Vertebrate Paleobiology and Paleoanthropology Series

Yohannes Haile-Selassie
Denise F. Su *Editors*

The Postcranial Anatomy of *Australopithecus afarensis*

New Insights from KSD-VP-1/1

Springer

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Cover illustration: Woranso-Mille team members excavating and sieving at the partial skeleton locality of KSD-VP-1/1, aka *Kadanuumuu* (left) and recovered elements of the partial skeleton arranged in their anatomical position (right). Photo credits: Yohannes Haile-Selassie and Elizabeth Russell.

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Foreword

I have been waiting a long time for a skeleton like this to be found. Many people have, some even longer than me. The KSD-VP-1/1 skeleton, nicknamed *Kadanuumuu*, is the first partial skeleton ever discovered of a large *Australopithecus afarensis* individual. It is the oldest partial skeleton of any *Australopithecus* individual and contains skeletal elements not previously known for *Au. afarensis*. As such, it has new stories to tell us about the biology and evolution of *Australopithecus*.

Until now, the only reasonably complete *Au. afarensis* skeleton known was the famous "Lucy" skeleton, A.L. 288-1. Lucy was discovered 40 years ago, and until the discovery of *Kadanuumuu* in 2005, she remained the earliest securely dated *Australopithecus* partial skeleton. Not only is Lucy a cultural icon within paleoanthropology and among the public worldwide, she is also significant because much of what we know about *Au. afarensis* comes from studies of her skeleton.

Lucy, along with isolated skeletal elements from the large sample of *Au. afarensis* recovered at the A.L. 333 site and other finds from the sites of Hadar, Maka, and Dikika over the years, has revealed that the small body size, nearly human-like pelvis, and bipedal locomotor adaptation seen in the more recent and less securely dated South African australopiths had appeared prior to three million years ago. These fossils have provided overwhelming and convincing evidence that the postcranial skeleton of *Au. afarensis* was adapted for habitual, committed terrestrial bipedal locomotion – long before human evolution witnessed an increase in brain size or reduction in the face and dentition characterizing the genus *Homo*.

Despite being the most well-represented, well-dated, and well-understood species of early hominin known so far, a vigorous and occasionally rancorous debate has surrounded the ways in which *Au. afarensis* differs from *Homo*. While there is no doubt that *Au. afarensis* individuals were committed terrestrial bipeds, they are not exactly like *Homo* in their postcranial anatomy. These differences have begged the question of why these differences exist; whether from active selection to retain some measure of arboreal competence, or whether these differences were adaptively neutral, and only disappeared later in the face of different selection either associated with improved terrestrial locomotor efficiency and/or positive selection for manipulatory or other behaviors with the origin of *Homo*. This debate is ongoing, and while *Kadanuumuu* does not resolve this debate, it does add key pieces of data that continue to shape it.

Kadanuumuu tells us many things that Lucy and the other fossils have not. A few in particular that stand out to me as particularly salient. Namely, *Kadanuumuu* has the first complete tibia length known for any *Australopithecus* individual, supporting the hypothesis that *Au. afarensis* did not have relatively short lower limbs like an ape, but rather long legs like humans. *Kadanuumuu* has ribs complete enough to reveal a broad upper thorax, reflecting vertebral invagination and fully upright posture in *Au. afarensis,* rather than the cone-shaped great ape-like rib cage previously inferred from less complete fossil material. *Kadanuumuu* also gives us the first fully described cervical vertebrae for any *Australopithecus*. The small upper and larger lower vertebra with long spinous processes and facet joints proportioned like those of humans appear to reflect human-like head carriage of a relatively small cranium with large prognathic face, but with larger neck musculature and likely lack of a nuchal ligament. *Kadanuumuu's* remarkably complete scapula and clavicle, the first known for an adult of this species, not only support the interpretation that the shoulder joint of *Au. afarensis* was indeed oriented more cranially than that of humans, but also show that the infraspinous fossa was large and the musculature of the clavicle and scapula were human-like, perhaps suggesting a shift from arboreal competence towards use of the upper limb in manipulatory function.

Significantly, unlike Lucy, who was much smaller than modern humans, *Kadanuumuu* is as large as a small human. As a consequence of Lucy's small size, there has been an inherent, lingering uncertainty as to whether her morphology differed from that of humans because she had different adaptations, or whether she was just small. *Kadanuumuu* nicely answers this question, confirming that *Au. afarensis* did indeed differ from those of humans, regardless of size.

This volume presents this information and much more in a series of chapters describing and analyzing the various bones of the *Kadanuumuu* skeleton, along with its geological and paleoecological context. The descriptive chapters provide thorough and detailed images, descriptions, and functional analysis. The authors then all take a further step and provide their interpretations of the implications of their findings, which are integrated and summarized in the last chapter to provide a cohesive interpretation of the biology of *Australopithecus afarensis*. From this interpretation, as in the individual analytic chapters, the authors put *Au. afarensis* into the context of other known hominin fossils and hypothesize about what this all means for the origin of hominins and the subsequent appearance of the genus *Homo*. The scenario presented here builds on analyses published recently by contributors to this volume and is consistent with much of the new fossil evidence that has been recovered over the past few years. It presents an exciting new perspective on hominin origins, and many testable predictions can be – and I am sure will be – drawn from it by these and other scholars for years to come.

So, while *Kadanuumuu* answers key questions about *Australopithecus afarensis*, like all good fossils, it raises at least as many questions as it answers. This skeleton, and this careful and thorough volume, provides a solid stepping-stone for future research on the early part of human evolution. This volume is sure to become a staple in every paleoanthropologist's library and an important reference work for generations to come.

Carol V. Ward
University of Missouri

Preface

The geological sequence in the Afar region of Ethiopia includes more than a kilometer-thick, stratified, fossiliferous sediments sampling the last six million years of vertebrate evolutionary history and provides one of the most important windows into our evolutionary past. The continuous fossil-bearing sedimentary sequence in this region is unparalleled by any other place in the world and has been a research target for a number of paleontologists for the last five decades. Since the discovery of Hadar in the late 1960s by the French Geologist Maurice Taieb and the subsequent initiation of paleontological field research at the site by the International Afar Research Expedition (IARE), a number of other projects have followed suit to extensively explore the region. Currently, there are more than eight paleontological and archeological research projects working in the Afar region; combined, they have yielded an uninterrupted fossil record documenting the last six million years of human evolutionary history with more than 12 early hominin species recovered thus far, some of them found only in the Afar region of Ethiopia.

The Woranso-Mille paleontological project is one of the relatively young projects working in the Afar region. Understanding the importance of locating new paleontological sites, one of us (YHS) initiated an extensive survey and exploration of the northern and central Afar region of Ethiopia in the fall of 2002 under a permit issued by the Authority for Research and Conservation of Cultural Heritage of the Ministry of Culture and Tourism of Ethiopia (ARCCH). Exploration and survey largely relied on aerial photographs, satellite imagery interpretations, and air survey in order to identify sediments with paleontological potential, followed by foot survey covering vast areas. It was not until the end of the 2004 survey and exploration season that the paleontological potential of the Woranso-Mille area was identified.

The Pliocene deposits of the Woranso-Mille are unique because they represent a geological time period (3.6–3.8 Ma) that is poorly sampled in the eastern African geological sequence. Moreover, recent investigations have also identified sediments within the study area that are older than 4.3 Ma, as well as sediments that are younger than 3 Ma and older than 5 Ma. Paleontological research at Woranso-Mille in the last 10 years has largely concentrated on the fossiliferous deposits dated to between 3.5 and 3.8 Ma, largely to address the ancestor-descendant relationship that has been widely hypothesized between *Australopithecus anamensis* (4.2–3.9 Ma) and *Australopithecus afarensis* (3.7–3.0 Ma). Although a number of morphological analyses support this hypothesis, the paucity of hominin fossils from the time between 3.6 and 3.9 Ma has been a major obstacle to understanding their phylogenetic relationship. The Woranso-Mille paleoanthropological research project has contributed significantly to our understanding of middle Pliocene hominin phylogeny and systematics with the recovery of hundreds of hominin fossils of the appropriate age. These fossils emphasized the mosaic nature of the dentognathic and postcranial morphology of these early hominins and showed unequivocally that the middle Pliocene of eastern Africa was populated by a diversity of hominin species.

One of the most spectacular fossil discoveries from the Woranso-Mille study area is a partial skeleton of *Au. afarensis* (KSD-VP-1/1), the subject of this volume. The first element of the specimen was found in February 2005 and the rest of its elements were recovered from excavations conducted over 4 years following the initial discovery. Partial skeletons are extremely rare in the fossil record, with only four known from the entire Pliocene hominin fossil record. One of these partial skeletons, A.L. 288-1 (Lucy), was discovered at Hadar in 1974. This 3.2 Ma specimen assigned to the species *Au. afarensis* has been a subject of intense research and used as the major source of information to understanding the paleobiology of the species. However, it has also raised a number of debates particularly in relation to early hominin body size, shoulder girdle anatomy, thoracic shape, and locomotor adaptation of *Au. afarensis*.

KSD-VP-1/1, nicknamed *Kadanuumuu*, which means "big man" in the local Afar language, not only is a much larger individual but also has almost complete elements of the shoulder and pelvic girdles, along with ribs, cervical vertebrae, and elements of both the fore- and hindlimb that, for the first time, shed light on the cervical anatomy of early hominins and allow for a deeper understanding of limb proportions and locomotion in *Au. afarensis*. A preliminary analysis of KSD-VP-1/1 was published in 2010 in the *Proceedings of the National Academy of Sciences* that highlighted the significance of the specimen for understanding the paleobiology of *Au. afarensis*. This volume, however, presents a detailed description and analyses of all of the elements recovered, with additional data derived from computed tomography (CT), along with a better understanding of its geological, taphonomical, and paleoenvironmental context. This volume will contribute greatly to our knowledge of the postcranial anatomy of *Au. afarensis* and towards a better understanding of its overall paleobiology.

Field research conducted by the Woranso-Mille paleoanthropological project was made possible under a permit from the Authority for Research and Conservation of Cultural Heritage (ARCCH) of the Ministry of Culture and Tourism of Ethiopia, the Afar Regional State, and all of its district administrations. We would like to particularly acknowledge Mohammed Bilay (Administrator of Mille district) and Habib Wogris (Chairman of the Gega and Burtele sub district) for their support of the project. Thanks to Alemayehu Asfaw who found the first skeletal element of KSD-VP-1/1 and to the colleagues and students who participated in the excavation: Mulugeta Alene, Joshua Angelini, Erin Benson, Alan Deino, Stephanie Melillo, Hailay Reda, Liz Russell, Beverly Saylor, Gary Scott, and Robin Shultz. We are also grateful to the many field assistants from Addis Ababa and the Afar people at Waki and Waylateyta without whose participation the excavation of KSD-VP-1/1 would not have been possible. The Paleoanthropology Laboratory of the ARCCH made its laboratory and fossil storage space available and we are grateful for the support provided by the curators in the laboratory. Field and laboratory research of the Woranso-Mille project was supported by The Leakey Foundation, The Wenner-Gren Foundation, The National Geographic Society, Cleveland Museum of Natural History, and National Science Foundation (BCS-0234320, BCS-0321893, BCS-0542037, BCS-1124705, BCS-1124713, BCS-1124716, BCS-1125157, BCS-1125345).

We thank all of the authors in this volume for their contribution to our understanding of *Australopithecus* paleobiology and paleoenvironment, and to the many colleagues who have provided comments, advice, and discussion to the research conducted at Woranso-Mille in general and to the research presented in this volume specifically. The chapters presented in this volume were extensively reviewed, and we are grateful to those colleagues who contributed their time and efforts to the review process. Alex Fadiga and Caitlin Schwartz provided editorial assistance. Our deepest thanks to Eric Delson and Eric Sargis, editors of the Vertebrate Paleobiology and Paleoanthropology Series, for their support throughout the process and their patience in seeing this volume to publication and to Shalini Selvam, Sherestha Saini and Jeffrey Taub for overseeing the production of this book.

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Chapter 1
Introduction to KSD-VP-1/1: The Earliest Adult Partial Skeleton of *Australopithecus afarensis*

Yohannes Haile-Selassie

Abstract Early hominin partial skeletons are extremely rare in the fossil record, particularly for the time predating 3 Ma (million years ago). As a result, most of our understanding of Pliocene hominin paleobiology and phylogenetic relationships is based on isolated and fragmentary specimens. The Middle Pliocene species *Australopithecus afarensis* is one of the best-known early hominin species, and yet only three adult partial skeletons of the species have been recovered thus far, including the one described in this volume. The best known of these is the 3.2 Ma partial skeleton of a small female (A.L. 288-1) from Hadar, Ethiopia, and much of our understanding of the paleobiology of this species has been influenced by this specimen. The newly recovered 3.6 Ma partial skeleton from the Woranso-Mille, Ethiopia (KSD-VP-1/1, aka *Kadanuumuu*) represents a much larger male individual and may provide us with fresh insights into the paleobiology of *Au. afarensis*. This specimen not only preserves elements of the forelimb and hindlimb, but also includes complete elements, such as the scapula and clavicle, which were previously known only from fragmentary specimens. This edited volume provides the taphonomy and paleoecology of the partial skeleton, as well as detailed comparative descriptions of the preserved elements of KSD-VP-1/1 and their implications for our understanding of early hominin paleobiology. This chapter will present a basic introduction to the discovery of KSD-VP-1/1 and provide a guide to the contents of the volume.

Keywords Woranso-Mille • Hominin • Paleobiology • Paleoecology • Middle Pliocene

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Introduction

Australopithecus afarensis is one of the best represented early hominin species in the fossil record, known from a number of cranial and postcranial elements collected from Middle Pliocene deposits of Ethiopia, Kenya, Tanzania, and possibly Chad that range in age from ca. 3.8 Ma (million years ago) to 2.9 Ma (Leakey et al. 1976; Aronson et al. 1977; White 1977, 1980; Johanson et al. 1978a, b, 1982; Harris 1987; Brunet et al. 1995, 1996; Brown et al. 2001; Alemseged et al. 2005, 2006; Campisano and Feibel 2008; Harrison 2011). A detailed review of the species is presented in Kimbel and Delezene (2009). However, since its initial naming (Johanson et al. 1978a), its taxonomy (Ferguson 1983; Richmond and Jungers 1995; Strait and Grine 2004; Grine et al. 2006) and locomotor adaptation (Stern and Susman 1983, 1991; Susman et al. 1984, 1985; Latimer et al. 1987; Lovejoy 1988; Latimer and Lovejoy 1990a, b; Latimer 1991; Stern 2000; Lovejoy et al. 2002; Ward 2002; Ward et al. 2011) have been subjects of great debate.

Due to the relatively abundant fossil remains of the species, the craniodental anatomy of *Australopithecus afarensis* has been the subject of intensive comparative studies. Most of the complete cranial and dentognathic specimens were recovered from Hadar, Ethiopia (see Kimbel et al. 2004; Kimbel and Delezene 2009, for review). The fossil remains of this species have served as the basis for what we know about the paleobiology of, and intraspecific variation in, early hominin taxa. Specimens attributed to *Au. afarensis* show substantial amount of size and shape variation related to sexual dimorphism (Johanson et al. 1978a, b; Johanson and White 1979; Kimbel et al. 1985, 2004; Kimbel and White 1988; Lovejoy et al. 1989, among many others). Reno et al. (2003) analyzed skeletal size dimorphism in *Au. afarensis* applying extensive simulations using the smallest individual A.L. 288-1, the large sample from A.L. 333, modern humans, chimpanzees, and gorillas, which indicated that skeletal size dimorphism in *Au. afarensis* was most

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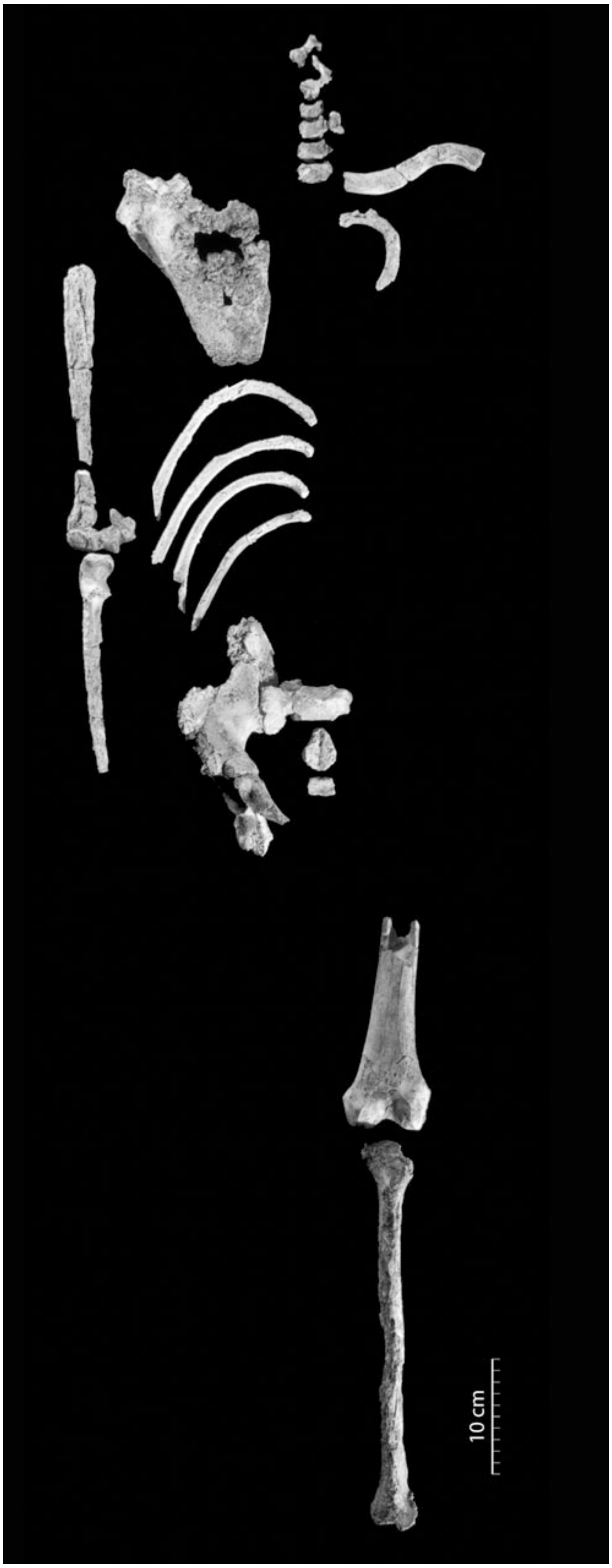

Fig. 1.1 KSD-VP-1/1 with elements arranged in their anatomical position. A complete list of elements is provided in Table 1.1. Photo courtesy of Elizabeth Russell

similar to that of modern humans. However, other comparative analyses (for example, Lague 2002) have shown that the variation falls within the range observed in gorillas and orangutans, and exceeds that of chimpanzees and humans. Some researchers have also suggested that the degree of variation seen in *Au. afarensis* is too great for a single species and proposed the possibility of multiple taxa within the hypodigm (for example, Coppens 1981, 1983; Olson 1981, 1985; Ferguson 1983, 1984; Senut 1983, 1986; Senut and Tardieu 1985; Zihlman 1985; Schmid 1989).

Until recently, only two adult partial skeletons of *Au. afarensis* with both forelimb and hindlimb elements have been reported since its initial description and naming – A.L. 288-1 (Johanson et al. 1982) and A.L. 438-1 (Drapeau et al. 2005). However, the unusually small body size of A.L. 288-1 has raised questions regarding allometry and its impact on the interpretation of *Au. afarensis* paleobiology and locomotor adaptation (e.g., Jungers 1982; Wolpoff 1983; Jungers and Stern 1983; Aiello 1992). A.L. 438-1, while a much larger individual, is missing key elements that preclude the analyses necessary to resolve the issue. Thus, there is still much to learn about the paleobiology of *Au. afarensis*. The recently announced partial skeleton, KSD-VP-1/1 (Fig. 1.1), from the Woranso-Mille study area is critically important as one of the only three known adult partial skeletons of *Au. afarensis*. KSD-VP-1/1 represents a moderately large-bodied individual, well within the range of living *Homo* in its size and certain aspects of its morphology (Haile-Selassie et al. 2010a, b); its preserved elements provide new data on limb proportions, shoulder girdle anatomy, thoracic form, and locomotor heritage in early hominins.

Background on the Woranso-Mille Study Area

The Woranso-Mille paleontological study area (WORMIL) is a relatively new hominin-bearing Mio-Pliocene site complex located in the central Afar region of Ethiopia, about 40 km north of the Hadar, Gona, and Dikika paleontological sites (Fig. 1.2). In the early 1970s, Kalb (1993, 2001) briefly visited the northern part of the study area along the old road from Mille town to Chifra and collected vertebrate fossils (mostly monkeys and pigs) from the area known as Am-Ado (Kalb's "Ahmado"). Kalb (1993, 2001) also identified some localities around the area locally known as Leadu on the Bati-Mille road further to the south. However, there is no record that exposures between Am-Ado and Leadu (ca. 12 km north–south stretch) were surveyed by Kalb or other paleontologists. A small team led by the author started intensive paleontological survey and exploration in this area in 2003. The team was able to identify a number of fossiliferous outcrops south of

Am-Ado and north of Leadu, signifying the need for long-term paleontological research in the area. In 2005, the Woranso-Mille project evolved from a small paleontological survey and exploration team to an international multidisciplinary team of scientists that began intensive and systematic research on the geology and paleontology of what is now known as the Woranso-Mille paleontological site.

A total of 85 vertebrate paleontological localities have been designated in the study area thus far, with more than 8,400 fossil specimens collected including 167 ($\sim$2% of the total fauna) hominin fossils (Haile-Selassie et al. 2007, 2010a, b, 2012; Haile-Selassie 2010). The faunal assemblage includes more than 70 mammalian species ranging in age from the Late Miocene to the Middle Pliocene. More than 95% of the specimens, including all of the hominins recovered thus far, are from sediments radiometrically dated to between 3.4 and 3.82 Ma (Deino et al. 2010; Haile-Selassie et al. 2012).

WORMIL is an important hominin-bearing site complex, sampling a time period that is poorly known in the human fossil record and providing significant fossil evidence that

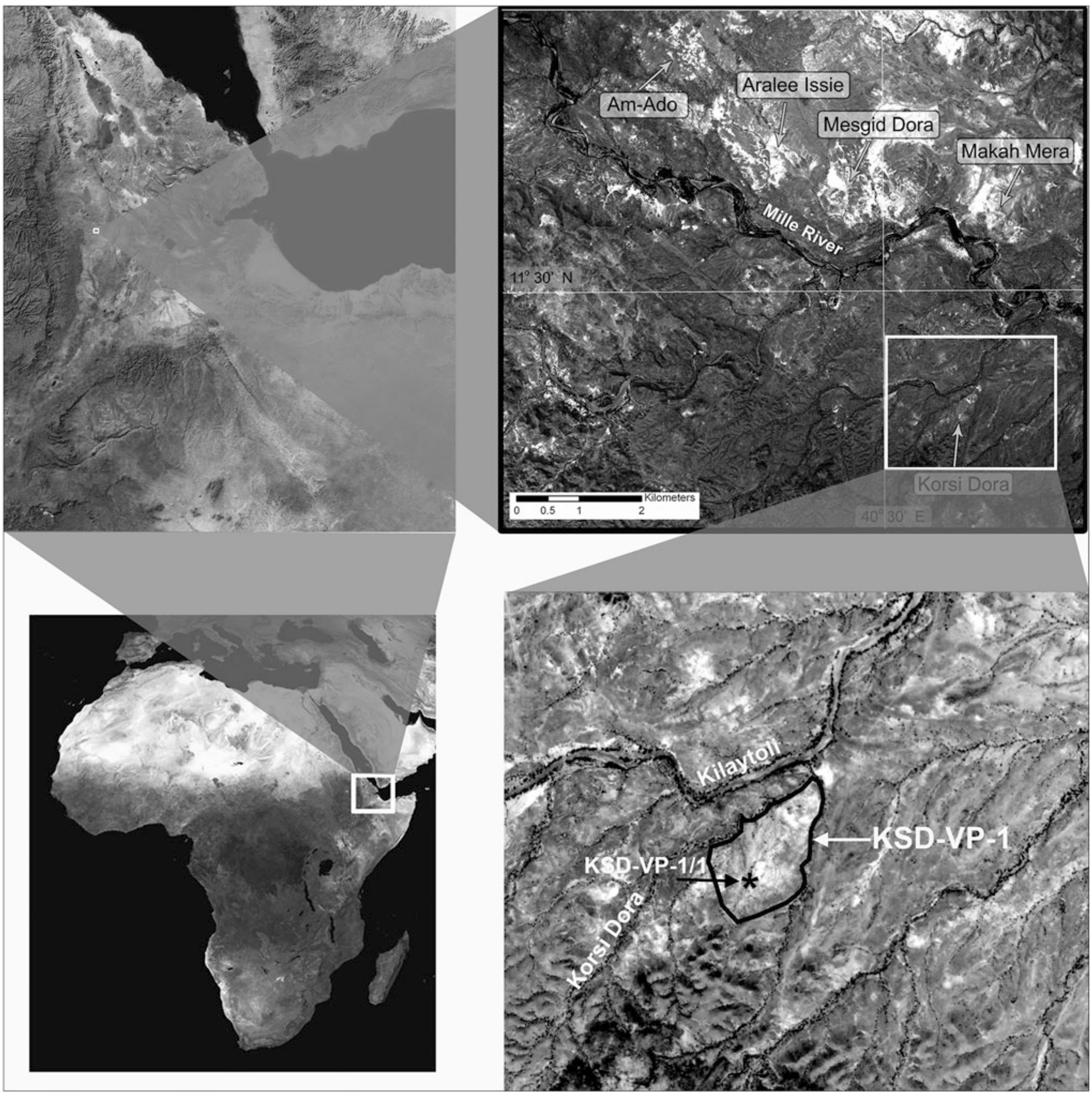

Fig. 1.2 Location map of the Woranso-Mille study area and locality boundaries of KSD-VP-1 locality (bottom right). The location of KSD-VP-1/1 is shown by a star

Fig. 1.3 Alemayehu Asfaw discovering the first element (proximal ulna) of KSD-VP-1/1 on February 10, 2005

could answer critical questions in human evolutionary studies. It is the only site, thus far, that has yielded incontrovertible evidence of multiple, contemporaneous hominin species from a single site during the Middle Pliocene (Haile-Selassie et al. 2012, 2015) and has yielded the oldest adult *Au. afarensis* partial skeleton, KSD-VP-1/1 (Haile-Selassie et al. 2010a).

Recovery, Excavation, and Preservation of KSD-VP-1/1

The partial skeleton is recovered from Korsi Dora vertebrate locality 1 (KSD-VP-1), one of the smallest and most paleontologically depauperate localities in the Woranso-Mille study area. The locality is about 300 m^2 in size, and fossiliferous sediments are exposed on the southern edge of a drainage system known as 'Kilaytoli' and east of 'Korsi Dora,' a small channel that drains to Kilaytoli (Fig. 1.2).

Recovery

The first element of KSD-VP-1/1, a proximal ulna fragment, was found by Alemayehu Asfaw (Fig. 1.3) on February 10, 2005 (11° 28′ 54.0″ N; 40° 30′ 39.3″ E [Reference Datum = WGS84]). Crawling and surface scraping in the immediate area resulted in the recovery of more parts of the ulna, fragments of the distal femur, bodies and pedicels of cervical vertebrae, humeral shaft fragments, and parts of the sacrum. Once the hominin horizon was identified, the team started excavating east and northeastward, where the surface

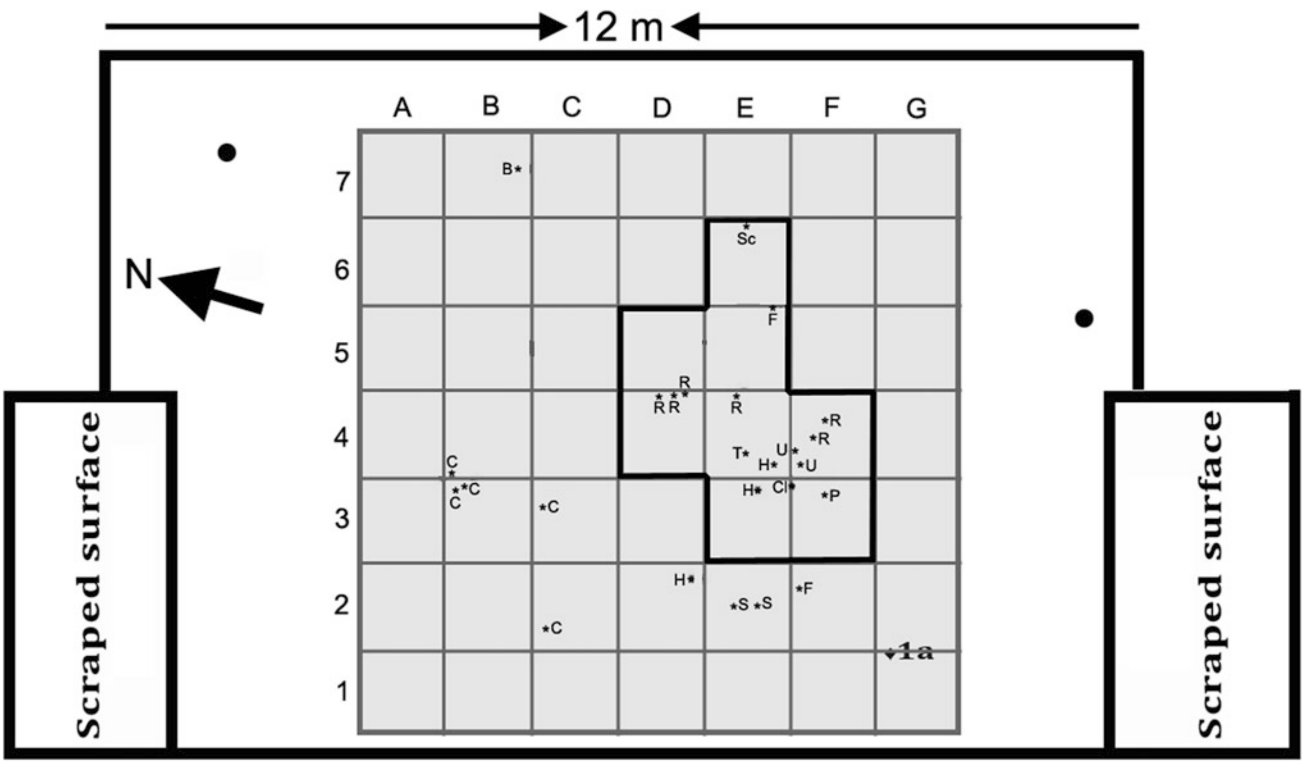

Fig. 1.4 Schematic diagram of the excavated area at KSD-VP-1/1 location. The gray area represents where most of the elements of the partial skeleton were collected. The area highlighted with the gray box is where the *in situ* specimens were recovered. 1a the first specimen (proximal ulna) that was discovered on the surface; *B* bovid molar fragment; *C* cervical vertebra; *Cl* clavicle; *F* femur; *H* humerus fragment; *R* rib; *Sc* scapula; *U* ulna fragment

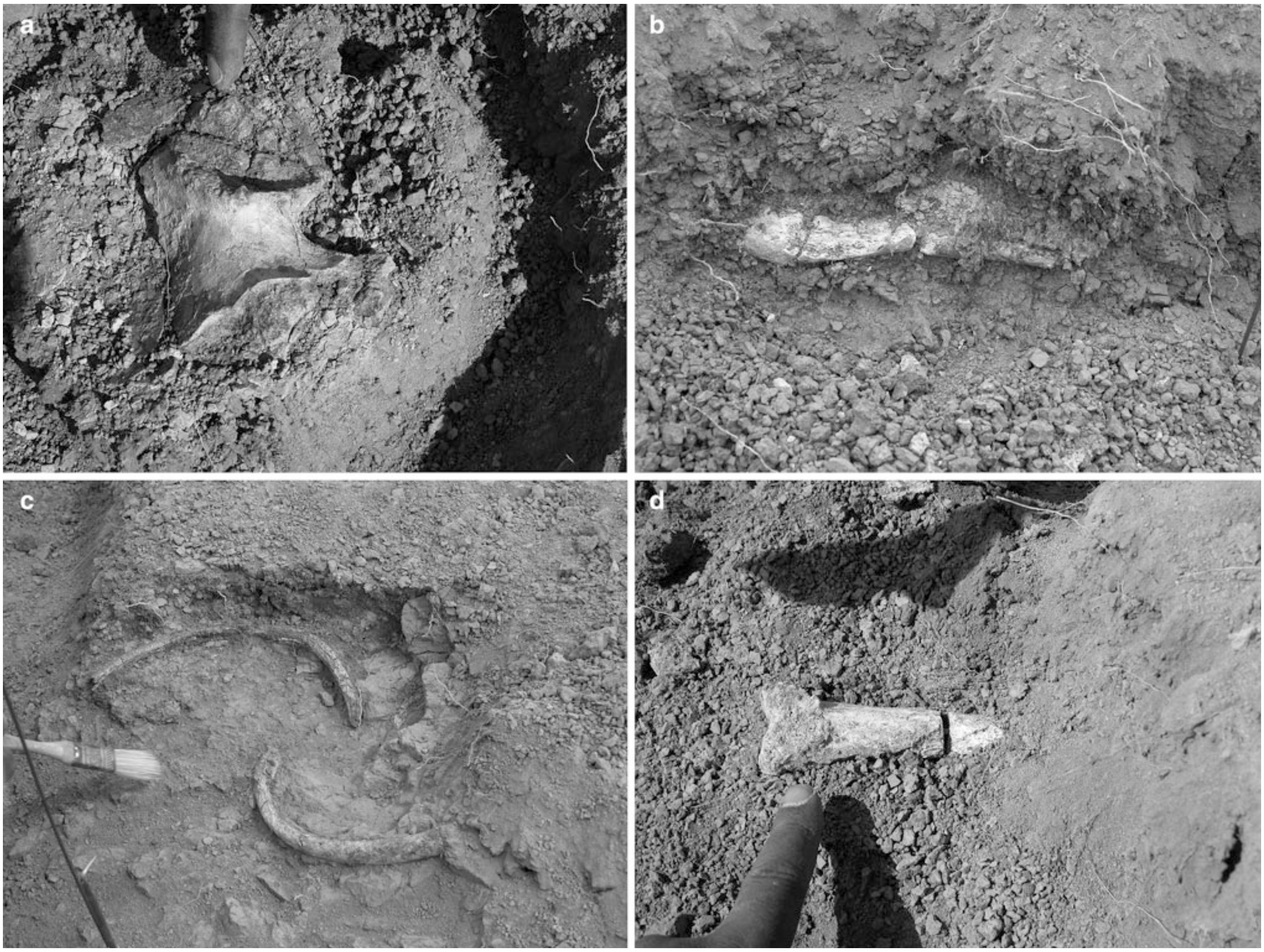

Fig. 1.5 Elements of KSD-VP-1/1 found *in situ*: **a** right innominate, **b** right clavicle, **c** lower ribs, **d** left tibia

finds were abundant, and resulted in further recovery of *in situ* skeletal elements including the left os coxa, right tibia, right clavicle, five ribs, and a left scapula (Fig. 1.4), all of which were excavated within an area of 8 m^2 (Fig. 1.5a–d) from a laminated mudstone and sandstone horizon at the base of upward-coarsening sequences that are interpreted as overbank deposits (Deino et al. 2010; Saylor et al. 2016).

Excavation

During the 2005 field season, an area of 49 m^2 was excavated, which covered the distribution of all surface fragments. A string grid was set up using metal pegs at the grid corners, and each 1 m^2 grid square was numbered with a combination of letters and numbers (Fig. 1.4). At the end of the 2005 excavation, long metal stakes were buried at all four corners of the grid perimeter, and each recovered specimen was marked with a long metal pin buried in the ground. The excavated surface and walls of the excavation were stabilized with rocks until the next field season. During the 2006 field season, the excavated area was expanded to the east and north, and numerous shaft fragments were excavated about 3 m northeast of the main bone concentration area. However, they were so fragmented that they could not be identified as belonging to KSD-VP-1/1 with any confidence. A single maxillary fragment of a bovid was also excavated about 3 m northeast of the easternmost excavated element (scapula) of KSD-VP-1/1 (Fig. 1.4).

The excavation continued for another 3 years until 2009 (Fig. 1.6a–c), with the participation of more than 45 individuals (Fig. 1.7). At the end of the 2009 field season, a total area of 85 m^2 with a vertical depth of 1.3 m on the eastern wall was excavated (Fig. 1.6d). No part of the cranium or dentition of KSD-VP-1/1 was ever recovered, and even though the enormous amount of excavated overburden was sieved, no additional bone fragments were retrieved from the sieving. Table 1.1 provides a list of the skeletal elements of KSD-VP-1/1 that are described in this monograph. It should be noted; however, that a few, mostly vertebral, fragments associated with the partial skeleton are neither listed nor described here because they cannot be identified with confidence.

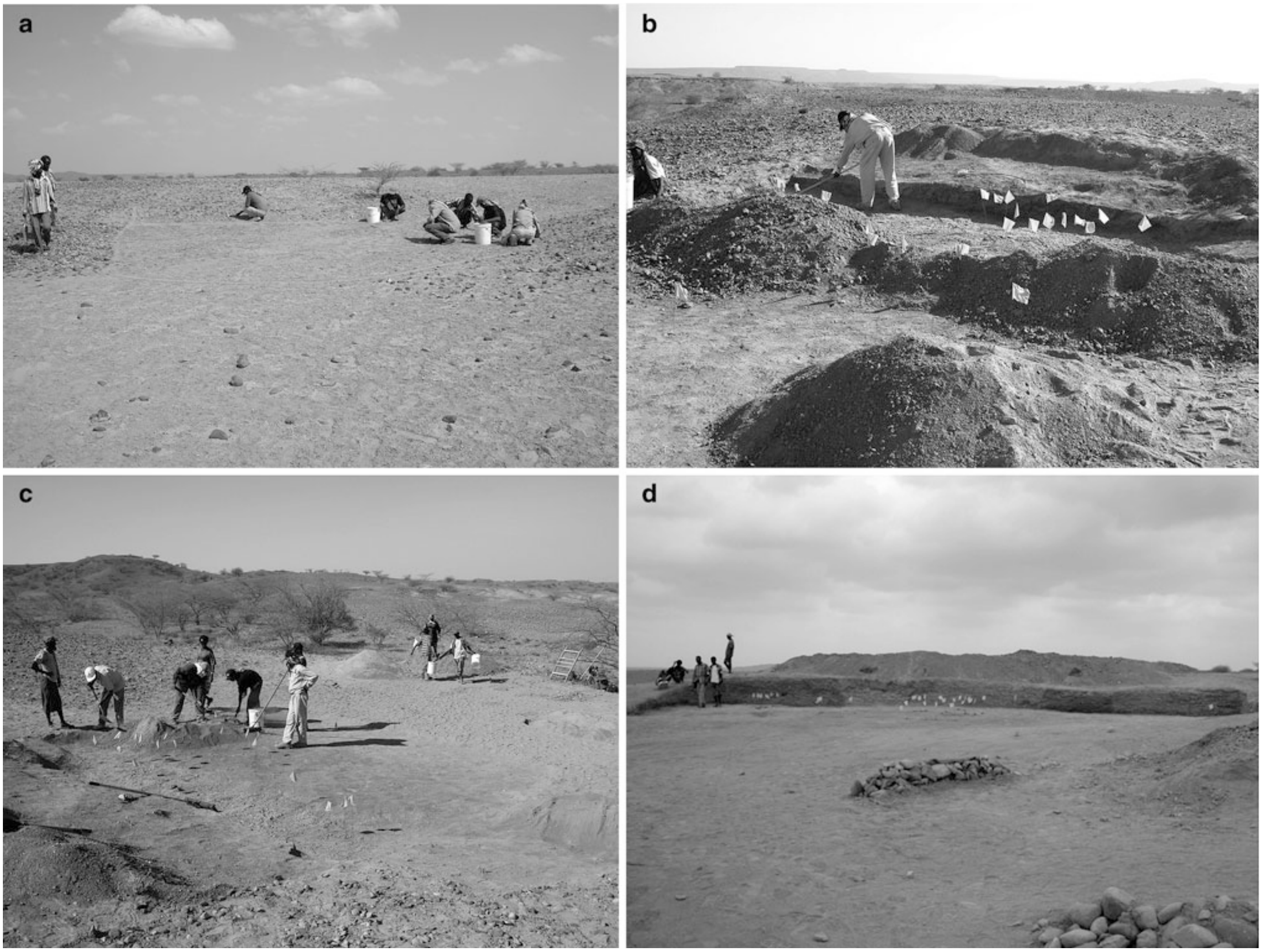

Fig. 1.6 Views of the KSD-VP-1/1 excavation location. **a** Initial surface scraping immediately after the discovery of the first element (February 10, 2005). **b** Piles of excavated sediments ready for sifting. **c** Excavation in 2005. Each flag represents a specimen that was found on the surface or excavated *in situ*. **d** View of the excavation site at the end of the 2005 field season

Fig. 1.7 The excavation team at the end of the 2005 field season. More than 45 people participated in the excavation of KSD-VP-1/1 between the 2005 and 2009 field seasons

Preservation

Elements of KSD-VP-1/1 that were excavated *in situ* (the right innominate, left tibia, the ribs, the left clavicle, and the right scapula) were highly fragile and had to be consolidated using a thin mixture of vinac beads and acetone before they were extracted. Additionally, the innominate had to be plaster-jacketed before removal. All other elements were recovered in the form of small fragments (Fig. 1.8). The distribution of the skeletal elements indicates that the carcass was more likely to have been surface scattered before fossilization either by trampling or erosion. However, none of the bones shows any carnivore damage or substantial transportation (see Su 2016, for details). Compression and deformation are apparent on some of the elements, particularly on the ribs, which is likely due to the contraction and expansion of the clay sediments in which they were buried. Almost all of the *in situ* skeletal elements were covered by a thin layer of gypsum that permeated through crevices extending from clay horizons higher in the section. The surface specimens, i.e., cervical vertebrae, humerus, femur, and ulna, were fragmented into numerous pieces although they did not require significant pre-collection treatment.

Fig. 1.8 Fragments of KSD-VP-1/1 collected by surface scraping, sieving, and excavation. More than 400 pieces were recovered representing parts of the cervical vertebrae, humerus, ulna, femur, and the sacrum. They were systematically conjoined by project scientists in the paleoanthropology laboratory of the National Museum in Addis Ababa. The fragments in the pan on top right corner belong to the innominate collected from the excavation in 2005

Table 1.1 KSD-VP-1/1 partial skeleton: inventory of preserved elements

Accession number	Element	Discovery
KSD-VP-1/1a	Right ulna	S
KSD-VP-1/1b	Right humerus	S
KSD-VP-1/1c	Left distal femur	S
KSD-VP-1/1d	Right os coxa	IS
KSD-VP-1/1e	Left tibia	IS
KSD-VP-1/1f	Right clavicle	IS
KSD-VP-1/1g	Right scapula	IS
KSD-VP-1/1h	Second cervical vertebra (C-2)	S
KSD-VP-1/1i and /1x	Third cervical vertebra (C-3)	S
KSD-VP-1/1j, /1z, and /1ac	Fourth cervical vertebra (C-4)	S
KSD-VP-1/1k, /1y and /1aa	Fifth cervical vertebra (C-5)	S
KSD-VP-1/1l	Sixth cervical vertebra (C-6)	S
KSD-VP-1/1m	Vertebral body	S
KSD-VP-1/1n	Left second rib	IS
KSD-VP-1/1o	Right lower rib (7th or 8th)	IS
KSD-VP-1/1p	Right lower rib (8th or 9th)	IS
KSD-VP-1/1q	Right upper rib (5th, 6th or 7th)	IS
KSD-VP-1/1r	Left 11th rib	IS
KSD-VP-1/1s	Middle rib fragment	S
KSD-VP-1/1t	Superior sacral body and ala	S
KSD-VP-1/1u	Posterior sacral spine fragment	S
KSD-VP-1/1v	Sacral spine fragment	S
KSD-VP-1/1w	Coccygeal body?	S
KSD-VP-1/1ab	Left articular process and articular pillar (C-7)	S
KSD-Vp-1/1ad	Right superior facet of vertebra (C-7)	S
KSD-VP-1/1ae	Right inferior facet of vertebra (C-7)	S
KSD-VP-1/1af	Posterior tubercle of the transverse process (C-7)	S
KSD-VP-1/1ag	Right lamina (C7)	S

S Surface; *IS In situ*

Fig. 1.9 Yohannes Haile-Selassie in the paleoanthropology laboratory of the National Museum of Ethiopia systematically conjoining the fragments of KSD-VP-1/1

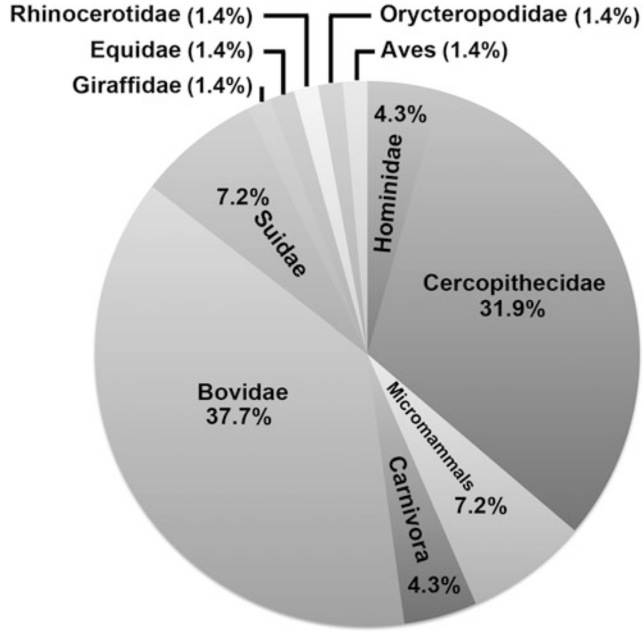

Fig. 1.10 Pie chart showing the percentage of mammalian families collected from KSD-VP-1/1 based on minimum number of individuals (MNI = 69). The micromammal percentage includes multiple families (see Table 1.2 for details)

Preparation and Curation

All original fossils collected from the study area are stored at the paleoanthropology laboratory of the National Museum of Ethiopia in Addis Ababa. Preparation of KSD-VP-1/1 included freeing elements from plaster jackets and cleaning the adhering matrix using an air scribe, at times under a microscope. Skeletal elements of KSD-VP-1/1 were joined together from over 300 bone fragments (Fig. 1.9), after which they were accessioned and photographed before being stored. The WORMIL project organizes its fossil collections by locality, taxon, and age so that project researchers can have easy access for analyses.

The Faunal Assemblage at KSD-VP-1

KSD-VP-1 is one of the smallest localities in the Woranso-Mille study area, with a total area of ca. 300 m^2. There are only 69 accessioned fossil specimens from the locality. However, a 100% collection for taphonomic analysis resulted in more than 700 mostly unidentifiable bone fragments (see Su 2016). Despite the small number of accessioned specimens, the taxonomic diversity of this locality is remarkable-23 mammalian species from 15 families are represented (Table 1.2). Bovids are the most abundant with six tribes identified, followed by cercopithecids represented by at least three species. Among the suids, *Kolpochoerus* and *Nyanzachoerus* are present. In addition to KSD-VP-1/1, two other specimens of *Au. afarensis*, an isolated lower molar (KSD-VP-1/52) and a child mandible with dentition (KSD-VP-1/39), have also been recovered from the locality. Two small carnivore species are also present: a herpestid and a lutrine (cf. *Torolutra* sp.). Among the small mammals, three genera (cf. *Serengetilagus*, *Thryonomys*, and *Hystrix*) are represented in the assemblage. Large-sized mammals are represented by Elephantidae, Rhinocerotidae, Hippopotamidae, Giraffidae, and Equidae, with at least one species identified from each family (Fig. 1.10).

Guide to Contents of the Book

This volume contains five chapters that provide detailed description and comparative analyses of KSD-VP-1/1, in addition to two chapters on its geological, taphonomic, and paleoecological context. Cumulatively, these chapters

Table 1.2 Faunal list of KSD-VP-1

Aves	Artiodactyla
Rodentia	Bovidae
Indet.	Indet.
Hystricidae	Alcelaphini
Hystrix sp.	Neotragini
Thryonomyidae	Hippotragini
Thryonomys sp.	Antilopini
Lagomorpha	*Gazella* sp.
Leporidae	Tragelaphini
cf. *Serengetilagus* sp.	*Tragelaphus saraitu*
Primates	*Tragelaphus* sp. indet.
Hominidae	Aepycerotini
Australopithecus afarensis	*Aepyceros* cf. *afarensis*
Cercopithecidae	Suidae
Indet.	Suinae
Papionini Indet.	*Kolpochoerus* cf. *millensis*
Theropithecus oswaldi aff. *darti*	Tetraconodontinae
Colobinae Indet.	*Nyanzachoerus kanamensis*
	Giraffidae
Carnivora	*Giraffa* cf. *stillei*
Viverridae	Hippopotamidae
cf. *Viverra* sp.	Perissodactyla
Mustelidae	Equidae
cf. *Torolutra* sp.	*Eurygnathohippus* sp.
	Rhinocerotidae
Proboscidea	Tubulidentata
Elephantidae	Orycteropodidae
Indet.	*Orycteropus* sp.
	Reptilia
	Crocodylidae

provide insights into the paleobiology and paleoecology of early *Au. afarensis* and the last chapter presents a synthesis of the broader implications of KSD-VP-1/1 for our interpretation of early hominin paleobiology.

Chapters 2 and 3 provide the geologic, taphonomic, and paleoenvironmental context of KSD-VP-1. While the fossiliferous areas within WORMIL have not yet been assigned to any specific geological formation or divided into subunits, radiometric ages have been obtained for most of the tuffs within the fossiliferous horizons (Deino et al. 2010; Haile-Selassie et al. 2010a, b, 2012, 2015). The geological age of KSD-VP-1/1 is therefore well-constrained using $^{40}Ar/^{39}Ar$ dating method. A thin tuff about 2.7 m below the partial skeleton yielded an age of 3.60 ± 0.03 Ma. Chapter 2 (Saylor et al. 2016) elaborates on the refinement of the geochronology of KSD-VP-1/1 and provides details on the sedimentological context of the locality.

Following that, Chapter 3 (Su 2016) explores the taphonomy and paleoenvironment of KSD-VP-1/1 based on faunal and geological data. The KSD-VP-1 faunal assemblage is likely autochthonous and transportation and disturbance of bones was minimal. The combined evidence indicates that the paleohabitat at KSD-VP-1 was a medium to dense woodland with some open areas of grassland or shrubland distal to the locality.

Chapters 4 through 8 provide detailed description and comparative analyses of the skeleton. One of the key pieces of information that was lacking from the preliminary description and analysis of KSD-VP-1/1 (Haile-Selassie et al. 2010a) was CT-scan data. With permission from the Ethiopian government, the original elements of the partial skeleton were transported to the United States, and each element was scanned using high-resolution computed tomography (HRCT) at the Center for Quantitative Imaging at the Pennsylvania State University. Chapter 4 (Ryan and Sukhdeo 2016) describes three-dimensional reconstructions and quantification of internal and external anatomical structures based on HRCT scan data.

KSD-VP-1/1 is the only early hominin adult specimen that preserves almost all of its cervical vertebrae and represents the oldest known cervical column in the hominin fossil record. Chapter 5 (Meyer 2016) presents a detailed description and comparative analysis of each cervical vertebra. The suite of characteristics in the KSD-VP-1/1 cervical centra is consistent with human-like orthograde posture and head carriage. However, the mosaic of derived anatomy