), the development of longer faces in large primates may have occurred independently in a number of anthropoind groups, possibly in response ro allometric effects." (Harrison 1982, p. 252).*

Harrison has subsequently revised his interpretation of the short face in *Oreopithecus* to be homoplastic or symplesiomorphic after the publication of *Ardipithecus* in 2009 (Wood and Harrison 2011, see Appendix 2).

Based on the available evidence, the position of the zygomatic root in *Oreopithecus* is similar to *Ardipithecus*, and is placed even more anteriorly. However, the extensive interspecific and infraspecific variation in this feature in the extant great apes reveals a flaw in the utility of this character in interpreting phylogenetic signal. Whereas *Pan* has a more posteriorly placed zygomatic root, some female gorillas have an anteriorly placed one, analogous to *Oreopithecus* and *Ardipithecus* (see Figure 3.3). For now, the most parsimonious interpretation of an anteriorly placed zygomatic root in *Oreopithecus* and hominids is that this character is a symplesiomorphy.

More fossil evidence from *Oreopithecus*, its yet to be recovered ancestor, and other outgrop taxa will be needed to further test this hypothesis.

Despite the possibility of symplesiomorphy, Alba *et al*. describe the reduced lower facial prognathism in *Oreopithecus* in terms of paedomorphic shifts (probably neoteny) in an insular context from a hypothesized *Dryopithecus* ancestor who was presumably more prognathic (2001a). In the limited sample for which implantation of incisors and zygomatic root positioning are observable, the *Oreopithecus* incisors are nearly vertically implanted and the position of the zygomatic root falls within the range of variation observed for *Ardipithecus*. Given the presently available evidence, the anterior zygomatic root in *Oreopithecus* is a likely symplesiomorphy while vertical implantation of incisors remains as a likely hominid homoplasy (see Table 3.3).

3.2 Reduced size and sexual dimorphism of the canines

As noted in Chapter 2, the second of the four craniodental characters claimed as hominid synapomorphies or homoplasies in *Oreopithecus* is relatively reduced canine size and dimorphism. Hominids have reduced canines relative to their postcanine dentition, a trend apparently beginning in the Late Miocene with *Ardipithecus* and progressing to the incisiform canines evident in modern *Homo sapiens*. In addition, the degree of sexual dimorphism evident in this tooth has also reduced within the hominid clade relative to other primates, which has led to many inferences about reduced social aggression in Hominidae (Lovejoy 1981, 2009; Plavcan *et al*. 1995, Plavcan 2001). The interpretation of the phylogenetic significance of this character/character complex in *Oreopithecus* has varied. When observing *Oreopithecus* dental remains, Hürzeler concluded that canine size in *Oreopithecus* was reduced relative to modern apes and interpreted this character as synapomorphic with Hominidae (Hürzeler 1958, 1968). Early investigators generally agreed (Schultz 1960, Straus 1963), whereas Harrison observed sexual dimorphism and large canines relative to postcanine teeth:

> *"There appears to be no metrical or morphological basis for Hürzeler's earlier conclusion that the canines of Oreopithecus foreshadow the development of the reduced, incisiform and slightly sexually dimorphic canines characteristic of hominids."* (Harrison 1987, p. 568)

Later investigators, however (including Harrison himself), have interpreted reduced canine size and sexual dimorphism in *Oreopithecus* as a hominid homoplasy (Moyà-Solà and Köhler 1997, Alba *et al*. 2001b, Wood and Harrison 2011).

Reduced canine size and sexual dimorphism are often treated as a "character" in the published literature, but these are actually two character complexes that I have subdivided into multiple characters each for the purpose of the comparative analysis that follows. Reduced canine size relative to the postcanine dentition in hominids involves "feminization" of the male canine shape (with height and other components; White *et al*. 2009a, Suwa *et al*. 2009b) as well as reduction in basal diameters. Reduced canine size thus involves the characters of upper and lower canine size relative to the postcanine dentition. The following are "feminization" characters of the upper and lower canines: shoulder height, shoulder flare, lingual marginal ridge, main mesial lingual ridge, and crown height of the upper canine and mesial shoulder height, lingual marginal ridge, distal crest, and distal tubercule of the lower canine. Therefore, reduced canine size is a character complex involving at least eleven (11) atomized characters beyond the simple size dimensions that are also related.

Reduced canine sexual dimorphism is a character complex composed of characters that practitioners of cladistic methodology might also subdivide: the degree of sexual dimorphism of canine size, and the relative size of the male and female canines.

Available *Oreopithecus* specimens bearing on this question are listed in Table 3.1 below. Canine crown maximum oblique basal (buccolingual) diameter and crown height were measured according to methodology outlined in Suwa *et al*. 2009b (see also White 1977, Johanson *et al*. 1982c, and Suwa 1990). Crown height measurements were taken from labial cervix to the extent of the cusp on the relatively little-worn specimens listed below. Per this method, caution was taken when correcting for wear only when labial and lingual surface wear profiles were present. Measurements were taken with Mitutoyo digital calipers. Raw measurements of the same *Oreopithecus* specimens used in the *Ardipithecus* analysis (Suwa *et al*. 2009b) were duplicated via the same methods, with inter-observer error at less than ~0.2mm. These measurements are presented in Table 3.1 below.

Table 3.1 *Oreopithecus* canine measurements by sex.

Male	UCMXOB	UCPP	UCHT	UM1MD	UM1BL	LCMXOB	LCPP	LCHT	LM1MD	LM1BL
BAC 60/43	9.32	7.99	15.49	8.25	7.98	–	–	–	–	–
BAC 64	8.50	7.41	16.1	8.58	8.24	–	–	–	–	–
BAC 94/95	9.55	8.30	X	–	–	–	–	–	–	–
IGF 11778	9.96	8.28	16.02	9.29	8.35	9.68	7.23	14.00	9.50	7.75
Female	UCMXOB	UCPP	UCHT	UM1MD	UM1BL	LCMXOB	LCPP	LCHT	LM1MD	LM1BL
BAC 61	7.00	6.15	X	7.68	7.85	–	–	–	–	–
BAC 66	–	–	–	–	–	6.95	5.10	X	8.70	7.65
BAC 92	7.60	6.45	10.15	–	–	–	–	–	–	–
BAC 111	–	–	–	–	–	6.82	5.10	10.00	–	–

Measurements in millimeters. X=broken or worn; – =not present. UCMXOB= upper canine maximum oblique diameter (~buccolingual breadth); UCPP=upper canine maximum diameter perpendicular to UCMXOB; UCHT=Upper canine height; LCMXOB= upper canine maximum oblique diameter (~buccolingual breadth); LCPP=upper canine maximum diameter perpendicular to LCMXOB; LCHT=Upper canine height; UM1MD=upper first molar mesiodistal length; UM1BL=upper first molar buccolingual breadth; LM1MD=lower first molar mesiodistal length; LM1BL=lower first molar buccolingual breadth. Data from personal observations.

3.2.1 Reduced canine size characters

The eleven subdivided characters that compose the reduced canine size character complex are summarized in Table 3.2, modified from White *et al*. (2009a:82) to include *Oreopithecus* observations. *Oreopithecus* and *Pan* character observations are novel to this study; *Ardipithecus* observations are from White *et al*. (2009).

Table 3.2 Reduced canine size characters.

Dental character	***O. bambolii***	***Pan troglodytes***	***Pan paniscus***	***Ar. ramidus***
Upper canine relative to upper first molar (UC basal diameter divided by UM1mesiodistal length)	small	large	moderate	small
Upper canine shape feminization	males unfeminized, higher crowned,	males unfeminized, higher crowned,	males unfeminized, higher crowned,	male C feminized in shape

	lower shoulder	lower shoulder	lower shoulder	
shoulder height	low	low	mid to low	mid to high
shoulder flare	weak	weak	weak	distinct flare
lingual marginal ridge	weak	weak	weak	fold-like
main mesial lingual ridge	moderate	secondarily weak	secondarily weak	basally broad
crown height	males tall, females moderate	overlap between sexes, males generally taller	overlap between sexes, males generally taller	UC height differentially reduced
Lower canine relative to lower first molar (LC basal diameter divided by LM1mesiodistal length)	small	large	moderate	small
Lower canine shape feminization	males higher crowned, modally low mesial shoulder, weak/no distal tubercle	males higher crowned, modally low mesial shoulder, weak/no distal tubercle	males higher crowned, modally low mesial shoulder, weak/no distal tubercle	feminized
mesial shoulder height	intermediate	intermediate	intermediate	intermediate?
lingual marginal ridge	weak or none	weak or none	weak or none	fold-like
distal crest	weak	weak or none	weak or none	weak
distal tubercle	weak	weak	weak	developed

C=canine, U=Upper, L=lower, M1=first molar. Observations for *Oreopithecus* and both *Pan* species from personal observations. *Ardipithecus* observations from White *et al*. 2009a.

Oreopithecus specimens showed reduction of the upper and lower canines relative to the first molars in the respective maxillary and mandibular tooth rows. *Oreopithecus* male upper and lower canine shape, however, was not feminized.

3.2.1.1 Comparison with *Ardipithecus*

Ardipithecus male upper and lower canine shape is feminized, with higher shoulders and generally lower relative crown heights. *Ardipithecus* also showed differential upper canine crown height reduction relative to their lower canine crown heights, a condition exclusively shared with hominids. By contrast, in *Oreopithecus*, male upper canine crown heights were larger (taller) than their lower canine crown heights, as with other non-hominid anthropoids.

3.2.1.2 Comparison with fossil and modern hominoids

Extant *Pan paniscus* shows reduced canines relative to their *Pan troglodytes* counterparts, though reduction is not to the extent seen in *Oreopithecus* specimens. Alba *et al*. also that *Oreopithecus* exhibited reduced canines relative to their upper first molar when compared to extant hominoids (except *Hylobates*) and especially when compared to *Dryopithecus*, a Middle Miocene hominoid that the authors speculate represents a candidate ancestor for *Oreopithecus* (Alba *et al*. 2001b). Based on the limited sample available, relative canine size appears reduced in *Oreopithecus* relative to extant and fossil hominoids, though not to the degree seen in *Ardipithecus*.

3.2.2 Reduced canine sexual dimorphism characters

As with reduced relative canine size, reduced canine sexual dimorphism is a character complex composed of characters that a practitioner of parsimony-based cladistic methodology might consider separately: the degree of sexual dimorphism of canine size, and female to male relative canine size. Canine dimorphism in *Oreopithecus* is apparent; male canines are absolutely and relatively larger than their female counterparts (the semi-circularity of this argument relative to sex identification of individual specimens is patent and recognized by the author, but the size and shapes of male individuals are almost always diagnosable for unworn and little worn crowns).

Alba *et al*. (2001b) measured relative canine area (product of mesiodistal and buccolingual basal lengths), canine height (maximum crown height on buccal aspect, correcting for wear), and upper first molar area (product of mesiodistal and buccolingual diameters) on 8 *Oreopithecus* and 9 *Dryopithecus* specimens, comparing these with published data for a broad sample of extant hominoids, fossil hominids, and modern humans. After using previously published body mass estimates (Jungers 1987, Smith and Jungers 1997) as a reference variable for allometrically corrected regressions comparing relative canine size to molar area, they reported that *Oreopithecus* was less sexually dimorphic than expected for a hominoid of its estimated body mass, on the order of *Pan paniscus* and *Australopithecus*, but more sexually dimorphic in the canine than modern humans and *Hylobates*.

3.2.2.1 Comparison with *Ardipithecus* specimens

In comparison with *Ardipithecus*, *Oreopithecus* female upper and lower crown heights are short relative to basal crown diameter and its postcanine teeth. However, the difference in male *Oreopithecus* male upper and lower crown heights relative to basal crown diameter and postcanine dentition in comparison to female *Oreopithecus* upper and lower crown heights relative to basal crown diameter and postcanine dentition is much greater than that seen in *Ardipithecus.*

3.2.2.2 Comparison with fossil and modern hominoids

While clearly sexually dimorphic in canine size, the degree of *Oreopithecus* canine sexual dimorphism is exceeded by all extant great apes besides *Pan paniscus.* Among fossil apes, the degree of canine sexual dimorphism in *Oreopithecus* is broadly comparable to that of *Ouranopithecus* and *Gigantopithecus*, two taxa whose canine size and degree of sexual dimorphism are interpreted to be reduced relative to their inferred large body masses.

3.2.3 Discussion and summary

The character complexes of reduced relative canine size and reduced canine sexual dimorphism in *Oreopithecus* have been evaluated quantitatively with regard to *Oreopithecus* on two published occasions. In addition to the Alba *et al*. (2001b) conclusions outlined above, Suwa *et al*. (2009b) calculated relative canine size for extant apes by dividing maximum canine diameter by first molar length in order to allow comparisons between *Ardipithecus*, *Australopithecus*, extant hominoids, *Oreopithecus*, *Gigantopithecus*, and *Ouranopithecus* (Alba *et al*. 2001b, Suwa *et al*. 2009b). They concluded that *Ardipithecus* and the fossil ape taxa all exhibit relatively small canines, and that the fossil ape taxa likely demonstrate parallel acquisitions of enlarged male canines. They also note that in two of the Miocene taxa, *Oreopithecus* and *Gigantopithecus*, female upper canine morphology is broadly comparable with hominid variation, though sexual dimorphism in canine size and morphology in these taxa is apparent.

Reduced canine size has apparently independently occurred in multiple anthropoid lineages among hominoids (*Oreopithecus*, *Gigantopithecus*, *Ouranopithecus, Pan paniscus, and* Hominidae*)*. At least two evolutionary explanations have been offered for apparent *Oreopithecus* canine reduction: diet and chewing (Harrison 1987, Hylander 2013) and paedomorphic neoteny and associated microdontia in an insular environment (Moyà-Solà and Köhler 1997; Alba *et al*. 1999, 2001a, 2001b). The hominid condition of reduced size and sexual dimorphism of canines is strongly linked with a scenario that asserts that canine size and sexual dimorphism were reduced as a result of reduced male-male agonism (Lovejoy 1981, 2009; Plavcan *et al*. 1995).

A greater fossil sample of *Oreopithecus*, *Dryopithecus,* and fossil sister taxa (*Pierolapithecus*, *Hispanopithecus*, *Ouranopithecus,* and *Rudapithecus)* contiguous dental material (that is, complete or nearly complete maxillary or mandibular tooth rows) will help to further test this potential homoplasy in *Oreopithecus*. At present, the available evidence indicates that *Oreopithecus* indeed exhibited relatively reduced canine size for its inferred body mass and some reduction of sexual dimorphism of the canine, with neither approaching the degree of reduction seen in Hominidae. However, as *Suwa et al*. note, the first molars of *Oreopithecus* are mesiodistally elongate relative to extant great apes, a likely consequence of folivory (Suwa *et al*. 2009b). This means that the ratio of canine basal diameter to mesiodistal length of the first molar may reflect small canines in a misleading way because canine height is not considered in this ratio. And as a cautionary note, it is already apparent by the principles of parsimony that in several ape species lineages the male canine may well have increased, rather than reduced in size, and a lineage-by-lineage assessment will be required to further understand the evolution of canine size and dimorphism among the hominoids. It is evident, however, that in terms of the honing function, lineages that reduced/increased male canine size fairly uniformly conserved the honing function, a topic of the next section.

3.3 Lack of a honing UC/LP3 honing complex

As noted in Chapter 2, the third of the four craniodental characters claimed as hominid synapomorphies or homoplasies in *Oreopithecus* is the alleged lack of a honing upper canine (UC)/lower third molar (LP3) complex (that is, that sharpening of the distolabial upper canine against the mesiobuccal face of the lower third premolar). As with the craniodental characteristics discussed previously in this chapter, a honing UC/LP3 complex is not a singular character as it is usually presented in the published literature. Rather, it is also a character complex comprising at least six (6) parsible characters I assess in the comparative analysis below. These characters are the presence of a distolabial sharpened edge of the worn upper canine, a mesiobuccal honing facet on the lower third premolar, basal crown size/shape of the lower third premolar, the absence of a lower third premolar metaconid, and the absence of a mesial marginal ridge.

Hürzeler remarked that *Oreopithecus* lower third premolars were not sectorial, were bicuspid, and homomorphic (same shape) with the lower fourth premolar (Hürzeler 1958, 1968).

Sarmiento (2010) and Wood and Harrison (2011) explicitly assert that this taxon, like hominids (and specifically *Ardipithecus*), lacked a honing upper canine/lower third molar complex (Sarmiento 2010, Wood and Harrison 2011). Curiously, the latter citation is in contrast to Harrison's earlier work with *Oreopithecus,* in which he asserted that the *reduction* of the upper canine lower third premolar honing complex relative to extant apes was sympleisomorphic for all hominoids (Harrison 1987, see Appendix 2).

Available *Oreopithecus* specimens that bear on this claim are a partial left maxilla preserving the left tooth row minus the first incisor (BAC 60/43) and the skull from the IGF 11778 skeleton, which preserves partial left and right maxillae, and partial left and right mandibles.

3.3.1 Honing UC/LP3 complex characters

The *Oreopithecus* male specimens demonstrate distinct distolingual honing on the upper canine and a clear mesiobuccal honing facet on the lower third premolar. These are pictured in Figure 3.4A. In addition, the lower third premolar has an obliquely elongate basal crown shape, a taller crown height than its adjacent lower fourth premolar, and features a weakly expressed metaconid and mesial marginal ridge. *Oreopithecus* lower third premolar morphology is highly variable, however, with isolated, presumably female elements featuring distinct metaconids (Abbazzi *et al*. 2008).

As for its Miocene ape counterparts, and in particular those with relatively small canines (such as *Ouranopithecus*; see section 3.2), *Oreopithecus* lower canines exhibit both a distal crest and distal tubercule (both are weakly expressed) with attendant "wear zones" in association with the UC/LP3 honing complex. The distal tubercule of the lower canine "guides" the upper canine against the honing plane of the lower third premolar (Suwa *et al*. 2009b).

3.3.1.1 Comparison with *Ardipithecus*

By contrast, *Ardipithecus* specimens completely lack the features associated with functional honing; see Figure 3.3D. In particular, worn *Ardipithecus* upper canines (ARA-VP-17-1, KUS-VP-2/100, SAG-VP-118) and lower third premolars (ARA-VP-1/128, ARA-VP-1/401), on which evidence of honing morphology would otherwise be apparent, show no evidence of honing. There is no distolabial sharpening of the upper canine and no lower third premolar mesiobuccal honing plane on the *Ardipithecus* specimens. The lower third premolar crown is basally expanded and there is a distinct mesial marginal ridge.

3.3.1.2 Comparison with fossil and modern hominoids

Functional honing is easily diagnosed in extant, large bodied hominoids and on well-preserved fossil specimens as illustrated in Figure 3.4B and 3.3C.

3.3.2 Discussion and summary

The lack of a honing upper canine complex in males is a diagnostic hominid characteristic (White *et al*. 1994, 2009a, 2015; Suwa *et al*. 2009). Relative to cercopithecoids, fossil and modern hominoids all exhibit(ed) some reduction of this complex, but retain the morphology of the distolingual upper canine and mesiobuccal lower third premolar, allowing facile diagnosis of the presence or absence of this complex. The available fossil evidence indicates that *Oreopithecus* was no exception.

3.4 Anteriorly placed foramen magnum

As noted in Chapter 2, the last of the four craniodental characters claimed as hominid synapomorphies or homoplasies in *Oreopithecus* is an anteriorly placed foramen magnum. The positioning of the foramen magnum in hominoids is a complex character involving basicranial length (Kimbel *et al*. 2014, White *et al*. 2015). In this dissertation, it is treated as a singular character for reasons owing to preservation of relevant elements. An anteriorly placed foramen magnum in association with orthograde posture has long been associated with a habitual bipedal locomotor mode as a hypothesized means of maintaining equilibrium atop the vertebral column while walking. This feature has also been characterized as a diagnostic hominid trait in terms of its anterior placement beginning with Dart's description of *Australopithecus* (1925) or its position relative to the carotid foramina (Dart 1925, White *et al*. 1994, Kimbel *et al*. 2014).

3.4.1 Foramen magnum positioning

The only available *Oreopithecus* specimen that potentially bears on the evaluation of this claim is the cranium IGF 11778, a very distorted specimen that preserves elements of the basicranium. However, positioning information of the foramen magnum can be realistically inferred; see Figure 3.1, which illustrates multiple views of this specimen, whose maximum mediolateral breadth prior to Clarke's (1997) reconstruction was ~30mm. Other *Oreopithecus* partial crania do not preserve this anatomy.

3.4.1.1 Comparison with *Ardipithecus*

The extreme flattening of the lone *Oreopithecus* specimen, mostly in a mediolateral/coronal dimension, renders the positioning of the foramen magnum speculative relative to the *Ardipithecus* fossils (evaluated by Kimbel *et al*. 2014).

3.4.1.2 Comparison with fossil and modern hominoids

Direct comparisons with hominoids of any taxon or chronological period are impossible, due to the preservation of the *Oreopithecus* specimen.

3.4.2 Discussion and summary

Despite Straus' (1963) inability to establish any certainty regarding the position of the foramen magnum, and the complete lack of mention in any of the published literature on *Oreopithecus* cranial anatomy, Wood and Harrison (2011) and others (Nelson and Rook 2016) list an "anteriorly situated foramen magnum" among similarities associated with bipedal locomotion shared with *Ardipithecus* and presumably other hominids. They cite Hürzeler (1958) as the source of this described anatomy, though Hürzeler makes no mention of this anatomy in that publication.

3.5 Conclusions

In this chapter, I have examined and evaluated three of the most frequently cited craniodental character complexes and one singular character claimed as hominid synapomorphies or homoplasies in *Oreopithecus*. Claims for a short face, reduced relative canine size and sexual dimorphism, and a lack of an upper canine lower third premolar honing complex are all based on evaluations of elements of character complexes whose constituent characters I have compiled from the published literature (or I have subdivided when no published constituent characters are mentioned) and evaluated in comparison with extant and fossil apes, *Ardipithecus*, and later hominids. The claim for hominid homoplasy of anterior zygomatic root position is not supported by the comparative evidence and is best interpreted as a hominoid (or catarrhine or anthropoid) syplesiomorphy. The claim for hominid homoplasy of vertically implanted incisors that constitute the claim of a short face in *Oreopithecus*, however, could not be falsified with the available evidence. This character therefore represents a potential homoplasy, but even on the basis of inadequate fossil samples of most hominoid taxa, this is a character that is much more widely shared than just between *Oreopithecus* and *Ardipithecus*.

The claim for hominid homoplasy of "reduced canines" in *Oreopithecus* is partially falsified. Of the 11 characters constituting the character complex of reduced canines in *Oreopithecus*, comparative analysis of nine (9) characters concerning feminization of canine crown shape reveal that unlike hominids (and specifically *Ardipithecus*), *Oreopithecus* male canine shape was not feminized. Comparative analysis of two singular characters, the reduction of the upper and lower canines relative to respective upper and lower postcanine dentitions, reveal similarity among *Ardipithecus*, *Ouranopithecus*, *Gigantopithecus*, *Oreopithecus,* and *Pan paniscus*. Therefore, the claim for hominid homoplasy in these characters in *Oreopithecus* could not be falsified. However, since the phyletic ancestor of *Oreopithecus* has not yet been found and the term "reduced" is inherently relative, further fossils and outgroup assessment will be required to confirm these potential homoplasies (see Table 3.3). Moreover, comparing ratios based on canine crown base measures are probably a relatively (relative to shape measures) poor means of evaluating canine evolution in the first place, despite their deep and often flawed historical use in paleoanthropology.

The claim that low sexual dimorphism of the *Oreopithecus* canine was evolved in parallel with hominids could not be entirely falsified and represents a potential homoplasy because comparative analysis of both of the subdivided characters constituting this character complex revealed a lower level of sexual dimorphism of the *Oreopithecus* canine relative to extant and fossil apes. However, the claim for hominid homoplasy in *Oreopithecus* with regard to a lack of an upper canine/lower third premolar honing complex was falsified on the basis of misinterpreted anatomy (see Table 3.3). The claim for an anteriorly positioned foramen magnum lacks evidentiary merit and is falsified because that anatomical region is insufficiently present in *Oreopithecus* fossils.

The results of the comparisons made in this chapter are summarized below in Table 3.3. The presently available evidence indicates that *Oreopithecus* had a (primitively) short face, reduced relative canine size (without the feminizing shape changes observed in hominids), and some degree of reduction of canine sexual dimorphism. However, the claim for a lack of an upper canine-lower third premolar honing complex in *Oreopithecus* is not supported by the evidence. Nor is the claim for an anteriorly situated foramen magnum, for the simple reason that this anatomy is not preserved. In the next chapter I will move inferiorly down the skeleton to evaluate claims for hominid homoplasy in the *Oreopithecus* axial skeleton.

Table 3.3 *Oreopithecus* and *Ardipithecus* craniodental characters

Craniodental character	***O. bambolii***	***Ar. ramidus***
Short face (character complex)	**anteroposteriorly short**	**anteroposteriorly short**
implantation of incisors	near vertical	near vertical
zygomatic root position	zygomatic root more anterior (M1)	zygomatic root more anterior (M1)
Upper canine relative to upper first molar (UC basal diameter divided by UM1mesiodistal length)	*small*	*small*
Upper canine shape feminization (character complex)	**males unfeminized, higher crowned, lower shoulder**	**male C feminized in shape**
shoulder height	low	mid to high
shoulder flare	weak	distinct flare
lingual marginal ridge	weak	fold-like
main mesial lingual ridge	moderate	basally broad
crown height	males tall, females moderate	UC height differentially reduced
Lower canine relative to lower first molar (LC basal diameter divided by LM1mesiodistal length)	*small*	*small*
Lower canine shape feminization (character complex)	**males higher crowned, modally low mesial shoulder, weak/no distal tubercle**	**feminized**
mesial shoulder height	intermediate	intermediate?
lingual marginal ridge	weak or none	fold-like
distal crest	weak	weak
distal tubercle	weak	developed
Sectorial UC/LP3 honing (character complex)	**present, strong in males**	**absent**
UC distolabial sharpening	present	absent
LP3 wear	hones UC	mostly horizontal?
LP3 basal crown size/shape	obliquely elongate	basally expanded and large
LP3 crown height	tall, slightly posteriorly oriented	low and squat
LP3 metaconid	weak	rudimentary
LP3 mesial marginal ridge	weak	distinct
Placement of foramen magnum	*unknown*	*anterior*

C=canine, U=Upper, L=lower, M1=first molar, P3=third premolar. Character complexes in **bold**. Singular characters are *italicized*. Character states for *Oreopithecus* from personal observations. Character states for *Ardipithecus* from personal observations, Suwa *et al*. 2009a, 2009b; and White *et al*. 2009a, 2015.

Cell color key:

Claimed as a homoplasy and probably is one.

Claimed as a homoplasy but is probably the primitive condition in *Oreopithecus* and *Ardipithecus*.

Claimed as a homoplasy but *Oreopithecus* anatomy is absent or has been misinterpreted.

Claimed as a homoplasy but further fossils/outgroup assessment required to confirm.

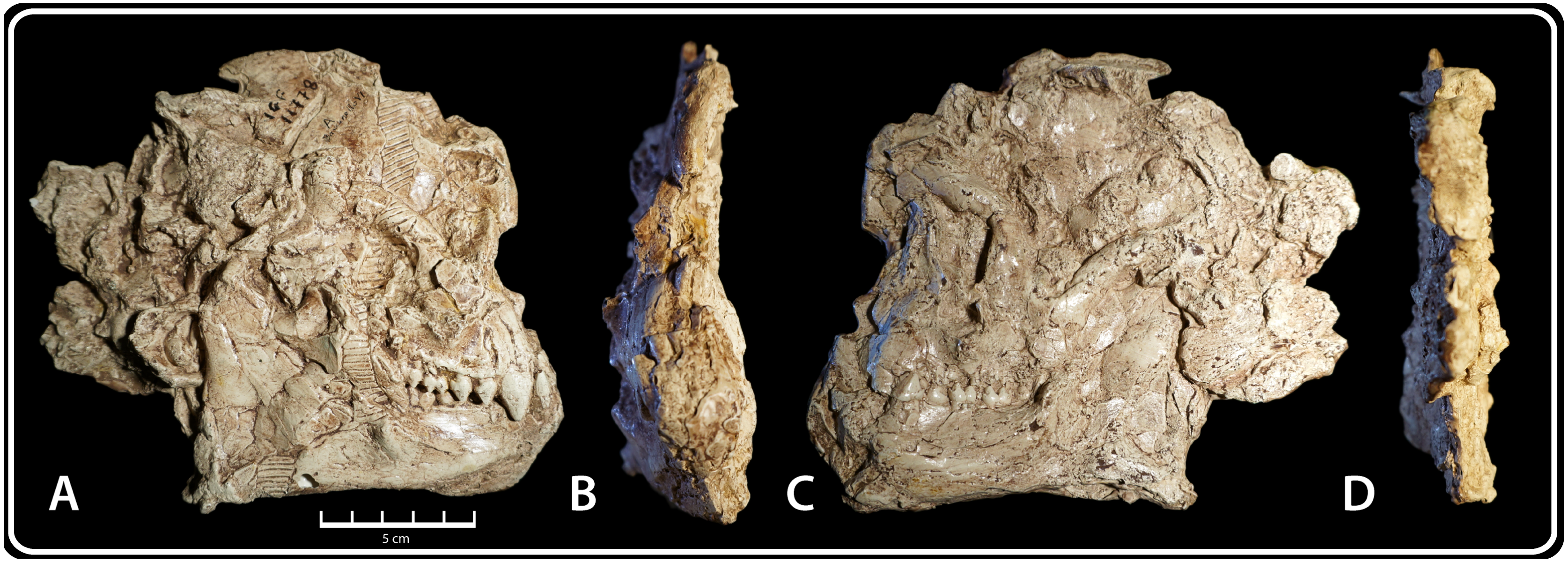

Figure 3.1: *Oreopithecus* IGF 11778 skull (cast) prior to 1997 R. Clarke reconstruction in A) lateral right B) anterior C) lateral left and D) posterior views. Maximum distorted mediolateral breadth of this specimen before preparation and reconstruction was approximately ~30 mm.

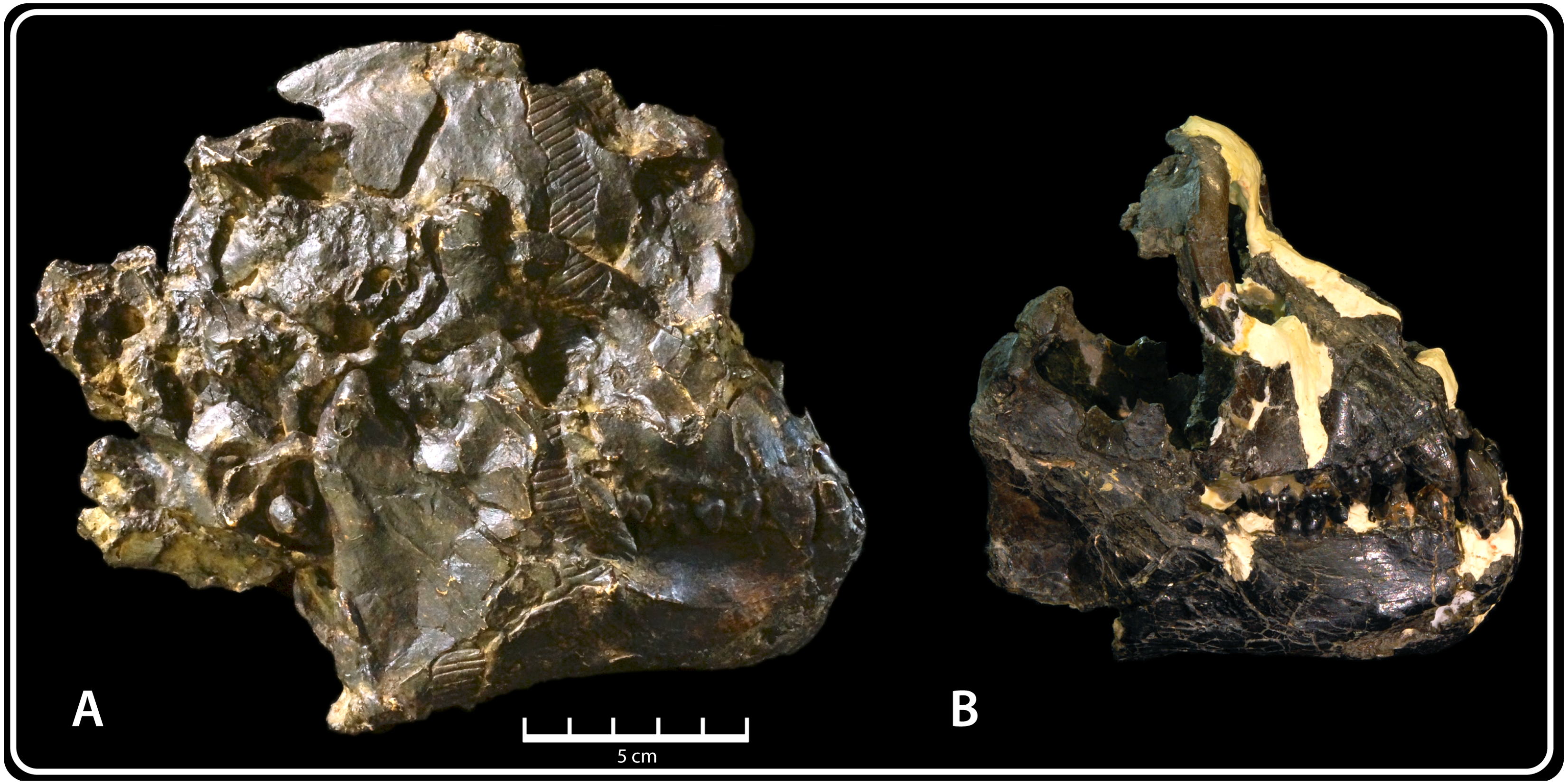

Figure 3.2: *Oreopithecus* IGF 11778 A) skull (cast) before the 1997 R. Clarke reconstruction, B) R. Clarke 1997 reconstruction.

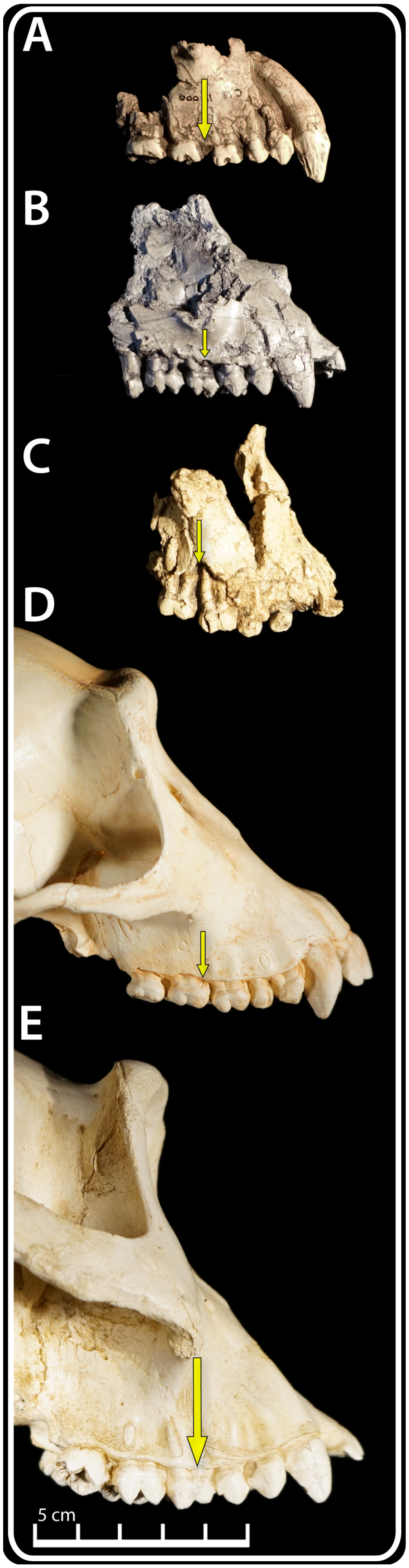

Figure 3.3: Position of the zygomatic root relative to tooth position. A) *Dryopithecus (Hispanopithecus) laietanus* CLI 18000 (cast) B) *Oreopithecus bambolii* IGF 11778 1987 reconstruction (cast) C) *Ardipithecus* ARA-VP-6/500 (cast) D) *Pan paniscus* (male, cast) E) *Gorilla gorilla* (female, cast). The base of each yellow arrow is a homologous point of the zygomatic root of each specimen (sensu Weidenreich 1943, Sergi 1947, Tobias 1967, and Hylander 1977, see text for details).

Figure 3.4: Upper canine/lower third premolar functional honing in *Oreopithecus*. A) *Oreopithecus* Upper BAC 60 maxilla and IGF 11778 mandible (both males), scaled to comparable length and reversed. B) *Pan troglodytes* (male) left upper and lower dentitions. C) *Dryopithecus* reconstruction (cast, male, reversed) right upper and lower dentitions. D) *Ardipithecus* ARA-VP-1/300 (male) right upper and lower dentitions (reversed, from Suwa *et al*. 2009b).

Chapter 4: Claimed Axial Skeleton Hominid-like Characteristics of *Oreopithecus*

4.0 Introduction

After the earliest descriptions and systematic interpretations of the *Oreopithecus* postcranial fossil remains from Baccinello (Hürzeler 1958, 1968; Schultz 1960, Straus 1963), much of the published literature of the past three decades has been devoted to the inference of locomotor behavior in this extinct Miocene hominoid taxon (Harrison 1991, Köhler and Moyà-Solà 1997, Rook *et al*. 1999, McCollum *et al*. 2009, Lovejoy and McCollum 2010, Russo and Shapiro 2013). This chapter presents an examination and evaluation of the key claimed hominid-like character complexes of the *Oreopithecus* axial skeleton and their subdivisions introduced in Chapter 2 (Sections 2.5.3.a-e).

As noted in Chapter 2, four *Oreopithecus* specimens necessary for evaluating claims of hominid homoplasy of the *Oreopithecus* axial skeleton were either unavailable for study or missing from the *Oreopithecus* collection in the Naturhistorisches Museum of Basel during my visit. These specimens include the IGF 11778 pelvis, BAC 76/49, a partial os coxa and associated proximal femur, and two partial ischia, BAC 182/50 (associated with a sacrum) and BAC 208. These specimens are discussed in more detail below.

4.1 Lordotic Lumbar spine consisting of 5 lumbar elements

As noted in Chapter 2, the first of the five axial skeleton characters claimed as hominid synapomorphies or homoplasies in *Oreopithecus* is a lordotic lumbar spine consisting of 5 lumbar elements. This is treated as a "character" in the published literature, but is actually a character complex that I have subdivided into two characters for the purpose of the comparative analysis that follows. These characters are 1) a lumbar spine consisting of five lumbar vertebrae and 2) the ability of those five lumbar elements to lordose, or to curve ventrally as a means of centering upper body mass over the lower body during orthograde posture and bipedal walking.

Oreopithecus fossil specimens that bear on these claimed synapomorphic or homoplastic characters are a partial and compressed third through fifth lumbar and first and second sacral vertebrae (BAC 72/35) as well as a partial lumbar spine and partial pelvis from the IGF 11778 skeleton. I examined BAC 72/35 in Basel and the partial lumbar spine from the IGF 11778 skeleton in Florence. As I have noted elsewhere in Chapter 2 and below, the original IGF 11778 pelvis was not made available to me during my visit. Instead, I have studied two casts, one in Florence and another housed in the Human Evolution Research Center in Berkeley.

First described by Hürzeler (1958), Schultz (1960) and later by Straus (1963), BAC 72/35 is a partial lower lumbosacral spine preserving partial third, fourth and fifth lumbar vertebrae and first and second sacral vertebrae (Schultz 1960, Straus 1963). It is multidimensionally crushed and flattened, predominantly in an anteroposterior dimension, with mediolateral displacement of vertebral portions. The IGF 11778 partial upper lumbar spine is disarticulated from the pelvis and preserves the first through third lumbar vertebrae as well as a portion of the most caudal thoracic vertebral centrum. The specimen is extremely distorted, crushed and nearly flattened in a dorsoventral dimension, with three adherent but displaced rib fragments. The IGF 11778 pelvis preserves left and right upper ilia, a left acetabulum, and a superior portion of the left ischial body. A displaced lumbar vertebra is lodged in the bi-iliac space. The specimen is nearly completely crushed and flattened in an anteroposterior dimension, obliterating and/or obscuring the morphology and positioning of important anatomical landmarks such as the acetabulum, aspects of the upper ilium (discussed in section 4.2 below), and the disposition of the entrapped lumbar vertebra. No sacral elements are preserved in the IGF 11778 specimen, and the lumbar vertebra is entrapped approximately ~2-3cm below the superior extent of the ilia.

4.1.1 Lumbar spine consisting of 5 lumbar vertebrae

Schultz examined BAC 72/35 and two elements of the IGF 11778 skeleton: a crushed and distorted upper lumbar spine and a partial pelvis described above (Schultz 1960). He identified the three first lumbar vertebrae on the IGF 11778 vertebral spine specimen based on proportions of those elements in comparison with extant apes. Schultz inferred that the displaced lumbar vertebra lodged in the bi-iliac space of the IGF 11778 specimen to be the fifth and most caudal lumbar because he had already identified the first, second, and third lumbar vertebrae on the other, disarticulated lumbar specimen belonging to this skeleton. He further identified fragments of another lumbar vertebra's centrum in association with this skeleton, which he inferred to belong to the fourth lumbar element. He strengthened his argument by comparing this entrapped lumbar element to the lumbar element immediately cranial to the first sacral vertebra in BAC 72/35 and concluded that the proportions and morphology of the centra of both elements were similar (Schultz 1960).

Schultz's identification and interpretation of a five-element lumbar spine in *Oreopithecus* was accepted and repeated by other early investigators without disagreement (Straus 1963). Hürzeler claimed that this lumbar count was a derived character *Oreopithecus* shared with Hominidae (Hürzeler 1968). Later investigators have also accepted Schultz' diagnosis and cited Schultz and Straus as the source of this claim (Harrison 1987, Sarmiento 1987, Harrison and Rook 1997, Köhler and Moyà-Solà 1997, McCollum *et al*. 2009, Lovejoy and McCollum 2010). Most of these later investigators, like Schultz, noted a five-element lumbar column in *Hylobates* as well as Hominidae. Many have interpreted this character as sympleisiomorphic in Hominiodea, as opposed to the derived, further shortened lumbar spine in *Pan*, *Gorilla*, and *Pongo*.

After examination of the BAC 72/35 and IGF 11778 partial lumbar spine specimens, as well as casts of the IGF 11778 pelvis, I am unable to falsify Schultz's assertion of a five-element lumbar spine in *Oreopithecus*. Though distorted, the mediolateral proportions of the vertebral body of the element immediately cranial to the first sacral vertebrae in BAC 72/35 are broadly similar to the vertebral element entrapped in the bi-iliac space in the IGF 11778 pelvis specimen (minimum width of 33mm, Schultz 1960). Schultz also appears to have been correct in his identification of the first three lumbar elements of the IGF 11778 partial lumbar spine specimen; a portion of the last thoracic vertebra above the first three lumbar preserves planar superior articular facets whereas the three lumbar elements below it have a lumbar pattern, with the third lumbar element preserving distinctly anterolaterally facing inferior articular facets.

I am also unable to falsify a hypothetical six-element lumbar spine in *Oreopithecus*, which is consistent with the inferred primitive hominoid condition of a lower spine consisting of 6-7 lumbar vertebrae (McCollum *et al*. 2009, Lovejoy *et al*. 2009d, Lovejoy and McCollum 2010, Machnicki *et al*. 2016 *contra* Williams and Russo 2015). There are no overlapping "fourth" lumbar vertebrae in the *Oreopithecus* hypodigm. There are fragments of vertebral centrum associated with the IGF 11778 skeleton that Schultz believed belonged to a missing fourth lumbar vertebra for this individual, but I am unable to "match" them to the penultimate lumbar vertebra on the BAC 72/35 specimen. This uncertainty is perhaps what has led some workers to avoid assigning *Oreopithecus* a lumbar vertebral count, using the words "ultimate," "penultimate," and "antepenultimate" to refer to the lumbar elements cranial to the first sacral vertebra on the BAC 72/35 specimen (Russo and Shapiro 2013, see also Williams and Russo 2015).

Therefore, it is currently not possible to determine the number of lumbar elements in *Oreopithecus* with the available fossil evidence. Further fossils, specifically those from multiple individuals with overlapping lumbar elements, will be needed to determine lumbar number in *Oreopithecus*.

4.1.1.1 Comparison with *Ardipithecus*

No *Ardipithecus* lumbar vertebrae have yet been found. Therefore, a direct comparison with *Oreopithecus* in order to evaluate the phylogenetic interpretation of vertebrae number in the lumbar spine is not yet possible.

4.1.1.2 Comparison with fossil and modern hominoids

No Miocene hominoid preserves a complete vertebral column. However, remains of several fossil taxa have yielded clues to lumbar vertebral count. The vertebral column for a *Nacholapithecus kerioi* skeleton (KNM-BG 35250) is nearly complete but very distorted, and its lumbar vertebral count is estimated to be six or seven (6-7) (Nakatsukasa and Kunimatsu 2009). Other Middle Miocene partial skeletons have been informative. Whereas *Pierolapithecus* lumbar vertebral count cannot be inferred on the basis of two preserved lumbar vertebrae (Moyà-Solà *et al*. 2004), *Hispanopithecus* is inferred to have had four or five (4-5) lumbar vertebrae (Susanna *et al*. 2014).

Extant great apes have three to four (3-4) lumbar vertebrae and have thus reduced their lumbar spines relative to the inferred primitive hominoid condition. This reduction, along with other modifications of the lower axial skeleton that restrict mobility, are interpreted as an adaptation to suspension and/or vertical climbing (Lovejoy 2005a, McCollum *et al*. 2009, Lovejoy *et al*. 2009b, 2009d).

4.1.2 Lumbar lordosis

The claim for lumbar lordosis in *Oreopithecus* originates with Köhler and Moyà- Solà on the basis of the BAC 72/35 specimen. These investigators contend it to be direct evidence of lordosis because of the human-like dorsal wedging (Köhler and Moyà- Solà 1997). Other workers have doubted this claim, noting that distortion on the specimen renders inference of lordotic curvature impossible (McCollum and Lovejoy 2010).

Köhler and Moyà-Solà (1997) posited that this specimen evinced vertebral wedging consistent with lordosis of the lumbar spine in association with habitual bipedal walking as in hominids. Their measurements of interfacet distances of the lumbar vertebrae and interpretation of caudally progressive decrease in those distances was vigorously questioned by Lovejoy and McCollum (2010). Though measurements and interpretation of zygopophyseal interfacet distance is inconceivable based on the preservation of this specimen, Russo and Shapiro presented evidence contradicting inferred lumbar lordosis in *Oreopithecus*, principally on the basis of anatomical distortion on the specimen and misinterpretation of relevant observable morphology (Russo and Shapiro 2013).

4.1.2.1 Comparison with *Ardipithecus*

While no *Ardipithecus* lumbar vertebrae have yet been recovered from the Aramis member localities, the ARA-VP-6/500-31 os coxa specimen yields important clues as to the potential for lordosis of the lumbar spine in this taxon. Specifically, the posterior retroauricular portion of the ilium did not extend sufficiently above the auricular surface (and therefore, the sacrum) to entrap and restrict the most caudal lumbar.

In contrast, the *Oreopithecus* os coxa entraps a lumbar vertebra in the bi-liac space (Figure 4.1A). The extent of lumbar entrapment is difficult to interpret due to the distortion and displacement of both the entrapped lumbar element and the adjacent ilia; it is unknown whether *Oreopithecus* entrapped a single caudal lumbar vertebra or the last two caudal lumbar vertebrae as in *Pan*.

4.1.2.2 Comparison with fossil and modern hominoids

The entrapment of at least one lumbar vertebra within the bi-iliac space is a significant part of a suite of characteristics of the lower spine associated with suspensory positional behaviors, along with mediolateral narrowing of the sacrum, superoinferior lengthening of the ilia, and reduction of lumbar elements from the inferred ancestral number (McCollum *et al*. 2009, Lovejoy and McCollum 2010). Chimpanzees and gorillas have both independently reduced their lumbar vertebral count to four (4) relative to the primitive condition, whereas *Hispanopithecus* appears to have had had 4 or 5 lumbar vertebrae (Susanna *et al*. 2014). A lumbar vertebral count of 5 or 6 in *Oreopithecus* is parsimoniously interpreted as a symplesiomorphy.

4.1.3 Discussion and summary

While lumbar number in *Oreopithecus* cannot be determined with the available fossil evidence, a count of 5 or 6 lumbar vertebrae is most parsimoniously interpreted as a hominoid symplesiomorphy. As mentioned previously, further, unambiguous fossil evidence will be needed to confirm lumbar vertebral count.

The evolution of a lordotic lumbar spine involves modifications of the ilia (reduced iliac height and more sagittal orientation) and the sacrum (mediolateral broadening) to allow for liberation of the lower lumbar column from the ilia (Lovejoy *et al*. 2009a, 2009b, 2009d; White *et al*. 2015). Russo and Shapiro (2013) examined the *Oreopithecus* BAC 72 specimen and concluded that dorsal wedging was not reliably interpretable from the damaged specimen, nor were the claims made by Köhler and Moyà-Solà (1997) for a caudally progressive increase in postzygopophyseal interfacet distance and associated increase in caudal surface of lumbar vertebrae laminar width that they observed as more consistent with that of modern hominoids and three-toed sloths. They also note that *Oreopithecus* possessed mediolaterally narrow sacral alae, concluding:

> *"…the lumbosacral morphology of* Oreopithecus *is fully encompassed within the range observed for mammals that exhibit skeletal adaptations for suspensory*

> *locomotion, and is inconsistent with the lumbosacral morphology associated with habitual bipedal posture and locomotion characteristic of modern humans."* (Russo and Shapiro 2013, p. 263).

At minimum, the narrow sacrum (BAC 72/35) and entrapped lumbar vertebra in the bi-iliac space (IGF 11778) are indicative of a suspensory locomotor repertoire and thus provide falsification of the hypothesis of hominid homoplasy or synapomorphy in this region of *Oreopithecus* anatomy.

4.2 Short and broad ilia

As noted in Chapter 2, the second of the five axial skeleton characters claimed as hominid synapomorphies or homoplasies in *Oreopithecus* is a short and broad pelvic ilium. I divided this morphological character complex into two characters: the height of the iliac isthmus and the relative breadth of the ilium. Hominid ilia are short and broad, rotated sagittally relative to modern and fossil apes, with relatively deep iliac fossae, short iliac isthmuses, and craniocaudally long and broad auricular surfaces for articulation with a mediolaterally broadened sacrum. The claim for hominid-like short and broad ilia on the *Oreopithecus* 1958 skeleton os coxa was made in the early 1960s and many times since (Schultz 1960, Straus 1963, Simons 1967, Hürzeler 1968, Köhler and Moyà-Solà 1997, Köhler and Moyà-Solà 2003, Moyà-Solà *et al*. 1999, Moyà-Solà *et al*. 2008, Rook *et al*. 1999, Wood and Harrison 2011). Hürzeler included this character complex in his list of the nineteen (19) derived characters that he believed *Oreopithecus* shared with hominids (Hürzeler 1968).

Later investigators have offered other phylogenetic interpretations of this character complex. Harrison has posited on multiple published occasions that a short, relatively broad ilium is a hominoid symplesiomorphic character (Harrison 1987, 1991; Harrison and Rook 1997), despite recently and strongly suggesting that the short, broad *Oreopithecus* ilium is was evolved in parallel with later hominids (a homoplasy; Wood and Harrison 2011). The Sabadell-Florence research group have asserted for the last two decades that the short, broad ilium in *Oreopithecus* is a hominid homoplasy (Köhler and Moyà-Solà 1997, Köhler and Moyà-Solà 2003, Moyà-Solà *et al*. 1999, Moyà-Solà *et al*. 2008, Rook *et al*. 1999).

Two specimens potentially bear on this claimed potential synapomorphic or homoplastic character complex. The first is the partial pelvis from the IGF 11778 skeleton. Neither this specimen (it was, and is still, at the Institut Català de Paleontologia Miguel Crusafont Sabadell, Spain for reconstruction and restricted study) nor the radiographs published in Rook *et al.* (1999) were made available to me for study during my visit to the Museo di Storia Naturale, Sezione di Geologia e Paleontologia dell'Università di Firenze. Three cast specimens were studied in order to evaluate this claim: a cast provided in Florence, a cast of similar provenance and quality available at the Human Evolution Research Center in Berkeley, and first generation anterior and posterior casts of the skeleton made "*in situ*" before it was extracted from the lignite block by preparator(s) at the museum in Florence in the late 1960s-early 1970s (Figure 4.2a).

The IGF 11778 pelvis specimen, a juvenile near-adult (its iliac crest is not fused), is anteroposteriorly flattened and preserves a lumbar vertebra between the left and right ilia (for discussion of this element, see section 4.1 above). It preserves distorted, fragmented and displaced left acetabular elements and the superior portion of the left ischial body. Because of the extreme anteroposterior crushing, assessment of lateral flare of the ilia and precise position of the left acetabulum is prohibitive.

The second specimen that potentially bears on the claim of potential synapomorphy or homoplasy in this character complex is BAC 76/49. Straus examined and illustrated this specimen. It preserves a right proximal femur (head, neck, lesser trochanter, and posteromedial portion of the greater trochanter) and an extremely distorted portion of right os coxa which preserves the portions of the acetabulum, lower iliac blade, and auricular surface (Straus 1963). Unfortunately, this specimen had been disarticulated and only the proximal femur was available for study in Basel during my visit in October 2013. The os coxa portion is missing from the collection and was not listed in the paperwork in association with the loan returned by the Spanish research group at Sabadell. Its current location is unknown; the last published mention of this specimen is contained within Rook *et al*. (1999), where they wrote:

> *"…BAC 76, a fragmentary blade and corpus of a right ilium…Preliminary radiographic and tomographic investigation of BAC 76 proved no specific trabecular features."* (Rook *et al*. 1999, p. 8795).

A subsequent, broader study also mentions this specimen, where the authors wrote:

> *"BAC 76 represents a freagmentary blade and corpus of a right ilium…A series of CT-scans and calibrated radiographs revealed cancellous bone preserved enough for digital image enhancement in both the right and left IGF 11778 fragments, but not in BAC 76."* (Macchiarelli *et al*. 2001).

Unfortunately, no casts of this specimen were available for study.

4.2.1 Short iliac isthmus

The iliac isthmus is defined as the inferior section of the ilium between the superior extent of the acetabulum and inferior extent of auricular surface for the sacrum (Schultz 1930, Straus 1962, 1963; Lovejoy *et al*. 2009b, White *et al*. 2015).

Straus wrote of the *Oreopithecus* iliac isthmus (though he did not call it "isthmus") with reference to the IGF 11778 and (now missing) BAC 76/49 specimens:

> *"In all living pongids and most cercopithecoids there is a comparatively long space between the upper margin of the acetabulum and the lower margin of the sacral surface, so that these two structures are well separated; in other words, the lower ilium is relatively long in simian catarrhines (Schultz, 1930; Fig. 13). In modem man (Schultz, 1930) and the Australopithecinae (Straus, 1962), however, acetabulum and sacral surface closely approach each other; thus the lower ilium is relatively short in hominids, this evidently being a stabilizing adaptation related to the erect bipedal posture (Straus, 1962; Fig. 13). In so far as I can determine from the two known but incomplete pelves (#49 and 1958) the distance between acetabulum and sacral surface is relatively shorter in* Oreopithecus *than in pongids-perhaps representing a more primitive or generalized hominoid condition. Indeed, if my interpretation of specimen #49 is correct, the acetabular-*

> *sacral relations closely approximate those found in hominids (Fig. 14).”* (Straus 1963, p. 167-168)

To date, Straus is the only investigator to make reference to this feature of the *Oreopithecus* lower ilium. He does not, however, quantify this as either a direct measurement or define it for comparative purposes as a ratio against another part of *Oreopithecus* anatomy. Nor does he mention that the inferior extent of the auricular surface on IGF 11778 is ***not preserved***.

Nevertheless, in order to make this comparison, he oriented os coxae of *Macaca mulatta*, *Gorilla*, and *Homo sapiens* in anterior view and rotated them slightly laterally such that the superior rim of the acetabulum and inferior extent of the auricular surface were both visible (Straus 1963, Fig. 13). According to gross comparisons made in this way, Straus concluded that this estimated vertical distance between the inferior extent of the auricular surface and the superior margin of the acetabulum in *Oreopithecus* (estimated from the BAC 76/49 specimen) was shorter than that in extant great apes (Straus 1963). This conclusion, however, is not supported by the available comparative evidence.

4.2.1.1 Comparison with *Ardipithecus*

As mentioned, IGF 11778 preserves only the most superior portion of the auricular surfaces of the left and right ilia. Because the inferior extent of the auricular surface is not present on the specimen, a direct comparison of iliac isthmuses cannot be made with certainty. However, an estimation of the inferior extent of the auricular surface may be made on the basis of extrapolations about the length of the sacrum evident in two other specimens (BAC 72/35 and BAC 182/50, Schultz 1960 and Straus 1963). These specimens, and in particular BAC 182/50, reveal a narrow, six element sacrum in *Oreopithecus* as in extant great apes. I estimated the general vicinity of the most inferior extent of the auricular surface in *Oreopithecus* based on the sacral specimens and inferred the most inferior extent of its articular position based on a chimpanzee model, who also have narrow, six element sacra (modally 5-7 between both species of *Pan*).

The *Ardipithecus ramidus* left os coxa (ARA-VP-6/500-31, Figure 4.2B) is almost complete, but suffers from some post-mortem depositional distortion (Lovejoy *et al*. 2009b). The ilium – in particular its anteroinferior portion and iliac fossa – are comparatively well-preserved. The acetabulum is reasonably intact and continuous bone surfaces allow for direct qualitative comparisons with the inferred position of the acetabulum on the *Oreopithecus* specimen (Rook *et al*. 1999).

By the methodology used by Straus (1963) and the *Ardipithecus* discovery team (Lovejoy *et al*. 2009b, White *et al*. 2015), I made direct comparisons between the *Oreopithecus* IGF 11778 specimen (cast) and the *Ardipithecus* ARA-VP-6/500-31 specimen. Though the most inferior extent of the auricular surface cannot be established with certainty in either specimen (because of crushing and bone loss in both), the vertical distance between the superior acetabular rim and the estimated most superior extent of the auricular surface in *Ardipithecus* appears to be relatively shorter than the estimated distance between the inferred superior acetabular rim in *Oreopithecus* (Rook *et al*. 1999) and where the inferior extent might have occurred in the *Oreopithecus* (see above and Figure 4.2). This estimation and resulting comparison is admittedly approximate and further fossils preserving both the auricular surface for the sacrum acetabulum in *Oreopithecus* will be needed to confirm my observation.

4.2.1.2 Comparison with fossil and modern hominoids

Based on my estimation outlined above, the *Oreopithecus* iliac isthmus appears as superoinferiorly tall (Figure 4.3) as in extant gorillas. This suggests that the superoinferior length of the iliac isthmus scales with body mass in large-bodied apes. As I mentioned, further fossils will be needed to confirm and phylogenetically interpret this anatomy.

4.2.2 Short and broad iliac blades

This character refers to the superoinferior length and mediolateral breadth of the superior portion of the ilia. Straus quantified this in *Oreopithecus* as an index of mediolateral iliac breadth divided by superoinferior iliac length which allowed comparisons between taxa (Straus 1963). Using this index, Straus calculated a value of 80 for *Oreopithecus* which was larger than *Pan* (66) and *Pongo* (74) but smaller than *Gorilla* (92) and *Homo sapiens* (125). Hürzeler interpreted these "short" and "broad" iliac blades as a derived character shared with hominids (synapomorphic) and later investigators interpreted this character as symplesiomorphic in hominoids (Hürzeler 1968, Harrison 1987, 1991; Harrison and Rook 1997). Recent workers have interpreted this character in *Oreopithecus* as a hominid homoplasy (Köhler and Moyà-Solà 1997, Köhler and Moyà-Solà 2003, Moyà-Solà *et al.* 1999, Moyà-Solà *et al.* 2008, Rook *et al.* 1999, Wood and Harrison 2011).

4.2.2.1 Comparison with *Ardipithecus*

In *Ardipithecus* (ARA-VP-6/500-31), the ilium broadens superior to the iliac isthmus and terminates below the iliac crest, which was not preserved (Lovejoy *et al.* 2009b). Posteromedially, the auricular surface is superoinferiorly tall and the posterolateral retroauricular surface is small relative to *Proconsul.*

The *in vivo* breadth of the upper ilium in *Oreopithecus* is ultimately indeterminate as the specimen was flattened and distorted by the laminar coal depositional substrate. The *Ardipithecus* specimen is also distorted, but preserves much more morphology than the flattened *Oreopithecus* specimen. Lovejoy and McCollum applied Straus' method to *Proconsul*, *Ardipithecus ramidus* (estimated, as the iliac crest is missing from this specimen), and *Australopithecus afarensis* and calculated values of 50, 113, and 137 for each respective taxon.

I confirmed the approximate *Oreopithecus* and *Ardipithecus* values reported by Straus and Lovejoy and McCollum, respectively (Straus 1963, Lovejoy and McCollum 2010). Though neither Straus nor Lovejoy and McCollum defined the chords used in this index, I used definitions for iliac length (or height) and upper iliac breadth from Martin (1928). Iliac length is measured using sliding calipers from the superior margin of the acetabular notch closest to the center of the triradiate suture to the most distant point on the iliac crest (Martin 1928). Upper iliac breadth is measured using sliding calipers is the maximum distance between the posterior and anterior superior iliac spines. Because some of the anatomy for both *Oreopithecus and Ardipithecus* specimens is missing or distorted, values are approximate.

These approximate values generally confirm gross observations of the specimens I made for both taxa. Both are inferred to have been large bodied and the *Ardipithecus* upper ilium is relatively mediolaterally broader compared to its estimated superioinferior length than that in *Oreopithecus*.

4.2.2.2 Comparison with fossil and modern hominoids

As mentioned previously, the upper ilium in the *Oreopithecus* specimen is broadly comparable with available fossil and extant ape os coxae. Iliac width/iliac length values indicate that *Oreopithecus* had mediolaterally broader iliac blades than *Proconsul* (KNM-MW 13142), *Pan*, and *Pongo* but mediolaterally narrower iliac blades relative to *Gorilla*. I am cautious in interpreting these comparisons because the apparent iliac breadth in *Oreopithecus* may well be an artifact of preservation. The postmortem anteroposterior/dorsoventral flattening of this specimen may have contributed artificially to the apparent mediolateral breadth of the *Oreopithecus* ilia, something better evaluated on the original, unavailable fossil. Despite this, others have noted the similarity in mediolateral breadth of *Oreopithecus* ilia and the ilia of *Pan*, *Pongo*, and *Gorilla* in their interpretations of symplesiomorphy (Harrison 1987), despite subsequent interpretations of this character as a hominid homoplasy (Wood and Harrison 2011).

4.2.3 Discussion and summary

The paucity and preservation of *Oreopithecus* iliac anatomical evidence with which to conduct gross qualitative comparisons hinders evaluation of the ilia in *Oreopithecus* in anything other than an approximate fashion. Also, the displaced, entrapped lumbar vertebra lodged in the bi-iliac space contributes to the illusion of hominid-like mediolateral expansion of the ilia. Indeed, when the entrapped lumbar vertebra is visually or photographically omitted from the *Oreopithecus* specimen, a realistic comparison with *Gorilla* reveals that *Oreopithecus* ilia are neither relatively superoinferiorly shorter nor mediolaterally broader than those of their gorilla counterparts (See Figure 4.1 and 4.3). Furthermore, the narrow, ape-like sacrum in *Oreopithecus* is incompatible with short, broad hominid-like ilia because it would not allow the anteromedial rotation of the iliac blades to the sagittal plane (as in hominids) without potentially damaging effects to the pelvic viscera (Lovejoy 1988).

Superoinferior shortening and broadening of the hominid pelvis (and consequently, the ilia) is evident in *Ardipithecus* at 4.4 Ma, albeit incompletely; the upper pelvis indicates a hominid increasingly committed to terrestrial bipedality whereas the lower pelvis demonstrates a retained capacity for vertical climbing (Lovejoy *et al*. 2009b). The treatment of one component of this structural, functional complex – the shortening and broadening of the ilium – as a singular signal of synapomorphy or as homoplastic noise is potential oversimplification, as the mosaic anatomical nature of the *Ardipithecus* os coxa attests. Of course, reliable reading of this anatomy is an essential first step. In the case of the *Oreopithecus* os coxa, depositional distortion of this anatomy allows only gross comparisons and those comparisons reveal similarities with extant apes.

4.3 Well-developed anterior inferior iliac spine

As noted in Chapter 2, the third of the five axial skeleton characters claimed as hominid synapomorphies or homoplasies in *Oreopithecus* is a well-developed anterior inferior iliac spine. The development of the anterior inferior iliac spine (AIIS) probably occurs as a result of the superoinferior shortening and mediolateral broadening of the ilium during growth and evolution in hominids (Lovejoy *et al*. 2009b, Lovejoy and McCollum 2010, Zirkle 2015). In hominids, this feature serves to anchor the iliofemoral ligament and gives origin to the rectus femoris muscle, both important stabilizers of the hip during thigh flexing and leg extension at the knee while walking bipedally.

4.3.1 The "anterior inferior iliac spine (AIIS)" in *Oreopithecus*

The claim for the hominid-like characteristic of a well-developed anterior inferior iliac spine in *Oreopithecus* originated with Straus' investigation of the Baccinello fossil material and Kummer's confirmation of Straus' observations (Straus 1963, Kummer 1965). Hürzeler interpreted this character in *Oreopithecus* as a derived character shared with hominids (a synapomorphy) (Hürzeler 1968). Interpretations since then have varied, with some investigators interpreting this character as "…a specialization of *Oreopithecus* that is peculiarly hominid-like, and represents an intriguing derived feature linking *Oreopithecus* with the hominids." (Harrison 1987, p. 559) while others interpret this character as a hominid homoplasy (Köhler and Moyà-Solà 1997, 2003; Moyà-Solà *et al*. 2008, Rook *et al*. 1999, Wood and Harrison 2011).

The only *Oreopithecus* specimen that bears on this claim is the IGF 11778 partial pelvis, a severely distorted, flattened partial pelvis preserving the superior portion of the right ilium, an entrapped, last lumbar vertebra, a partial left ilium preserving anterolateral anatomy relevant to the evaluation of this claim, and a partial ischial body. For further discussion about the preservation of this specimen, see Section 4.2 and the discussion that follows.

4.3.1.1 Comparison with *Ardipithecus*

The anterior margin of the ARA-VP-6/500-31 os coxa is well-preserved and evinces a distinct, mediolaterally thick AIIS whose size, shape, and disposition make it likely to have emerged from a separate bone growth physis. The AIIS in *Ardipithecus* is therefore evidence of the presence of a diagnostic hominid apomorphy. White *et al*. recently described this feature in Ardipithecus, where they wrote:

> *"The AIIS is placed immediately above the acetabulum, and forms a localized thick protuberance that terminates abruptly superiorly. It is distinctly curved (medially convex) in anterior view, and is flanked by a localized concavity on the lateral iliac surface just above the acetabular margin. This morphological complex is commonly seen in* Australopithecus *and later hominids, likely reflecting the separate ossification center of the hominid AIIS."* (White *et al*. 2015, p. S5)

In *Oreopithecus*, there is a protuberance in the region immediately superior to the inferred acetabular rim. Published radiographs have been claimed to show dense trabecular bundles

(Rook *et al*. 1999) within. However, there is no evidence of a growth physis, which is a reasonable expectation given the juvenile status of this individual; see Figure 4.5.

It is possible that this apparent bony prominence is, at least in part, an artifact of preparation either during the removal of the lignite block from the Baccinello coal mine, or after the skeleton was fully exposed in the laboratory at the Naturhistorisches Museum, Basel. Evaluating the shape and thickness of the anterior edge of this os coxae is therefore challenging without access to the original fossil. Indeed, even on the best casts, discriminating between carved coal and bone is impossible (see Figure 4.6).

4.3.1.2 Comparison with fossil and modern hominoids

The presence of a mediolaterally thin anterior inferior iliac spine occurs in low frequency in *Pan* and *Gorilla* (see figure 4.7), and seems to be associated with loading as a consequence of allometric increase in body mass. (Lovejoy *et al*. 2009b, Zirkle 2015). Rook *et al*. also note the similarity of the *Oreopithecus* AIIS with that of *Gorilla*, but provide no illustrative evidence (Rook *et al*. 1999).

4.3.2 Discussion and summary

Whether an artifact of preparation or a loading/allometric effect due to increased body mass, which seems at least in part likely given the claim of dense trabecular bundles in radiographs of this morphological feature (though the appearance of density may itself be due to the depositional compression of the fossil), the protuberance of bone immediately superior to the approximated superior extent of the acetabular rim on the *Oreopithecus* ilium is not especially remarkable because large-bodied *Pan* and *Gorilla* occasionally develop a bony protuberance in this region. Therefore, the claim for hominid homoplasy in this character in *Oreopithecus* is falsified both because of the poor preservation of the fossil *and* because what anatomy has been preserved has been misinterpreted. The 4.4 Ma *Ardipithecus ramidus* os coxa illuminates the nature of the hominid apomorphy in that it is not the mere presence of this feature that is homologous among hominids; rather, it is its relative size, robusticity, and probable ontogenetic emergence from a secondary ossification center.

4.4 Superoinferiorly short pubic symphysis

As noted in Chapter 2, the fourth of the five axial skeletal characters claimed as hominid synapomorphies or homoplasies in *Oreopithecus* is a superoinferiorly short pubic symphysis. A superoinferiorly short pubic symphysis likely occurs as a consequence of morphogenetic field shifts, effecting systematic shortening and broadening of the entire pelvis during early hominid evolution, a speculation (Lovejoy *et al*. 1999) confirmed, albeit incompletely, in *Ardipithecus* (Lovejoy *et al*. 2009b, 2009d; White *et al*. 2009a, 2015). As the ilia and later the ischium adaptively shortened in response to selective processes favoring habitual bipedalism, the pubic rami lengthened and the symphysis shortened (Lovejoy 2005a).

4.4.1 Pubic symphyseal superoinferior "length"

Schultz observed the pubic symphysis in *Oreopithecus* and concluded that it was superoinferiorly short relative to cercopithecoids, as in other hominoids (Schultz 1960). Harrison argued that this feature was not a diagnostic hominoid character because there is extensive interspecific variation in the character among catarrhines (Harrison 1987).

Nevertheless, Hürzeler (1968), Köhler and Moyà-Solà (1997), and Moyà-Solà *et al.* (2008) have asserted that the *Oreopithecus* pubic symphysis is superoinferiorly short, unlike modern apes, and approximating the condition of *Australopithecus* and modern humans. Interpretations of the phylogenetic significance of this character in *Oreopithecus* have varied, with Hürzeler including it in his list of 19 derived characters that *Oreopithecus* shares with hominids (synapomorphies), and later investigators claiming it as homoplastic with hominids (Köhler and Moyà-Solà 1997, Moyà-Solà *et al*. 2008, Sarmiento *et al*. 2002, Sarmiento 2010, Wood and Harrison 2011).

The only *Oreopithecus* specimen that bears on this claim is one preserving medial portions of the left and right pubic rami and symphysis, which is cemented at the midline (BAC 71/44). Moyà-Solà *et al*. noted, based on the BAC 71/44 specimen (Figure 4.9A), that the pubic ramus showed evidence of rugose bony attachment sites for perineal ligaments and musculature as in modern humans (Moyà-Solà *et al*. 2008). However, the pectineal line claimed as evidence for this part of their claim is not preserved on the BAC 71/44 specimen (Köhler and Moyà-Solà 1997, Moyà-Solà *et al*. 2008).

4.4.1.1 Comparison with *Ardipithecus*

A "short" pubic symphysis is a misleading description of this anatomy. It is unclear whether the investigators that describe the pubic symphysis as short actually mean the superoinferior length (height) of the pubic body (the portion of the os pubes immediately lateral to the symphysis itself) or the outline shape of the pubic symphysis itself. In extant great apes, the superoinferior length (height) of the pubic body is elongate relative to that in hominids, and *Ardipithecus* is very different. The outline of the pubic symphysis, or the long axis of the pubic symphyseal face, is a different matter. The long axis of the pubic symphyseal face is vertical in anatomical orientation, and is a long and thin oval in extant great apes and more rounded oval in hominids.

The pubis in the *Ardipithecus* specimen has a superoinferiorly elongate pubic body, reflecting the primitive nature of its lower pelvis (Lovejoy *et al*. 2009b). However, in *Ardipithecus* the outline of the pubic symphyseal face is a rounded ovoid, as in *Australopithecus afarensis* (A.L. 288-1) and all chronologically younger hominids (see Figure 4.8).

The pubic body of the of the *Oreopithecus* specimen is inferred to have belonged to a small female based on the dubious proposition that the ventral curvature on its anteroinferior border is shared with female humans (Moyà-Solà *et al*. 2008). This pubic body is not particularly elongate relative to that in female chimpanzees. However, the specimen preserves only the left and right pubic bodies and the symphysis. Because the rest of the os coxae are missing, it is impossible to determine the relative proportions of this specimen. Though the pubic symphysis of this specimen is distorted (especially on the left side) and cemented at the midline, the outline of the pubic symphyseal face observed by orienting the fossil in oblique view appears to be a thin oval, as in extant great apes (see figure 4.9). However, due to diagenetic damage to the specimen, the precise outline of the symphysis is indeterminate. Further fossils will be needed to confirm my interpretation of this ape-like anatomy.

4.4.1.2 Comparison with fossil and modern hominoids

There are currently no fossil European Miocene pubic symphyses with which to compare *Oreopithecus*, beyond a recently recovered and as yet undescribed *Rudapithecus* partial innominate preserving a superior pubic ramus (Ward *et al*. 2008, Shapiro and Begun 2015, 2016).

In the Lower Miocene of Africa, *Proconsul nyanzae* (KNM-MW-13142) exhibits a superoinferiorly tall pubic body and thin oval outline of the pubic symphyseal face. A recently published Middle Miocene *Sivapithecus indicus* innominate is missing the entirety of the medial portion of the os pubis (Morgan *et al*. 2015).

4.4.2 Discussion and summary

The *Oreopithecus* pubic body appears to be superoinferiorly short relative to that in extant apes, at least on the basis of this single specimen. Such anatomy may be biologically incompatible with the superoinferiorly tall iliac isthmus on the IGF 11778 os coxa (discussed in section 4.2 above), as suggested by the series of morphogenetic field changes suggested for *Ardipithecus* and all later hominids. As Harrison noted, however, there is interspecific variation in this character among catarrhine primates (Harrison 1987). Furthermore, the outline of the pubic symphyseal face of this single, distorted *Oreopithecus* specimen appears to be a thin oval as in extant great apes. At present, the interpretation of this characteristic as a potential homoplasy in *Oreopithecus* is indeterminate, pending further fossils, and additional outgroup assessment.

4.5 Large ischial spine

The last of the five axial skeleton characters claimed as hominid synapomorphies or homoplasies in *Oreopithecus* is a large ischial spine. The ischium is composed of the ischial body and two rami. The ischial body terminates in a rugose, massive ischial tuberosity. The ischial spine is a bony projection located at approximately the midpoint of the ischial body, approximately inferior to the greater sciatic notch and superior to the lesser sciatic notch. It anchors the sacrospinous ligament, whose primary role is to prevent rotation of the ilium past the sacrum during bipedal walking.

In a comprehensive study of 143 mammals, Abitbol (1988) noted the unique role of the sacrospinous ligament in humans relative to quadrupeds in giving a substrate to pelvic diaphragmatic musculature that forms a support system for human abdominal organs. He concluded that the size and orientation of the ischial spine in humans was the result of a compromise between a rotation-inhibitor and abdominal organ support, and that African apes and fossil hominids demonstrate an intermediate size of the ischial spine relative to tailed quadrupedal mammals and modern humans (Abitbol 1988). Others have noted the role of parturition in determining the size and orientation of the ischial spine (Gruss and Schmitt 2015).

4.5.1 Ischial spine relative size

The claim for hominid homoplasy in this character in *Oreopithecus* is relatively recent. Köhler and Moyà-Solà 1997, Köhler and Moyà-Solà 2003, Moyà-Solà *et al*. 1999, Moyà-Solà *et al*. 2008, Rook *et al*. 1999, Sarmiento *et al*. 2002, Wood and Harrison 2011). Regarding the ischial spine in the *Oreopithecus*, Köhler and Moyà-Solà argue:

> *"This specimen [BAC 71/44] retains a surprisingly short ischium. A further previously undescribed partial ischium with acetabulum (BA182, Fig. 2C) exhibits an extraordinarily large ischial spine (present and of similar size and form in two other partial ischia, BA71 and BA208, although less well preserved). This spine is much larger than in apes, but identical to that of Homo."* (1997, p. 11747).

However, the caption in Figure 2C in that publication indicates BAC 71/44 rather than BAC 182. The specimen drawn in Figure 2C, however, is not BAC 71/44 (See Figure 4.10A). At any rate, neither the BAC 182 nor BAC 208 ischia they reference were in Naturhistorisches Museum Basel when I visited. It is possible these two specimens were not yet returned to the museum from the loan these researchers secured for study during the time of my visit.

Therefore, the only *Oreopithecus* specimen available to me (there are no photos of either missing specimen mentioned above in the published literature) in that bears on this claim is the specimen BAC 71/44 (See Figure 4.10A). Schultz (1960) published this specimen as part of a discussion about a spatially associated pubic symphyseal specimen (see previous section). In the caption for the drawing he provided for these specimens, Schultz identified this specimen as a right ischium on the basis of what he interpreted as an ischial tuberosity at its inferior extent (Schultz 1960). This tuberosity was also noted by Straus (1963) to be low and rounded, resembling that of large-bodied extant hominoids (Schultz 1960, Straus 1963). Despite its spatial association with the os pubes specimen discussed in section 4.4, this specimen may in fact be neither a fragment of ischium nor belong to *Oreopithecus* (see discussion that follows in sections 4.5.1.2 and 4.5.2).

Like most other fossils from Baccinello, this specimen is crushed and flattened. Despite this distortion, Köhler and Moyà-Solà (1997) assert the ischial body is short and the ischial spine is large (relative to the length of the ischial body). These authors provide quantification for the claim beyond the (confusing) illustration mentioned above.

4.5.1.1 Comparison with *Ardipithecus*

The region of the *Ardipithecus* ischium (ARA-VP-6/500) that might have evidenced an ischial spine is damaged and the ischial spine is missing. Therefore, no comparisons with *Oreopithecus* can be made.

4.5.1.2 Comparison with fossil and modern hominoids

The BAC 71/44 fragment was found in spatial association with the specimen preserving a pubic symphysis discussed in Section 4.4 but its anatomy does not resemble any other known hominoid, including *Australopithecus afarensis* (see figures 4.10 and 4.11). In view of the dramatic anatomical difference between the *Oreopithecus* fragment and other smaller and larger extinct and extant hominoids, the BAC 71/44 specimen cannot presently be confirmed as belonging to an *Oreopithecus* pelvis, and indeed might well represent some other vertebrate. Assessment of the IGF 11778 subadult specimen is not helpful in this regard due to the fact that it also does not preserve an ischial spine.

4.5.2 Discussion and summary

The claim for the large size of the ischial spine in *Oreopithecus* relative to its "…surprisingly short ischium…" (Köhler and Moyà-Solà 1997, p. 11747) cannot be supported by the fossil evidence. The specimen (BAC 71/44) is flattened and distorted and despite the spatial association with the specimen preserving a pubic symphysis discussed in Section 4.4, the anatomy of the claimed ischial spine on this specimen is completely incompatible with that of any known fossil or extant hominoid. The fragment may well represent another skeletal part of the BAC 71/44 individual or belong to another vertebrate in the assemblage. Further comparisons with the unavailable published specimens offered as evidence for this claim (BAC 182 and BAC 208, see above) will clarify both the correct identification of this specimen and perhaps the anatomy of the ischial spine in *Oreopithecus*.

The phylogenetic interpretation of this character in *Oreopithecus* must, for now, be that this potential homoplasy requires access to the full range of original fossils, and further comparisons with other extinct and extant primates.

4.6 Conclusions

I have examined 5 of the most frequently cited claims of similarity between *Oreopithecus* and hominids. *Oreopithecus* may well have possessed 5 lumbar vertebrae as some investigators have claimed (Schultz 1960, Straus 1963), but there is insufficient evidence that this portion of the spine lordosed (Russo and Shapiro 2013, McCollum and Lovejoy 2010), especially considering that a lumbar vertebra would have been entrapped lumbar in the bi-iliac space.

There is likewise insufficient evidence that *Oreopithecus* possessed short and broad iliac blades, because the *Oreopithecus* iliac isthmus is tall and narrow as in extant apes. Furthermore, the specimen is anteroposteriorly flattened, precluding meaningful interpretation of the upper ilium. The preservation of this specimen (IGF 11778) also affects the evaluation of the claim of a hominid-like anterior inferior iliac spine in *Oreopithecus*, whose morphology may well have been partially altered by extraction of the fossil from the lignite block, and which nevertheless resembles the bony protuberance that sometimes occurs in extant African apes in this region. This caveat is strengthened by the fact that in the key juvenile specimen where it would be expected, the bony protuberance in the anterior inferior iliac spine region in *Oreopithecus* lacks a separate ossification physis, a feature restricted to hominids.

The morphology of the pubic symphysis and ischial spine are no more easily read. Both fossils are distorted and claims of *Oreopithecus* similarity with hominids appear unsubstantiated. A superoinferiorly short pubic body (the portion of the os pubes immediately lateral to the symphysis itself) in *Oreopithecus* is incompatible with morphogenetic field shifts hypothesized to have shortened and broadened the hominid pelvis. *Oreopithecus* ilia were likely as superoinferiorly tall relative to iliac breadth as they are in extant apes, particularly the gorilla.

Extant and fossil apes are instructive in the evaluation of the claim for a hominid-like, relatively large ischial spine in *Oreopithecus*. Comparisons with hominids, extant apes, and fossil apes reveal dramatically different ischial spine anatomy in the sole *Oreopithecus* specimen available upon which the claim for hominid similarity is based. Access to all the published specimens claimed to preserve an ischial spine will be necessary to evaluate this potential homoplasy.

In summary, claims for hominid homoplasy in characters of the *Oreopithecus* axial skeleton presented in this chapter are almost entirely falsified, with only the superoinferiorly short pubic symphysis and relatively large ischial spine uncertain in terms of phylogenetic interpretation. These characters in *Oreopithecus* may well be homoplasies or even hominoid symplesiomorphies; further fossils and outgroup assessment will be needed to confirm (See Table 4.2).

In the next chapter, I will proceed to the appendicular skeleton, in particular *Oreopithecus* hand and foot morphology, and will examine and evaluate claims of hominid homoplasy made for characters in these organs.

Table 4.1 *Oreopithecus* and *Ardipithecus* axial skeleton characters

Axial skeleton character	***O. bambolii***	***Ar. ramidus***
Lordotic lumbar spine consisting of 5 lumbar vertebrae (character complex)	**5 or 6 (indeterminate), no lordosis**	**lordosis likely, lumbar vertebral count unknown**
lumbar vertebral count	5 or 6 (indeterminate)	unknown, likely 6 (Lovejoy and McCollum 2010)
lordosis of the lumbar column	no lordosis, entrapment of at least one lumbar vertebra	likely; no entrapment is evident
Short and broad ilia (character complex)	**no shorter or broader than extant large bodied apes**	**ilium short and broad as in later hominids**
iliac isthmus	likely tall as in large bodied extant great apes	short as in chronologically younger hominids
iliac blades	intermediate between *Pongo* and *Gorilla*	short and broad as in later hominids
Well-developed anterior inferior iliac spine	*protuberance likely developed as a consequence of loading during life; no separate growth physis*	*proportionally large and developed from a separate growth physis as in later hominids*
Short pubic symphysis	*pubic body superoinferiorly short, outline of the pubic symphysis probably thin oval*	*pubic body superoinferiorly elongate, outline of the pubic symphysis rounded oval*
Size of the ischial spine relative to the ischial body	*large****	*ischial spine is not preserved*

Character complexes in **bold**. Singular characters are *italicized*. Character states for *Oreopithecus* from personal observations. Character states for *Ardipithecus* from personal observations, White *et al*. 2009a, 2015; and Lovejoy *et al*. 2009b. ***= pending examination of two published specimens, BAC 182 and BAC 208.

Cell color key:

Claimed as a homoplasy and probably is one.

Claimed as a homoplasy but is probably the primitive condition in *Oreopithecus* and *Ardipithecus*.

Claimed as a homoplasy but *Oreopithecus* anatomy is absent or has been misinterpreted.

Claimed as a homoplasy but further fossils/outgroup assessment required to confirm.

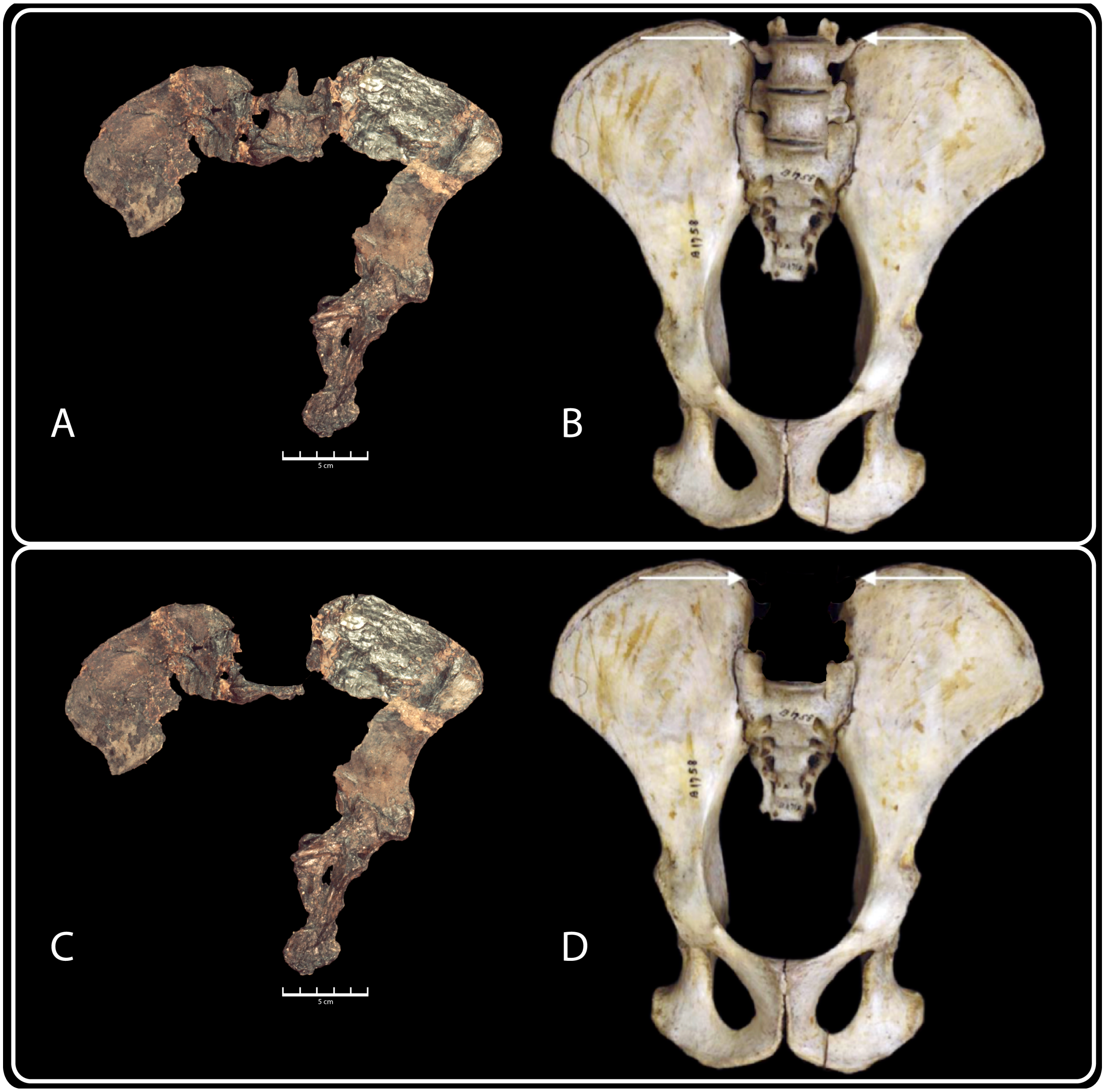

Figure 4.1: Lower lumbar vertebral entrapment in the bi-iliac space in A) *Oreopithecus* IGF 11778 (original, photo taken in 1973) and B) *Pan troglodytes*. The entrapped lumbar has been digitally removed in C) and D).

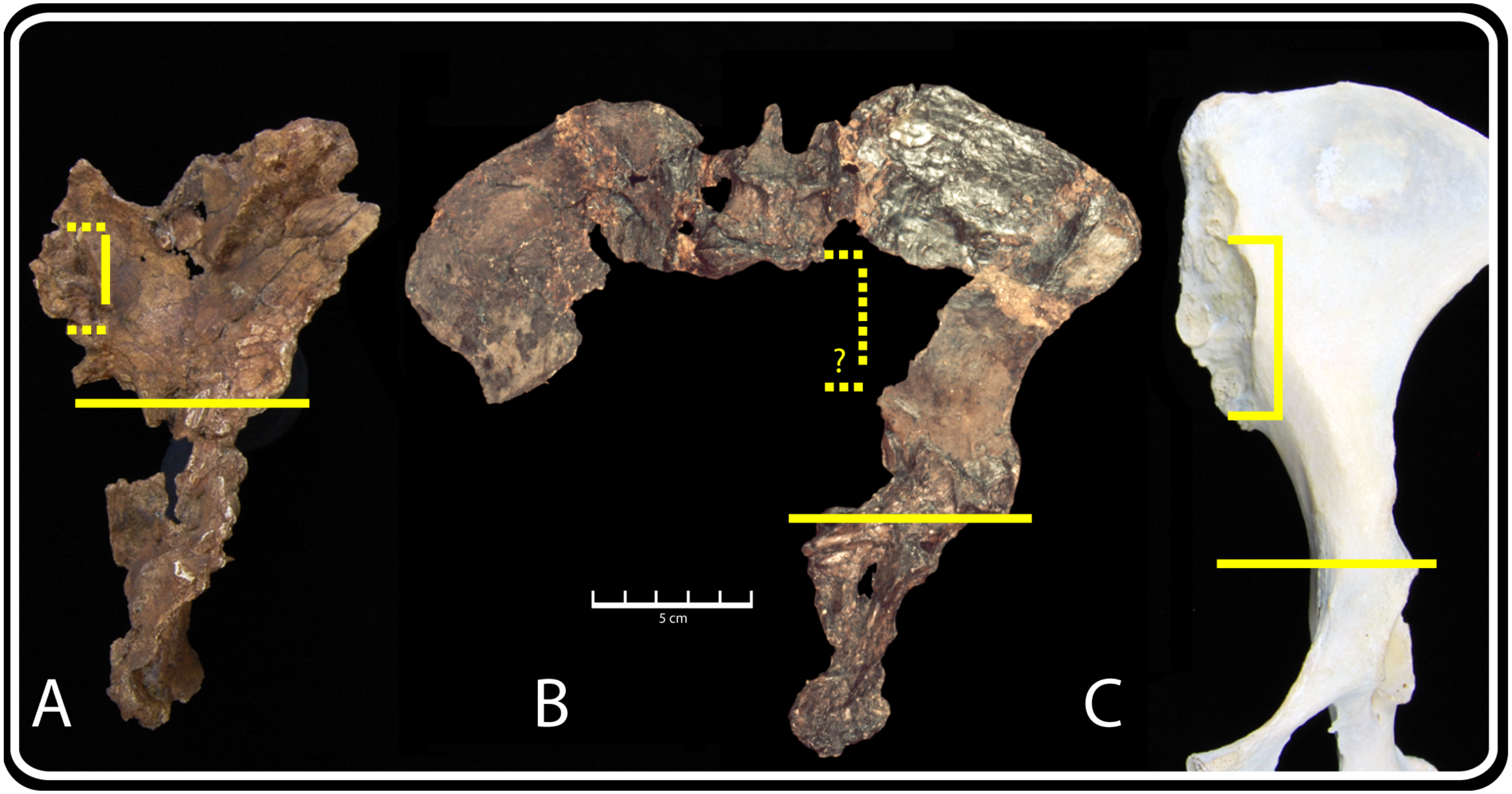

Figure 4.2 Iliac isthmus height in A) *Ardipithecus* ARA-VP-6/500, B) *Oreopithecus* IGF 11778, and C) *Pan troglodytes*. Brackets show the superior and inferior extents of the sacral auricular surface. The extremities for *Ardipithecus* (because of bone loss and crushing) cannot be established with certainty. The extremities of the *Oreopithecus* auricular surface are estimated based on sacral element below the entrapped lumbar and the six-element sacrum from other individuals). The solid line in the brackets for *Ardipithecus* and *Pan* illustrate the anterior margin of the auricular surface. Horizontal lines indicate the upper margin of the acetabulum (its position is estimated in *Oreopithecus* from Rook *et al*. 1999, p. 8797, Fig. 2). The vertical distance between the acetabulum and auricular surface in *Ardipithecus* is short, as in later hominids. Modified from White *et al*. 2015, p. S5, Fig. S4 (see text for discussion).

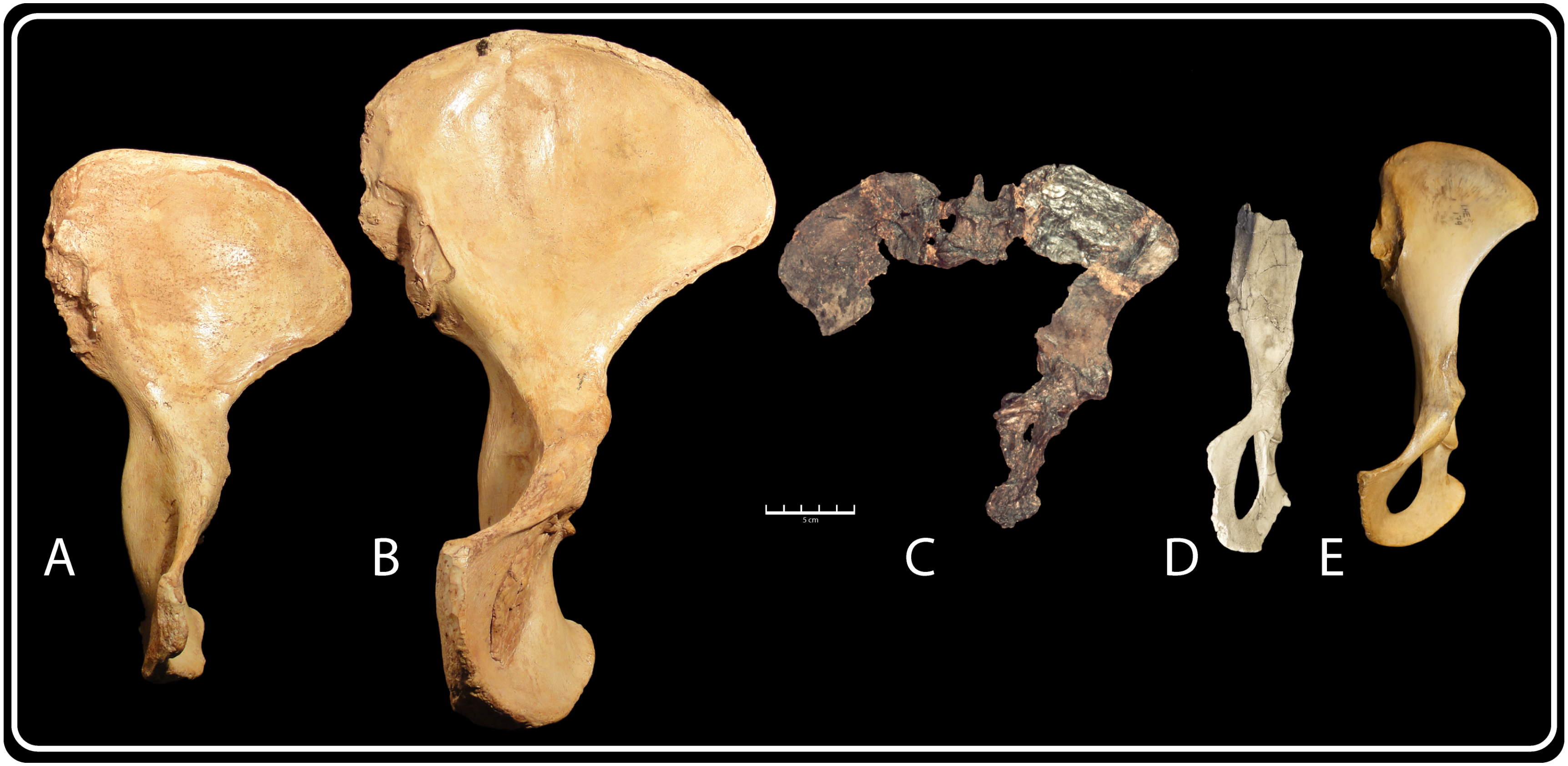

Figure 4.3: Comparative iliac breadth in Hominoidea. A) *Gorilla gorilla* (female) left os coxa, B) *Gorilla gorilla* (male, reversed) right os coxa, C) *Oreopithecus* IGF 111778 right and left os coxae, D) *Proconsul nyanzae* KNM-MW-13142 left os coxa (cast), E) *Pan troglodytes* left os coxa. In this comparison, *Oreopithecus* iliac breadth is most comparable to that of Gorilla.

Figure 4.4: *Oreopithecus* and hominid anterior inferior iliac spine (AIIS) comparisons. Anteromedial view, A) *Ardipithecus ramidus* ARA-VP-6/500 (cast), B) *Australopithecus afarensis* A.L. 288-1 (cast), D) *Australopithecus africanus* STS 14 (cast, reversed), E) *Homo sapiens* (reversed). Yellow arrows indicate the position of the AIIS in the hominid taxa; a blue arrow indicates the position of the "AIIS" in *Oreopithecus*.

Figure 4.5: *Oreopithecus* IGF 11778 radiograph illustrating trabecular bundle density, modified from Rook *et al*. 1999, p. 8797, Fig. 2) Blue oval indicates the position of the claimed anterior inferior iliac spine in *Oreopithecus*.

Figure 4.6: *Oreopithecus* IGF 11778 (cast), whose extraction and preparation now makes interpretation of the anterior inferior iliac spine (AIIS) difficult. In this zoomed view of the claimed AIIS, white arrows indicate carved laminar coal; blue arrows indicate potential bone.

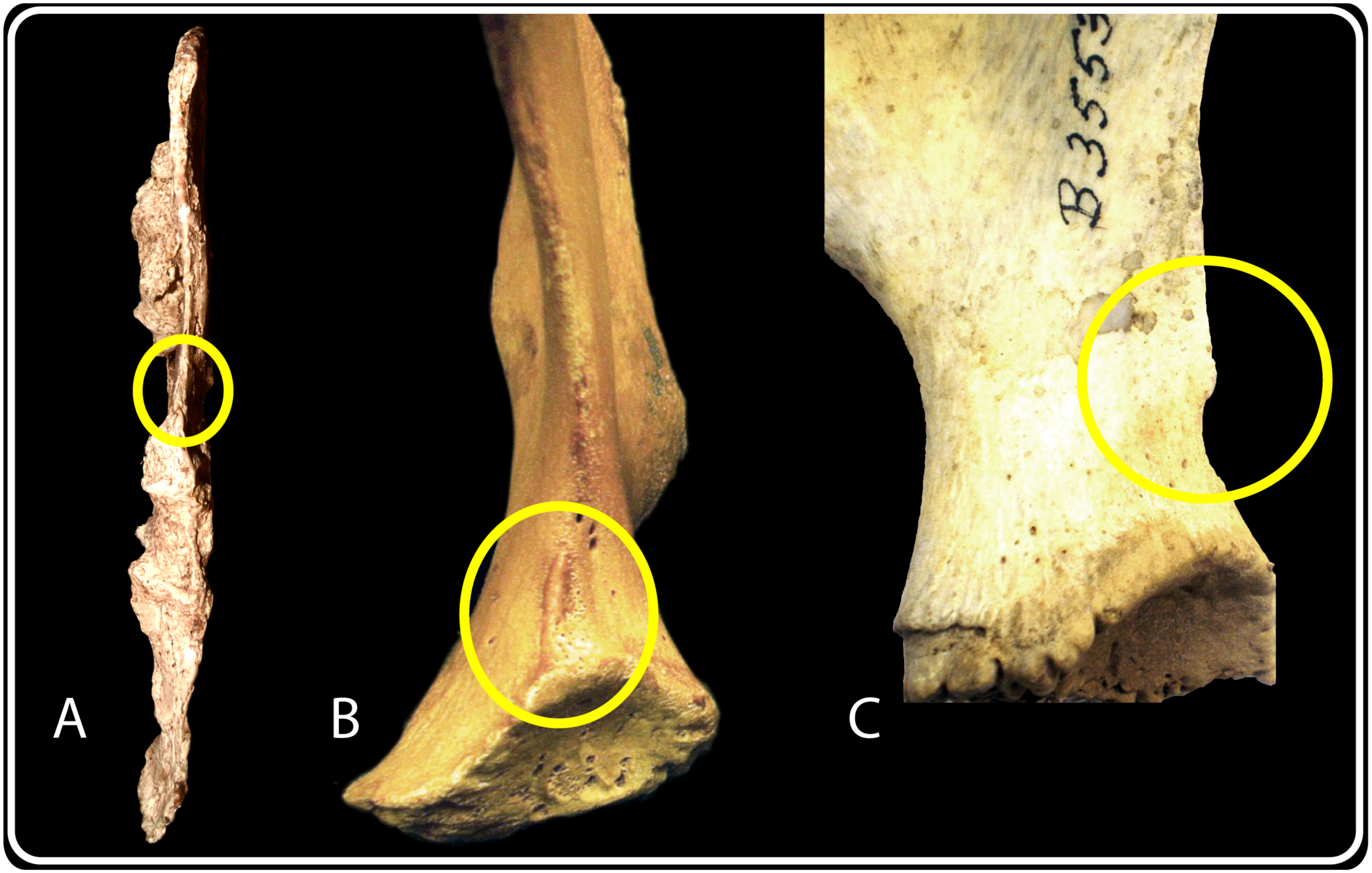

Figure 4.7: *Oreopithecus* and extant African ape "AIIS" comparisons. Anteromedial view; A) IGF 11778 (cast), B) *Gorilla,* C) *Pan*. Yellow circles indicate bony protuberances in this region. B) *Gorilla* and C) *Pan* modified from Zirkle 2015, p. 48 (Fig.19) and p. 45 (Fig. 17), respectively.

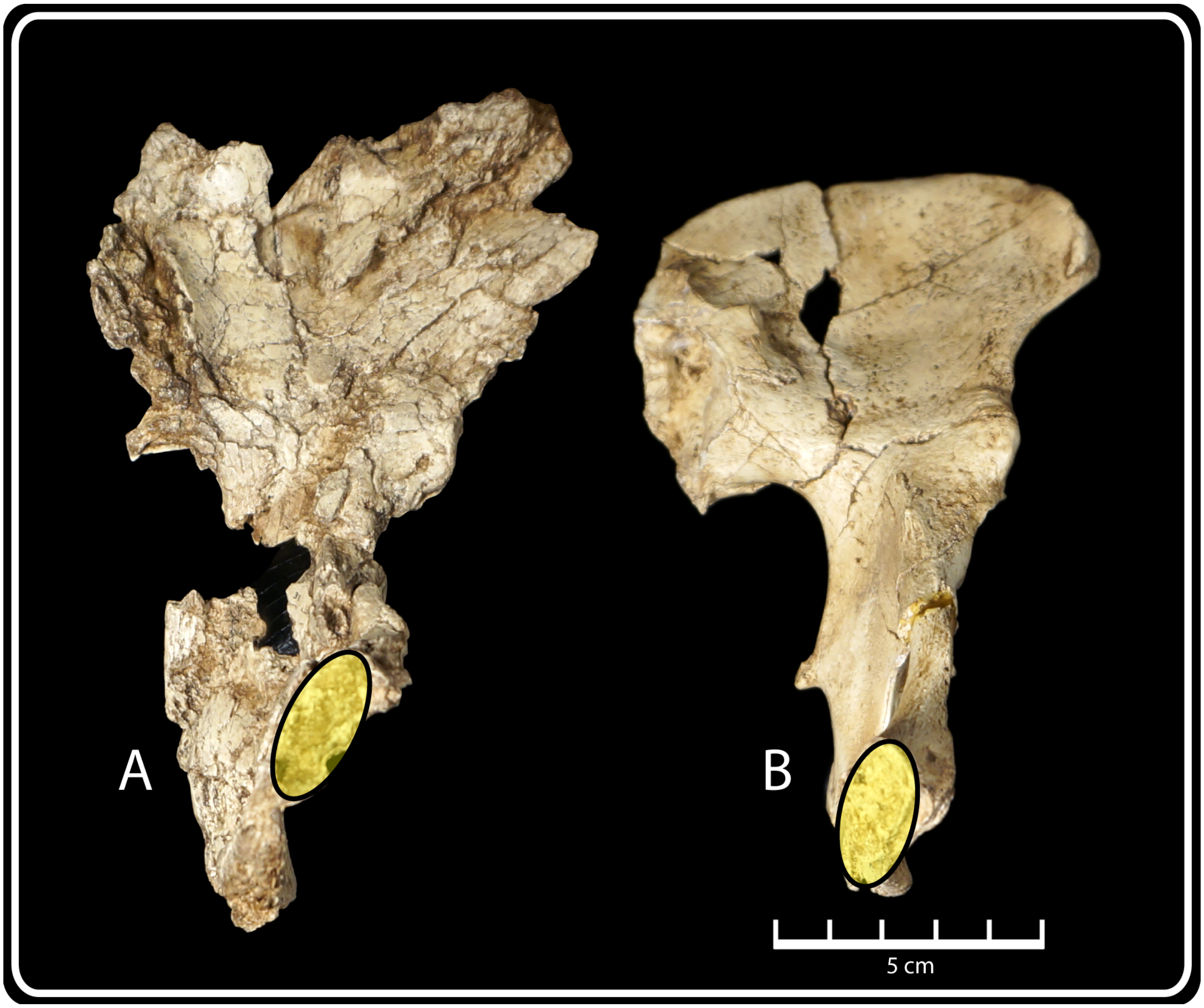

Figure 4.8: Medial views of the pubic symphyses in early hominids. A) *Ardipithecus ramidus* ARA-VP-6/500 (cast, posteromedial view), and B) *Australopithecus afarensis* A.L. 288-1 (cast, posteromedial view). Semi-transparent yellow ovals trace the shape of the pubic symphyseal surface outline.

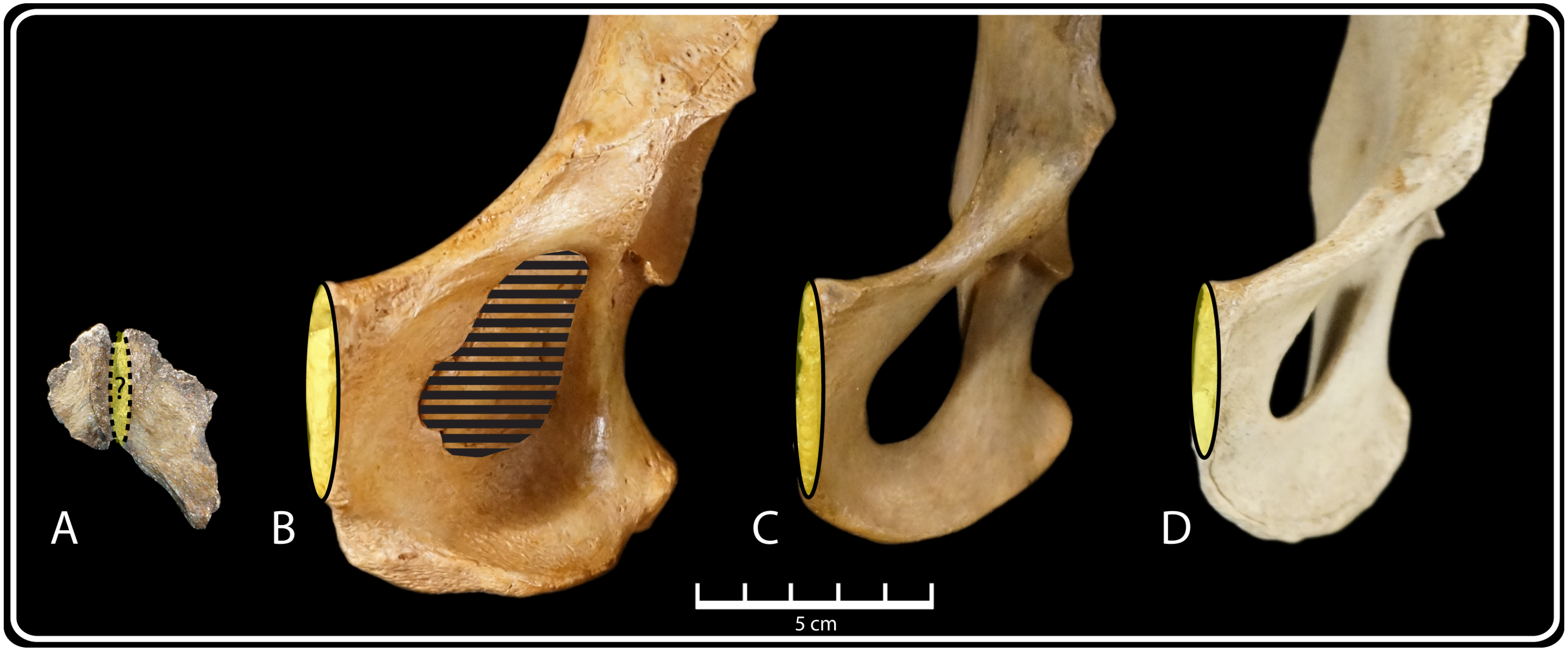

Figure 4.9: Hominoid pubic symphyses. Medially offset anterior view. A) *Oreopithecus bambolii* BAC 71/44, B) *Gorilla gorilla* (cast, plaster-filled obturator foramen is indicated by black striped lines), C) *Pan troglodytes*, and D) *Pongo pygmaeus* (cast). Semi-transparent yellow ovals trace the shape of the pubic symphyseal surface outlines. Like extant great apes, the outline of the pubic symphyseal surface outline appears to be a thin oval in *Oreopithecus*. However, the posterior portion of this fossil is damaged and invaded with coal, preserving no meaningful morphology, so this observation is provisional pending further *Oreopithecus* fossils preserving this anatomy. See text for details.

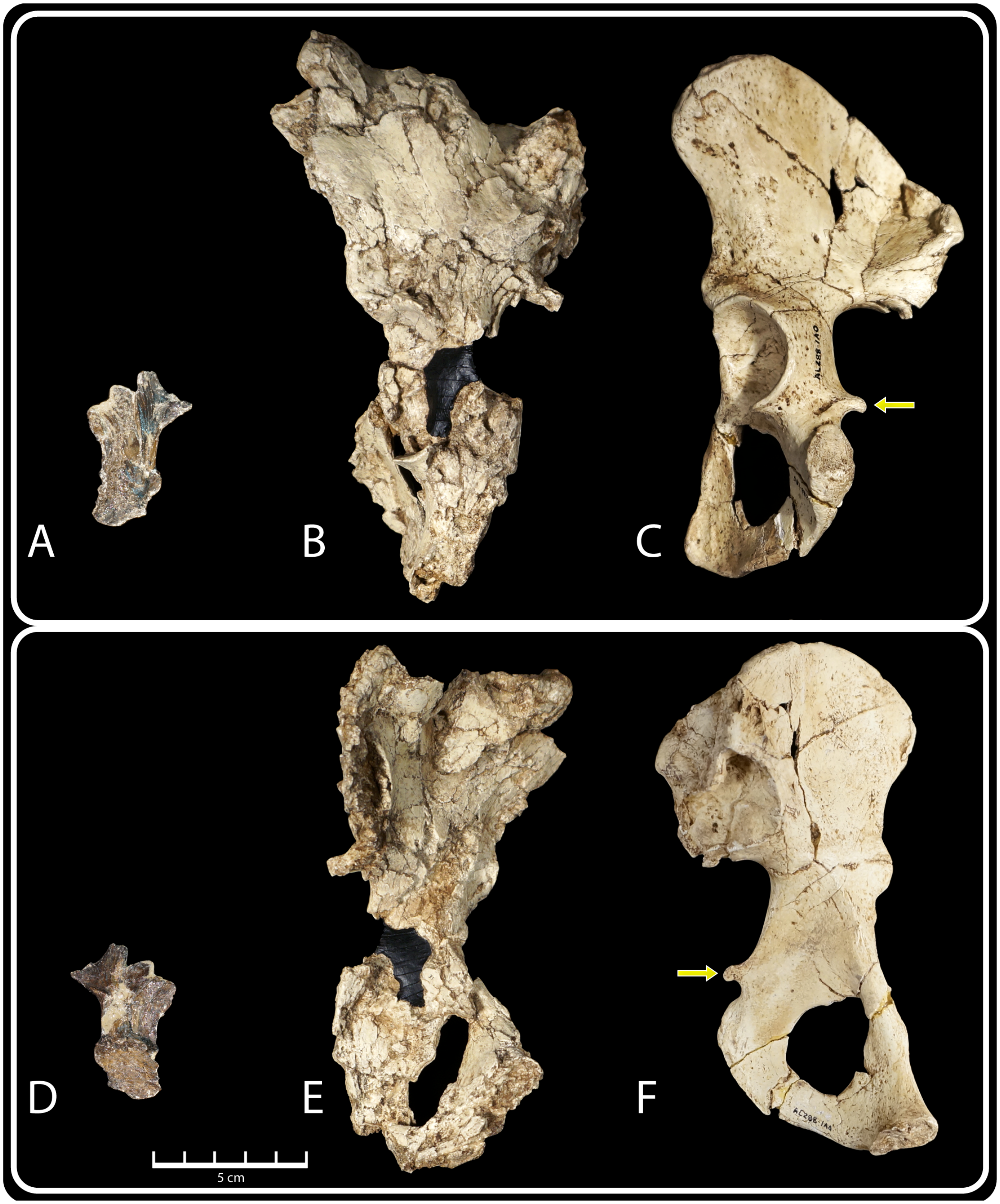

Figure 4.10: *Oreopithecus*, *Ardipithecus*, and *Australopithecus* ischia. A-C: lateral views, D-F: medial views. Arrows indicate the position of the ischial spine in C) and F). A) and D) *Oreopithecus bambolii* BAC 71/44. This specimen was published by Schultz (1960) as a right ischium fragment. Köhler and Moyà-Solà (1997) asserted that this specimen showed evidence of a large ischial spine relative to the length of the ischial body. This specimen was found in spatial association with the specimen in Figure 4.9A, but its anatomy does not resemble any other known hominoid, including *Au*. *afarensis* (see also Figure 4.11 and text for details). B) and E) *Ardipithecus* ARA-VP-6/500 (cast). The region of of the *Ardipithecus* os coxa that might have evidenced an ischial spine is missing, so no comparisons can be made. C) and F) *Australopithecus afarensis* A.L. 288-1 (cast).

Figure 4.11: Hominoid ischial spines. A-E: lateral views, F-J: medial views. Arrows indicate the position of ischial spines in B-E and G-J. A) and F) *Oreopithecus bambolii* BAC 71/44 (see Figure 4.10 caption and text for details), B) and G) *Hyobates sp*., C) and H) *Proconsul nyanzae* KNM-MW-13142 (cast), D) and I) *Pan paniscus* (cast), E) and J) *Pan troglodytes*.

Chapter 5: Claimed Appendicular Skeleton Hominid-like Characteristics of *Oreopithecus*

5.0 Introduction

Elements of the *Oreopithecus* appendicular skeleton have been described and interpreted in a comparative context since Hürzeler's report (1958) on the skeleton (IGF 11778) recovered from Baccinello. Since then, investigators have examined the arms and legs of this skeleton (to date, the only near-complete arms and legs known for this taxon), noting the high intermembral index compared to modern apes (119%, slightly above the range exhibited by *Pan*, Straus 1963) and concluded that it belonged to at least a part-time suspensory ape (Harrison 1987, Jungers 1988, Harrison and Rook 1997).

Hürzeler noted three (3) *Oreopithecus* appendicular skeletal characters that he interpreted as derived and shared (synapomorphies) with hominids (Hürzeler 1968). On the *Oreopithecus* forelimb, he noted that the ulnar attachments for extrinsic muscles of the hand were similar to those in humans. Harrison, however, noted that the extremely poor condition of the complete ulna of the IGF 11778 skeleton prohibited detailed anatomical observations (Harrison 1987). Since then, this potential hominid synapomorphy or homoplasy of the *Oreopithecus* skeleton has not been revisited in the published literature.

The second and third *Oreopithecus* appendicular skeleton characters Hürzeler interpreted as derived and shared (synapomorphies) with hominids concern the femur (Hürzeler 1968). Hürzeler noted a human-like fovea capitis on the *Oreopithecus* femur, and, because *Pongo* lacks this feature and *Pan* expresses it variably, he reasoned that this character must be a derived character shared by *Oreopithecus* and hominids. Harrison noted the prominent fovea capitis in *Oreopithecus* and defined the lack of a fovea capitis in *Pongo* as uniquely derived (autapomorphic) in that genus (Harrison 1987). This character in *Oreopithecus* has not been revisited in the published literature. The third *Oreopithecus* appendicular skeleton character that Hürzeler interpreted as derived and shared (synapomorphic) with hominids is actually a character complex that affects functional diaphyseal angulation of the femur. Hürzeler noted femoral condyles of nearly the same size, with the medial condyle projecting more distally than the lateral condyle, which affects a condition known as genu valgum, or the angling of the distal femora medially, placing the center of mass over the line of gravity. He interpreted this as a hominid synapomorphy in *Oreopithecus* (Hürzeler 1968). Straus had earlier urged caution in the interpretation of this feature in the *Oreopithecus* femur, when he wrote:

> *"But this determination is only an approximation-and hence without deep significance-since it is based upon considerable reconstruction of the badly fractured 1958 left femur."* (Straus 1963, p. 159).

Straus also noted that the nearly equal femoral condyle sizes was a condition more like that in cercopithecoids and hominids than in extant *Pongo*, suggesting that this character in *Oreopithecus* could be primitively shared in *Oreopithecus* and hominids (Straus 1963). Harrison generally agreed, noting that nearly equal femoral condyles (with the medial condyle slightly larger) was a condition common in *Hylobates* and *Cebus* (Harrison 1987). About the interpretation of these condyles as participating in the genu valgum of the distal femora that Hürzeler had asserted, Harrison wrote:

> *"The similarity is not compelling, however, and in view of the crushed and fragmentary nature of the material it provides rather tenuous evidence of a close relationship between* Oreopithecus *and hominids."* (Harrison 1987, p. 555).

Despite these cautions, Köhler and Moyà-Solà attempted to resurrect this claim of hominid similarity in the suite of characters associated with hominid bipedalism that they claimed to be homoplastic in *Oreopithecus*, initially without any data or evidence for their claim (Köhler and Moyà-Solà 1997). Their claim was recently repeated in a far less assertive manner, and in contrast with one of that author's (Harrison) previous work:

> *"Shared similarities associated with bipedal behaviour include… medial and lateral condyles of the distal femur similar in size, possibly associated with a bicondylar angle."* (Wood and Harrison 2011, p. 350)

It is the opinion of this author, in agreement with Straus (1963), the distal femur evidence in *Oreopithecus* is far too fragmentary to evaluate comparatively and/or interpret phylogenetically.

Oreopithecus hand and foot elements, in contrast to the major limb bones, are comparatively better preserved because of their smaller size and higher density. Hand and foot elements were not recovered from the *Oreopithecus* localities until the 1950s. Once recovered from Baccinello, they suffered from poor preservation or a lack of extraction from lignite blocks. The hand from the 1958 IGF 11778 skeleton (it does not preserve pedal elements) and hands and feet from other individuals from Baccinello were not extracted from lignite blocks until the late 1960s-early 1970s (IGF 11778 skeleton, in Florence, Italy) and 1990s (hands and feet belonging to other individuals from Baccinello, extracted in Sabadell, Spain).

These remains were not the subject of extensive published research until the 1980s. Since then, researchers have interpreted the *Oreopithecus* hand as one employed in suspensory behaviors (Susman 1985, 2004, 2005; Marzke and Shrewsbury 2006) or one capable of a hominid-like "precision grip" (Moyà-Solà *et al*. 2004, 2005). Despite the primitive characteristics of the feet noted by most researchers (Riesenfeld 1975, Sarmiento 1987, Szalay and Langdon 1988), Köhler and Moyà-Solà (1997) claimed that the *Oreopithecus* foot was uniquely (to the exclusion of any other primate, save for hominids) adapted for bipedal walking. Here I examine and evaluate each of the two broadly claimed hominid-like character complexes and their subdivided characters of the *Oreopithecus* hand and foot.

5.1 Hand: Human like precision grip

Napier distinguished between "power" and "precision" grips in primates, defining a "power" grip as one where an object is gripped between the palmar surface of the hand and the clenched fingers, with the thumb offering support. He defined a "precision" grip as one of minimal angulation and maximum opposition of the thumb; an object is held between the thumb and finger(s) in pad-to-pad contact (Napier 1956). Great apes and cercopithecoid monkeys employ either type of grip to greater or lesser degree depending on the context (power grip=maximum support when grasping a support object, precision grip=maximum dexterity when grasping an object).

A "precision grip" in hominids has been claimed as an important component in hand-eye coordination and tool-making behavior (Marzke 1997, Marzke *et al*. 1997, Reece *et al*. 1997, Susman 1994, 1998). This characteristic has been similarly invoked as a uniquely hominid trait by others (Alba *et al*. 2003, Almécija and Alba 2014), but not without some controversy (Rolian and Gordon 2014). Moyà-Solà *et al*. argued for the parallel acquisition of a "precision grip" in *Oreopithecus* on the basis of hand length relative to body mass and humeral length, thumb length relative to ray 2 length, the presence of a deep, palmar pit for insertion of the flexor pollicis longus on the terminal pollical phalanx, and the orientation of the capitate/metacarpal 2 articulation (Moyà-Solà *et al*. 1999, 2005). These subdivided characters of the character complex of a hominid-like precision grip are examined and evaluated here.

The *Oreopithecus* hand element sample comprises a partial adult left hand (IGF 11778), a partial juvenile right hand (BAC 140/34), and several partial hands (BAC 151/85, BAC 89/114, BAC 200) preserving mostly broken phalanx shaft fragments. Because BAC 140/34 is a juvenile specimen, and because inferences made on the basis of measured lengths of immature elements are problematical, I do not include them in my analysis. Measurements for the long bones of the adult left hand of the IGF 11778 skeleton are presented in Table 5.1. The IGF 11778 hand elements are illustrated in Figure 5.1.

All *Oreopithecus* specimens are depositionally deformed relative to their *in vivo* anatomy, but relative to other anatomical zones of the skeleton, the two mostly complete hands (IGF 11778 and BAC 140/34) are comparatively well preserved. That said, the deformation of even these elements has led investigators to be mostly conservative in their assignment of individual elements to rays and in their interpretations of these fossils (Straus 1963, Harrison 1987, 1991; Begun 2002, Susman 1985, 2004, 2005). A notable exception to this conservative approach is the examination and interpretation of *Oreopithecus* by Moyà-Solà *et al*. (1999, 2005).

5.1.1 Hand length

Moyà-Solà *et al*. claimed that unlike extant *Pan*, *Pongo*, and fossil *Dryopithecus* (*Hispanopithecus*), who have elongate hands relative to body mass as an adaptation to suspension or vertical climbing, *Oreopithecus* had short hands like pronograde monkeys, *Gorilla*, and hominids (Moyà-Solà *et al*. 1999). These authors further claimed that the elongation of the second through fifth fingers in extant *Pan*, *Pongo*, and fossil *Dryopithecus* had an effect on their ability to execute a precision grip:

> *"Because of their climbing and suspensory behavior, their second-through-fifth fingers are elongated in relation to the body mass (Fig. 1a) whereas the thumb length remains unchanged. The difference in length between the thumb and index finger makes a precision pad-to-pad grip impossible (1, 3). In apes, orthograde body structure and elongated hands are linked inseparably, as they form part of the same adaptative* [sic] *complex functionally related to suspension and vertical climbing."* (Moyà-Solà *et al*. 1999, p. 316).

This claim for hominid homoplasy of this subdivided character of the character complex of a hominid like precision grip in *Oreopithecus* hand is closely related to relative thumb length discussed in Section 5.2.1. Moyà-Solà *et al*. defined hand length as the combined lengths of the lunate, capitate, third metacarpal, third proximal phalanx, third intermediate phalanx, and third distal phalanx (Moyà-Solà *et al*. 1999). They later revised hand length to include only the third metacarpal, third proximal phalanx, third intermediate phalanx in order to allow comparisons with *Hispanopithecus*, which lacks carpal bones (Moyà-Solà *et al*. 2005). In both cases, they normalized hand length by body mass (to account for body size allometry) and humeral length, with the justification that the hands of orthograde apes with large body mass are expected to be long to support their mass while engaging in vertical climbing or suspensory behaviors. Though there was disagreement between Moyà-Solà *et al*. and Susman regarding the correct identification of ray 3 elements, both arrived at a hand length for *Oreopithecus* that, when normalized by body mass, was intermediate between the highly suspensory *Pongo*, *Pan*, and *Hispanopithecus* and the hand lengths of gorillas, *Proconsul*, and *Papio* (Moyà-Solà *et al*. 1999, 2005; Susman 2004, 2005). My examination and measurements of the fossils failed to falsify these findings (See Table 5.1). *Oreopithecus* hands, while more elongate than those of hominids, appear to have not been as elongate as those in *Pongo*, *Pan*, and *Hispanopithecus* relative to body mass.

5.1.1.1 Comparison with *Ardipithecus*

Ardipithecus hand elements from multiple individuals reveal a hominid with short metacarpals and long phalanges (shorter than *Pan*, longer than *Gorilla*). Lovejoy *et al*. described the metacarpals of *Ardipithecus* as shorter than those of African apes, and the phalanges of *Ardipithecus* to be shorter than those of *Pan* but longer than those of *Gorilla*, relative to body mass (Lovejoy *et al*. 2009a). This helps to explain why *Ardipithecus* hand length (as defined by Moyà-Solà *et al*. 1999, 2005 – see above) appears elevated relative to *Homo*.

5.1.1.2 Comparison with fossil and modern hominoids

Oreopithecus hand length relative to body mass is intermediate between the hand lengths of *Gorilla* and its extant suspensory ape counterparts. The relationship between hand length and body mass in orthograde apes appears to be related to locomotor behaviors; for example, relative to *Pan* and *Pongo*, gorillas have short hands relative to their body mass and are primarily terrestrially quadrupedal.

5.1.1.3 Discussion and summary

For fossil taxa, hand length measurements depend on the correct assignment of metacarpals and phalanges to ray and an accounting for any distortion in these elements. Despite disagreements about element identification, it appears that *Oreopithecus* hand length is best interpreted as a symplesiomorphy in *Oreopithecus* and hominids, whereas suspensory *Pan*, *Pongo*, and *Hispanopithecus* have converged on elongate hands by comparison.

Table 5.1 Measurements of the “long bones” of the *Oreopihecus* (IGF 11778) hand.

Element	**Max length**	**Base DP Height**	**Base Max Breadth**	**Base Dorsal Max***	**Base Breadth Volar Max**
MC1	X	X	X	X	X
MC2	(64.62)	(10.67)	(9.84)	X	X
MC3	(65.60)	(10.88)	(9.84)	(9.72)	(8.10)
MC4	(64.62)	(10.58)	(8.21)	(8.16)	(6.39)
MC5	X	X	X	X	X
	Max length	**Base max ML Breadth**	**Base Max DP HT**	**Head Max ML Breadth**	**Head Max DP Height**
PHP1	X	X	X	X	X
PHP2	[42.50]	X	X	{6.50}	{5.50}
PHP3	(46.66)	(10.25)	(8.46)	(7.52)	(7.58)
PHP4	(39.18)	(10.39)	(8.57)	{6.67}	(5.31)
PHP5	(37.97)	(10.27)	(7.19)	(6.29)	(5.70)
IHP2	(25.71)	(9.74)	(7.26)	(7.47)	(4.42)
IHP3	(34.18)	(10.09)	(8.07)	(8.67)	(5.31)
IHP4	(29.98)	(9.66)	(6.72)	(8.25)	(4.90)
IHP5	(23.91)	(8.51)	(7.37)	(7.94)	(4.20)
THP1	(16.36)	(8.42)	(5.31)	(5.87)	(3.84)
THP2	(17.25)	(7.52)	(5.88)	(4.57)	(3.40)
THP3	(20.09)	(8.53)	(5.50)	(5.85)	(3.98)
THP4	(18.77)	(7.74)	(5.49)	(4.60)	(3.71)
THP5	(17.40)	(7.65)	(5.46)	(5.55)	(3.62)
	Max length				
CAP	(14.50)				
LUN	(15.70)				

Measurements in millimeters (mm). X=not present; MC=metacarpal; PHP=proximal hand phalanx; IHP=intermediate hand phalanx; THP=terminal hand phalanx; CAP=capitate; LUN=lunate. ( ) estimated length within 1 mm on distorted elements. [] missing base, length is estimated based on PHP3 and PHP4 bases. {} distorted, estimated based on PHP3 head.

Hand length= MC3 length+PHP3 length+IHP3 length (Moyà-Solà *et al*. 2005). In this *Oreopithecus* specimen, hand length is approximately 146.44mm. See text for details. Data collected from the original fossils by the author.

5.1.2 Thumb length

Moyà-Solà *et al*. contend that *Oreopithecus*, in addition to having short hands, had a long thumb relative to extant great apes (Moyà-Solà *et al*. 1999, 2005). These researchers posit that *Oreopithecus* had a proximal pollical phalanx that was subequal in length to the second ray proximal phalanx. These assertions of course critically depend on the correct identification of phalanges by ray.

Moyà-Solà *et al*. are the first and only investigators who have worked with *Oreopithecus* fossils to identify a thumb proximal phalanx in the IGF 11778 hand (Moyà-Solà *et al*. 1999, 2005). Susman vigorously disagreed with this identification, observing that among other problems, Moyà-Solà *et al*. had incorrectly identified thumb proximal and index finger phalanges and thus used the wrong elements in calculating their thumb/index finger ratios, which they had claimed to demonstrate a relatively long thumb in *Oreopithecus*, similar to that in hominids (Susman 2004, 2005). Specifically, Susman asserted that a ray 5 proximal phalanx was misidentified as by Moyà-Solà *et al*. as a ray 2 proximal phalanx. In addition, Susman claimed that a ray 3 intermediate phalanx was misidentified by Moyà-Solà *et al*. as a pollical proximal phalanx.

I examined the IGF 11778 hand in Florence and concluded that Moyà-Solà *et al*. (1999, 2005) correctly identified (at least in their Figure 3b) the ray 5 proximal phalanx. However, in agreement with Susman (2004, 2005), I found that the phalanx identified by Moyà-Solà *et al*. (1999, 2005) as a proximal pollical phalanx is more likely an intermediate phalanx from ray 3 or ray 4. The bipartite facet for the head of the proximal phalanx on this specimen is not as apparent that in *Pongo* and more closely approximates the shape of the facet in *Pan*, in which the bipartite articular surface for the head of the proximal phalanx is less concave by comparison. In addition, this IGF 11778 phalanx has medial and lateral raised mid-shaft ridges for attachment of the tendons of the flexor digitorum superficialis muscle, a characteristic of intermediate hand phalanges.

Moyà-Solà *et al*. defended their initial identification of the IGF 11778 phalanx as a pollical phalanx by contrasting it with other *Oreopithecus* phalanges that they identified as pollical proximal phalanges (Moyà-Solà *et al*. 2005). These specimens (BAC 200, BAC 83/36, and the juvenile BAC 140/34) are all considerably proximodistally shorter (by ~5-8mm) than the IGF11778 phalanx in question. BAC 200, BAC 83/36, and the juvenile BAC 140/34 may all well by pollical proximal phalanges as Moyà-Solà *et al*. (2005) contend, because their proximal articular surfaces feature a single concavity for the first metacarpal. However, in comparison with the *Hispanopithecus* pollical proximal phalanx that is presented in their Figure 1, the *Oreopithecus* phalanges that the authors contend are pollical proximal phalanges are approximately the same proximodistal length (Moyà-Solà *et al*. 2005).

5.1.2.1 Comparison with *Ardipithecus*

Ardipithecus had short ray 2 through ray 5 metacarpals and a longer ray 1 metacarpal relative to those in extant great apes. In addition, it had longer phalanges than those of chronologically younger hominids. Lovejoy *et al*. demonstrated a metacarpal 1/metacarpal 5 ratio in *Ardipithecus* that approximated that of *Proconsul* and exceeded that of extant apes, concluding that *Ardipithecus* metacarpals were primitively proportioned relative to those of the suspension derived hands of extant great apes (Lovejoy *et al*. 2009a). While a complete thumb from an adult

Oreopithecus individual precludes direct comparisons with *Ardipithecus*, the distorted ray 2 through ray 5 metacarpals in *Oreopithecus* are elongate compared to those in *Ardipithecus* based on a ratio between length and body mass. This observation, in addition to those made in comparison with extant and fossil hominoids (see below), indicate that the *Oreopithecus* thumb was probably proximodistally shorter relative to its rays 2 through ray 5 than those of *Ardipithecus* and chronologically younger hominids.

5.1.2.2 Comparison with fossil and modern hominoids

Relative to extant great apes and fossil *Hispanopithecus,* who have/had extremely short thumbs relative to their elongate rays 2-5, *Oreopithecus* likely had proximodistally longer thumbs. Whereas the adult *Oreopithecus* (BAC 200 and BAC 83/36) proximal pollical phalanges are of similar proximodistal length to the *Hispanopithecus/Dryopithecus* proximal pollical phalanx (Moyà-Solà *et al*. 2005; there is currently no secure taxonomic designation for this element, see Alméija 2012), *Hispanopithecus* ray 2 through ray 5 metacarpals and phalanges were considerably proximodistally longer. The same observation applies to *Oreopithecus* proximal pollical phalanges relative to those in *Pan*, *Pongo*, and to a lesser extent, *Gorilla*. Moyà-Solà *et al*. interpret this difference as consequence of a homoplastic reduction of index fingers in *Homo*, *Papio*, *Theropithecus*, and *Oreopithecus* relative to *Pan*, *Pongo, Hispanopithecus*, and *Gorilla* (Moyà-Solà *et al*. 2005). This hypothesis, however, does not adequately address the elongate metacarpals in *Oreopithecus* relative to those in hominids.

5.1.2.3 Discussion and summary

Ardipithecus fossil hand material reveal that the anatomy, proportions, and function of the hands of extant and fossil large-bodied great apes to be homoplastically derived for suspension, terrestrial knuckle walking, or both (Lovejoy *et al*. 2009a, 2009d, White *et al*. 2009a, 2015). The primitive hand of *Ardipithecus* and chronologically younger hominids reveal that similarities of thumb length relative to ray 2 in *Oreopithecus*, *Proconsul*, *Papio*, and *Theropithecus* are more parsimoniously interpreted as a catarrhine or hominoid symplesiomorphy. Moreover, it is likely, based on its very long forelimbs, very short hindlimbs, and modifications of the lower back (see Chapter 4), that *Oreopithecus* also had a short thumb relative to its other, much longer manual rays, though not to the extent seen in *Hispanopithecus*. This hypothesis awaits testing with further fossils.

5.1.3 Deep pit on terminal pollical phalanx for insertion of the flexor pollicis longus tendon

Moyà-Solà *et al*. describe this character and interpret the fossils in the following fashion:

> *"The application of considerable force to precision grips [precision pinching sensu (2)] is a distinctive human character, and it largely depends on the strength of the flexor pollicis longus, the main muscle that flexes the thumb. All distal thumb phalanges of* Oreopithecus *(IGF 11778, BA#85, BA#140, BA#130, and BA#170) are broad-based and flat proximally, as in hominids and baboons. They show a large, deep, and rough excavation for the insertion of the flexor pollicis longus tendon (Fig. 4 b and c), comparable in size and depth only to that of*

> *hominids. Although apes and monkeys are reported to lack this pit (16), a weak and shallow excavation is found in hylobatids (17),* Papio*, and* Theropithecus *(S.M.-S., M.K., and L.R., unpublished observations). However, it is never as deep as in* Oreopithecus*. All other primates, including* Proconsul*, lack this pit. In* Oreopithecus*, the size and depth of the pit suggest considerable strength for the flexor pollicis longus muscle."* (Moyà-Solà *et al*. 1999, p. 314)

Although it is cited in this paragraph and nine (9) other times in this paper, Marzke wrote of this character:

> *"The fibers supplying the deep pollical flexor tendon generate flexion of the distal phalanx of the thumb, and thus are capable of maintaining both the orientation of its pad toward the fingers and its flexion against pressure by the fingers. Presence of the muscle does not necessarily reflect an emphasis on thumb pad/finger pad grips."* (Marzke 1997, p. 100).

The "deep" pit on the palmar surface of the terminal pollical phalanx in *Oreopithecus* for insertion of the flexor pollicis longus, responsible for opposition of the thumb with the index finger, is shown in the inset in Figure 5.1. The depth of this feature is variable in hominoid taxa, and all are capable, to some degree, of a "precision grip." Indeed, Marzke wrote of the capability of the *Papio hamadryas* hand to execute a precision grip:

> *"The morphological features of particular interest here are those facilitating the thumb pad-index finger distal pad grip, the so-called ''acme'' of human precision gripping stressed in the literature on hominid hand evolution. The features are built into a morphological pattern specialized (with relatively short phalanges) for semi-digitigrade locomotion. First, the index finger is particularly short relative to the thumb (Etter, 1973). Second, the distal interphalangeal joints are capable of extending fully and hyperextending, allowing much of the distal volar pad of the thumb to oppose its counterpart on the index finger (Jude, 1993). This pad-to-pad grip thus provides a relatively large surface area for maintaining hold of small objects. Third, as in the chimpanzee and humans, there is a saddle joint with incongruent surfaces (Rose, 1992) between the trapezium and first metacarpal, which allows the thumb pad to be brought into opposition to the pad of the index finger. Fourth, a tendon originating from the central fibers of the flexor digitorum profundus muscle at the level of the wrist inserts into the base of the distal phalanx of the thumb, in a position to effect the application of pressure by the volar pad against the object held on the volar pad of the index finger. These findings on hamadryas baboons return the thumb pad/index finger pad grip from the exclusive realm of ''refined'' human behavior to membership among grips merely shared with humans. Morphological correlates of the grip in the baboons should be considered among features that might have existed in the hominid ancestral hand prior to abandonment of quadrupedal locomotion."* (Marzke 1997, p. 104).

5.1.3.1 Comparison with *Ardipithecus*

Like *Oreopithecus*, the *Ardipithecus* terminal pollical phalanx showed a "…symmetrically constructed, rugose insertion gable for the flexor pollicus longus, in contrast to African apes, where it is reduced or absent." (Lovejoy *et al*. 2009a, p. 70e1).

5.1.3.2 Comparison with fossil and modern hominoids

Moyà-Solà *et al*. note similarities of *Oreopithecus* and hamadryas baboon hand, and dismiss baboon similarity as a locomotor adaptation. The depth of the attachment site for the tendon of the flexor pollicis longus muscle was not quantified in association with this claim in the original papers where this claim was made (Moyà-Solà *et al*. 1999, 2005). A recent study included a morphometric analysis of the *Oreopithecus* pollical phalanx and conceded morphological similarities of the terminal pollical phalanx in *Oreopithecus* that are shared with chimpanzees and *Proconsul* (Almécija *et al*. 2014). These authors speculated that these similarities suggest that this character is a symplesiomorphy. However, they also posited that nonmetrical traits of the terminal pollical phalanx in *Oreopithecus* (such as the mediolaterally wide tuft and palmarly elevated attachment of the tendon of the flexor pollicis longus) are most similar to hominids, supporting earlier claims of homoplasy in this character (Almécija *et al*. 2014). These authors also note palmarly protruding, mediolaterally wide tufts on the two *Oreopithecus* terminal pollical phalanges, an observation also made for *Orrorin* (Almécija *et al*. 2014, Gommery and Senut 2006).

5.1.3.3 Discussion and summary

Morphological similarities of the attachment site for the flexor pollicis longus on the palmar side of the terminal pollical phalanx in *Papio*, *Proconsul*, *Oreopithecus*, *Ardipithecus*, and all chronologically younger hominids suggest that this character is primitively shared in all hominoids, and that extant African and fossil apes that showed reduced or absent attachment sites may have been derived in parallel with one another.

5.1.4 Capitate/metacarpal 2 articulation

Moyà-Solà *et al*. observed similarities of the capitate-second metacarpal articulation in hominids and *Oreopithecus*. They wrote:

> ''*In* Oreopithecus*, the facet for the capitate on the metacarpal 2 shows a hominid-like transversel [sic] orientation, perpendicular to the facet for metacarpal 3.''* (Moyà-Solà *et al*. 1999: 317).

These observations of a transverse capitate articulation for the second metacarpal (that is, the facet for the second metacarpal is oriented distally and medially on the bone in palmar view) are set against observations these authors made for *Papio*, *Dryopithecus*, and *Pan*, for which this articulation has a sagittal orientation (that is, the facet for the second metacarpal is oriented medially, toward the thumb, and perpendicular to the facet for the third metacarpal in palmar view). Based on my examination of the original fossils, I agree with Moyà-Solà *et al.*'s observations, but not their interpretation of this morphology (see discussion below).

5.1.4.1 Comparison with *Ardipithecus*

The *Oreopithecus* IGF 11778 hand preserves a second and third metacarpal and a capitate with which to compare with *Ardipithecus* and modern hominoids. In addition, an isolated capitate (BAC 151) and second metacarpal (BAC 165) exist for comparisons. In *Ardipithecus*, the capitate-second metacarpal articulation has a transverse orientation (that is, the facet for the second metacarpal is oriented distally and medially on the bone in palmar view) as in *Oreopithecus*.

5.1.4.2 Comparison with fossil and modern hominoids

Marzke summarized the differences between the extant great apes and human capitate-second metacarpal joints. She wrote:

> *''...the joint between the second metacarpal and capitate was oriented distally, away from the sagittal plane, compared with a sagittal orientation in nonhuman hominoid hands.''* (Marzke 1997, p. 101).

In a review of this joint in *Oreopithecus*, Susman observed similarities between *Oreopithecus* and *Homo*, and differences setting both apart from extant great apes (Susman 2005). However, he also observed transverse orientations of the capitate-second metacarpal joint in *Macaque* and *Procolobus* as well as in *Oreopithecus* and *Australopithecus*, and therefore concluded that this character was a primitive character (symplesiomorphy) shared among *Oreopithecus* and Hominidae. Unfortunately, a capitate for *Hispanopithecus* has not yet been recovered. The facet for the capitate on the second metacarpal in this taxon, however, is sagitally oriented, as in extant great apes.

5.1.4.3 Discussion and summary

The characters associated with a hominid-like hand capable of a hominid-like precision grip that are examined and interpreted as homoplastic by Moyà-Solà *et al.* (1999, 2005) are better interpreted as symplesiomorphies after issues of misidentification of elements and mischaracterization of morphology are accounted for in a broadly comparative context. Moyà-Solà *et al.* also claim that the *Oreopithecus* capitate lacks ape-like "waisting" (constriction distal to the capitate head) (Moyà-Solà *et al.* 1999, 2005). This feature has been noted as a suspensory adaption in order to facilitate midcarpal locking (Lewis 1971, 1989). Given the fact that synovial joints do not "lock," (Lovejoy *et al.* 2001) capitate "waisting" is of little utility in interpreting the phylogenetic significance of the *Oreopithecus* capitate. Lovejoy *et al.* wrote in 2009:

> *"Frictionless synovial diarthroses promote motion, and joints do not normally lock because it is hazardous to their structure (41). In most joints, stability is instead almost entirely the responsibility of ligaments and soft tissues [contractile and connective tissue (noncontractile) components of the joint's surrounding*

> *muscles (63)]. If these did not arrest motion at and near full midcarpal dorsiflexion (64), the capitate's precipitous distal expansion would habitually strain the scaphoid-lunate syndesmosis, leading to its deterioration and instability…functions assigned to minor surface topographic fluctuations of the scaphoid, capitate, and hamate reflect only the ontogenetic interplay of cartilage modeling, positional information, and the stabilizing soft tissues surrounding these joints. Mere concavities (or ridges) on synovial surfaces are almost never able to restrict motion and are more likely to merely reflect its limits as dictated by the joint's surrounding soft tissues (63). These features reflect the joint's likely kinematics, but little about its kinetics."* (Lovejoy *et al*. 2009a).

Whereas the presence or absence of ape-like "waisting" of the capitate is thus irrelevant to whether or not *Oreopithecus* engaged in suspensory activities, other aspects of the "central joint complex" of the *Oreopithecus* hand perhaps are. The proximal base of the third metacarpal (left side, IGF 11778) in *Oreopithecus* features a convex palmar capitate surface, a dorsolateral styloid element, and a medial canal for a large carpometacarpal ligament (also present on the medial capitate) as in *Pan*. As Susman (2004) notes, morphology of the scaphoid (which serves as a sort of anchor for the long bones of the thumb) is not addressed in the Moyà-Solà *et al*. (1999, 2005) arguments. In *Oreopithecus* the scaphoid is proximodistally thin with an unfused os centrale, as in *Pongo*.

Ardipithecus and indeed all later hominids have hands with several primitive characters relative to extant apes – thumb lengths are not reduced relative to metacarpal lengths, hands are not elongate relative to *Pan* and *Pongo*, there is no morphology consistent with knuckle-walking, and there are no modifications of the CJC to prevent palmar rotation during suspension. In contrast, the *Oreopithecus* hand, whose moderately long hand length and short thumb length relative to that in hominids, is consonant with an aggregate pattern of below-branch suspensory behavior. Though not as derived for suspensory behavior as *Hispanopithecus* (whose long hands resemble *Pongo*), its long forelimbs terminated in a long hand with curved phalanges, with a *Pongo*-like scaphoid supporting a putatively short (relative to hominids) thumb.

5.2 Foot: A grasping organ deployed in bipedal locomotion

The hominid foot is an important component of an orthograde, bipedal locomotor repertoire, functioning to absorb shock and to act as a propulsive lever during toe-off while walking. As such, any inferential claims of facultative or habitual bipedality relative to pelvic and hindlimb anatomy of fossil hominoids by definition must reconcile the functional morphology of the foot in taxa for which foot elements are available. Fortunately for *Oreopithecus*, there are two partial feet of the same individual, along with a few isolated pedal elements of other individuals.

Straus (1963) commented briefly on the isolated tarsal elements, and Riesenfeld (1975) determined *Oreopithecus* metatarsal robusticity compared to humans and gorillas. Szalay and Langdon (1987) delivered a complete report of a partial composite foot comprising elements of the left and right feet from a presumed single individual from Baccinello (described below; the 1958 IGF 11778 skeleton does not preserve the feet). Szalay and Langdon (1987) concluded that the *Oreopithecus* foot was chimpanzee-like in its form and function, with "loose" tarsal articulations facilitating climbing but not leaping (as in cercopithecoids) or hanging (as in *Pongo*).

Köhler and Moyà-Solà, in their comprehensive attempt to argue for hominid-like positional and locomotor behavior for *Oreopithecus* (1997), disagreed with Szalay and Langdon (1987) and claimed a completely autapomorphic foot for *Oreopithecus*. They claimed a "permanent" lateral abduction of rays 1-4 away from the hallux, midfoot rigidity of the second and third metatarsals along their articulations with the cuneiforms, a medial deviation of force transmission unlike all other primates, minimally curved metatarsals, and a calcaneal tuber perpendicular to the ground, suggesting orthogonal orientation of the tibia-astragalar orientation (for their reconstruction of the *Oreopithecus* foot, see figure 5.2). Moreover, they claimed that *Oreopithecus* would have been a poor climber because it lacked the ability to "…transmit support reaction forces acting on the lateral border of the foot" because of what they inferred is a novel fifth metatarsal-cuboid articulation (Köhler and Moyà-Solà 1997, p. 11748). They further argued that foot proportions (power/load arm ratio, which scales allometrically with body mass) of *Oreopithecus* reflect a short-footed, large-bodied animal capable of propulsive forward foot movements on the ground, like gorillas (because of body mass) and humans (because of bipedality). The authors concluded that *Oreopithecus* feet were deployed as "tripods" capable of "bipedal shuffling" during food harvesting in a predator-less environment (Köhler and Moyà-Solà 1997).

No investigators have explicitly itemized the *Oreopithecus* pedal characters that they interpret as derived and shared (synapomorphies) or acquired in parallel (homoplasies) with hominids. Köhler and Moyà-Solà list a suite of characters of the *Oreopithecus* foot that they interpret as follows:

> *"Compared with the postcranial anatomy of the suspensory vertical climber and hypothetical ancestor,* Dryopithecus*, we interpret these many morphological features of* Oreopithecus *as autapomorphies and not as primitive retentions."* (Köhler and Moyà-Solà 1997, p. 11749)

Sarmiento asserted that qualitative pedal characters of *Ardipithecus* listed as exclusively shared with later *Australopithecus* in White *et al*. (2009a) were invalid hominid synapomorphies because "…nearly all…appear in early hominoids (i.e., *Oreopithecus* and *Dryopithecus*)." (Sarmiento 2010, p. 1105-b). Included in Sarmiento's list of postcranial characters were the following pedal characters: robust second metatarsal base and shaft, dorsally domed second to fifth metatarsal heads, and upwardly canted proximal foot phalanges. It is unclear which of these characters (or taxa) Sarmiento is arguing possessed these anatomical characters. Moreover, Sarmiento's previous work with *Oreopithecus* foot elements suggested a primitive rather than derived hominoid pattern:

> *"…the ratios of the tarsus and metatarsus of* Oreopithecus *as well as those features which are associated with restricted movement at the midtarsal and tarsometatarsal joint are what may actually be expected in a generalized hominoid."* (Sarmiento 1987, p. 25).
>
> *"The Oreopithecus navicular best corresponds to the foot of an arboreal vertical climber. A relatively mobile foot with a wide opposable grasp, this foot could be*

> *apposed against vertical trunks when climbing, or used along horizontal supports of diameters permitting hallucal grasps."* (Sarmiento and Marcus 2000)

Despite the lack of claims for hominid pedal syanapomorphies or homoplasies in *Oreopithecus* in the published literature, an examination of the asserted bipedal propensity of the *Oreopithecus* foot offered in Köhler and Moyà-Solà (1997) follows below.

5.2.1 The *Oreopithecus* evidence

Table 5.2 List of elements of *Oreopithecus* partial feet

Specimen Number	Elements
BAC 79/37	L. FOOT (AST, CAL, NAV, MED. CUN)
BAC 83/36	R. FOOT (AST frag, CUB, MED. CUN, INT. CUN, LAT. CUN. MT1-5, PFP, TFP)
BAC 120	R. MT2 (prox), IPX (n=2), TPX (n=2)
BAC 136/50	Lignite block: FOOT (L. MED CUN + MT frag (prox) + 3 MT shafts + 3 PPX + 3 IPX + 3 TPX)
BAC 151/85	MT (shaft) + 2 PPX + 2 TPX
BAC 152/37	L. INT. CUN+ L. MT3 + PPX (frag) + L. MED CUN+ R. MT4 (prox.) (associated with BAC 79/37)
BAC 154/94	L. MT2 (prox.)
BAC 158/71	FOOT: R. MT1 (dist) + L.MT3 (prox) + R. MT4 (prox) + PFP1 + CUB
BAC 159/111	L. MT2 (prox) + 3 PPX (dist) + IPX (dist) + IPX + PHX (shaft) + TPX (prox)
BAC 160/77	MTP (dist frag) + IPX (prox) + 2 IPX (dist)
BAC 165/72	R. LUN + R. CUB (frag) + L. MEDCUN + R. MT3 + SESAMOID
BAC 166	L. MT1 (prox) + IPX (prox)
BAC 171	MT (dist) + PPX + PPX (dist) + IPX + TPX + 3 PHX frags
BAC 179	L. MT4 (prox)
BAC 208	L. MT4 (prox)

AST=astragalus; CAL=calcaneus, NAV=navicular; MED. CUN=medial cuneiform; INT. CUN=intermediate cuneiform; LAT. CUN=lateral cuneiform; CUB=cuboid; MT=metatarsal; PFP=proximal foot phalanx; TFP=terminal foot phalanx; PPX=proximal phalanx; IPX=intermediate phalanx; TPX=terminal phalanx.

A lignite block from Baccinello was prepared at the Naturhistorishes Basel in the 1970s and it contained the remains of the right and left feet of presumably the same individual (see Table 5.2); the medial cuneiforms are reasonably inferred to be antimeres. Preservation of the fossils, particularly the tarsal elements, is comparatively better than most of the *Oreopithecus* assemblage, with only the right astragalus demonstrating the typical crushing distortion. The hallux is nearly complete, and as for all other apes and the hominid *Ardipithecus*, it is abducent relative to the other pedal rays. These *Oreopithecus* metatarsals do not preserve their heads. BAC 83/36 preserves single proximal and terminal phalanges.

5.2.2 Comparison with *Ardipithecus*

The *Ardipithecus* foot reveals a mosaic; it had an abducted hallux that aided in grasping during climbing and a rigid midfoot interpreted to function as a lever during toe-off during bipedal walking (in *Ardipithecus*, the lever was ray 2 rather than ray 1 as in all later hominids) (Lovejoy *et al*. 2009c). The abducted hallux in *Ardipithecus* is similar to that in *Oreopithecus*; however, both the medial cuneiform and the articular surface with which it articulates in *Ardipithecus* is proximodistally longer. Where the *Ardipithecus* and *Oreopithecus* feet differ most is the lateral midfoot.

The *Ardipithecus* cuboid is proximodistally long relative to *Oreopithecus*, with a distinct facet for the os peroneum of the fibularus longus tendon, a feature that is absent on the *Oreopithecus* cuboid. The articulation for fifth metatarsal on the *Ardipithecus* cuboid is flat; on the *Oreopithecus* cuboid this articulation swoops laterally and slightly posteriorly, suggesting a slightly greater range of mobility in this articulation.

5.2.3 Comparison with fossil and modern hominoids

Several features of the *Oreopithecus* tarsus resemble their extant ape counterparts. The lateral foot is short, with a proximodistally short cuboid (see Figure 5.3). This cuboid features a narrow and deep groove for passage of the fibularus longus that participates in adducting the hallux, as with chimps, gorillas, and orangutans and unlike the fibularus longus in *Australopithecus* and all later hominids, where it serves as support during plantarflexion (Lovejoy *et al.* 2009c). Contrary to Köhler and Moyà-Solà's (1997) observations of nearly equal medial and lateral crests of the *Oreopithecus* astragalus, the lateral crest is higher and longer, as in all other extant apes. The navicular is relatively proximodistally short, with articular facets for the cuneiforms that follow the curve of its distal surface, as in *Proconsul* and *Pongo*, and in contrast to cercopithecoids. This feature has been interpreted to relate to climbing (Langdon 1986, Sarmiento and Marcus 2000).

Unlike modern apes, *Oreopithecus* metatarsals have been reported to be short relative to body mass (Riesenfeld 1975, Szalay and Delson 1979, Szalay and Langdon 1987). This appears to be the case in the single specimen preserving all metatarsals.

5.2.4 Discussion and summary

The *Oreopithecus* foot superficially resembles that of *Ardipithecus* in that both taxa possessed an abducent hallux (Szalay and Dagosto 1988, Lovejoy *et al*. 2009c). However, the midfoot of both reveal divergent evolutionary paths. In *Ardipithecus*, the midfoot is relatively elongate and laterally rigid, suggesting terrestrial, bipedal competence in its utility as a propulsive lever, despite retaining the ability for hallucial grasping while climbing. *Ardipithecus* retained an os peroneum as indicated by the facet for it on the elongate cuboid, an important clue for what would eventually be an important character in *Homo* (Lovejoy *et al.* 2009c).

Oreopithecus demonstrated mobility for climbing in its proximodistally shortened midfoot, as in the great apes, and this mobility would have made for poor propulsion in association with what Köhler and Moyà-Solà (1997) interpret as "bipedal shuffling". While the *Ardipithecus* mosaic foot form suggests rapid evolution under strong selection in hominids that chronologically followed it (with the notable and currently unresolved exception of the Burtele foot, see Haile-Selassie *et al*. 2012), the *Oreopithecus* foot is consistent with other aspects of its postcranial anatomy in suggesting below-branch suspensory and vertical climbing locomotion.

5.3 Conclusions

In this chapter, I have examined and evaluated claims of hominid similarity of the *Oreopithecus* appendicular skeleton, particularly the hand and foot. These claims relate primarily to proportions of key elements and resultant interpretations of function in these organs. The claim for a hominid-like, pad-to-pad precision grip relates to inferred relative pollical length and overall hand length (Moyà-Solà *et al*. 1999, 2005), assertions that are not supported by the comparative evidence. In turn, this suggests that *Oreopithecus* relied most frequently on an ape-like power grip. Likewise, the claim for a foot as a grasping organ deployed in bipedal locomotion in *Oreopithecus* (Köhler and Moyà-Solà 1997) is incompatible with its ape-like short and mobile midfoot.

In summary, claims for hominid homoplasy in characters of the *Oreopithecus* appendicular skeleton presented in this chapter are uniformly falsified. These characters in *Oreopithecus* are likely hominoid symplesiomorphies; further fossils and outgroup assessment will be needed to confirm these inferences (See Table 5.3).

In the concluding chapter, I will summarize my examination and evaluation of claims of homoplasy made for all characters of the *Oreopithecus* skeleton and suggest directions for future research.

Table 5.3 *Oreopithecus* and *Ardipithecus* appendicular skeleton characters

Appendicular skeleton character	***O. bambolii***	***Ar. ramidus***
Human-like precision grip (character complex)	**partially capable, likely relied on power grip (see text)**	**present**
short hand length	intermediate-long (long metacarpals and long phalanges)	intermediate-long (short metacarpals and long phalanges
long thumb	intermediate between *Proconsul* and hominids?	present
long proximal pollical phalanx	intermediate relative to PHP2 comparison with extant great apes?	intermediate relative to PHP2 in comparison with extant great apes
deep pit on THP1 for attachment of flexor pollicis longus tendon	present	present
Capitate-metacarpal 2 articulation	transverse	transverse
Grasping and bipedally efficient foot	prehensile midfoot, no more bipedal than *Gorilla*	rigid midfoot, facultatively bipedal

Character complexes in **bold**. Character states for *Oreopithecus* from personal observations. Character states for *Ardipithecus* from personal observations, White *et al*. 2009a, 2015; and Lovejoy *et al*. 2009a, 2009c.

Cell color key:
Claimed as a homoplasy and probably is one.
Claimed as a homoplasy but is probably the primitive condition in *Oreopithecus* and *Ardipithecus*.
Claimed as a homoplasy but *Oreopithecus* anatomy is absent or has been misinterpreted.
Claimed as a homoplasy but further fossils/outgroup assessment required to confirm.

Figure 5.1: *Oreopithecus* (IGF 11778) left hand, palmar view. Yellow circle indicates the phalanx claimed by Moyà-Solà *et al*. (1999, 2005) to be a pollical proximal phalanx but is in fact an intermediate third ray phalanx (see text for details). **Inset**: Pit (indicated by semi-transparent yellow outline) on terminal pollical phalanx for insertion of the flexor pollicis longus tendon in A) *Oreopithecus bambolii* BAC 130/99 and B) *Ardipithecus ramidus* ARA-VP-6/500-049 (cast).

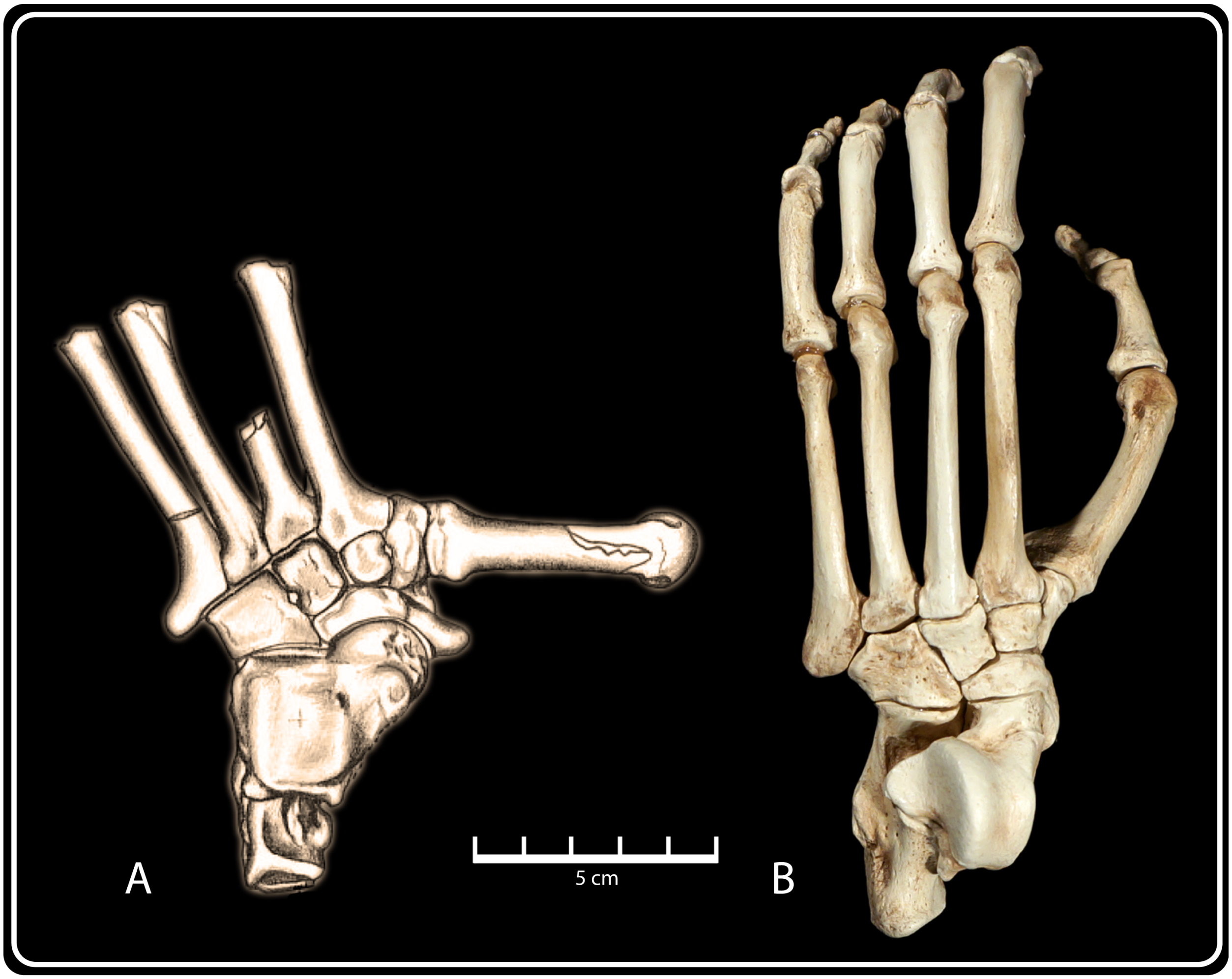

Figure 5.2: *Oreopithecus* foot reconstruction. A) Illustration of left foot modified from Köhler and Moyà-Solà 1997 (p. 11749, Fig. 3) based on BAC 79/37 and BAC 83/36, right and left foot of the same individual and B) *Pan troglodytes*, right foot (cast, reversed).

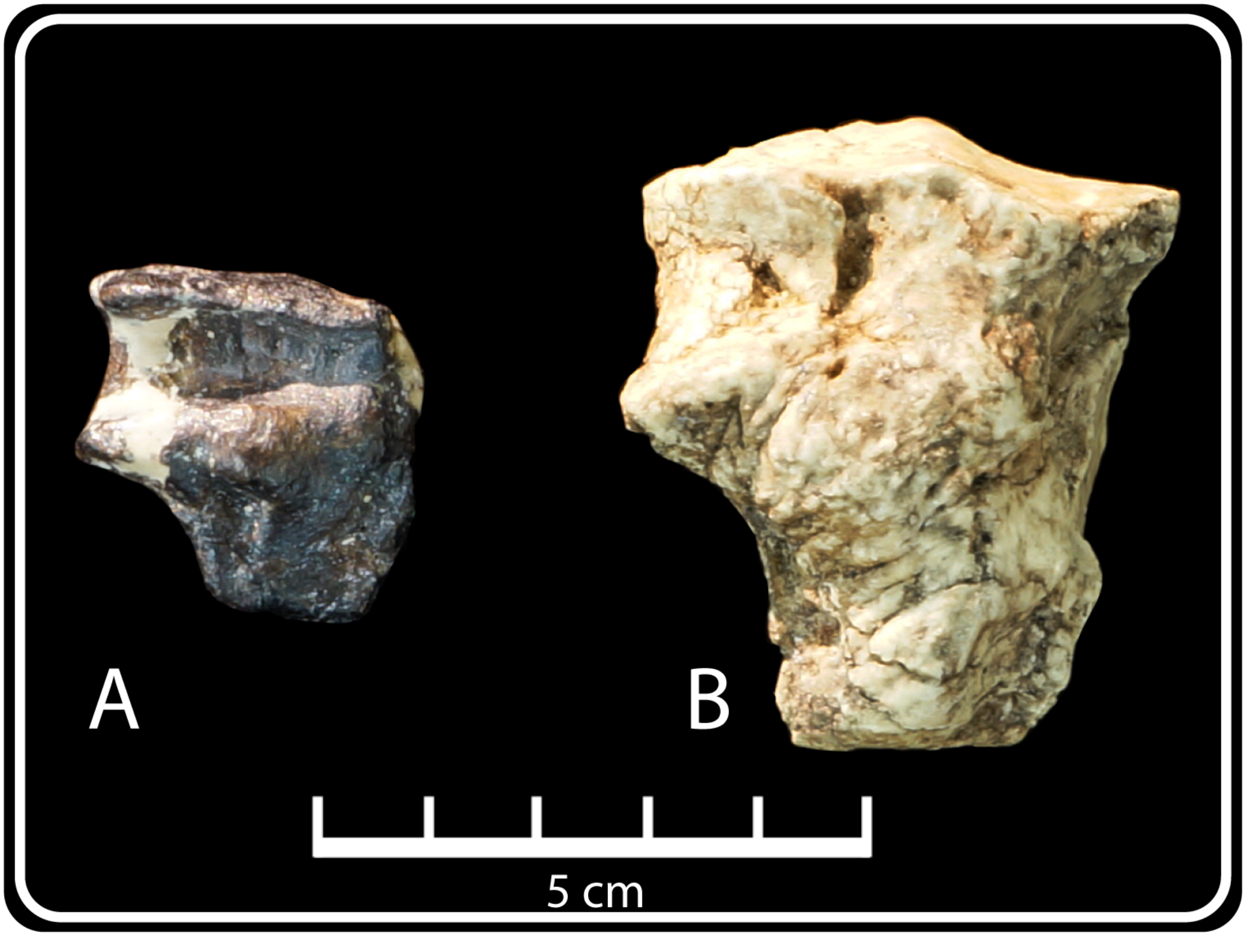

Figure 5.3: *Oreopithecus* and *Ardipithecus* cuboids. Plantar view, distal is up. A) *Oreopithecus bambolii* BAC 83/36 and B) *Ardipithecus ramidus* ARA-VP-6/500-081.

Chapter 6: Conclusions

6.0 Introduction

This dissertation examined key skeletal and dental characters claimed historically to be hominid synapomorphies or homoplasies in *Oreopithecus* (see Appendix 2). All of these have recently been featured in arguments regarding the placement of *Ardipithecus* as a phylogenetic hominid (in the sense of the nomenclature outlined in Chapter 1). This study is the first to evaluate decades-old claims of hominid similarity in *Oreopithecus* and recent comparisons of this taxon with *Ardipithecus ramidus*. Indeed, many of the old claims of *Oreopithecus* hominid-like similarity have been recently resurrected in attempts to deploy them as evidence of homoplasy in Hominoidea in general, and in particular, to raise doubts about the hominid status of *Ardipithecus* (Sarmiento 2010, Wood 2010, Wood and Harrison 2011).

The paramount goal of my study has been to address both the original and the more recent claims of hominid similarity in *Oreopithecus* (see Chapter 2, section 2.5; Chapters 3-5) in a descriptive, qualitative fashion (and quantitatively where preservation of the fossils has allowed). The approach centered on determining whether the claims for hominid anatomical similarity in *Oreopithecus* are based on morphology that 1) can actually be confidently observed; 2) has been reported accurately; and 3) represents anatomy that is primitive relative to *Oreopithecus*, or evolved in parallel (homoplasy) or exclusively (synapomorphy) with *Ardipithecus* and later hominids.

6.1 Research questions

Three research questions were presented in Chapter 2, Section 2.4:

(1) Is the claimed morphological feature present/observable, or can it be reasonably inferred on the basis of the actual fossil evidence?

(2) If the claimed morphological feature is verified as present/observable, has the feature been accurately diagnosed in hominids (*Australopithecus, Ardipithecus*, and others)?

(3) Can allegedly shared characters that remain after testing per (1) and (2) be diagnosed as symplesiomorphic (shared primitive), synapomorphic (shared derived), autapomorphic (uniquely derived) or homoplastic (evolved in parallel)?

The descriptive comparisons made between *Oreopithecus* and *Ardipithecus* (as well as with other hominoids) in the context of the claims of hominid synapomorphy or homoplasy in *Oreopithecus* presented in Chapter 3 (craniodental), Chapter 4 (axial skeleton), and Chapter 5 (appendicular skeleton) directly bear on these research questions. The results of those comparative tests are presented below.

6.2 Findings

6.2.1 Response to research questions

The results of each tested hypothesis for hominid-similiarity (research question 2) presented in Chapter 2, section 2.5, and evaluated in Chapters 3 (craniodental), 4 (axial skeleton), and 5 (appendicular skeleton) are presented in Table 6.1 below, with background found in the previous three chapters and in Appendix 2 (that outlines sources of various claims).

Table 6.1 *Oreopithecus* and *Ardipithecus* skeletal characters.

KEYS: C=canine, U=Upper, L=lower, M1=first molar, P3=third premolar. Character complexes in **bold**. Singular characters are *italicized*. ***= pending examination of two published specimens, BAC 182 and BAC 208. Character states for *Ardipithecus* from personal observations, Lovejoy *et al*. 2009a, 2009b, 2009c*;* Suwa *et al*. 2009a, 2009b; and White *et al*. 2009a, 2015.

Cell color key:
Claimed as a homoplasy and probably is one.
Claimed as a homoplasy but is probably the primitive condition in *Oreopithecus* and *Ardipithecus*.
Claimed as a homoplasy but *Oreopithecus* anatomy is absent or has been misinterpreted.
Claimed as a homoplasy but further fossils/outgroup assessment required to confirm.

Craniodental character	***O. bambolii***	***Ar. ramidus***
Short face (character complex)	**anteroposteriorly short**	**anteroposteriorly short**
implantation of incisors	near vertical	near vertical
zygomatic root position	zygomatic root more anterior (M1)	zygomatic root more anterior (M1)
Upper canine relative to upper first molar (UC basal diameter divided by UM1mesiodistal length)	*small*	*small*
Upper canine shape feminization (character complex)	**males unfeminized, higher crowned, lower shoulder**	**male C feminized in shape**
shoulder height	low	mid to high
shoulder flare	weak	distinct flare
lingual marginal ridge	weak	fold-like
main mesial lingual ridge	moderate	basally broad
crown height	males tall, females moderate	UC height differentially reduced
Lower canine relative to lower first molar (LC basal diameter divided by LM1mesiodistal length)	*small*	*small*
Lower canine shape feminization (character complex)	**males higher crowned, modally low mesial shoulder, weak/no distal tubercle**	**feminized**
mesial shoulder height	intermediate	intermediate?
lingual marginal ridge	weak or none	fold-like

distal crest	weak	weak
distal tubercle	weak	developed
Sectorial UC/LP3 honing (character complex)	**present, strong in males**	**absent**
UC distolabial sharpening	present	absent
LP3 wear	hones UC	mostly horizontal?
LP3 basal crown size/shape	obliquely elongate	basally expanded and large
LP3 crown height	tall, slightly posteriorly oriented	low and squat
LP3 metaconid	weak	rudimentary
LP3 mesial marginal ridge	weak	distinct
Placement of foramen magnum	*unknown*	*anterior*
Axial skeleton character	***O. bambolii***	***Ar. ramidus***
Lordotic lumbar spine consisting of 5 lumbar vertebrae (character complex)	**5 or 6 (indeterminate), no lordosis**	**lordosis likely, lumbar vertebral count unknown**
lumbar vertebral count	5 or 6 (indeterminate)	unknown, likely 6 (Lovejoy and McCollum 2010)
lordosis of the lumbar column	no lordosis, entrapment of at least one lumbar vertebra	likely; no entrapment is evident
Short and broad ilia (character complex)	**no shorter or broader than extant large bodied apes**	**ilium short and broad as in later hominids**
iliac isthmus	likely tall as in large bodied extant great apes	short as in chronologically younger hominids
iliac blades	intermediate between *Pongo* and *Gorilla*	short and broad as in later hominids
Well-developed anterior inferior iliac spine	*protuberance likely developed as a consequence of loading during life; no separate growth physis*	*proportionally large and developed from a separate growth physis as in later hominids*
Short pubic symphysis	*pubic body superoinferiorly short, outline of the pubic symphysis probably thin oval*	*pubic body superoinferiorly elongate, outline of the pubic symphysis rounded oval*
Size of the ischial spine relative to the ischial body	*large****	*ischial spine is not preserved*
Appendicular skeleton character	***O. bambolii***	***Ar. ramidus***
Human-like precision grip (character complex)	**partially capable, likely relied on power grip (see text)**	**present**
short hand length	intermediate-long (long metacarpals and long phalanges)	intermediate-long (short metacarpals and long phalanges
long thumb	intermediate between *Proconsul* and hominids?	MC1 + PHP1 long relative to extant great apes
long proximal pollical phalanx	intermediate relative to PHP2 comparison with extant great apes	intermediate relative to PHP2 in comparison with extant great apes
deep pit on THP1 for attachment of flexor pollicis longus tendon	present	present
Capitate-metacarpal 2 articulation	transverse	transverse
Grasping and bipedally efficient foot	prehensile midfoot, no more bipedal than *Gorilla*	rigid midfoot, facultatively bipedal

Seven (7) morphological character complexes (in **bold** in Table 6.1) composed of twenty-six (26) subdivided characters and six (6) other singular characters (*italicized* in Table 6.1) that have been claimed by other authors as hominid synapomorphies or homoplasies in *Oreopithecus* were culled from the published literature and objectively examined and evaluated in comparison with *Ardipithecus*, *Australopithecus*, *Homo sapiens*, extant hominoids, and fossil hominoids. Five (5) morphological character complexes are revealed to have been based on *Oreopithecus* anatomy that is either absent, or has been misinterpreted (red cells in Table 6.1). The remaining two (2) character complexes were similar in *Oreopithecus* and *Ardipithecus* either because they are probably the primitive condition for the two taxa (cyan blue cells in Table 6.1). All but one (1) of the twenty-six (26) subdivided characters that comprise the seven (7) morphological character complexes examined in this study are revealed to be either based on *Oreopithecus* anatomy that is absent or has been misinterpreted or represent the probable primitive condition in *Oreopithecus* and *Ardipithecus* (red and blue cells in Table 6.1). Of the six (6) singular characters claimed as hominid homoplasies in *Oreopithecus* (themselves reducible to indices or ratios of different kinds, but presented as individual characters in the literature), two (2) are revealed to have been based on *Oreopithecus* anatomy that is absent or has been misinterpreted, and four (4) represent possible homoplasies but further fossils and outgroup analysis will be required to confirm them (yellow cells in table 6.1). A discussion of these largely falsified claims of homoplasy follows.

Claims of hominid homoplasy in five (5) character complexes and eighteen (18) of their subdivided characters of *Oreopithecus* skeletal anatomy are falsified because relevant *Oreopithecus* anatomy is absent or has been misinterpreted (red cells in Table 6.1). The same true for two (2) singular characters claimed as hominid homoplasies in *Oreopithecus*. In the craniodental skeleton, *Oreopithecus* upper and lower canines exhibit none of the morphology indicative of morphological feminization of these teeth as in hominids. The claim of a lack of a functional upper canine/lower third premolar sectorial (honing) complex in *Oreopithecus* is easily falsified, because all of the morphology involved in this character complex in extant and fossil great apes is also present in *Oreopithecus* male specimens. In particular, a distolabial shearing plane is clearly present on male upper canines, as is a concomitant mesiobuccal honing plane on the mesiobuccal third premolar. The claim for hominid homoplasy for the character of an anteriorly placed foramen magnum in *Oreopithecus* is falsified because this anatomy is not preserved in the available *Oreopithecus* fossils.

In the axial skeleton, a lumbar vertebral count of 5 or 6 in *Oreopithecus* is most parsimoniously interpreted as a hominoid symplesiomorphy. The claim of homoplasy in the character complex of lumbar lordosis is falsified because the relevant *Oreopithecus* anatomy has been misinterpreted. Indeed, as noted by Lovejoy and McCollum (2010) in their cursory assessment of the lumbosacral *Oreopithecus* specimen (BAC 72/35), that anyone (Kohler and Moyà-Solà 1997) would attempt to measure interfacet distances of caudal lumbar elements on such a distorted specimen and then conclude that those measurements are evidence of vertebral wedging (which contributes to the lordotic curve) in association with lordosis is inconceivable (Kohler and Moyà-Solà 1997, Lovejoy and McCollum 2010).

Claims of hominid homoplasy in the character complex of short and broad ilia and the character of a well-developed anterior inferior iliac spine in *Oreopithecus* are likewise falsified on the basis of misinterpreted *Oreopithecus* anatomy. The claim for short and broad iliac blades does not appear to be valid; *Oreopithecus* ilia are no shorter or broader than those in extant great apes.

The claimed well-developed anterior inferior iliac spine in *Oreopithecus* was first made by Straus (1963) and reiterated by Wood and Harrison (2011). It is based on a small protrusion above the estimated most superior extent of acetabulum on the single os coxa specimen IGF 11778. The "feature" may well be partly an artifact of preparation, having been "carved" while extracting the overlying lignite from the flattened skeleton's surface. Even if the morphology is real, a bony protuberance in this area occurs at relatively low frequency in gorillas and chimpanzees. Gorillas and chimpanzees, with large body masses, likely develop a bony protuberance in the region above the acetabulum in response to loading (Zirkle 2015).

Two characters of the *Oreopithecus* postcranial skeleton claimed as hominid homoplasies remain as potential homoplasies but require further fossils and outgroup assessment in order to confirm. These are a superoinferiorly short pubic body and a large ischial spine relative to the length of the ischial body.

In the appendicular skeleton, the claim of hominid homoplasy in the subdivided character of a long thumb as part of a human-like hand capable of a precision grip is falsified because a longer thumb relative to extant great apes is probably the primitive condition in *Oreopithecus* and *Ardipithecus*. Claims of hominid homoplasy in four (4) other characters of the character complex of a hand capable of a human-like precision grip in *Oreopithecus* are falsified because the evident similarities between *Oreopithecus* and *Ardipithecus* may in fact be the primitive condition in these two taxa (cyan blue cells in Table 6.1). A pad-to-pad precision grip is not uncommon among catarrhines; the frequency and reliance upon this grasping mode is highest in modern humans, who are also capable of an ape-like power grip.

Despite the lack of claims for hominid pedal synapomorphies or homoplasies in *Oreopithecus* in the published literature, the anatomy of the *Oreopithecus* foot appears incompatible with frequent bipedal locomotion. The short, prehensile mid-tarsus and curved phalanges of the *Oreopithecus* foot are characteristics shared with modern large-bodied apes.

Whereas the character complex of an anteroposteriorly short face and the subdivided character of an anteriorly placed zygomatic root in *Oreopithecus* are most parsimoniously interpreted as the probable primitive condition in *Oreopithecus* and *Ardipithecus*, the interpretation of the subdivided character of vertical implantation of the incisors could not be falsified with the available fossil evidence and therefore represents a probable homoplasy. The singular craniodental characters in *Oreopithecus* that remain as potential homoplasies are small upper and lower canine basal diameter lengths relative the mesiodistal lengths of the first molars in their respective tooth rows.

Because the “zygomatic root” is not clearly and consistently defined and applied in the published literature, phylogenetic interpretations made about its position relative to the upper tooth row are problematic. Moreover, inter- and infraspecific variation in this feature is poorly appreciated (see Chapter 3 and Figure 3.3). Because of these concerns and because of the paucity of fossil evidence, the phylogenetic polarity of this character across all of Hominoidea is difficult to ascertain. A question remains: which taxa represent the derived condition, the anteroposteriorly long-faced chimpanzees or the short-faced *Oreopithecus* and hominids?

A similar question might be posed regarding the small basal canine diameter lengths relative to mediodistal lengths of the first molar in respective upper and lower tooth rows in *Oreopithecus* and hominids. Because the underpinnings of this and other upper/lower homologs is genetically and developmentally constrained (Delezene 2011, 2015; Grieco *et al*. 2013), subdivision into two characters seems inappropriate. However, in this dissertation, I tested characters of other workers, so I enumerated these characters in this fashion for maximum assessment. Nevertheless, the claims for hominid homoplasy in these characters could not be falsified as potential hominid homoplasies in *Oreopithecus* and will require further fossils and outgroup testing to confirm them. As mentioned in Chapter 3, however, the reduction of canine basal diameter relative to the mesiodistal length of the first molar in a respective tooth row has been observed in other fossil taxa and at least in *Oreopithecus*, may have a dietary explanation (elongate mesiodistal length of the first molars as an adaptation to folivory, see Suwa *et al*.

2009b). Also, this ratio of tooth lengths does not consider canine height, however, and it is already apparent by the principles of parsimony that in several ape species lineages, the male canine may well have increased, rather than reduced in size. A lineage-by-lineage assessment will be required to further understand the evolution of canine size and dimorphism among the hominoids.

The above discussion and arising questions prompt future directions for research, the topic of the next section.

6.3 Future directions and conclusions

The results of this study form a foundation for future comparative work to test the potential hominid homoplasies in *Oreopithecus* summarized in the last section. The claim of hominid homoplasies of the superoinferiorly short pubic "symphysis" (more accurately, the pubic body, immediately lateral to the symphysis on both sides – the outline of the symphysis itself was probably ape-like, see Chapter 4) and large ischial spine relative to the ischial body could be further evaluated with the examination of all the original fossils, to some of which I was denied access (see Chapter 2 and 4). In addition, these claims could be further tested on a large inter-specific sample of all primates to better capture the variation of these anatomical characters across various primate locomotor modes.

The claim of hominid homoplasy for the character complex of an anteroposteriorly short face in *Oreopithecus* (parsimoniously interpreted as a symplesiomorphy in *Oreopithecus* and *Ardipithecus* in this study) and its subdivided characters (vertical incisor implantation and anterior position of the zygomatic root) may be further tested with a broadened sample of all the known Miocene hominoid forms. Moreover, this broader comparison could assess whether Clarke's observation of incisors being in line with the canines in *Oreopithecus* is a character separate from incisor implantation (Clarke 1997). The subdivided character of the anterior position of the zygomatic root may also be approached comparatively across a broader cross section of primates, and indeed all mammals. The claim for potential hominid homoplasy of reduced canines relative to cheek teeth in *Oreopithecus* compared with a putative, relatively large-canine *Dryopithecus* ancestor could also be approached comparatively across a broader cross section of primates, and taking into account more than simple basal crown diameters.

Of course, further *Oreopithecus* fossils suffering from comparatively less distortion of relevant anatomy would greatly help, as would complete access to all *Oreopithecus* fossils that form the basis of past claims. So too would greater clarity on the underlying developmental genetic relationship of these morphological characters.

Some investigators (Moyà-Solà and Kohler 1997, Alba *et al*. 2001a, 2001b) interpret *Oreopithecus* craniodental anatomy in the context of paedomorphy, with heterochronic shifts in development responsible for the anteroposteriorly short face (or a reduced rostrum length) relative to its putative ancestor, *Dryopithecus*. They observed that a similarly short rostrum and reduced canines occurs in in juvenile great apes and in adult *Pan paniscus*, with the caveat that only *Oreopithecus* exhibited microdontia of the postcanine dentition (Alba *et al*. 2001b).

Many authors have hypothesized that a shortened face and reduced canines relative to cheek teeth in *Oreopithecus* has a dietary explanation in association with extreme folivory (Szalay and Delson 1979, Harrison 1987, Harrison and Rook 1997). These conclusions deal with ultimate causation in their attempts to explain an apparent similarity. Proximate explanations, in the form of underlying developmental genetic mechanisms, have the power to reveal the nature of the similarities and to determine whether characters of teeth, such as whether canine basal diameter, lateral profile, or crown height are deeply conserved homologies, parallelisms (same genetic mechanisms), or convergences (different genetic mechanisms).

Whether or not an anteroposteriorly short face (based on the position of the zygomatic root relative to the upper tooth row) and small canine diameter relative to first molar length are derived conditions (as the above authors contend) or the primitive conditions in Hominoidea, the two characters may be functionally and developmentally linked. With respect to *Oreopithecus*, in the primitive condition scenario, an anteroposteriorly short face and relatively small canines would have been retained from the common ancestor of Hominoidea, and the anteroposteriorly long faces and relatively large canines of its fossil sister taxa and extant chimpanzees homoplastically derived. In a derived condition scenario, it is possible that anteroposterior length of the face, or rostral (or muzzle) length, is a collateral effect of reduction of the canines relative to the cheek teeth. This anteroposterior shortening of the face in turn might have affected the orientation of incisor implantation. For example, as canines reduced in *Oreopithecus* lineage after its split from a longer-faced, larger-canine *Dryopithecus* ancestor, the anteroposterior length of the face reduced relative to that of its ancestor, which in turn affected the verticality of incisor implantation.

Tests of these hypotheses require first establishing a functional/developmental link between these characters and secondly, determining the genetic mechanisms that underlie the reduction of the canines in concert with the shortening of the face. Understanding the developmental underpinnings of these potential hominid homoplasies shared in *Oreopithecus* is currently impossible from fossils alone. Rather, we need to turn to research on extant organisms for insight, especially animal models commonly used in genetics research such as mice, dogs, and baboons.

Double knockout of *Msx1* and *Msx2* homeobox genes responsible for neurocranial patterning in mice produce a reduced rostrum with more domed neurocrania, shortened nasal bones, and shortened maxillae (Han *et al*. 2007, Sun *et al*. 2016). This is similar to the condition seen in the facial region of bracycephalic dogs, where this facial profile is associated with broader midfaces in some breeds (Rizk 2012). Another study dealing with the rostrum of mice and potential application to human-specific morphology (McLean *et al*. 2011) found that knockouts of an androgen receptor enhancer in mice affected vibrissae and baculum formation in mice, suggesting that the corresponding deletion in the human genome may have had profound effects on secondary sexual characteristics of the face. Vibrissae in mice primarily occur in the anterolateral regions of the face, just superior to the mouth, in an area analogous to the canine jugum and canine fossae in humans.

Unfortunately, mice are uninformative as model organisms for the question of canine reduction because they lack canines. They are also evolutionarily distant from hominoids, separated by ~140 million years (70 million years on either side of the split with mice). Though not concerned with canines and anterior facial morphology, a recent study identifying two phenotypes of the primate postcanine dentition illuminated promise for non-human primates as model organisms for identifying genetically patterned phenotypes in hominoids (Hlusko *et al*. 2016). Studies conducted with panionins reveal a probable functional link between canine eruption, adult male canine size and degree of dimorphism, and muzzle length (Leigh *et al*. 2005, Leigh 2006, 2007), revealing homoplasy in panionin cranial anatomy variation among sub-clades via different ontogenetic trajectories. Another study found phenotypic (and presumably underlying genotypic) correlations between the anteroposterior length of the papionin muzzle and the mediolateral breath at the canines of South African fossil papionins (Monson *et al*. 2016).

The results of this study falsify many of the claims for parallel acquisition of hominid characters in *Oreopithecus* on the basis of poor preservation of relevant morphology, mischaracterized anatomy, or misinterpretations of similarity in the context of interspecific ape anatomical variation. In the characters hypothesized to be similar to hominids, I have proposed hypotheses to explain the potential development of those characteristics as a means of illustrating the need to understand the developmental foundations of such similarity. A future direction of such research will be to examine similarities in patterns of canine and rostrum covariance in anthropoid primates to determine the developmental timing of the co-occurrence of a short face with relatively small canines (or a long face with relatively large canines) under different selective pressures. This would facilitate the determination of the nature of the development of these perhaps functionally linked and probably homoplastic characteristics in some hominoids.

While the supermajority of *Oreopithecus* hypotheses of hominid similarity evaluated in this dissertation are falsified, this taxon remains no less remarkable as an exemplar, along with extant apes, as a relict species of a once vast adaptive radiation of Hominoidea, relegated to refugia and, in the case of *Oreopithecus*, now extinct. Whereas the insular sequestration and late Miocene persistence of *Oreopithecus* is remarkable, its suspensory *bauplan* and incidental, potentially homoplastic craniodental anatomy do not inform the condition of the ancestor we shared with chimpanzees (CLCA). Claims to the contrary based on mischaracterizations of severely distorted morphology of a limited sample size of fossils, are obstructive. Indeed, this distantly related, “enigmatic” taxon is interesting because it illuminates the diversity of an adaptive radiation long ago usurped by Ceropithecoidea.

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Appendix 1: *Oreopithecus* Specimen list

Element Abbreviations:

Abbreviation	Element Name
AST	Astragalus
ATL	Atlas (1st cervical vert.)
AXIS	Axis (2nd cervical vert.)
C	Canine
CAL	Calcaneus
CAR	Carpal
CER	Cervical vertebra
CLA	Clavicle
CMC	Carpometacarpal
COC	Coccyx
COR	Coracoid
CRA	Cranium
CUB	Cuboid
d	Deciduous tooth prefix
FEM	Femur
FIB	Fibula
FPX	Foot phalanx
FRO	Frontal
HAM	Hamate
HPX	Hand phalanx
HUM	Humerus
I	Incisor
IFP	Intermediate foot phalanx
IHP	Intermediate hand phalanx
ILI	Ilium
INT CUN	Intermediate cuneiform
IPX	Intermediate phalanx
ISCH	Ischium
L	Lower (tooth)
LAT CUN	Lateral cuneiform
LUM	Lumbar vertebra
LUN	Lunate
LUN	Lunate
M	Molar
MAN	Mandible
MAX	Maxilla
MC	Metacarpal
MED CUN	Medial cuneiform
MT	Metatarsal
MTP	Metapodial
NAV	Navicular

Abbreviation	Element Name
OCC	Occipital
OCX	Os coxae
OSS	Ossicone
P	Premolar
PAR	Parietal
PAT	Patella
PFP	Proximal foot phalanx
PHP	Proximal hand phalanx
PHX	Phalanx
PPX	Proximal phalanx
PUB	Pubis
RAD	Radius
RIB	Rib
SAC	Sacrum
SCP	Scapula
SKULL	Mandible and cranium
SPD	Scaphoid
STE	Sternum
TAL	Talus
TEM	Temporal
TFP	Terminal foot phalanx
THO	Thoracic vertebra
THP	Terminal hand phalanx
TIB	Tibia
TPX	Terminal phalanx
TRQ	Triquetrum
TZD	Trapezoid
TZM	Trapezium
U	Upper (tooth)
ULN	Ulna
VER	Vertebra
ZYG	Zygomatic

Specimen Number	Field Number	Elements Preserved	Locality	Repository	Repository Location	References
BAC 60	43	CRA (R. M1-3; L. I1, C-M2)	Baccinello	Naturhistorisches Museum	Basel	Hürzeler 1958 (Fig. 5, 21A); Alba *et al*. 2001a and 2001b
BAC 61	119	CRA (R. I1-M3)	Baccinello	Naturhistorisches Museum	Basel	Alba *et al*. 2001a
BAC 62	117	CRA (R. P3-M3; L. M1-3)	Baccinello	Naturhistorisches Museum	Basel	Straus 1963
BAC 63	40	CRA (R. + L. P4-M3)	Baccinello	Naturhistorisches Museum	Basel	Straus 1963, Alba *et al*. 2001a
BAC 64	122	R. MAX (C-M1)	Baccinello	Naturhistorisches Museum	Basel	
BAC 65	121	R. + L. MAN (R. I1-M3; L. I2-M3)	Baccinello	Naturhistorisches Museum	Basel	
BAC 66	46	R. + L. MAN (R. C-M3; L. P3-M1)	Baccinello	Naturhistorisches Museum	Basel	
BAC 67	48	R. + L. MAN imm (R. I1-2, dP3-M1; L. I1-C, dP3-M1) + I1-C, M1 germs	Baccinello	Naturhistorisches Museum	Basel	
BAC 68	105	R. MAN (C-P4); L. UP3-4, M1	Baccinello	Naturhistorisches Museum	Basel	
BAC 69	30	L. MAN (M1-2; M2 damaged)	Baccinello	Naturhistorisches Museum	Basel	

BAC 70	42	L. PFP1	Baccinello	Naturhistorisches Museum	Basel	Hürzeler 1958 (Fig. 18A)
BAC 71	44	OCX (PUB symph + ISCH)	Baccinello	Naturhistorisches Museum	Basel	Schultz 1960; Straus 1963; Hürzeler 1958 (Fig. 20), Köhler 1997, Moyà-Solà *et al* 2008
BAC 72	35	VER (3 LUM + 2 SAC)	Baccinello	Naturhistorisches Museum	Basel	de Terra 1956; St 1957; Schultz 1960 (Fig. 3); Hürzeler 1958 (Fig. 15), Köhler and Moyà-Solà 1997; Lovejoy and McCollum 2010; Russo and Shapiro 2013
BAC 73	123	FEM head (in acetabulum)	Baccinello	Naturhistorisches Museum	Basel	
BAC 74	97	FEM head	Baccinello	Naturhistorisches Museum	Basel	
BAC 75	68	FEM head	Baccinello	Naturhistorisches Museum	Basel	
BAC 76	49	R. + L. OCX; SAC, R. FEM (prox)	Baccinello	Naturhistorisches Museum	Basel	Straus 1963 (Fig. 14), Rook *et al* 1999
BAC 77	66	R. FEM (dist frag)	Baccinello	Naturhistorisches Museum	Basel	Straus 1963 (Fig. 9); Hürzeler 1968 (Fig. 23)

BAC 78	65	R. AST frag	Baccinello	Naturhistorisches Museum	Basel	
BAC 79	37	FIB frag (shaft), L. AST, L. CAL, L. NAV, L. ECTOCUN, L. MT3	Baccinello	Naturhistorisches Museum	Basel	Straus 1963 (Fig. 11); Szalay and Langdon 1987; Köhler and Moyà-Solà 1997
BAC 80	41	L. ECTOCUN	Baccinello	Naturhistorisches Museum	Basel	Hürzeler 1958 (Fig. 17A); Straus 1963
BAC 81	65	L. ECTOCUN	Baccinello	Naturhistorisches Museum	Basel	
BAC 82	118	L. AST (damaged)	Baccinello	Naturhistorisches Museum	Basel	Straus 1963 (Fig. 10)
BAC 83	36	R. HAM + R. FOOT (MT1-4, PFP, 3 CUN, CUB, AST frag)	Baccinello	Naturhistorisches Museum	Basel	Riesenfeld 1975, Szalay and Langdon 1987, Köhler and Moyà-Solà 1997
BAC 84	51	R. HUM (dist) + R. ULN (prox) + R. RAD (prox)	Baccinello	Naturhistorisches Museum	Basel	Straus 1963 (Fig. 1,3)
BAC 85	82	R. HUM (shaft), HAND elements?	Baccinello	Naturhistorisches Museum	Basel	Moyà-Solà 1999; Susman 2004; Moyà-Solà 2005
BAC 86	90	FEM head	Baccinello	Naturhistorisches Museum	Basel	
BAC 87	82	R. ULN (prox) + R. RAD (prox)	Baccinello	Naturhistorisches Museum	Basel	

BAC 88	98	AXIS	Baccinello	Naturhistorisches Museum	Basel	
BAC 89	114	Lignite block: MT + PHX frags)	Baccinello	Naturhistorisches Museum	Basel	Moyà-Solà 1999; Susman 2004; Moyà-Solà 2005
BAC 90	109	R. MAX (P3-M1, M1 damaged)	Baccinello	Naturhistorisches Museum	Basel	
BAC 91		L. MAX imm (C germ)	Baccinello	Naturhistorisches Museum	Basel	
BAC 92		R. UC	Baccinello	Naturhistorisches Museum	Basel	
BAC 93	39	L. UdP3	Baccinello	Naturhistorisches Museum	Basel	Hürzeler 1958 (Fig. 14)
BAC 94	78	R. UC (broken)	Baccinello	Naturhistorisches Museum	Basel	
BAC 95	78	L. UI1	Baccinello	Naturhistorisches Museum	Basel	
BAC 96	61	R. UI1	Baccinello	Naturhistorisches Museum	Basel	
BAC 97	7	R. UI1	Baccinello	Instituto Tecnico Statale per Geometri "Gaetano Salvemini"	Florence	Hürzeler 1958 (Fig. 8)
BAC 97		L. UI1	Baccinello	Naturhistorisches Museum	Basel	

BAC 98	7	L. + R. UC	Baccinello	Instituto Tecnico Statale per Geometri "Gaetano Salvemini"	Florence	Hürzeler 1958 (Fig. 6)
BAC 98		R. UC	Baccinello	Naturhistorisches Museum	Basel	
BAC 99	7	R. LI2	Baccinello	Instituto Tecnico Statale per Geometri "Gaetano Salvemini"	Florence	
BAC 99		LI1	Baccinello	Naturhistorisches Museum	Basel	
BAC 100	95	R. LM2 frag	Baccinello	Naturhistorisches Museum	Basel	
BAC 101	60	L. MAX (dP4-M1)	Baccinello	Naturhistorisches Museum	Basel	Alba *et al*. 2001a
BAC 102	88	L. UM3 germ	Baccinello	Naturhistorisches Museum	Basel	
BAC 103	120	R. + L. MAN (L. M1-3; R. M2-3) (cast)	Baccinello	Naturhistorisches Museum	Basel	
BAC 104	54	R. MAX (M2-3)	Baccinello	Naturhistorisches Museum	Basel	
BAC 105	31	R. LP3, C (frag), M1-2	Baccinello	Naturhistorisches Museum	Basel	
BAC 106	64	R. UC + L. UM2	Baccinello	Naturhistorisches Museum	Basel	

BAC 107	100	L. U12	Baccinello	Naturhistorisches Museum	Basel	
BAC 108		AXIS frag (dens)	Baccinello	Naturhistorisches Museum	Basel	
BAC 109	64	MTP frag (dist)	Baccinello	Naturhistorisches Museum	Basel	
BAC 110	33	R. MAN (I1-M1)	Baccinello	Naturhistorisches Museum	Basel	
BAC 111		R. LC	Baccinello	Naturhistorisches Museum	Basel	
BAC 112	115	R. + L. MAN (L. I1-2, C?, R. P3)	Baccinello	Naturhistorisches Museum	Basel	
BAC 113		PHX frag.	Baccinello	Naturhistorisches Museum	Basel	
BAC 114		L. UM3	Baccinello	Naturhistorisches Museum	Basel	
BAC 114a	53	CRA frag, R. dI2-dP3 (imm)	Baccinello	Naturhistorisches Museum	Basel	
BAC 115		PHX frag	Baccinello	Naturhistorisches Museum	Basel	
BAC 116		PHX frag	Baccinello	Naturhistorisches Museum	Basel	

BAC 117	91	R. MEDCUN	Baccinello	Naturhistorisches Museum	Basel	
BAC 118		PPX2 frag (dist), PPX3 in situ	Baccinello	Naturhistorisches Museum	Basel	
BAC 119	104	3 PPX, MTP (frag)	Baccinello	Naturhistorisches Museum	Basel	
BAC 120		R. MT2 (prox), IPX (n=2), TPX (n=2)	Baccinello	Naturhistorisches Museum	Basel	
BAC 121	67	PPX (dist frag)	Baccinello	Naturhistorisches Museum	Basel	
BAC 122	70	L. PAT	Baccinello	Naturhistorisches Museum	Basel	
BAC 123		IPX	Baccinello	Naturhistorisches Museum	Basel	
BAC 124		L. HUM (trochlea)	Baccinello	Naturhistorisches Museum	Basel	
BAC 125		PFP1 (dist)	Baccinello	Naturhistorisches Museum	Basel	
BAC 126	81	R. HUM (prox) + PPX	Baccinello	Naturhistorisches Museum	Basel	
BAC 127		L. SCAP (glenoid, coracoid, detached acromion)	Baccinello	Naturhistorisches Museum	Basel	

BAC 128		FEM (head)	Baccinello	Naturhistorisches Museum	Basel	
BAC 129		TPX + IPX (prox+shaft)	Baccinello	Naturhistorisches Museum	Basel	
BAC 130	99	MC frag (dist) + TPX (dist+shaft) + TPX1 + IPX (prox)	Baccinello	Naturhistorisches Museum	Basel	Moyà-Solà *et al*. 1999 (Fig 4)
BAC 131		TPX (dist) + IPX (dist)	Baccinello	Naturhistorisches Museum	Basel	
BAC 132	70	TPX	Baccinello	Naturhistorisches Museum	Basel	
BAC 133	108	R. FRO (supraorbital frag)	Baccinello	Naturhistorisches Museum	Basel	
BAC 134	89	CRA frag + AXIS frag	Baccinello	Naturhistorisches Museum	Basel	
BAC 135	112	TPX + MC (dist epiphysis)	Baccinello	Naturhistorisches Museum	Basel	
BAC 136	50	Lignite block: FOOT (L. MED CUN + MT frag (prox) + 3 MT shafts + 3 PPX + 3 IPX + 3 TPX)	Baccinello	Naturhistorisches Museum	Basel	
BAC 137	62	Lignite block: MAN frag + CER frags + OCC (condyle) + R. UP4+ R. M1 frag + L. M3 + R. LM2	Baccinello	Naturhistorisches Museum	Basel	
BAC 138		THP1 + 3 IPX (dist) Probably imm.	Baccinello	Naturhistorisches Museum	Basel	

BAC 139		PPX (dist) + 2 IPX (dist) + IPX (prox	Baccinello	Naturhistorisches Museum	Basel	
BAC 140	34	Lignite block: CLAV (midshaft) + R. HAND (MC 1-4 shafts + 3 PHP (dist+shaft) + PHX + IHP)	Baccinello	Naturhistorisches Museum	Basel	de Terra 1956 (Fig. 2), Moyà-Solà *et al* 1999; Susman 2004; Moyà-Solà *et al*. 2005
BAC 141	84	L. HUM (dist)	Baccinello	Naturhistorisches Museum	Basel	Straus 1963
BAC 142	29	TPX	Baccinello	Naturhistorisches Museum	Basel	Hürzeler 1958
BAC 143	32	Upper dentition (L. I2-P4)	Baccinello	Naturhistorisches Museum	Basel	
BAC 144	107	L. FRO (supraorbital)	Baccinello	Naturhistorisches Museum	Basel	
BAC 145		CRA (R. M1-3; L. P4-M2)	Baccinello	Instituto di Geologia e Paleontologia dell Universita Roma	Rome	
BAC 146		L. SCAP (glenoid, neck, coracoid)	Baccinello	Naturhistorisches Museum	Basel	
BAC 147	79	MC1 (dist + shaft) + PFP1 (dist) + PPX	Baccinello	Naturhistorisches Museum	Basel	
BAC 148		PPX + PPX (dist) + IPX (dist) + 2 IPX (prox) + 2 TPX + TFP1	Baccinello	Naturhistorisches Museum	Basel	

BAC 149	72	PPX (prox damaged) + PPX (dist) + IPX + IPX (dist)	Baccinello	Naturhistorisches Museum	Basel	
BAC 150		CRA frags (R. FRO + ?) + L. UI1	Baccinello	Naturhistorisches Museum	Basel	
BAC 151	85	CAP + MT (shaft) + 2 PPX + 2 TPX	Baccinello	Naturhistorisches Museum	Basel	Moyà-Solà 1999; Susman 2004; Moyà-Solà 2005
BAC 152	37	R. MT4 (prox) + L. MT3 + PPX (frag) + L. MED CUN	Baccinello	Naturhistorisches Museum	Basel	
BAC 153		R. SCAP (glenoid + neck)	Baccinello	Naturhistorisches Museum	Basel	
BAC 154	94	L. MT2 (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 155	76	L. CAL (dist) + L. CUB (prox) + 2 IPX (dist) + TPX	Baccinello	Naturhistorisches Museum	Basel	
BAC 156	75	L. AST (frag) + R. NAV (frag) + PPX (dist+shaft) + IPX + TPX	Baccinello	Naturhistorisches Museum	Basel	
BAC 157	80	L. HUM (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 158	71	FOOT: R. MT1 (dist) + L.MT3 (prox) + R. MT4 (prox) + PFP1 + CUB	Baccinello	Naturhistorisches Museum	Basel	

BAC 159	111	L. MT2 (prox) + 3 PPX (dist) + IPX (dist) + IPX + PHX (shaft) + TPX (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 160	77	MTP (dist frag) + IPX (prox) + 2 IPX (dist)	Baccinello	Naturhistorisches Museum	Basel	
BAC 161		R. ULN (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 162	72	R. MC2-4 and CRA frag	Baccinello	Naturhistorisches Museum	Basel	
BAC 163	110	R. PAT	Baccinello	Naturhistorisches Museum	Basel	
BAC 164	83	R. TIB (dist) + L. TIB (dist) + FIB (shaft)	Baccinello	Naturhistorisches Museum	Basel	
BAC 165	72	R. LUN + R. CUB (frag) + L. MEDCUN + R. MT3 + SESAMOID	Baccinello	Naturhistorisches Museum	Basel	
BAC 166		L. MT1 (prox) + IPX (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 167	74	RAD (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 168	73	MTP (frag) + IPX + TPX + R. ULN (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 169		2 MTP (frag) + PPX (dist) + IPX (dist) + TPX + PHX (shaft)	Baccinello	Naturhistorisches Museum	Basel	

BAC 170		3 VER frags + RIB frags + 6 PHX frags	Baccinello	Naturhistorisches Museum	Basel	
BAC 171		MT (dist) + PPX + PPX (dist) + IPX + TPX + 3 PHX frags	Baccinello	Naturhistorisches Museum	Basel	
BAC 172	63	L. AST (crushed)	Baccinello	Naturhistorisches Museum	Basel	
BAC 173		Dentition (R. LM1 + L. UP4 + tooth frags)	Baccinello	Naturhistorisches Museum	Basel	
BAC 174		RAD (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 175		L. SCAP (glenoid+ neck)	Baccinello	Naturhistorisches Museum	Basel	
BAC 176		L. MAN (I2-C)	Baccinello	Naturhistorisches Museum	Basel	
BAC 177		TEM (EAM)	Baccinello	Naturhistorisches Museum	Basel	
BAC 178		2 PPX (dist) + TPX frag + PHX (shaft)	Baccinello	Naturhistorisches Museum	Basel	
BAC 179		L. MT4 (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 180	98	ATLAS frag	Baccinello	Naturhistorisches Museum	Basel	

BAC 181		R. LM1	Baccinello	Naturhistorisches Museum	Basel	
BAC 182	50	SAC + ISCH?	Baccinello	Naturhistorisches Museum	Basel	Straus 1963 (Fig. 6), Köhler and Moya Sola 1997 (see text, Chapter 4)
BAC 183	103	CRA imm (R. + L. M3)	Baccinello	Naturhistorisches Museum	Basel	
BAC 184	126	FEM (prox) + L. OCX (ILI) + FIB (dist+shaft) + R. AST (frag)	Baccinello	Naturhistorisches Museum	Basel	
BAC 185	45	Lignite block: CRA imm (frag) + dP3-M2 impressions	Baccinello	Naturhistorisches Museum	Basel	
BAC 186	38	Lignite block: TPX (dist) + IPX (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 187		R. TIB (dist)	Baccinello	Naturhistorisches Museum	Basel	
BAC 188		R. SPD (frag)	Baccinello	Naturhistorisches Museum	Basel	
BAC 189		R. MAN frag (edentulous)	Baccinello	Naturhistorisches Museum	Basel	
BAC 190	106	R. ULN (prox:olecranon) + L. MED CUN	Baccinello	Naturhistorisches Museum	Basel	

BAC 191	72	SCAP frag + L. OCX frag	Baccinello	Naturhistorisches Museum	Basel	
BAC 192		?RAD (dist)	Baccinello	Naturhistorisches Museum	Basel	
BAC 193	86	L. MAN (condyle)	Baccinello	Naturhistorisches Museum	Basel	
BAC 194		R. LI1 + M frag + CER2 frag (dens)	Baccinello	Naturhistorisches Museum	Basel	
BAC 195	85	HUM (shaft)	Baccinello	Naturhistorisches Museum	Basel	
BAC 196	85	2 PHX frags + MTP frag	Baccinello	Naturhistorisches Museum	Basel	
BAC 197	87	L. CLAV (lateral)	Baccinello	Naturhistorisches Museum	Basel	
BAC 198		L. MAN (P3-M2)	Baccinello	Naturhistorisches Museum	Basel	
BAC 199	101	R. + L. OCX + FIB (shaft) + 2 PHX frags	Baccinello	Naturhistorisches Museum	Basel	
BAC 200		R. HAND (LUN + 2MC (dist) + 6 HPX)	Baccinello	Naturhistorisches Museum	Basel	Moyà-Solà 1999; Susman 2004; Moyà-Solà 2005
BAC 201		4 RIB frags + 4 PHX frags	Baccinello	Naturhistorisches Museum	Basel	

BAC 202		R. OCX + PHX frags	Baccinello	Naturhistorisches Museum	Basel	
BAC 203		L. HUM (dist+shaft) + ?CLAV frag + MTP + PPX (dist)	Baccinello	Naturhistorisches Museum	Basel	
BAC 204		4 CER frags + RIB frags + long bone (shaft)	Baccinello	Naturhistorisches Museum	Basel	
BAC 205		R. AST (head frag)	Baccinello	Naturhistorisches Museum	Basel	
BAC 206		L. MT4 (prox)	Baccinello	Naturhistorisches Museum	Basel	
BAC 207		UC root	Baccinello	Naturhistorisches Museum	Basel	
BAC 207		UC root	Baccinello	Naturhistorisches Museum	Basel	
BAC 208		CRA imm (L. TEM complete + M1 + M2 germ) + ISCH?	Baccinello	Naturhistorisches Museum	Basel	Köhler and Moya Sola 1997, Rook *et al*. 2004
BAC 208		L. MC2	Baccinello	Naturhistorisches Museum	Basel	
BAC 552		R. ZYG frag	Baccinello	Naturhistorisches Museum	Basel	Rook *et al*. 1996
BAC 553		L. LM3	Baccinello	Naturhistorisches Museum	Basel	Rook *et al*. 1996

BAC 554		L. UM2 (germ)	Baccinello	Naturhistorisches Museum	Basel	Rook *et al*. 1996
BAC 555		L. UdP4 (dist)	Baccinello	Naturhistorisches Museum	Basel	Rook *et al*. 1996
BAC 556		L. LC	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Rook *et al*. 1996
BAC 557		L. PAT	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Rook *et al*. 1996
Bb. 31	4	R. UM3 (germ)	Monte Bamboli	Naturhistorisches Museum	Basel	Hürzeler 1949 (Fig. 11)
Bb. 32	3	R. UM2	Monte Bamboli	Naturhistorisches Museum	Basel	Hürzeler 1949 (Fig. 11); Hürzeler 1958 (Fig. 2-3)
Bb. 33	5	R. MAN (M1)	Monte Bamboli	Naturhistorisches Museum	Basel	Hürzeler 1949
BM 11555	24	MAX (R. UC-M3, R. Udm1-2; L. UC-M3)	Monte Bamboli	British Museum of Natural History	London	Butler and Mills 1959 (Fig. 1-12; Pl. 1-2)
FS1995#0001		R. UM2	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0002		L. UM2	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0003		L. LP3	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)

FS1995#0004		R. LM3	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0005		L. UM1	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0006		L. UM3	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0007		R. LM2	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0009		R. dP4	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0010		R. UM3	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0011		L. UM1	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0012		R. UM3	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
FS1995#0013		L. LI1	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
IGF 10882	6	L. UM1 germ	Monte Bamboli	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1949
IGF 10883	26	PFP1	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1958 (Fig. 19)

IGF 10884		P	Monte Bamboli	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1959 (Fig. 19)
IGF 10885	7	R. + L. MAX frag. (L. P3-4, M2; R. P4-M2) Imm. (P3 in crypt, M3 removed from crypt)	Monte Bamboli	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Ristori 1890 (Fig. 3)
IGF 10886	26	MAX frags w/ L. I2-M2; R. I2-P3	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1958 (Fig. 7)
IGF 10890	17	L. MAN (P4-M1)	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Ristori 1890 (Tab. 7, Fig. 9); Hürzeler 1958 (Fig. 26A); de Terra 1956 (Fig. 3)
IGF 11778	116	MAN	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778	26	L. SPD + R. MT3 + PPX + IPX + TPX + L. FEM (prox)	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Harrison 1986; Susman 2004
IGF 11778	8	CRA frag (R. ZYG. + OCC? frag)	Monte Bamboli	Academia del fisiocritici, Siena	Siena	de Terra 1956; Hürzeler 1958
IGF 11778	8	FEM head	Montemassi	Academia del fisiocritici, Siena	Siena	
IGF 11778	18	R. + L. MAX (R. P3-M3; L. C-P4)	Ribolla	Naturhistorisches Museum	Basel	Merciai 1907 (Tab. 3; Fig. 3)

IGF 11778	19	R. + L. MAN (R. P4-M1; L. I1-M1)	Ribolla	Naturhistorisches Museum	Basel	Merciai 1907 (Tab. 3; Fig. 5), Szalay and Delson 1979 (Fig. 217 G-F)
IGF 11778	21	R. + L. MAX (R. I1-M3; L. I1-M3)	Ribolla	Naturhistorisches Museum	Basel	Merciai 1907 (Tab. 3; Fig. 1), Szalay and Delson 1979 (Fig. 217 G-F)
IGF 11778	22	R. + L. MAX (R. M2-3; L. M3)	Ribolla	Naturhistorisches Museum	Basel	Merciai 1907 (Tab. 3; Fig. 264)
IGF 11778A	116	CRA	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987, Clarke 1997, Alba *et al*. 2001a
IGF 11778B	116	OCX	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987, Rook *et* al. 1999
IGF 11778C	116	HUM + ULN	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987

IGF 11778D	116	R. FEM	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778E	116	L. FEM (distal)	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778F	116	RAD	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778G	116	THO (4 VER + RIBS)	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987

IGF 11778H	116	?	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778I	116	R. RIB	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778J	116	3 RIB	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778K	116	3 RIB	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987

IGF 11778L	116	RIB	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778M	116	RIB	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778N	116	RIB	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778O	116	RIB	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987

IGF 11778P	116	RIB	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778Q	116	RIB	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778R	116	?	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 11778S	116	PAT	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987

IGF 11778T	116	L. HAND (SPD, LUN, CAP, HAM, MC2-5, PHP3-5, IHP2-5, THP1-5	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987; Moyà-Solà *et al*. 1999; Susman 2004; Moyà-Solà *et al*. 2005
IGF 11778W	116	MT	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1960 (Fig. 3-5); Schultz 1960 (Fig. 3-5); Straus 1963 (Fig. 12); Szalay and Delson 1979; Harrison 1987
IGF 2011V	26	R. ULN (prox)	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1958 (Fig. 16); Straus 1963 (Fig. 8); Hürzeler 1968 (Fig. 21)
IGF 4000		R. HUM (dist)	Monte Bamboli	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	
IGF 4330	13	R.+ L. MAN (L. I1; R. I1-P4)	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1949 (Fig. 8-9), Hürzeler 1968 (Fig 14)
IGF 4331	14	R.+ L. MAN (R. M3; L. I1-P3, M3)	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Ristori 1890 (Tab. 7, Fig. 6); Hürzeler 1949 (Fig. 4a)

IGF 4332	10	R. + L. MAX (I1-M3)	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Ristori 1890 (Tab. 7, Fig. 4); Schwalbe 1915 (Fig. 1, 3); Hürzeler 1949 (Fig.10, 12b)
IGF 4333	9	CRA (L. I2-M3; R. C-M3)	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Ristori 1890 (Tab. 7, Fig. 2); Hürzeler 1949 (Fig. 12a)
IGF 4334	9	L. MAN (P3-4)	Monte Bamboli	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Ristori 1890 (Tab. 7, Fig. 5); Hürzeler 1949 (Fig. 6-7); Hürzeler 1958 (Fig. 24A)
IGF 4335	1	R. + L. MAN imm (R. I2, P3-M3; L. P3-M3)	Monte Bamboli	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Gervais 1872 (Fig. 1-3, Pl. 14); Ristori 1890 (Tab. 7, Fig. 8); Schwalbe 1915 (Fig. 10-11); Hürzeler 1949 (Fig. 1-2); Hürzeler 1958 (Fig. 9); Simons 1960 (Fig. 1);
IGF 4335	1a	L. dP4	Monte Bamboli	Laboratoire de Paleontologie, Museum National Histoire Naturelle	Paris	Gervais 1872 (Fig. 2, Pl. 14); Gervais 1876 (Pl. 5);
IGF 4336A	25	RAD	Monte Bamboli	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1949
IGF 4336B	25	R ULN (proximal) frags	Monte Bamboli	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1949
IGF 4350	20	R. MAN (P3-M3)	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Ristori 1890 (Tab. 8, Fig 7); Hürzeler 1949 (Fig. 3,5)

IGF 4350	23	L. MAN (P3-M3)	Montemassi	Naturhistorisches Museum	Basel	Hürzeler 1958 (Fig. 12)
IGF 4350	28	CRA (L. P4-M2; R. M1-M3)	Baccinello	Instituto di Geologia e Paleontologia dell Universita Roma	Rome	
IGF 4350	55	UM	Baccinello	Jean Piveteau	Paris	
IGF 4350	56	UM	Baccinello	American Museum of Natural History	New York	
IGF 4350	57	R. UM1	Baccinello	Adolf Schultz Collection, Anthropologishes Institute, Universitat Zurich	Zurich	
IGF 4350	58	R. MAX (M3)	Baccinello	Bryan Patterson, Harvard University	Cambridge, MA	
IGF 4350	59	UM	Baccinello	A.C. Blanc	Rome	
IGF 4350	?	L. UM1-3 (M3 damaged)	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	
IGF 4350	?	R. MAX (P4-M2)	Baccinello	Forschungs-Institut, Senchenberg	Frankfurt	
IGF 4351		R. MAN (M2-3)	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Ristori 1890 (Tab. 7, Fig. 1); Hürzeler 1949 (Fig. 4b)
IGF 4580	12	R. + L. MAN (M3)	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1949

IGF 4581	12	L. UI1	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Ristori 1890 (Tab. 7, Fig. 7); Hürzeler 1949 (Fig. 13)
IGF 4582	16	R. MAX (M2-3)	Casteani	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Hürzeler 1949
IGF 4883V		R. + L. MAN (R. P3-4, M2-3, L. P4, M1-3 roots)	Baccinello	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Rook 1993, Rook *et al* 1996
IGF 7516V		L. HAND (Partial-carpals)		Museo di Geologia e Paleontologia dell Universita Firenze	Florence	
IR#63900		L. UM2	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
IR#63901		L. UM3	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
IR#63902		R. UP3	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
IR#63903		R. UM2	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
IR#63904		R. UP4	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
IR#63905		L. LM1	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
IR#63906		R. MAN (P3-4)	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Cordy and Ginesu 1994, 1995; Abbazzi *et al*. 2008 (Pl.1, Tab. 2)

IR#64427		L. LM1 (dist tigonid only)	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
IR#64428		L. LP4	Fiume Santo	Museo di Geologia e Paleontologia dell Universita Firenze	Florence	Abbazzi *et al*. 2008 (Pl.1, Tab. 2)
	92	CAL (missing)	Baccinello	Naturhistorisches Museum	Basel	Straus 1963
		HUM (dist)		Naturhistorisches Museum	Basel	
		THOs		Naturhistorisches Museum	Basel	
		MC3? (prox. frag.)		Naturhistorisches Museum	Basel	
		PHX (prox. frag. + shaft)		Naturhistorisches Museum	Basel	
		PHX (dist. frag.)		Naturhistorisches Museum	Basel	
		PHX frags.		Naturhistorisches Museum	Basel	
		MC5 (dist. frag.)		Naturhistorisches Museum	Basel	
		2 PHX frags.		Naturhistorisches Museum	Basel	

		MT2 (prox. frag.)		Naturhistorisches Museum	Basel	
		MT3 (prox. frag.)		Naturhistorisches Museum	Basel	
	99?	CLAV		Naturhistorisches Museum	Basel	
		PHX frag.		Naturhistorisches Museum	Basel	
		MTP frag.		Naturhistorisches Museum	Basel	
		NAV + frags.		Naturhistorisches Museum	Basel	
		ULN (olecranon frag.)		Naturhistorisches Museum	Basel	
		UC germ + PAT		Naturhistorisches Museum	Basel	
	77?	TZD		Naturhistorisches Museum	Basel	
		MTP frags.		Naturhistorisches Museum	Basel	
		RIB frags.		Naturhistorisches Museum	Basel	

		2 LUM		Naturhistorisches Museum	Basel	
		frags. (no ID)		Naturhistorisches Museum	Basel	
		frags. (no ID)		Naturhistorisches Museum	Basel	
		frags. (no ID)		Naturhistorisches Museum	Basel	
		frags. (no ID)		Naturhistorisches Museum	Basel	
		frags. (no ID)		Naturhistorisches Museum	Basel	
		frags. (no ID)		Naturhistorisches Museum	Basel	
		frags. (no ID)		Naturhistorisches Museum	Basel	
		CRA (L. UM1-3; R. UM1-3) + THP1	Casteani	Museum "G. Capellini" (University of Bologna)	Bologna	Gentili *et al*. 1998, Alba *et al*. 2001a
		L. + R. MAN	Casteani	Museum "G. Capellini" (University of Bologna)	Bologna	Gentili *et al*. 1998, Alba *et al*. 2001a

Green highlighted rows cells indicate specimens unavailable for study (see text).

Appendix 2: Table of claims of hominid-like smiliarity in *Oreopithecus* and associated citations by investigators

	Forsyth Major 1880	Hürzeler 1968	Harrison 1987	Sarmiento 1987	Harrison 1991	Harrison and Rook 1997	Köhler and Moyà Solà 1997	Moyà Solà and Köhler 1997	Moyà Solà *et al*. 1999	Sarmiento *et al*. 2002	Sarmiento 2010	Wood and Harrison 2011
Craniodental												
Short face	X	SYA	AUT	SYP	SYP	AUT	X	HOM	X	X	X	HOM/SYP
Zygomatic root position: above UP4/UM1	X	SYA	AUT	SYP	SYP	AUT	X	HOM	X	X	X	HOM/SYP
Vertically implanted incisors	X	SYA	AUT	SYP	X	AUT	X	HOM	X	X	X	HOM/SYP
Reduced (male) canines	X	SYA	SYP	X	X	X	X	HOM	X	HOM	X	HOM/SYP
Reduced sexual dimorphism of the canine	X	SYA	SYP	X	X	X	X	HOM	X	X	X	X
Absence or reduction of UC/LP3 honing complex	X	SYA	SYP	SYP	X	SYP	X	X	X	HOM	HOM	HOM/SYP
Homomorphic, bicuspid lower premolars	SYA	SYA	HOM	HOM	X	AUT	X	X	X	HOM	X	X
Foramen magnum: anterior	X	X	X	X	X	X	X	X	X	X	X	HOM/SYP
Postcranial												
Lumbar vertebrae count: 5	X	SYA	SYP	SYP	SYP	SYP	HOM/SYP	X	X	X	X	X
Lumbar lordosis	X	X	X	X	X	X	HOM	X	X	X	X	X
Short, broad ilia	X	SYA	SYP	HOM/SYP	SYP	SYP	HOM	X	X	HOM	HOM	HOM/SYP
Short iliac isthmus	X	X	X	X	X	X	X	X	X	X	HOM	X
Short and broad iliac blades	X	SYA	SYP	HOM/SYP	SYP	SYP	X	X	X	HOM	HOM	HOM/SYP
Well-developed AIIS	X	X	SYA	X	SYP	SYP	HOM	X	X	X	HOM	HOM/SYP
Short pubic symphysis	X	SYA	INDET.	X	X	X	HOM	X	X	HOM	HOM	HOM/SYP
Relatively large ischial spine	X	X	X	X	X	X	HOM	X	X	HOM	X	HOM/SYP
Human-like precision grip	X	X	X	X	X	X	X	X	HOM	X	X	X
Short hand length	X	X	SYP	LONG	LONG	LONG	X	X	HOM	X	X	X
Long thumb	X	X	X	X	SHORT	SHORT	X	X	HOM	X	X	X
Long proximal pollical phalanx	X	X	X	X	SHORT	SHORT	X	X	HOM	X	X	X
Deep pit on THP1 for attachment of flexor pollicis longus tendon	X	X	X	X	X	X	X	X	HOM	X	X	HOM/SYP
Capitate/metacarpal 2 articulation	X	X	X	X	X	X	X	X	HOM	X	X	X
Grasping and bipedally efficient foot	X	X	X	NOT BIPEDAL	X	X	AUT	X	X	X	X	X

SYA=claimed synapomorphy, AUT=claimed autapomorphy, SYP=claimed symplesiomorphy, HOM=claimed homoplasy, and X=no claim made in the given publication. Cells with multiple values (e.g., HOM/SYP) indicate that the authors of the claim propose either character state interpretation. For example, *"…these features are most parsimoniously interpreted as either homoplasies or retained primitive hominid features.* Oreopithecus *is a classic example of how a late Miocene hominid can independently acquire a suite of structural-functional complexes of the dentition, cranium, hand, hip and hindlimb that closely parallel the specialized features uniquely associated with the hominin lineage, and thereby encourage researchers to generate erroneous assumptions about evolutionary relationships.* Oreopithecus *highlights the dangers inherent in uncritically assuming that shared similarities are a secure indication of relationship or that extant primates are an adequate guide to the potential behavioural diversity of extinct taxa."* (Wood and Harrison 2011, p. 351).