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Edited by Sally C. Reynolds and Andrew Gallagher

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1 *African Genesis: an evolving paradigm*

SALLY C. REYNOLDS

Introduction

The Late Miocene and Early Pliocene hominin fossil record confirms Africa as the birthplace of humanity. Raymond Dart's announcement of the first species of 'ape-man' in the journal *Nature* (Dart, 1925) forever changed our perceptions of Africa's place in the 'human story' and firmly established the field of African palaeoanthropology. We palaeoanthropologists, past, present and future, owe a significant debt to Dart's discovery and his recognition of its importance. But Dart's work was just the beginning of a long and proud legacy of excavation and research in southern Africa, and new discoveries continue to confirm the importance of this region to our understanding of human evolution.

The African Genesis symposium, held at the University of the Witwatersrand Medical School, Johannesburg, South Africa between 8 and 14 January 2006, celebrated the 80th anniversary of Dart's publication of the Taung child and the 80th birthday of a remarkable man, Professor Phillip V. Tobias. Tobias continued the tradition established by his mentor Dart, and his mentor before him: a long line of mentors and students stretching back more than 500 years (Ungar and Tobias, Chapter 2). Tobias, in turn, continues to collaborate with colleagues and former students on a variety of new perspectives on the fossil hominin material (e.g. Lockwood and Tobias, 2002; Holloway *et al.*, 2004; Curnoe and Tobias, 2006; Moggi-Cecchi *et al.*, 2006). His commitment to education and scientific rigour established a strong foundation for our scholarly community.

Phillip Tobias's contributions encompass the systematic study of all aspects of human evolution and he continues to inspire students and colleagues worldwide. In his role of palaeoanthropologist, he described new fossil discoveries (Leakey *et al.*, 1964; Hughes and Tobias, 1977), headed the excavation programme at Sterkfontein for many years and studied deposits of Sterkfontein,

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such as the Silberberg Grotto in which Ron Clarke would later discover a near -complete *Australopithecus* skeleton (Tobias, 1979; Clarke and Tobias, 1995). Tobias's seminal publications include two monographs on the comparative morphology and evolutionary significance of two hominin taxa, *Australopithecus boisei* and the enigmatic *Homo habilis* from Bed 1 Olduvai Gorge, Tanzania (Tobias, 1967, 1991).

The African Genesis conference and this subsequent volume outline the major developments since Dart's announcement and description of Taung and gauge the consensus between various subdisciplines concerning the broader issues of hominin emergence in our ancestral homeland. This chapter reviews and summarises the main topics linking the contributions in this volume. These are loosely grouped into four parts: (I) the search for origins, whether these be in the earliest African Miocene deposits, in new excavations or in the new interpretation of previously studied hominin assemblages (Chapters 3–7); (II) hominin cranial, postcranial and dental morphology (Chapters 8–16); (III) the processes of modern human origins and dispersals (Chapters 17–21) and (IV) faunal context of hominin discoveries and the inferences about the evolution of human behaviour through time (Chapters 22–27).

At the end of the volume overview, I discuss the other significant discoveries of the last two decades that have helped to change our perspectives of our science and our origins.

Part I (Chapters 3–7)

In search of origins: evolutionary theory, new species and paths into the past

Colin Groves (Chapter 3) reviews the search for a species concept that is grounded in biology, but still applicable to the fossil record. He examines this important concept in three parts: first, how species can be identified; second, how speciation occurs and third, how these concepts can be meaningfully applied to the diversity of species of hominins identified in the fossil record. Groves also offers a new scheme of classification for the hominins and posits the modes of speciation and dispersal that may have led to the fossil evidence observed.

Michel Brunet (Chapter 4) discusses the environment of a new hominin genus, *Sahelanthropus tchadensis*, from the Chadian deposits of Toros-Menalla that date to approximately 7.0 million years old (Ma). Evidence that this hominin lived in an environment similar to the modern-day Okavango Delta (Botswana) provides an important reminder of how much the interpretation

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of early hominin environments has changed since Yves Coppens's 'East Side Story' (Coppens, 1983). The prevailing view of human evolution from Dart (1925) until the discovery of *Sahelanthropus* was that early (Miocene) hominins evolved in savannah environments, specifically in southern and eastern Africa. Recent discoveries, both within Africa and elsewhere, show that several other regions contain important aspects of the human story and that our Miocene ancestors were clearly not exclusively associated with savannah environments (e.g. Brunet *et al.*, 2002).

Brigitte Senut (Chapter 5) provides an insightful and thorough review of Miocene hominoids, with a consideration of their modes of locomotion. While most Miocene hominoids can be considered primarily adapted to arboreal locomotion, significant morphological differences exist in the shoulder, elbow and wrist joints of known Miocene apes, which indicate considerable diversity in locomotor mode, relative to modes seen in extant primates. Senut also explores the possibility that hominin adaptations to bipedality may have arisen in closed, forested environments.

Martin Pickford (Chapter 6) echoes the idea that recent fossil discoveries have radically altered our understanding of Miocene hominins. The discovery of the 6.0 million-year-old bipedal hominin *Orrorin tugenensis* in the Lukeino Formation, Kenya, in 2000, has shed doubt on what the last common ancestor (LCA) between humans and apes may have looked like. *Orrorin* appears very different from the hypothetical LCA, which was predicted to possess large canines and be a knuckle-walker (Pickford *et al.*, 2002). Ape-like specimens recovered in the same levels as *Orrorin* (Pickford and Senut, 2005) suggest that the LCA must have existed some time before the appearance of *Orrorin* at 6 Ma (Senut and Pickford, 2004). These finds indicate that *Orrorin*, along with the older *Sahelanthropus* from Chad and the somewhat younger *Ardipithecus* from the Lower Aramis Member of the Sangatole Ethiopia were all bipedal and inhabiting closed, forested environments.

Ronald J. Clarke (Chapter 7) presents an historical review of 40 years of excavation at the world famous site of Sterkfontein, where the first adult specimen of *Australopithecus africanus* was discovered by Robert Broom in 1936 (Broom, 1936). Clarke reviews the most important fossil discoveries made at Sterkfontein during the long-running research project started by Phillip V. Tobias and A. R. Hughes in 1966. The Sterkfontein excavation project has had several remarkable results, not just in terms of impressive hominin discoveries such as the StW 53 cranium (Hughes and Tobias, 1977), which has been recently redated to 1.8–1.4 Ma based on seriation methods (Herries *et al.*, 2009) but also insight into fossil plants (Bamford, 1999), in-depth taphonomic studies (Pickering, 1999; Kibii, 2004; Pickering *et al.*, 2000) and a deeper understanding of the complexity of cave breccias and site formation processes

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(Kuman, 1994; Clarke, 1994; Kuman and Clarke, 2000; Reynolds *et al.*, 2007). Clarke's discovery of a near-complete hominin skeleton (StW 573), dating to between 3.3 Ma and 2.2 Ma (Partridge *et al.*, 1999; Walker *et al.*, 2006) has shed much light on aspects of the *Australopithecus* postcranial morphology (e.g. Clarke and Tobias, 1995; Clarke, 1998, 1999).

Part II (Chapters 8–16)

Hominin morphology through time: brains, bodies and teeth

Dean Falk (Chapter 8) reviews the development of endocast studies, comparing the scientific and public response to the first endocast to be discovered and described by Dart (1925; see also Holloway, Chapter 9) to the most recent endocast to cause controversy and comment within the palaeoanthropological community, that of *Homo floresiensis*, LB1, which was found on the Indonesian island of Flores in 2004 and is dated to between 38 ka and 18 ka (Morwood *et al.*, 2004). Work by Falk and colleagues on the endocast of the *H. floresiensis* specimens indicate that 'global, rather than mosaic, cortical reorganisation' occurred and that the cerebral cortex of this species has derived features that span the entire surface (Falk *et al.*, 2005; 2007). She concludes that both brain size and neurological reorganisation characterise human evolution (Gould, 2001; Falk, Chapter 8).

Ralph L. Holloway (Chapter 9) provides his perspective on Dart's original interpretation of the position of the lunate sulcus in *Australopithecus africanus* (Dart, 1925). Holloway reviews the issue of brain reorganisation and the development of the three areas of brain research (i.e. palaeoneurology, comparative neuroanatomy and molecular genomics). As Holloway and other authors point out, the process of *Australopithecus* brain reorganisation was probably more complex than that first envisioned by Dart (1925), with a mosaic pattern of brain enlargement and simultaneous reorganisation of the brain being a likely scenario (Falk, Chapter 8; Holloway, Chapter 9). More recently, work undertaken by Holloway and colleagues on the Sterkfontein *Australopithecus* cranium StW 505 suggests 'cortical reorganisation preceded brain enlargement in hominin evolution' (Holloway *et al.*, 2004: 290).

In Chapter 10, Paul R. Manger and his colleagues explore the relationship between hominin body size and brain size, compared with other primates. The analysis by Manger and colleagues of body and brain size estimates of a range of humans and extant primates, as well as fossil hominins, indicates that the relationship between brain and body size is the same for fossil hominins and modern humans (Manger *et al.*, Chapter 10). They propose two

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key transitions that have shaped our present brain–body mass relationship. The first occurred at the origin of the primates, where scaling laws governing non-primate mammalian orders diverged from the Order Primates. The second putative event occurred at the origin of the hominin lineage, where scaling laws appear altered in favour of further positive allometry. When they are combined, these two shifts towards positive allometry together explain the present *H. sapiens*' large brain relative to all other mammals. The authors suggest that the large human brain is a highly successful 'spandrel' (*sensu* Gould and Lewontin, 1979), for which the causes are as yet unclear, but which may well be environmental in origin.

Henry M. McHenry's contribution (Chapter 11) is a case study of recent comparative physiological investigations into hominin energetics. Recent experimental data reveal that energy expenditure during bipedal progression in chimpanzees (*Pan*) does not substantially exceed that incurred during terrestrial quadrupedalism. These results confirm earlier ideas that energetics imposed no obstacle to the transition from a terrestrial quadrupedal gait to bipedalism and that even the earliest bipeds may have enjoyed an energetic advantage (Taylor and Rowntree, 1973). The extant African hominins (*Gorilla*, *Pan*, *Homo*) display poorly adapted terrestrial gaits compared with quadrupedal mammals of a similar size, including the large cercopithecine monkeys such as *Papio* (McHenry, Chapter 11).

Michelle S. M. Drapeau (Chapter 12) presents a novel perspective on the 'transitional' morphology of the upper limb in *Australopithecus afarensis*. Drapeau and her colleagues have undertaken a revised synthesis of comparative hominin upper limb morphology during the past decade (Drapeau, 2004; Drapeau *et al.*, 2005). While the upper limb of the earliest hominins remains undoubtedly primitive, tantalising evidence has emerged for a remarkable suite of morphological features that strongly suggest that *Australopithecus* engaged their upper limbs in novel manual activities that have no corollaries among the extant hominins. This new evidence may provide some support for the cladistic inference that the common ancestor of the panin–hominin dichotomy may have regularly engaged in enhanced manual activities as part of an expanding and more sophisticated terrestrial ecological repertoire (e.g. Panger *et al.*, 2002).

The contribution by Brian G. Richmond and William L. Jungers (Chapter 13) examines the proximal femoral morphology of Plio-Pleistocene early hominins with specific reference to the femoral specimens assigned to the 6-Ma *O. tugenensis* from Kenya and the Indonesian small hominin species, *H. floresiensis* (Senut *et al.*, 2001; Brown *et al.*, 2004). As discussed in an earlier section, the precise biomechanical attributes of the *Orrorin* femoral neck are problematic, but morphometric analysis by Richmond and Jungers (2008; Chapter 13) confirm that the affinities of the *Orrorin* specimen are in

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agreement with the Upper Miocene age and its being a bipedal, basal hominin with similarities to Plio-Pleistocene *Australopithecus* and *Paranthropus* rather than with Lower Pleistocene *Homo* (McHenry and Corruccini, 1976, 1978). As for the much-debated ‘Hobbit’ species, the study by the authors of the proximal femoral anatomy of the *H. floresiensis* specimen (LB1/9) indicate that it is not a small modern human, but possesses a primitive morphology suggesting that it is a distinct hominin species that existed on the island of Flores in the Late Pleistocene (Morwood *et al.*, 2004).

M. Christopher Dean (Chapter 14) explores the types of data that can be gleaned from even very badly weathered dental specimens that preserve little macroscopic detail. The specimen discussed is a hemimandible fragment (KNM-ER 1817) recovered from the Okote Member of Koobi Fora, Kenya, dating to between 1.65 and 1.55 Ma (Wood, 1991). This specimen could be assigned only to Hominidae gen. et sp. indet., but the size of the mandible suggested that it probably represents *Paranthropus boisei* (Leakey, 1974; Wood, 1991). Using microscopy techniques, Dean provides information about rates of dentine formation and root extension times and offers insights into differences between dental traits in modern humans and extinct hominins. His results indicate that molar roots in *P. boisei* may have had faster rates of root extension than those of modern human molars at the same developmental stage and illustrate the powerful insights that can be gained using microscopic techniques.

Kevin L. Kuykendall (Chapter 15) examines the evolutionary development, in particular the morphology of the cusps and the enamel–dentine junction (EDJ), of the *Paranthropus* molar specimen from the Pliocene site of Gondolin. This site lies within the Cradle of Humankind, (South Africa) and has been dated faunally to between 2.0 and 1.5 Ma (Menter *et al.*, 1999). Initial published reports described the isolated lower molar (GDA-2) as ‘*Paranthropus* sp. indet.’ (Menter *et al.*, 1999). The specimen is an ‘unexpected variant’; exceeding the size variation for all known southern African *Paranthropus* specimens and falling more closely within the range of eastern African specimens. Although a larger sample of the ‘hyper-robust’ variant form would allow further investigation into the environmental context and life history of what was, presumably, a large body-sized *Paranthropus* subpopulation, Kuykendall points out that such investigations must await the further recovery of more ‘hyper-robust’ specimens for study.

Gerhard W. Weber and his colleagues (Chapter 16) review how technology is being used to digitise and analyse specimens as part of a new subdiscipline of anthropology called ‘virtual anthropology’ (VA; Weber *et al.*, 2001). As an illustration of this new approach, reconstructions of fossil specimens are presented, including that of a Makapansgat cranium (MLD37/38) and Sterkfontein crania Sts 71 and StW 505. New analyses can correct for various

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taphonomic problems associated with fossil specimens, such as deformation or incomplete preservation. It is also possible to compare digitally enhanced reconstructions to several other reconstructions simultaneously. Virtual anthropology promises many benefits to students of palaeoanthropology, since several teams of researchers can work on different digital versions of the same fossil specimen simultaneously. Comparisons between fossils can be made without the constraints of travel or funding, thus aiding the access of researchers to fossils around the world and also facilitating new and integrative analyses, which have hitherto been difficult, if not almost impossible, to undertake.

Part III (Chapters 17–21)

Modern human origins: patterns and processes

Steven E. Churchill and his colleagues (Chapter 17) present new body-size estimations of fossil *Homo* species of the African Middle Pleistocene, from such sites as Berg Aukas (Namibia) and Kabwe (Zambia). When orbit and femur data are compared with modern sub-Saharan African *H. sapiens*, the data suggest that the majority of Middle Pleistocene *Homo* individuals are larger than both early and modern *H. sapiens* counterparts. A possible reason for the increased body size may have been the requirement for increased body mass and muscularity to ensure success in hunting large-bodied prey species (Churchill and Rhodes, 2006).

Milford H. Wolpoff and Sang-Hee Lee (Chapter 18) consider the role that the continent of Africa played in providing significant genetic contributions to the modern human gene pool. Given the limited genetic data available, the authors instead employ measures of phenetic, rather than phylogenetic, similarities. The authors consider the hypothesis that the taxon represented by the Middle Pleistocene Bodo cranium (Middle Awash region, Ethiopia) is ancestral to lineages of later hominins, represented by the morphology of the Herto cranium from Herto Bouri (Ethiopia), dating to between 160 ka and 154 ka (Clark *et al.*, 2003) as well as samples of European Neandertals. Their results do not support the hypothesis that Herto and European Neandertals are the very different endpoints of two divergent lineages. Instead, the authors contend that some amount of gene flow, perhaps facilitated by as little as 24 to 74 matings between archaic and anatomically modern humans, would preserve overall levels of genetic similarity (Hawks and Cochran, 2006). The authors conclude that the genetic origins of modern humans must comprise combinations of African *H. sapiens* and Neandertal genes.

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Fred H. Smith and his colleagues (Chapter 19) consider how within-African population movements have affected the morphological patterns observed within anatomically modern humans. Based on the geologically earliest fossils of anatomically modern humans from eastern Africa (specifically the sites of Omo Kibish and Herto, Ethiopia, which date to between 196 ka and 104 ka, and 160 ka and 154 ka, respectively), Smith and colleagues propose an assimilation model whereby these original populations spread out from eastern Africa and into southern and northern Africa and gradually assimilated the pre-existing archaic humans in these regions. Later and better dated sites in this region, such as Border Cave, show no such mosaic of features, suggesting that by approximately 74 ka (Grün *et al.*, 2003), the assimilation of modern humans into southern Africa is already complete. The authors contend that this is essentially extinction by assimilation, similar to a process of extinction by hybridisation (Levin, 2002). Given the wealth of sites in Africa, the process of human population movements and developments indicates that within-African movements were as important as those that occurred when modern humans left Africa.

The contribution by Emma Mbua and Günter Bräuer (Chapter 20) considers the exact mode of speciation prior to the emergence of the suite of facial and cranial features considered ‘anatomically modern’. Several authors approach the fossil variation in *H.sapiens* differently, with some considering the mixture of archaic and modern *Homo* specimens as the African transitional group (ATG; Smith 1993, 2002). Mbua and Bräuer address this issue with a new morphological analysis of cranial features, designed to differentiate between long-term, diachronic changes and multiple speciation events. Rather than splitting the Middle Pleistocene anatomical variation into a range of separate species (as discussed in Bräuer, 2008), the authors advocate the approach that the modernisation of the *Homo* lineage began with the species represented by the Bodo cranium and continued to develop as a single species, *H. sapiens*, dispersing out from eastern Africa, as is suggested by Smith and colleagues (Chapter 19).

Osbjorn M. Pearson (Chapter 21) examines the genetic, anatomical and archaeological data available for the emergence of modern humans. The definition of what exactly constitutes modern human behaviour has long been subject to debate and McBrearty and Brooks (2000) have shown that the Later Stone Age (LSA) appearance was not a sudden revolution from the Middle Stone Age (MSA), rather a gradual accretion of increasingly modern behavioural and technological traits. Pearson considers that ‘precocious’ early behavioural changes such as the use of ochre and backed pieces by 300 ka at the Zambian sites of Twin Rivers and Kalambo Falls (Barham, 2002a,b) and the even earlier appearance of prepared core technology and blade production at Kapthurin,

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Kenya, by 500 to 400 ka (McBrearty, 2001) represent nascent modern behaviours, which, in some cases, became locally extinct and were later re-invented (Shennan, 2001; d'Errico, 2003). Pearson contends that the capacity for 'modern' behaviour may have preceded the appearance of anatomically modern humans.

Part IV (Chapters 22–27)

In search of context: hominin environments, behaviour and lithic cultures

Darryl J. de Ruiter and colleagues (Chapter 22) examine the fauna associated with the extinct hominin *P. robustus*, from the Cradle of Humankind sites (Gauteng Province, South Africa). Using faunal data from Pleistocene sites such as Sterkfontein, Swartkrans and Kromdraai, they identify a pattern of arid-habitat avoidance for this species, which is in agreement with stable light isotope studies that indicate that this species had a mixed diet (Sponheimer *et al.*, 2006). The authors suggest that this species would have modified its landscape use in times of environmental and climatic fluctuations to make use of open grassland areas (their less favoured habitats) in order to exploit fall-back resources such as insects, sedges and tubers.

Extant primates and their extinct counterparts form the basis of Sarah Elton's contribution (Chapter 23), which reviews the community of 11 monkey species in southern Africa that underwent fundamental community changes and extinctions during the Plio-Pleistocene. The South African cercopithecoid fossil record over the past 3 Ma is characterised by high species diversity at the beginning of the period, followed by a reduction in diversity in the Pleistocene, which appears to have been due in part to cooling, drying shifts in climate and the spread of grassland habitats. The surviving monkey species, the baboon (*Papio hamadryas ursinus*) and vervet monkey (*Chlorocebus aethiops*) are eclectic feeders that can exist in environments extensively modified by humans. This ability to coexist with humans, since as early as the Late Pleistocene, has probably been the key to their ongoing success in Africa. In addition, the inferred role of the hominins during the Plio-Pleistocene may have been the generalist niche presently occupied by the baboons and vervets.

Travis R. Pickering's contribution (Chapter 24) considers our evolving view of hominin behaviour by reviewing Raymond Dart's 'killer ape' hypothesis (Dart, 1949), an idea much popularised in the decades after its publication (Ardrey, 1961). Central to this idea was the notion that broken bones found with the hominins were used by them as tools for inter- and intraspecies

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violence. Subsequent careful research by C. K. (Bob) Brain illustrated the role of carnivore damage in creating the distinctive damage patterns, thereby refuting Dart's killer ape model and establishing the subdiscipline of taphonomy (Brain, 1981). Pickering also reviews one of the present debates of hominin behaviour, the issue of when and how hominins gained access to carcasses. Did hominins obtain animal tissue by scavenging carnivore kills, or instead by hunting and /or aggressive scavenging? Dart's killer ape hypothesis may have a ring of truth to it in at least one instance: the evidence for cannibalism suggested by butchery marks on the StW 53 cranium does suggest that early hominins may have been capable of violence, although the context and intention of this behaviour is as yet unclear (Pickering *et al.*, 2000).

John A. J. Gowlett (Chapter 25) examines Acheulean stone tools from African sites dating to between 1.1 and 0.2 Ma, such as Casablanca (Morocco) and Kilombe and Baringo (Kenya), to deduce the internalised, shared concepts of desirable tool attributes in the minds of the toolmakers. Acheulean bifaces, while showing much size variation, possess a consistent pattern of production that remains constant at a variety of sites across Africa. As tools became larger, the increasing size and weight demanded that stone tool makers adjust their designs to preserve the utility of these tools (e.g. Crompton and Gowlett, 1993). These demands suggest that ancient humans were capable of controlling four or five of the most important lithic variables simultaneously (Gowlett, 2006). They indicate that the toolmakers tended to manipulate the variables relating to the tool-forms in a consistent manner, across temporal and geographic ranges, leading Gowlett to conclude that the concepts were affected by external experiences and their unique cultural traditions. Based on this evidence, he also argues that the shared attributes indicate systematic or collective social communication by the Acheulean toolmakers.

Lyn Wadley (Chapter 26) discusses the interpretations and significance of the Sibudu Cave (KwaZulu-Natal Province). Sibudu is the third South African site to document the transition between the Middle Stone Age Still Bay industry and the subsequent enigmatic, microlithic, Howiesons Poort industry (Wadley, 2007). The sequence is detailed enough to offer intriguing signs of behaviour: changes in the types of species hunted through time, as well as changes in the use of raw materials for tools. Wadley observes that notable shifts in material culture and subsistence strategies appear to coincide with marked changes in the environment at the site. She stresses the need for ongoing excavation efforts in southern Africa, since more evidence for the Still Bay and Howiesons Poort succession, such as has been recovered at Sibudu, is necessary to understand the origins of modern behaviour in the region.

Avraham Ronen (Chapter 27) explores the development of the awareness of death, combined with a review of deliberate funerary practices. The oldest