

Vertebrate Paleobiology and Paleoanthropology Series



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Richard E. Leakey
Editors

The Paleobiology of *Australopithecus*

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Vertebrate Paleobiology and Paleoanthropology Series

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The Paleobiology of *Australopithecus*

Contributions from the Fourth Stony Brook
Human Evolution Symposium and Workshop,
Diversity in Australopithecus: Tracking the First Biped
September 25–28, 2007

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For Charles Abram Lockwood and Elizabeth Hunt Harmon, young researchers whose creativity, resourcefulness, energy, and ideas remain with us through their work.



Charlie at breakfast at the Ledi-Geraru field camp, and showing his strength (with pumice). Photos by Kaye Reed.



E (as we called her) driving a field vehicle while surveying near the Omo, and smiling—although she had stepped in mud in her only shoes. Photos by Michelle Drapeau.

Preface

Australopithecus holds a special place in the study of human evolution. From the initial description of the genus by Dart in 1925 through the present, there has been ongoing discussion and debate about whether this genus is best viewed as an ape with some human features or an old, somewhat primitive version of modern humans. How much like modern humans was *Australopithecus* in its locomotion, its social behavior, and its life history? As the hominid fossil record has expanded, indeed exploded, over the nearly nine decades since *Australopithecus* was first described, it has become the most speciose genus of human ancestors with no consensus regarding how many species should actually be recognized. Similarly, there is ongoing debate about the distinctions, boundaries, and phylogenetic relationships between *Australopithecus* and related genera, including *Homo*, *Paranthropus*, and *Kenyanthropus*. What kinds of biogeographical scenarios can best explain the evolution of *Australopithecus*?

In order to address these and other issues regarding the biology of *Australopithecus*, we organized the Fourth Stony Brook Human Evolution Workshop in 2007 with the title of “*Diversity in Australopithecus: Tracking the Earliest Bipeds*”. A group of scholars and students from all over the world assembled in Stony Brook New York between September 25 and September 29, 2007 for five days of presentations, discussions, and collegiality in an informal setting. This volume is derived from that workshop.

The workshop was sponsored by Stony Brook University and the Turkana Basin Institute, and was generously hosted by the President of Stony Brook, Dr. Shirley Strum Kenny in her home at Sunwood. The workshop and associated symposium were only possible through the efforts and contributions of many people and institutions, including the Provost of Stony Brook University, the LSB Leakey Foundation, Jim and Marilyn Simons, Mrs. Kay Harrigan Woods, Mrs. Mary Armour, Elizabeth Wilson, and Lawrence Martin. In addition to the contributors to this volume, numerous other people attended all or part of the workshop and contributed to the discussions (Fig. 1), including Meave Leakey, Terry Harrison, Bill Kimbel, Gary Schwartz, Fredrick Manthi, Francis Kirera, Jack Stern, Bill Jungers, Randall Susman, James Rossie, Kathryn Twiss, Lawrence Martin, Aryeh Grossman, Chris Gilbert, Ian Wallace, Jessica Lodwick.

The chapters in this monograph were formally peer-reviewed and we thank those reviewers for their time and effort in making this volume better. We thank Eric Delson, senior co-editor of the *Vertebrate Paleobiology and Paleoanthropology* Series, for his patience, guidance, good humor, and more patience in helping to publish this volume. Christopher J. Campisano, David A. Feary, and William H. Kimbel were of great support to Kaye Reed during the editorial work on this volume. In addition, we thank Andrea Baden and Ian Wallace for providing editorial and bibliographic assistance.



Fig. 1 Workshop participants. *Back row, left to right:* William Kimbel, Ron Clarke, Frank Brown, Richard Leakey, Matt Sponheimer, David Strait, Adam Gordon, Charlie Lockwood, John Shea; *Middle row, left to right:* Susan Larson, Terry Harrison, Carol Ward, John Fleagle, Andy Herries, Zeray Alemseged, Fred Grine, Gary Schwartz. *Front row, left to right:* Meave Leakey, Elizabeth Harmon, Kay Behrensmeyer, Fredrick Manthi, Kaye Reed, Francis Kirera, Robert Foley

Kaye E. Reed
John G. Fleagle
Richard E. Leakey

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Chapter 1

Introduction: Issues in the Life and Times of *Australopithecus*

Kaye E. Reed

Abstract *Australopithecus* species have been a topic of debate in paleoanthropology since the original description by Dart in 1925. The Stony Brook University/Turkana Basin Institute sponsored workshop on this subject occurred in September 2007. Participants designated various *Australopithecus* species as knowns, others as known unknowns (i.e., those for which there was limited fossil material), and “biological realities?” such as *Australopithecus bahrelghazali*. The chapters in this volume address many questions that arose from these discussions—especially those regarding the paleobiology of the genus: phylogenetic validity, dating problems, biogeography, diet and especially fallback foods, sexual dimorphism, use of stone tools, and reconciling pattern and process in a fossil record of unequal scales.

Keywords Biogeography • Fallback foods • Microwear • Phylogeny • Paleobiology

Raymond Dart described the first *Australopithecus* fossil from Taung, South Africa in 1925. Since that time, numerous species attributed to that genus have been recovered, deriving from southern, eastern, and north central Africa. These species have created excitement in the general public, as they know that one of these species was likely ancestral to our own genus *Homo*. Paleoanthropologists respond in the same manner, although there is much more scientific insight into what each species may mean in the evolutionary history of the genus, and indeed, “discussion” as to whether various specimens belong in the genus or not. To address some of these issues regarding specimens and various contextual and behavioral evidence of the genus, contributors to this volume attended a workshop in the fall of 2007, sponsored by the Turkana Basin Institute and Stony Brook University and entitled *Diversity*

in *Australopithecus: Tracking the First Biped*s. Various questions were asked in the public lecture session on the opening day of the workshop, and potential answers and problems were discussed in subsequent days. Contributors were asked to provide rough drafts of manuscripts on particular topics before the workshop, and then, based on extensive conversations at the workshop, they were asked to revise their manuscripts for this volume.

There were lively discussions, as no one actually presented a paper except at the public session, but all present were asked to discuss the various questions. Ron Clarke told everyone that at Wenner-Gren workshops, formerly held in the Burg Wartenstein castle in Austria, there were often suggestions to “get out the swords.” That set the tone for our discussions, with contributors often beginning a contra argument with, “Bring out the swords!” At the time, there was no extensive knowledge of *Ardipithecus ramidus* (White et al. 2009), nor were there any recovered specimens of *Australopithecus sediba* (Berger et al. 2011), but many of the authors here have added references to those taxa to their manuscripts, and the discoverers of *A. sediba* provided a chapter.

The questions that the participants of the workshop asked fell into four major groups: phylogeny, dating, paleobiology (including diet, fallback foods, sexual dimorphism, use of stone tools, and biogeography), and reconciling pattern and process in a fossil record of unequal scales. Phylogenetic questions ranged from how many species might be found at the sites of Sterkfontein and Makapansgat to what can phylogeny tell us about fallback foods? Dating questions and current problems involved emphatic statements regarding what was seen as a mistake, trying to date South African sites using only East African fauna, that is, other methods should be used and developed to help clarify the sequence of events in South Africa. Another focus was to urge understanding the tectonic patterns and their influence in the East African fossil record. Paleocological and paleobiological questions were numerous, although many participants were interested in fallback foods and their

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importance to the genus, and how fallback foods may have been utilized in different regions. It was also noted that there was a strong provinciality in the populations of various species, which breaks down in the Pleistocene with other hominin taxa—what might this mean paleoecologically and biogeographically? Several people wondered if *Australopithecus* actually used stone tools—note that this was long before the discovery of putative cut marked bones at Dikika (McPherron et al. 2010). Many participants would still wonder where the stone tools are if there are cut marks. Scale was another issue—species or paleodemes; time-averaging and understanding sexual dimorphism; time-averaging within depositional environments—are we always looking at the dry season, for example? How can we map life history patterns onto the different species of *Australopithecus*? What can better knowledge of the postcranial skeleton—from juveniles and different *Australopithecus* species—tell us about diversity in function, sexual dimorphism, and foraging strategies? Biogeographical questions included whether the capability for dispersals of *Australopithecus* can be determined; what is the influence of large rivers within basins for limiting dispersals; and why have no Plio-Pleistocene hominins been recovered from Angola, North Africa or Uganda? And finally, how can we understand selection processes from patterns that are at a much greater scale than these processes likely occur?

The participants also made lists of knowns, known unknowns, and biological realities (the latter followed by a question mark). The list of known taxa included *Australopithecus afarensis*, *Australopithecus africanus*, and *Australopithecus anamensis* to which one could add the species classified by many as *Paranthropus*: *Paranthropus robustus* and *Paranthropus boisei*; known unknowns were those in which only one or very few specimens are known: *Paranthropus aethiopicus*, *Australopithecus garhi*, and *Kenyanthropus platyops*. Finally, there were questions regarding the biological reality of *Australopithecus bahrelghazali*, a second species of *Australopithecus* at Sterkfontein, and, indeed, what exactly was the species at Makapansgat—is it actually *A. africanus*? Obviously, none of the participants was aware of *A. sediba* in the fall of 2007, but we asked for a contribution from its discoverers to add to the depth of the volume. This new species may belong in the category of known unknowns for some researchers, but that is for another discussion and another workshop. The organizers of the workshop limited the discussions to the *Australopithecus* species mentioned above and decided that *Paranthropus* and *Kenyanthropus* would be the subjects of other workshops.

The name of this volume does not match the name of the workshop, because as the discussion progressed and the papers were submitted, it seemed that the incorporation of the diversity of *Australopithecus* species was in reference to

their overall paleobiology. Part 1 of this volume, the context of *Australopithecus* evolution, sets up the geological and paleoecological context within which all of the *Australopithecus* species, as well as some of the other genera, occur. From these papers we learn that the genus ranges over about 2.3 million years, with the oldest species recovered in East Africa and the youngest species recovered in South Africa (Malapa). The Taung child, once thought to be among the youngest of representatives, is now in the middle of the *A. africanus* species range—with *A. sediba* now the youngest. The *Australopithecus* specimens from Sterkfontein and Malapa postdate the enigmatic specimen of *A. garhi* from the Middle Awash of Ethiopia, as well as specimens of *P. aethiopicus*. The dispersal and speciation of various species across the landscape is thus bracketed within dates that are not intuitive, and create more questions and some answers about the biogeographical patterns that we see in this genus. Within Part 1 the information we know about the paleoecology of each *Australopithecus* site is discussed, and the authors elucidate what is known about each species' habitat. In general, *Australopithecus* species appear to be habitat generalists, which simply provokes further questions about fallback foods, disparate diets among species, and apparent lack of continuous dispersal across the landscape.

Part 2 of the volume covers site distribution and issues regarding the phylogeny within the genus as well as its origination. These authors also pose more questions regarding the earliest members of the genus, such as understanding the variation and biogeographic distribution of *A. anamensis* in light of the newer recoveries in northern Ethiopia; understanding the temporal range of *A. afarensis* because there is a widespread unconformity in the northern Awash basin that likely eliminates much of the data necessary to understand its LAD there; and understanding the phylogenetic connections to possible descendants such as *Homo* and *Paranthropus*. Later members of the genus also supply controversy of a sort, for example, the longevity of what is known as the *A. africanus* lineage and the variation among specimens begs the question as to how many species of *Australopithecus* are represented by the individuals currently assigned to that taxon in South Africa. There appear to be as many phylogenetic solutions to this question as there are researchers, and there are key specimens that are involved in this debate with StW 53 being among the most controversial. Finally, the newest member of the genus, *A. sediba*, is also discussed with regard to its relationship to other *Australopithecus* and to *Homo*.

Part 3 examines various biogeographical perspectives and evolutionary models and how they can be used to examine evidence regarding ancestor–descendant relationships. This section addresses questions of scale and processes in considering the adaptive radiation of the genus—and arrives at an interesting conclusion that

Australopithecus evolution falls short of a true adaptive radiation, and is better explained by other evolutionary models. None of the authors in this section questioned the hypothesis of an anagenetic lineage from *A. anamensis* to *A. afarensis* (Kimbel et al. 2006), although there are researchers who do not accept that view. Lockwood (2013) asks what is the evidence for a member of the *A. anamensis*–*A. afarensis* lineage as an origin for the *A. africanus* like hominins in South Africa? Can one explain the many cranial features present in both *A. africanus* and *Homo* through a biogeographical model of ancestor–descendant relationships? There are hints of answers to these questions in these chapters, and Foley (2013), Lockwood (2013), and Strait (2013) all mention the provinciality of these early species. If we agree that evolution occurs in small, isolated populations, then some of the biogeographical patterning that we see is necessary and, indeed, we expect to recover new members of the genus through time in some of these insulated regions, e.g., northern Ethiopia (*A. garhi*) and southern Africa (*A. sediba*), and possibly another species now included in *A. africanus*.

Part 4 considers aspects of the paleobiology of the genus. These topics include diet (as informed by microwear and isotopic data), locomotor adaptational and ontogenetic differences, as well as sexual dimorphism. These chapters explore the myriad of questions that were proposed—but still leave questions: Why is the microwear of *Australopithecus* so different among species recovered from East and South Africa? What do the differences in isotopes among species actually mean? That is, even if a taxon is mixed C3 or all C4, what does that suggest about the actual food items ingested? Newer studies in microwear (Grine et al. 2013) suggest that the purported *A. anamensis*–*A. africanus* lineage varied little in the overall food properties that were consumed and that hard-object feeding was not involved. These authors imply that their diet may have included some type of vegetation, but we are still not sure of the actual food items utilized. There are differing opinions as to the details of locomotion of some of the *Australopithecus* species. Although everyone agrees the species were bipedal, not all agree on whether their forelimbs were used for climbing, as some contend that the relevant features are just primitive retentions. Were there different modes of locomotion among species? While discovered after the workshop, *A. sediba* at least has some different, and interesting, skeletal morphology suggesting more differences in bauplan than previously expected.

Tragically, two of the young researchers who attended the workshop and provided initial manuscripts have been lost to the field of paleoanthropology since those fall 2007 discussions. Charlie Lockwood died in the summer of 2008 and Elizabeth Harmon in the spring of 2009. For me, editing

this volume was intertwined with their lives and deaths, and having their papers, rough or not, included here was extremely important. Elizabeth’s paper had been submitted and reviewed before her death, and Will Harcourt-Smith incorporated the reviewers’ comments into her manuscript. Charlie’s paper had not been submitted in final form, but the latest version was recovered from his computer. David Strait and John Fleagle kindly revised his manuscript, as we felt Charlie’s scientific viewpoint was important to incorporate here.

It has taken a long time for this book to see the light of day, but the research described and the analyses discussed are as important today as they were in September of 2007. All of the authors provide some tentative answers to the questions posed at the workshop, and many suggest new research that should likely be done to answer some of the questions posed. But what is research that does not lead to further questions about a field? It is likely time for another workshop and further discussion on the genus *Australopithecus*, given all of the unique discoveries in the past 5 years.

References

- Berger, L. R., de Ruiter, D. J., Churchill, S. E., Schmid, P., Carlson, K., Dirks, P. H. G. M., et al. (2011). *Australopithecus sediba*: A new species of *Homo*-like australopithec from South Africa. *Science*, 328, 195–204.
- Foley, R. A. (2013). Comparative evolutionary models and the “Australopithecine Radiations.” In K. E. Reed, J. G. Fleagle, & R. E. Leakey (Eds), *The paleobiology of Australopithecus* (pp. 163–174). Dordrecht: Springer.
- Grine, F. E., Ungar, P. S., Teaford, M. F., & El-Zaatari, S. (2013). Molar microwear, diet and adaptation in a purported hominin species lineage from the Pliocene of Africa. In K. E. Reed, J. G. Fleagle, & R. E. Leakey (Eds), *The paleobiology of Australopithecus* (pp. 213–223). Dordrecht: Springer.
- Kimbel, W. H., Lockwood, C. A., Ward, C. V., Leakey, M. G., Rak, Y., & Johanson, D. C. (2006). Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record. *Journal of Human Evolution*, 51, 134–152.
- Lockwood, C. A. (2013). Whence *Australopithecus africanus*? Comparing the skulls of South African and East African *Australopithecus*. In K. E. Reed, J. G. Fleagle, & R. E. Leakey (Eds), *The paleobiology of Australopithecus* (pp. 175–182). Dordrecht: Springer.
- McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., et al. (2010). Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, 466, 857–860.
- Strait, D. S. (2013). The biogeographic implications of early hominin phylogeny. In K. E. Reed, J. G. Fleagle & R. E. Leakey (Eds), *The paleobiology of Australopithecus* (pp. 183–191). Dordrecht: Springer.
- White, T. D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C. O., Suwa, G., et al. (2009). *Ardipithecus ramidus* and the paleobiology of early hominids. *Science*, 326, 75–86.

Part I

Geological and Paleontological Context

The chapters in this section provide the background for later parts of the volume by placing *Australopithecus* fossils in a broader temporal and deposition framework. In “Age Ranges of *Australopithecus* Species, Kenya, Ethiopia, and Tanzania” Francis Brown, Ian McDougall, and Patrick Gathogo review and summarize all of the geological information about the age of *Australopithecus* fossils from Eastern Africa and also the specimen of *Australopithecus bahrelghazali* from Chad. They provide charts showing correlations between geological formations and individual sites that have yielded fossils of *Australopithecus* and related taxa, as well as comparing the ranges of the different species of *Australopithecus*. The genus *Australopithecus* is found in East Africa in deposits ranging in age from 4.2 Ma to less than 2.5 Ma. *Australopithecus anamensis* has been described from sites ranging from 4.2 Ma to just under 3.80 Ma. *Australopithecus afarensis* has a well-documented range from over 3.6 Ma to just less than 3.0 Ma. However, several associated teeth from the site of Fejej in southernmost Ethiopia, dated ca. 4.2–4.0 Ma, have been attributed to that species, and some authors have suggested that *A. anamensis* and *A. afarensis* are chronospecies of a single lineage. *A. bahrelghazali* from Chad has an estimated date, based on faunal correlations of between 3.4 and 3.0 Ma. *Australopithecus garhi* is known from a single site in Ethiopia and has a well-constrained age of just slightly less than 2.5 Ma. Fossils attributed to *Kenyanthropus platyops* from northern Kenya range in age from 3.6 to 3.25 Ma.

In “A Multi-Disciplinary Perspective on the Age of *Australopithecus* in Southern Africa”, Andy Herries and colleagues review and summarize the ages of *Australopithecus* species from Southern Africa and compare them with the ages of other species from Eastern Africa. They base their results on a combination of paleomagnetic correlation, electron spin resonance (ESR), and uranium lead (U-Pb) analyses as well as biochronological and stratigraphic data. They find that the oldest fossils attributed to *Australopithecus africanus* are from the Makapansgat Limeworks site dated to between 3.0 and 2.6 Ma. The type specimen of *A. africanus* from Taung is most likely in the same age range as the Makapansgat fossils. *Australopithecus* fossils from the rich but complex site of Sterkfontein are dated to between 2.6 and 2.0 Ma. However the number of contemporaneous species is a subject of debate. *Australopithecus* fossils from Gladysvale are dated to between 2.4 and 1.9 Ma. *Australopithecus sediba* from Malapa is well-dated at 2.05–1.98 Ma. Thus, *Australopithecus* fossils from Southern Africa are generally much younger than *Australopithecus* in East Africa and are contemporaneous with *Homo* and *Paranthropus*.

In “Reconstructing the Habitats of *Australopithecus*: Paleoenvironments, Site Taphonomy, and Faunas”, Kay Behrensmeyer and Kaye Reed review what can be reconstructed regarding the paleoecology of each of the species of *Australopithecus* in the context of a broader consideration of the many factors involved in deducing ecological information from the geological and paleontological records. They find that as a genus, *Australopithecus* likely occupied a wide range of habitats, and that there is evidence that the species *A. afarensis* occupied multiple habitats. However, they also note that different types of information sometimes yield conflicting evidence about the paleoecology of *Australopithecus* species.

The Editors

Chapter 2

Age Ranges of *Australopithecus* Species, Kenya, Ethiopia, and Tanzania

Francis H. Brown, Ian McDougall, and Patrick N. Gathogo

Abstract *Australopithecus anamensis*, *Australopithecus afarensis*, *Australopithecus bahrelghazali*, *Australopithecus garhi*, and *Kenyanthropus platyops* have all been described from eastern Africa and Chad. Principal results presented are the age of specimens assigned to these taxa that derive from sedimentary formations of the Omo Group in the Omo-Turkana Basin of Kenya and Ethiopia. Also included are ages of relevant fossils from various sites in sediments of similar age preserved in the Ethiopian Rift Valley (e.g., Hadar, Asa Issie, Aramis, Maka, Bouri), and at Laetoli in Tanzania. All $^{40}\text{Ar}/^{39}\text{Ar}$ ages were recalculated to a common age for the Fish Canyon sanidine fluence monitor (FCs) to eliminate small differences in age caused by different choices for this value. The value chosen for the age of the Fish Canyon sanidine monitor (28.10 Ma) is that of Spell and McDougall (2003). The overall effect is to increase ages computed using 27.84 Ma for the age of the monitor by 0.93 %, and to increase ages computed using 28.02 Ma for the age of FCs by 0.29 %. An age of 4.000 Ma using the 27.84 Ma age for FCs is thus increased to 4.037 Ma; whereas the same age computed using 28.02 Ma is increased to 4.011 Ma. Thus the differences in the stated ages are on the order of 0.02 Ma—up to about twice the length of a precessional orbital cycle. Excellent age information is available on most specimens principally due to the efforts of Paul Renne and coworkers at the Berkeley Geochronology Center (BGC), and Ian

McDougall and coworkers at the Research School of Earth Sciences, Australian National University; some other information (e.g., Walter and Aronson 1993) is also useful, but less extensive than the results obtained by the workers mentioned above.

Keywords Hominin evolution • Geology • Tephrostratigraphy • Radiometric dating • Turkana Basin • Omo Group

Introduction

The principal formations of interest are those of the Omo Group in the Omo-Turkana Basin of northern Kenya and southern Ethiopia, the Sagantole, Hadar, and Bouri formations of northeast Ethiopia, and the Laetoli Formation of northern Tanzania (Fig. 2.1). At other localities, such as that at Bahr al Ghazal (KT-12), Chad, australopithecus fossils are dated by faunal comparison and $^{10}\text{Be}/^9\text{Be}$ determinations; in some cases it is not evident what area or thickness of strata is included in the fauna being compared.

For the present chapter, we use ages for magnetostratigraphic boundaries given in Table 2.1. These generally follow Gradstein et al. (2004) and Horg et al. (2002), with those of Kidane et al. (2007) used for the Reunion I and Reunion II subchrons. Although stated without error estimates, in many instances errors of up to 0.03 Ma are associated with each of these ages. Further, we use ages given in Table 2.2 for dated volcanic materials in the Omo-Turkana Basin, and ages listed in Table 2.3 are for dated volcanic materials at sites in Ethiopia and Tanzania, recomputed where necessary, so that the Fish Canyon Tuff sanidine reference age is identical to that used for ages in the Omo-Turkana Basin (i.e., 28.10 Ma).

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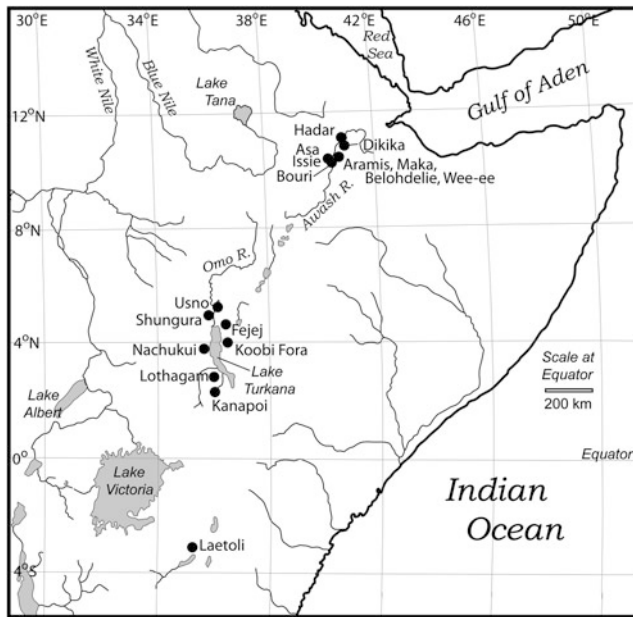


Fig. 2.1 Map of eastern Africa showing locations of most of the fossil sites mentioned in the text. Locations are generalized because some formations (e.g., Koobi Fora Formation; Shungura Formation) extend over large areas

Table 2.1 Ages of magnetostratigraphic and stratigraphic boundaries

Designation	Age (Ma)	Alternate name ^a
C1n	0.000–0.781	Brunhes
C1r	0.781–2.581	Matuyama
C1r.1n	0.988–1.072	<i>Jaramillo Normal</i>
C1r.2n	1.173–1.185	<i>Cobb Mt. Normal</i>
C2n	1.778–1.945	<i>Olduvai Normal</i>
C2r.1n	2.06–2.08 ^b	<i>Reunion II Normal</i>
C2r.2n	2.15–2.20 ^b	<i>Reunion I Normal</i>
C2An.1n and C2An.3n	2.581–3.596	Gauss
C2An.1r	3.032–3.116	<i>Kaena Reversed</i>
C2An.2n	3.116–3.207	
C2An.2r	3.207–3.33	<i>Mammoth Reversed</i>
C2An.3n	3.33–3.596	
C3r	3.596–6.033	Gilbert
C3n.1n	4.187–4.3	<i>Cochiti Normal</i>
C3n.2n	4.493–4.631	<i>Nunivak Normal</i>
C3n.3n	4.799–4.896	<i>Sidufjall Normal</i>
C3n.4n	4.997–5.235	<i>Thvera Normal</i>

Sources Gradstein et al. (2004) and Horng et al. (2002)

^a Subchrons in italics

^b Age estimates based on Kidane et al. (2007)

Table 2.2 ⁴⁰Ar/³⁹Ar ages of dated units in the Omo-Turkana Basin

Unit	Age and standard deviation (Ma)	
Silbo	0.751 ± 0.022	Anorthoclase ^a
U. Nariokotome	1.230 ± 0.020	Anorthoclase ^a
M. Nariokotome	1.277 ± 0.032	Anorthoclase ^a
L. Nariokotome	1.298 ± 0.025	Anorthoclase ^a
Gele	1.326 ± 0.019	Anorthoclase ^a
Chari	1.383 ± 0.028	Anorthoclase ^a
Ebei	1.475 ± 0.029	Anorthoclase ^a
Karari Blue	1.479 ± 0.016	Anorthoclase ^a
Koobi Fora	1.485 ± 0.014	Anorthoclase ^a
Lower Koobi Fora	1.476 ± 0.013	Anorthoclase ^a
Morte	1.510 ± 0.016	Anorthoclase ^a
Lower Ileret	1.527 ± 0.014	Anorthoclase ^a
Morutot	1.607 ± 0.019	Anorthoclase ^a
Malbe	1.843 ± 0.023	Anorthoclase ^a
KBS	1.869 ± 0.021	Anorthoclase ^a
Kangaki	2.063 ± 0.032	Anorthoclase ^b
G-3	2.188 ± 0.036	Anorthoclase ^b
Kalochoro	2.331 ± 0.015	Anorthoclase ^b
Tuff F	2.324 ± 0.020	Anorthoclase ^b
Tuff D-3-2	2.443 ± 0.048	Anorthoclase ^b
Lokalalei	2.526 ± 0.025	Anorthoclase ^b
Burgi	2.622 ± 0.027	Anorthoclase ^b
B-10	2.965 ± 0.014	Anorthoclase ^b
Ninikaa	3.066 ± 0.017	Anorthoclase ^b
Toroto	3.308 ± 0.022	Anorthoclase ^b
Tulu Bor	3.438 ± 0.023	Anorthoclase ^b
Lokochot	3.596 ± 0.045	Anorthoclase ^b
Moiti	3.970 ± 0.032	Anorthoclase ^b
Topernawi	3.987 ± 0.025	Anorthoclase ^b
Kanapoi Tuff	4.108 ± 0.029	Anorthoclase ^b
Upper pumiceous siltstone, Kanapoi	4.147 ± 0.019	Anorthoclase ^b
Lower pumiceous siltstone, Kanapoi	4.195 ± 0.033	Anorthoclase ^b
Pumice clasts, Apak Mb., Lothagam	4.244 ± 0.042	Anorthoclase ^b
Lothagam Basalt	4.23 ± 0.03	Whole rock ^c

All ages calculated relative to a reference age of 28.10 Ma for the Fish Canyon Tuff sanidine fluence monitor. All results on anorthoclase are arithmetic mean ages with uncertainties the standard deviation of the population. Most pooled ages are based on multiple single crystal total fusion measurements

^a McDougall and Brown (2006)

^b McDougall and Brown (2008)

^c McDougall and Feibel (1999, 2003)

Table 2.3 K/Ar and $^{40}\text{Ar}/^{39}\text{Ar}$ ages of dated units at Ethiopian sites other than Omo, and at Laetoli standardized to a value of 28.10 Ma for the Fish Canyon sanidine fluence monitor

Unit	Age and standard deviation (Ma)	
<i>Sagantole, Hadar, and Bouri formations</i>		
Maoleem vitric tuff (MOVT)	2.519 ± 0.008	Sanidine ^a
Bouroukie tuff 3 (BKT-3)	2.35 ± 0.07	Alkali feldspar ^b
Bouroukie tuff 2 (BKT-2U)	2.978 ± 0.038	Alkali feldspar ^c
Bouroukie tuff 2 (BKT-2L)	2.971 ± 0.017	Alkali feldspar ^c
Kada hadar tuff (KHT)	3.205 ± 0.012	Alkali feldspar ^d
Triple Tuff (TT-4)	3.250 ± 0.010	Alkali feldspar ^d
Kadada momou basalt (KMB)	3.311 ± 0.040	Whole rock ^e
Sidi hakoma tuff (SHT)	3.430 ± 0.030	Anorthoclase ^f
Wargolo tuff (VT-3)	3.783 ± 0.023	Alkali feldspar ^g
Cindery tuff (CT)	3.883 ± 0.083	Plagioclase ^h
Moiti tuff (VT-1)	3.925 ± 0.030	Sanidine ^h
Unnamed tuff, Sagantole Fm. (94–55 °C)	4.052 ± 0.060	Sanidine ^g
Unnamed basaltic tuff (MA02-13)	4.128 ± 0.074	Basaltic glass ⁱ
Marker tuff sibabi	4.303 ± 0.019	Alkali feldspar ^h
Kullunta basaltic tuff (KUBT)	4.329 ± 0.055	Basaltic glass ^g
Igida tuff complex (IGTC)	4.344 ± 0.011	Plagioclase ^g
Gaala tuff complex (GATC)	4.430 ± 0.031	Mainly sanidine ^g
Daam aatu basaltic tuff (DABT)	4.429 ± 0.053	Volcanic glass ^g
Unnamed tuff, Sagantole Fm. 94–58	4.605 ± 0.121	Plagioclase ^g
Abeesa tuff (ABCT)	4.863 ± 0.073	Plagioclase ^g
Unnamed tuff, Sagantole Fm. 94–32	4.895 ± 0.083	Plagioclase ^g
Gawto basalt	5.234 ± 0.083	Whole rock ^g
<i>Upper unit Laetolil beds</i>		
Yellow marker tuff	3.614 ± 0.018	Alkali feldspar ^j
Tuff 8	3.46 ± 0.12	Biotite ^k
Tuff 8	3.618 ± 0.018	Alkali feldspar ^j
Between tuffs 7 & 8 (MM25)	3.49 ± 0.11	Biotite ^k
Between tuffs 7 & 8 (75-7-7E)	3.56 ± 0.02	Biotite ^k
Tuff 7A	3.65 ± 0.02	Biotite ^j
Tuff 7	3.56 ± 0.19	Biotite ^k
Tuff 6	3.77 ± 0.05	Biotite ^j
Tuff 5	3.61 ± 0.19	Biotite ^j
Tuff between 4 & 5	3.78 ± 0.11	Biotite ^j
Tuff 4	3.80 ± 0.04	Alkali feldspar ^j
Tuff 4	3.85 ± 0.02	Biotite ^j
Tuff 3	3.71 ± 0.04	Biotite ^j
Tuff 2	3.78 ± 0.04	Alkali feldspar ^j
Tuff 2	3.85 ± 0.03	Biotite ^j
Tuff 1	3.74 ± 0.02	Biotite ^j
Base of upper unit, Laetolil beds	3.76 ± 0.03	Biotite ^k
<i>Lower unit Laetolil beds</i>		
Uppermost lower Laetolil beds	3.84 ± 0.02	Alkali feldspar ^j

Most results on alkali feldspar are based upon single crystal total fusion measurements, whereas most whole rock or glass measurements are from step heating experiments. In most cases the age and uncertainty are based upon a weighted mean calculation

^a de Heinzelin et al. 1999

^b Kimbel et al. 1996

^c Dimaggio et al. 2008

^d Walter 1994

^e Renne et al. 1993

^f Walter and Aronson 1993

^g Renne et al. 1999

^h White et al. 1993

ⁱ White et al. 2006

^j Deino 2011; preferred ages

^k Drake and Curtis 1987

Pliocene Formations of the Omo-Turkana Basin (the Omo Group)

Hominin taxa described from sedimentary deposits of the Omo Group in northern Kenya and southern Ethiopia include *Australopithecus anamensis*, *Australopithecus afarensis*, *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Kenyanthropus platyops*. The Omo Group was defined originally by de Heinzelin (1983) as a general term to include tilted and faulted sedimentary strata of Pliocene and Pleistocene age in the Lower Omo Valley. Within the Omo Group, de Heinzelin (1983) included the Mursi, Nkalabong, Usno, and Shungura formations, and also what he termed the Loruth Kaado and Naiyena Epul beds, which are now included within the Nachukui Formation. By extension, the Koobi Fora Formation (Brown and Feibel 1986), and the Nachukui Formation (Harris et al. 1988a, b) are now included in the Omo Group. These formations consist dominantly of sands, silts and clays, deposited in fluvial, deltaic and lacustrine, environments. The Omo River, which drains the Ethiopian highlands, transported much of the sediment to the basin but there are also important contributions from lateral streams along the basin margin in many places. Two lacustrine intervals are especially prominent, one between ~4.3 and 4 Ma, and a second between ~2.0 and 1.6 Ma. Two of the formations of interest are located in the Lower Omo Valley of Ethiopia—the Shungura and Usno formations. Chronological control on formations of the Omo Group derives principally from $^{40}\text{Ar}/^{39}\text{Ar}$ ages measured at the Australian National University, Canberra. Directly measured ages are now available for 33 individual volcanic ash layers (Table 2.2). Because of the reasonably closely spaced direct age measurements, additional control can be added by knowing the levels of transition from normal to reversed paleomagnetic polarity and assigning the transitions to previously established chrons and subchrons of the Geomagnetic Polarity Time Scale.

Shungura Formation

The 766 m thick Shungura Formation is beautifully documented by de Heinzelin and coworkers (see de Heinzelin and Haesaerts 1983a, b). It crops out in a long (~65 km), narrow (1–9 km), north–south trending belt west of the Omo River in southern Ethiopia, and it is faulted, with most blocks having been dropped down on the east and strata dip ~10°W. de Heinzelin and Haesaerts (1983a) divided the formation into a Basal Member, followed upward by members A to L (omitting I). The base of the formation is taken as the lowest strata exposed below Tuff A; nowhere is the contact with underlying rocks exposed. A silicic tuff lies at the base of

each member except for the Basal Member, which is defined as those strata which lie beneath Tuff A. Tuff A lies at the base of Member A. de Heinzelin and Haesaerts (1983a) divided each member into submembers on the basis of fining upward sequences and/or erosional surfaces, and labeled them numerically from the base upward within each member (e.g., D-3); some submembers are divided internally, and these too are numbered from the base upward within each submember (e.g., D-3-2). Tuffs not used to define members are designated by the submember or unit in which they occur (i.e., D-3-2). Fossils are abundant from Member A to Member L, and have provided an important set of fossil mammals useful for biochronology in East Africa. Below submember G-14, the formation consists principally of fluvial sediments arranged in fining upward cycles, commonly with a paleosol at the top of each. Many fossils derive from sandstones at the base of each fining upward sequence, but others come from less energetic conditions representing ancient floodplains. Chronological control is provided by direct determinations on materials from the Shungura Formation, and also by tephrostratigraphic correlations to dated units in other formations of the Omo Group. For example, Tuff C-4 of the Shungura Formation correlates with the Ingumwai Tuff of the Koobi Fora Formation, and lies below the Burgi Tuff which has been dated at 2.62 Ma. Hence C4 is somewhat older than 2.62 Ma. Other correlations provide still additional information.

Usno Formation

de Heinzelin and Haesaerts (1983b) described the 172 m thick Usno Formation that is exposed ~20 km northeast of the Shungura Formation in several small (named) patches. Fossils come principally from two of these exposures—White Sands and Brown Sands—at stratigraphic levels near the middle of the formation above tuffs U-10 and U-11, which correlate with tuffs B- α and B- β . Like the Shungura Formation, the fossils derive from fluvial deposits.

Koobi Fora Formation

Bowen and Vondra (1973; see also Bowen 1974) first provided a stratigraphy of Pliocene and Pleistocene deposits in the Koobi Fora region east of Lake Turkana. Brown and Feibel (1986) revised the stratigraphy, and defined all Pliocene and Early Pleistocene strata as part of the 525 m thick Koobi Fora Formation. The latter authors divided the

Koobi Fora Formation into eight members based on chemically distinct tephra marker horizons. From bottom to top the member names are: Lonyumun, Moiti, Lokochot, Tulu Bor, Burgi, KBS, Okote, and Chari. A major discontinuity occurs within the Burgi Member, which has a duration of ~ 0.5 Ma. This separates the informal lower Burgi Member (which extends upward to Lokalalei Tuff; 2.52 ± 0.03 Ma), from the informal upper Burgi Member (for which deposition begins approximately 2 Ma ago; McDougall and Brown 2008). Part of the interval missing in the Koobi Fora region is preserved in exposures of the Koobi Fora Formation at Loiyangalani (Gathogo et al. 2008), where deposits include the Kokiselei Tuff, and the depositional break occurs after eruption of flows of the Lenderit Basalt (2.02 ± 0.02 to 2.51 ± 0.03 Ma). The Koobi Fora Formation records a variety of fluvial, lacustrine, and deltaic environments, but fossils of *Australopithecus* sp. are principally known from fluvial channel deposits (see Coffing et al. 1994).

Kanapoi Formation and Nachukui Formation

These units lie disconformably above Miocene volcanic rocks. In other locations in the Omo-Turkana Basin deposition of Omo Group sediments began shortly before or after eruption of basalts of the Gombe Group (Watkins 1983; Haileab et al. 2004).

The Kanapoi Formation, located southwest of Lake Turkana in the Kerio River Valley is 37.3 m thick in its type section (Feibel 2003a). It records both lacustrine deposition and deltaic deposition by a river entering the basin from the south or southwest. Specimens recovered from this locality led Leakey et al. (1995) to propose a new species of hominin—*A. anamensis*.

At Lothagam, also located southwest of Lake Turkana ~ 65 km north of Kanapoi, the 37–113 m thick Apak Member of the Nachukui Formation disconformably lies above fluvial strata of the Nawata Formation (7.4 ± 0.1 to 6.5 ± 0.1 Ma; McDougall and Feibel 1999; Feibel 2003b), and below the 59 m thick Muruogori Member. The 94 m thick Kaiyumung Member lies above the Muruogori Member (McDougall and Feibel 1999). The Apak Member records rapid deposition by a meandering river on a floodplain, perhaps related to that at Kanapoi (Feibel 2003b). It is succeeded by lacustrine strata of the Muruogori Member, and then a return to fluvial conditions recorded in the Kaiyumung Member. Despite considerable effort, hominin fossils from Lothagam remain scant. A mandible recovered in 1967 is said to be from the Apak Member, and Leakey and Walker (2003) assigned four dental specimens from the Kaiyumung Member to *Australopithecus* cf. *A. afarensis*.

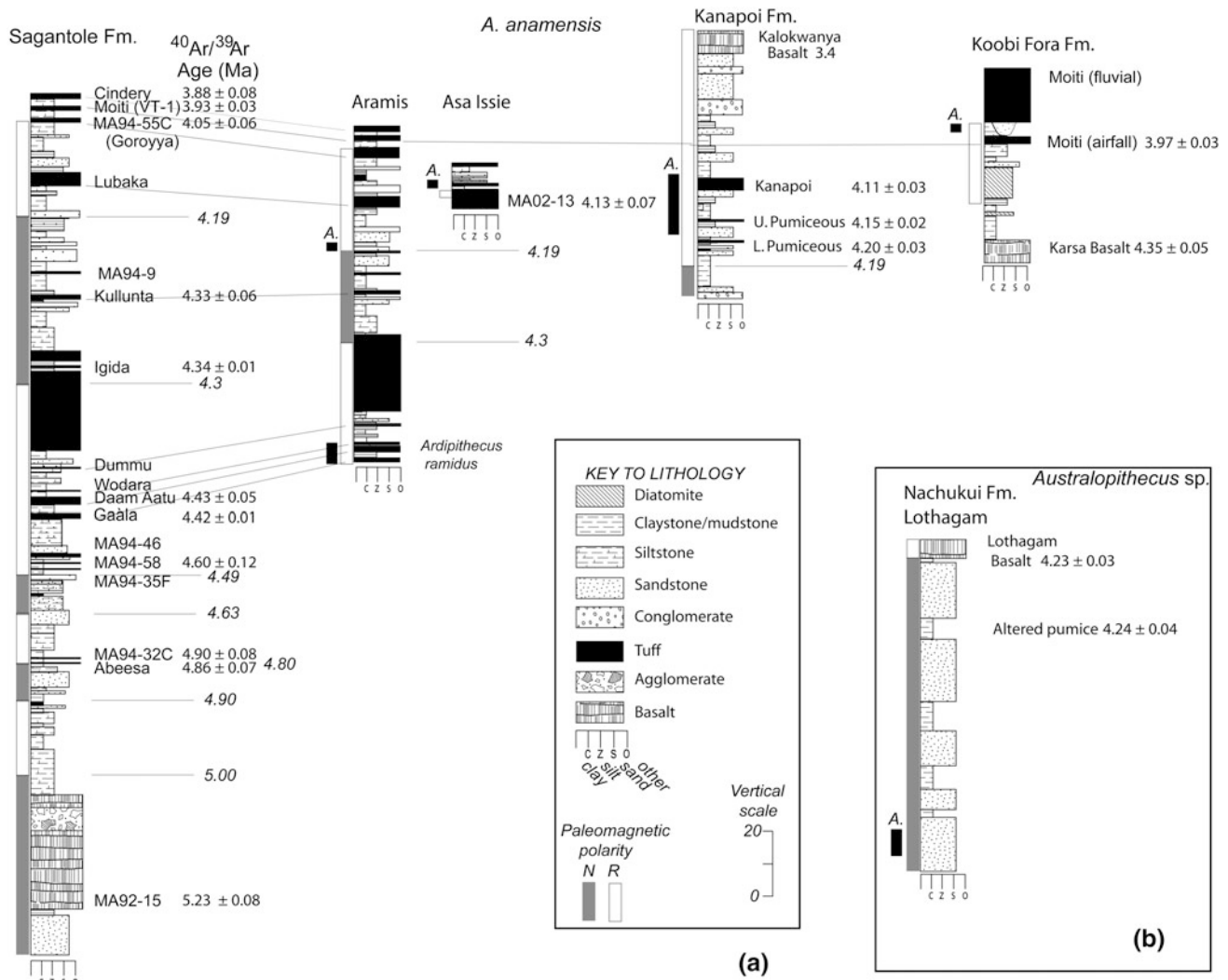
Where exposed west of Lake Turkana between ~ 3.75 and 4.25°N latitude (i.e., between the towns of Kataboi and Lowarengak), the Nachukui Formation has an aggregate thickness of 730 m (Harris et al. 1988a, b). The formation in this region is divided into the Lonyumun (4.2–4 Ma), Kataboi (3.9–3.4 Ma), Lomekwi (3.4–2.5 Ma), Lokalalei (2.5–2.3 Ma), Kalochoro (2.3–1.9 Ma), Kaitio (1.9–1.6 Ma), Natoo (1.6–1.3 Ma), and Nariokotome (1.3–0.6 Ma) members. Remains of *Australopithecus* sp. are known from the Lomekwi Member, and those of *Kenyanthropus* are known from the Kataboi Member. Facies variations occur over short lateral distances in some parts of the Nachukui Formation, and it records lacustrine, fluvial, and alluvial fan environments as described in previous publications (e.g., Harris et al. 1988a, b). Remains of *Australopithecus* sp. were recovered from alluvial plain environments, and those of *Kenyanthropus* were recovered from lacustrine margin deposits.

Pliocene Formations in Ethiopia Outside the Omo-Turkana Basin

Along the Awash River in Ethiopia several paleontological sites have yielded specimens ascribed to *Australopithecus*. Geological units include the Sagantole Formation, the Hadar Formation, and the Bouri Formation.

Sagantole Formation

With important fossils, a thickness over 200 m, and a quasi-continuous temporal record extending over ~ 1.5 Ma, the Sagantole Formation has received special attention. A complete section shown in Fig. 2.2 demonstrates that sedimentary units extending back well over 5 Ma in age exist in the region. Renne et al. (1999) have reviewed the geology, dating, and magnetostratigraphy of this unit, which is very well controlled, and later White et al. (2006) added still more temporal information. The Sagantole Formation has been divided into seven members (Renne et al. 1999). From the base upward these are the Kuseralee, Gawto, Haradaso, Aramis, Beidareem, Adgantole, and Belohdelie members. The Kuseralee Member consists of gypsiferous siltstones and claystones with interbedded bentonite layers and sandstones. A sandstone with a rich vertebrate fauna is succeeded by the lowermost flow of the Gawto Member. Basaltic lava flows and an agglomerate make up the Gawto Member. Fine-grained strata of the overlying Haradaso Member are succeeded by thick, cross-bedded sandstones,



and conglomerate lenses near the top. Vertebrate fossils are abundant in the silty sandstones and coarser sandstones. The Haradaso Member contains at least seven tephra (mainly altered), including the Abeesa Tuff. At the base of the Aramis Member is the Gàala Tuff Complex, which is overlain by silt, clay, and sand with calcareous layers some of which contain vertebrate fossils and fossilized seeds and dung. A coarse-grained cross-bedded sandstone at the top of the Aramis Member contains vertebrate fossils, but the member also includes gastropod-bearing limestones. Most of the Aramis Member probably records fluvial sedimentation with shallow lacustrine environments represented

near the top. The Beidareem Member consists of altered basaltic tephra and locally 2–4 m of silts and silty clays between the basaltic tuffs enclose the Igida Crystal Tuff. Some 80 m of strata comprise the Adgantole Member, which is dominated by silt, clay, and sand, but also has coarse sandstone and conglomerate near the top. It contains several tuffs (e.g., Kullunta Basaltic Tuff, Lubaka Vitric Tuff, Goroyya Tuff Complex). The Goroyya Tuff Complex crops out ~3 m below Tuff VT-1 (=Moiti Tuff) which defines the base of the Belohdelie Member. The Moiti Tuff was defined in the Omo-Turkana Basin (Cerling and Brown 1982; Haileab and Brown 1992). Extending upward to the

base of the Cindery Tuff, the Belohdelie Member consists of clay, silt, and fine sand with a few thin, coarser-sand horizons, several laterally extensive vitric tephra, and a gastropod-bearing limestone beneath the Cindery Tuff. Deposition in a fluctuating shallow- to deep-lacustrine system, including swamp and lake-margin facies is suggested for this member (Renne et al. 1999). White et al. (2006) report on specimens of *A. anamensis* from this formation at Aramis, and also at Asa Issie.

Hadar Formation

The Hadar Formation, a minimum of 280 m thick, is exposed along the Awash River adjacent to the eastern escarpment of the Ethiopian Plateau (Johanson et al. 1982). The principal area (~10 km²) from which fossils of *Australopithecus* were collected is located north of the Awash River. The strata are essentially flat lying, and have been divided into four members, the Basal, Sidi Hakoma, Denen Dora, and Kada Hadar members from the base upwards. The sedimentary strata are generally similar to those of the Sagantole Formation, but lack basaltic tephra that are so prominent in the former. Like the Sagantole Formation, the Hadar Formation contains several vitric tuffs (e.g., the Sidi Hakoma Tuff (SHT), the Kada Hadar Tuff (KHT), the Triple Tuff (TT), the Bouroukie Tuffs (BKT), etc.), which have provided material for ⁴⁰Ar/³⁹Ar dating. Lacustrine, lake margin, fluvial and flood plain environments are well represented, and described elsewhere (e.g., Taieb et al. 1972, 1976; Johanson et al. 1982). Near the base of the formation is the Sidi Hakoma Tuff, which correlates with the β -Tulu Bor Tuff of the Omo-Turkana Basin (Brown 1982; Walter and Aronson 1993). The site is justly famous for the discovery of many fossils now ascribed to *A. afarensis* (e.g., Taieb et al. 1976; Johanson et al. 1978; Johanson and White 1980). At Dikika, the Hadar Formation has a maximum thickness of ~160 m, and many of the units defined at Hadar itself are still recognizable (SHT, KHT, TT-4, etc.; see Wynn et al. 2006). Below the Sidi Hakoma Tuff, lacustrine clays resting on older basalts give way to shoreline facies with gastropod bearing sandstones. These are transitional to delta plain facies that contain the splendid juvenile skeleton attributed to *A. afarensis* described by Alemseged et al. (2005, 2006). Still higher in the section, lacustrine deposition resumes, and is then once again replaced by predominantly fluvially deposited strata in the upper part of the formation. In addition to the juvenile hominin, a partial mandible with associated dentition has been recovered from the area which is also attributed to *A. afarensis* (Alemseged et al. 2005).

Bouri Formation

de Heinzelin et al. (1999) named the Bouri Formation for its location on the Bouri Horst, and divided it into three members (the Hata, Daka, and Herto members) with a combined thickness of 80 m. Of interest here is the Hata Member, which is 40 m thick in its type locality. The lower part of this member is made up of silty claystones, tuffs, and mudstone, with sandstones and mudstones in the upper part. These units are interpreted as having been deposited in fluvial settings close to a shallow fluctuating lake (de Heinzelin et al. 1999). Three tuffs were recognized—the Maoleem Vitric Tuff (MOVT), a yellow-green zeolitized unit, a diatomaceous tuff 14 m higher in the section, and a bentonitic tuff with accretionary lapilli 4 m above that. This is the site from which Asfaw et al. (1999) described the new taxon *Australopithecus garhi*.

Laetolil Beds

Hay (1987) described a representative section of the Laetolil Beds exposed in northern Tanzania, and divided it into a lower unit (64 m), and an upper unit (59 m). His lower unit consists principally of aeolian tuff interbedded with air-fall and water-worked tuffs, and in some sections also contains conglomerates and a mudflow. His upper unit consists largely of aeolian tuff, but also contains air-fall tuffs and several horizons of angular rock fragments, or xenoliths. As sub-aerial deposits, probably on a grassland savanna, the Laetolil Beds differ sharply from other units discussed previously. K/Ar age measurements along with one ⁴⁰Ar/³⁹Ar age determination, principally on biotite from airfall tuffs within the sequence are the basis for the chronology of these beds (Drake and Curtis, 1987). More recent detailed ⁴⁰Ar/³⁹Ar age measurements on biotite and alkali feldspar by Deino (2011) are now the basis for the age assignments. Hominin fossils derive from the upper unit of the Laetolil Beds from levels 7 m below Tuff 3 to 9 m above Tuff 8 (Leakey, 1987).

Temporal Distribution of *Australopithecus* Species

Australopithecus anamensis

Chronologic information on this taxon is summarized in Fig. 2.2, where all columns are drawn, insofar as possible,

to a standard format for ease in comparison. The position of *Ardipithecus ramidus* is also shown on this figure where it is apparent that this taxon predates the earliest occurrences of *A. anamensis* by at least 100 ka.

Representative fossils of *A. anamensis* at Kanapoi, southwest of Lake Turkana, come principally from a lower channel sandstone and overbank mudstone complex, and a distributary channel associated with the Kanapoi Tuff (4.108 ± 0.029 Ma; McDougall and Brown 2008). Altered pumiceous clasts occur in two siltstones in the lower levels of the Kanapoi sequence, and alkali feldspar crystals from them yielded ages of 4.195 ± 0.033 and 4.147 ± 0.019 Ma (Leakey et al. 1995, 1998; McDougall and Brown 2008). The oldest dated level (4.195 ± 0.033 Ma) is below the lowest *A. anamensis* specimen yet recovered. Most hominins from Kanapoi occur in strata between the lowest dated level and the Kanapoi Tuff. Fossils of *A. anamensis* have also been recovered from the Koobi Fora Formation in paleontological collecting Area 261 of the Allia Bay region. In the latter locality the specimens lie ~ 5 m below the Moiti Tuff (Coffing et al. 1994), within the Lonyumun Member as currently defined. However, an airfall equivalent of the Moiti Tuff lies lower in the section in Area 260 (Brown unpublished) to which the age of 3.970 ± 0.032 Ma should most likely be attributed.

Australopithecus anamensis is also known from Aramis and Asa Issie, Ethiopia, probably from the Adgantole Member of the Sagantole Formation. A single specimen from Aramis, Ethiopia, from near the base of paleomagnetic chron C2Ar (4.18 Ma) is attributed to *A. anamensis* (White et al. 2006). At Asa Issie specimens of *A. anamensis* derive from strata above a basaltic tephra layer for which the weighted mean of two plateau ages is 4.128 ± 0.074 Ma (recomputed from 4.116 ± 0.074 in White et al. 2006). These strata are of reversed paleomagnetic polarity, and assigned to chron C2Ar (4.19–3.61 Ma). The younger age limit is more difficult to assess, but White et al. (2006) suggest that the fossils lie below a vitric tuff (VT-3) correlated with the Wargolo Tuff of the Omo-Turkana Basin by Haileab and Brown (1992). White et al. (1993) reported an average age of 3.78 ± 0.02 Ma for this unit. deMenocal and Brown (1999) estimated the age of the Wargolo Tuff at 3.80 ± 0.01 Ma from its correlate in ODP Site 721. Thus, all known specimens attributed to *A. anamensis* lie between 3.8 and 4.2 Ma.

Australopithecus afarensis

Figure 2.3 shows the stratigraphic distribution of this taxon in its principal occurrences: the Hadar region and Laetoli. Some specimens from Koobi Fora, Lothagam and Fejej have also been attributed to *A. afarensis*.

Specimens attributed to *A. afarensis* at Hadar are found in the Sidi Hakoma and Denen Dora members of the Hadar Formation, bounded by the Sidi Hakoma Tuff below, and by BKT-2 above. *Australopithecus* specimens come from a variety of depositional settings; the most famous (A.L. 288-1; “Lucy”) derives from a channel fill of a small stream. Site A.L. 333, which has yielded remains of at least 13 individuals, may have been preserved in overbank sediments related to an adjacent channel fill. Hominin fossils have been retrieved from floodplain, delta plain and delta-margin facies in addition to shallow lacustrine deposits in the Sidi Hakoma Member. In the Denen Dora Member, which has shallow lacustrine deposits in the lower part transitional to swamp and floodplain deposits above, hominins have been recovered not only from the sandy units, but also from finer grained deposits. Chronological control is provided not only by K/Ar and $^{40}\text{Ar}/^{39}\text{Ar}$ dates on intercalated volcanic ash layers, but also by paleomagnetic polarity transitions representing the Mammoth and Kaena subchrons.

K/Ar data reported by Drake and Curtis (1987) establish the general age for the Laetolil Beds, the source of the holotype of *A. afarensis* (L.H. 4; Johanson et al. 1978) but the data set is not as robust as it might be, and additional work would be of interest. In particular, errors on the age determinations are larger than those obtained for materials of comparable age in the Kenyan and Ethiopian materials, partly because biotite normally contains a much smaller fraction of radiogenic argon than feldspars. Recently, Deino (2011) provided new $^{40}\text{Ar}/^{39}\text{Ar}$ ages on the entire succession at Laetoli that are in general agreement with the earlier results of Drake and Curtis (1987), Harrison and Msuya (2005), and Manega (1993). Deino’s preferred ages are shown on the column in Fig. 2.3, and document convincingly that the fossils from the Upper Laetolil Beds lie between 3.63 and 3.8 Ma in age.

Perhaps the best known specimen from Lothagam is a mandible (KNM-LT 329) recovered by Bryan Patterson from the lowest part of the Apak Member of the Nachukui Formation in 1967. It derives from the lowest 3 m of this member, so we only know that it is $>4.22 \pm 0.03$ Ma in age. Leakey and Walker (2003) note that it has affinities to both *A. ramidus* and *A. afarensis*, but attribute the specimen to Hominidae indeterminate. Four dental specimens from the Kaiyumung Member of the Nachukui Formation at Lothagam were assigned to *Australopithecus* cf. *A. afarensis* by Leakey and Walker (2003). On the basis of the known paleomagnetic record, the base of the Kaiyumung Member must be ~ 3.5 Ma (scaling linearly between 3.58 and 3.33 Ma), but probably greater than 3.11 Ma, as only one reversed magnetozone has been reported (Powers 1980; see also McDougall and Feibel 2003). Details of the stratigraphic placement of the specimens within this

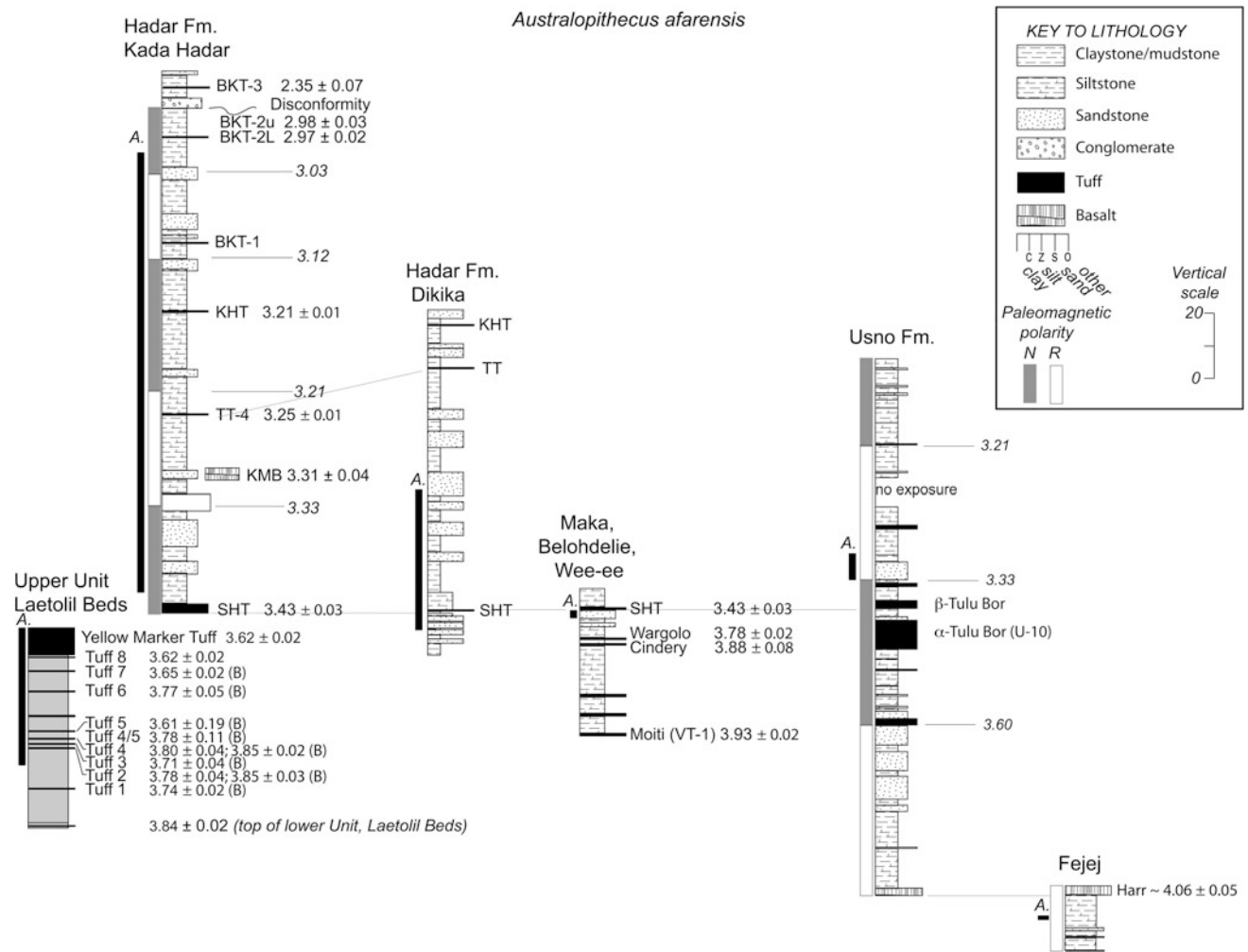


Fig. 2.3 Schematic stratigraphic columns for localities from which fossils ascribed to *Australopithecus afarensis* have been recovered. The column for the Laetolil Beds is after Hay (1987); that for Hadar is after Bonnefille et al. (2004); that for Dikika is after Wynn et al. (2006); that for Maka/Belohdelie/Wee-ee is after White et al. (1993); that for the Usno Formation is after de Heinzelin and Haesaerts (1983b); that for Fejej is after Kappelman et al. (1996). To the left of each stratigraphic column is a column showing paleomagnetic polarity

(if known). Left of that is a *small solid bar* capped with “A.” showing the known range of fossils in each section. Dated units are identified by name, or if a name is lacking, by sample number; $^{40}\text{Ar}/^{39}\text{Ar}$ ages shown with error are recalculated to an age of 28.10 Ma for the Fish Canyon sanidine fluence standard (FCs) so that ages on all columns are comparable. Ages assigned from paleomagnetic transition boundaries are shown without error and italicized

member are lacking, so the specimens can only be said to lie between 3.11 and 3.5 Ma.

At Fejej, Ethiopia (Asfaw et al. 1991), there is evidence for the existence of a species of *Australopithecus* older than 4.0 Ma, but probably not more than 4.2 Ma, based on fossil material from a 25 m section below the Harr Basalt (Fleagle et al. 1991; Kappelman et al. 1996). On the basis of worn and fragmentary teeth they ascribed these specimens to *A. afarensis* following comparison with similar teeth from Hadar. The age of these specimens is nearly 400 ka older than *A. afarensis* at Laetoli. Provided the taxonomic attribution is correct (see Alemseged 2013)—and we stress that this

determination should be based on morphology, not age—it would appear that *A. afarensis* overlaps temporally with *A. anamensis*. Thus, the temporal range of *A. afarensis*, insofar as it is currently known is from ~4.1 Ma at Fejej, to ~2.9 Ma at Hadar. On the other hand, Kimbel et al. (2006), and also White et al. (2006), argue for a linear progression from *A. anamensis* to *A. afarensis*. If the former view is correct, it would suggest that the two taxa were not a strictly anagenetic lineage, but overlapped for an extended time (see Kimbel et al. 2006). Therefore it is of the highest importance that the taxonomic identity of the specimens from Fejej be confirmed.

