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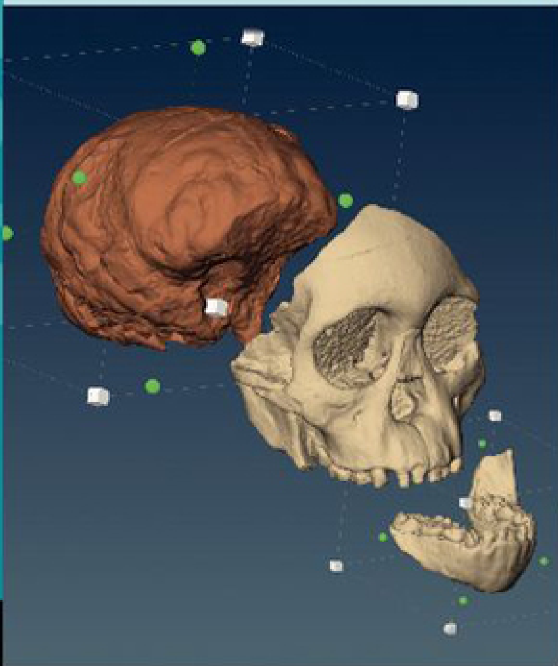
African Genesis

Perspectives on Hominin Evolution

Edited by
Sally C. Reynolds and
Andrew Gallagher



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African Genesis: Perspectives on Hominin Evolution

The announcement of the first African hominin species, *Australopithecus africanus*, from Taung, South Africa in 1924, launched the study of fossil man in Africa. New discoveries continue to confirm the importance of this region to our understanding of human evolution.

Outlining major developments since Raymond Dart's description of the Taung skull, and, in particular, the impact of the pioneering work of Phillip V. Tobias, this book is a valuable companion for students and researchers of human origins. It presents a summary of the current state of palaeoanthropology, reviewing the ideas that are central to the field, and provides a perspective on how future developments will shape our knowledge about hominin emergence in Africa. A wide range of key themes are covered, from the earliest fossils from Chad and Kenya, to the origins of bipedalism and the debate about how and where modern humans evolved and dispersed across Africa and beyond.

SALLY C. REYNOLDS is an honorary research staff member of the Institute for Human Evolution, University of the Witwatersrand, South Africa and Liverpool John Moores University, UK. She conducts research on the world-famous Sterkfontein Cave fossils and is interested in the relationships between geomorphology, mosaic habitats and extinction in hominins and other mammals.

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African Genesis

Perspectives on Hominin Evolution

Edited by

SALLY C. REYNOLDS

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Foreword

As the Honorary President of the African Genesis symposium committee, it was a great pleasure to welcome delegates from many countries to a meeting that served two purposes: to celebrate the discovery of the Taung child, the type specimen of *Australopithecus africanus* and, secondly, to honour Professor Phillip Tobias, the doyen of palaeoanthropology in Africa, the continent from which humanity evolved.

It was awesome to hear presentations by Michel Brunet, Brigitte Senut and Martin Pickford, regarding the type specimens of *Sahelanthropus* and *Orrorin*, from Chad and Kenya respectively, dated between 6 and 7 million years before the present. To place things in perspective there was a lecture by David Begun on African hominin origins, with reference to Miocene primates. This was followed by colloquia on the origin, adaptations and radiations of australopithecines; on hominid evolutionary ecology in the Plio-Pleistocene; on origins and diversity of *Homo* in the early Pleistocene; and on the origins, evolution and behaviour of *Homo sapiens* in the Late Pleistocene.

Speaker after speaker paid tribute to Professor Tobias whose enthusiasm has evidently encouraged many palaeoanthropologists who have worked on hominid fossils curated by the School of Anatomical Sciences at the University of the Witwatersrand. The collections at Wits have grown substantially since the description of the Taung child by Professor Raymond Dart in 1925.

The description of ‘Little Foot’, an extraordinary australopithecine discovered at Sterkfontein by Ron Clarke, Nkwane Molefe and Stephen Motsumi, was dramatic. Here was a palaeoanthropologist’s dream. If *Sahelanthropus* and *Orrorin* were breathtaking, this new discovery in the Cradle of Humankind was even more so. A virtually complete skeleton, initially dated at 3.3 million years on the basis of fauna and palaeomagnetism, has been found *in situ* in the Silberberg Grotto and awaits formal description. Ron Clarke’s presentation made South Africans proud of their heritage, and proud of the work that is being done in this part of the African continent.

In addition to formal lectures by invited speakers, there were many excellent posters presented by students who represent a new generation of palaeoanthropologists.

I would like to express my sincere gratitude to the organising committee of the African Genesis symposium for their dedicated efforts that made the event the stunning success that it was. Thanks are also extended to the many sponsors, especially to De Beers, the Department of Science and Technology, the Anglo-American Chairman's Fund, the Wenner Gren Foundation for Anthropological Research, the National Research Foundation, the Palaeontology Scientific Trust (PAST), First National Bank, the French Embassy in South Africa, the Canadian Embassy and the School of Anatomical Sciences at the University of the Witwatersrand. Special thanks are extended to Sally Reynolds for her sterling efforts with regard to the publication of this compilation of papers, and to Cambridge University Press for accepting the proceedings of the African Genesis symposium as part of their Cambridge Studies in Biological and Evolutionary Anthropology series.

Francis Thackeray
Honorary President
African Genesis: a symposium on hominid evolution in Africa

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We would like to extend our thanks to the University of the Witwatersrand Medical School for hosting the conference and to all the participants who joined us for this marvellous event. Francis Thackeray, in his role as President of the Symposium, was a kind and genial host. We would like to acknowledge the hospitality of the Mayor of the City of Johannesburg, Amos Masondo and the staff of the Cradle Restaurant (Cradle of Humankind) for our delegates. We are grateful to Professor Laurence Chait for the bust of Phillip Tobias that has been installed at Sterkfontein.

Our generous sponsors made this symposium unforgettable; specifically we acknowledge De Beers, the Department of Science and Technology (DST), the Anglo-American Chairman's Fund, the Wenner Gren Foundation for Anthropological Research, the National Research Foundation (NRF), the Palaeontology Scientific Trust (PAST), First National Bank, the French Embassy in South Africa, the Canadian Embassy and Rick Menell. The fossil exhibit was a highlight of the conference and Stephanie Potze and the staff of the Ditsong National Museum of Natural History (formerly the Transvaal Museum, Pretoria) are thanked for granting permission to display the original fossils of Sterkfontein's 'Mrs. Ples' and Raymond Dart's 'Taung child' together for the first time.

To all our colleagues and friends at Wits Medical School, including Colin Menter, Muhammad 'Spoc' Spocter, Meredith Robinson, Jason Hemingway, Manoj Chiba, Kavita Chibba, Ishana Ryan, Candice Hutchinson, Adhil 'Bugs' Bhagwandin and the late Heather White: thank you for your camaraderie, patience and loyal support.

Our thanks are due to Martin Griffiths and Lynette Talbot at Cambridge University Press for their invaluable help in the production of this volume. We also owe a special mention to Bernard Wood for his support of this project.

Finally, Sally would like to extend her gratitude to her parents, Chris and Jenni Reynolds for all their support of this volume. In particular, she would like to acknowledge the patience, encouragement and editorial support of her mother, Jenni.

Sally C. Reynolds
Andrew Gallagher

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-Cecci *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

of early hominin environments has changed since Yves Coppen'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

(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 that 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

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

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

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.

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,

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 cercopithecid 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

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

known burials of both *H. neanderthalensis* and *H. sapiens* date to the Middle Palaeolithic period (specifically between 130 and 100 ka) and were found in the Mount Carmel and Galilee regions of Israel. Ronen argues that burial practices indicate that both humans and Neandertals likely possessed similarly developed syntactical language skills, an awareness of death and, possibly, a concept of an afterlife.

Review of other scientific developments

The African Genesis conference aimed to review the major developments since Dart's description of the Taung skull and to gauge consensus between various subdisciplines. Major groundbreaking work has been done in the intervening decades and we now possess greater insight into the biology, intelligence, genetics and behaviour of hominins.

In the last two decades, rich new fossil hominin sites at Drimolen and Malapa, both in the Cradle of Humankind have been discovered (Keyser *et al.*, 2000; Berger *et al.*, 2010). The new species of *Australopithecus sediba* from Malapa dating to 1.95 to 1.78 Ma has been interpreted as representing a species of late *Australopithecus* – early *Homo* (Berger *et al.*, 2010). Other well known and much debated fossils, such as Sterkfontein cranium StW 53, first assigned to *H. habilis*, have been reassigned as the type specimen of a new species: *H. gautengensis* (Curnoe, 2010). Re-examination of *Paranthropus robustus* males has provided insights into the life histories and social organisation of an extinct hominin (Lockwood *et al.*, 2007). We have shifted our emphasis from single sites and have started to widen our view and examine the landscape around hominin sites and consider what features attracted the hominins to these regions (Bailey *et al.*, 2011; Reynolds *et al.*, 2011).

Hominins from Late Miocene and Pliocene, such as *Sahelanthropus*, *Orrorin*, *Ardipithecus* and *Kenyanthropus* have been discovered in central and eastern Africa and, surprisingly, these species appear to have lived in closed, wooded or mosaic environments (Senut *et al.*, 2001; Leakey *et al.*, 2001; Brunet *et al.*, 2002; White *et al.*, 2009). This lays to rest the savannah hypothesis (Dart, 1925), at least for the earlier part of the hominin fossil record, that was long considered pivotal to our African genesis.

In southern Africa, stable light isotope analysis has enabled us to gain insight into the diets of hominin species, leading to unexpectedly high levels of variation, both in *Australopithecus africanus* from Sterkfontein (e.g. van der Merwe *et al.*, 2003) and clear evidence of seasonal and annual dietary variation in *Paranthropus robustus* (Sponheimer *et al.*, 2006). Recent microwear texture analysis results for these hominins are consistent with this result (Scott *et al.*,

2005). Later genera, such as *P. robustus*, show a pattern of habitat avoidance of open, grassland habitats (de Ruiter *et al.*, Chapter 22). Our interpretation of cave deposits now encompasses the appreciation of climate- and time-averaging, which has bearing on how morphological variation and faunal communities should be interpreted in the fossil record (O'Regan and Reynolds, 2009; Hopley and Maslin, 2010).

New species, such as the 'Hobbit' (*H. florisensis*) from Indonesia and early *Homo* dating to approximately 1.75 Ma from the site of Dmanisi, Republic of Georgia (Vekua *et al.*, 2002) clearly show that important chapters of our ancestors' history were written outside of Africa. Other important firsts, such as abstract art and personal adornment, long thought to have developed outside of Africa, appear to have originated in Blombos Cave in South Africa at about 75 ka (Henshilwood *et al.*, 2004, 2009). Genetic studies on modern humans have shed light onto our evolution in unexpected ways: a genetic mutation that may be in part responsible for speech – the *FOXP2* gene – has been found (Enard *et al.*, 2002) and more importantly, a later study indicated that the Neandertals also possessed this critical mutation (Krause *et al.*, 2007). We have sequenced the genome of Neandertals and discovered that they are 'likely to have had a role in the genetic ancestry of present-day humans outside of Africa' (Green *et al.*, 2010: 722).

Recent excavations in the rainforests of central Africa have yielded a Chimpanzee Stone Age and a history of stone tool modification that stretched back at least 4300 years in the Côte d'Ivoire (Mercader *et al.*, 2007). Stone tool using and possibly even stone tool manufacture may no longer be exclusively associated with our lineage.

All of these discoveries have given us insights into what makes us human. Previously our concept of human behaviour included bipedality, syntactical speech, toolmaking and an awareness of death. Slowly but surely, these definitions are being revised as new discoveries challenge our perceptions. Through it all, the efforts and creativity of palaeoanthropologists all over the world ensure that the next 80 years of our field will continue to surprise, shock and delight all of us who follow the paths into the past.

Conclusion

The study of human origins from southern African sites began in the 1920s and the pace of the field has quickened considerably over the last two decades or so. When Raymond Dart's description of the Taung child was first published in 1925, his ideas met with mixed reactions. Recent discoveries at the Cradle of Humankind fossil sites, as well at Blombos Cave, illustrate how the southern

African region continues to produce new evidence to aid our understanding of human evolution and the role southern Africa played in the human story. It is thanks to tireless pioneers working in Africa that the important role of this continent can be fully appreciated. Phillip V. Tobias is one of those pioneers and he in turn has nurtured and encouraged several new generations of researchers. His scholarly legacy is that the systematic study of all aspects of human evolution continues, both in South Africa, where so many human 'firsts' have been recorded, but also all around the world.

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References

Ardrey R. (1961). *African Genesis: a Personal Investigation into the Animal Origins and Nature of Man*. New York: Atheneum.

Bailey, G. N., Reynolds, S. C. and King, G. C. P. (2011). Landscapes of human evolution: models and methods of tectonic geomorphology and the reconstruction of hominin landscapes. *Journal of Human Evolution*, **60**(3): 257–80.

Bamford, M. (1999). Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. *South African Journal of Science*, **95**: 231–7.

Barham, L. S. (2002a). Systematic pigment use in the Middle Pleistocene of South-Central Africa. *Current Anthropology*, **43**: 181–90.

(2002b). Backed tools in Middle Pleistocene Central Africa and their evolutionary significance. *Journal of Human Evolution*, **43**: 585–603.

Berger, L. R., de Ruiter, D. J., Churchill, S. E. *et al.* (2010). *Australopithecus sediba*: a new species of *Homo*-like australopith from South Africa. *Science*, **328**: 195–204.

Brain, C. K. (1981). *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. Chicago: University of Chicago Press.

Bräuer, G. (2008). The origin of modern anatomy: by speciation or intraspecific evolution? *Evolutionary Anthropology*, **17**: 22–37.

Broom, R. (1936). A new fossil anthropoid skull from South Africa. *Nature*, **138**: 486–8.

Brown, P., Sutikna, T., Morwood, M. J. *et al.* (2004). A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature*, **431**: 1055–61.

Brunet, M., Guy, F., Pilbeam, D. *et al.* (2002). A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, **418**: 145–51.

Churchill, S. E. and Rhodes, J. A. (2006). How strong were the Neandertals? Leverage and muscularity at the shoulder and elbow in Mousterian foragers. *Periodicum Biologorum*, **108**: 457–70.

Clark, J., Beyene, Y., WoldeGabriel, G. *et al.* (2003). Stratigraphic, chronological and behavioural context of Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature*, **423**: 747–52.

Clarke, R. J. and Tobias, P. V. (1995). Sterkfontein Member 2 foot-bones of the oldest South African hominid. *Science*, **269**: 521–4.

Clarke, R. J. (1994). On some new interpretations of Sterkfontein stratigraphy. *South African Journal of Science*, **90**: 211–14.

(1998). First ever discovery of a well-preserved skull and associated skeleton of *Australopithecus*. *South African Journal of Science*, **94**: 460–3.

(1999). Discovery of complete arm and hand of the 3.3 million-year-old *Australopithecus* skeleton from Sterkfontein. *South African Journal of Science*, **95**: 477–80.

Coppens, Y. (1983). Les plus anciens fossiles d'Hominidés. In *Recent Advances in the Evolution of Primates*. Pontificiae Academiae Scientiarum Scripta Varia, pp. 1–9.

Crompton, R. H. and Gowlett, J. A. J. (1993). Allometry and multidimensional form in Acheulean bifaces from Kilombe, Kenya. *Journal of Human Evolution*, **25**: 175–99.

Curnoe, D. (2010). A review of early *Homo* in southern Africa focusing on cranial, mandibular and dental remains, with the description of a new species (*Homo gautengensis* sp. nov.). *Homo – Journal of Comparative Human Biology*, **6**(31): 151–77.

Curnoe, D. and Tobias, P. V. (2006). Description, new reconstruction, comparative anatomy and classification of the Sterkfontein StW 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. *Journal of Human Evolution*, **50**: 36–77.

Dart, R. A. (1925). *Australopithecus africanus*: the man-ape of South Africa. *Nature*, **115**: 195–9.

(1949). The bone-bludgeon hunting technique of *Australopithecus*. *South African Journal of Science*, **2**: 150–2.

Enard, W., Przeworski, M., Fisher, S. E. *et al.* (2002). Molecular evolution of *FOXP2*, a gene involved in speech and language. *Nature*, **418**: 869–72.

d'Errico, F. (2003). The invisible frontier: a multiple species model for the origin of behavioral modernity. *Evolutionary Anthropology*, **12**: 188–202.

Drapeau, M. S. M. (2004). Functional anatomy of the olecranon process in hominoids and Plio-Pleistocene hominins. *American Journal of Physical Anthropology*, **124**: 297–314.

Drapeau, M. S. M., Ward, C. V., Kimbel, W. H. *et al.* (2005). Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *Journal of Human Evolution*, **48**: 593–642.

Falk, D., Hildebolt, C., Smith, K. *et al.* (2005). The brain of LB1, *Homo floresiensis*. *Science*, **308**: 242–5.

(2007). Brain shape in human microcephalics and *Homo floresiensis*. *Proceedings of the National Academy of Sciences, USA*, **104**: 2513–18.

Gould, S. J. (2001). Size matters and function counts. In Falk, D. and Gibson, K. R. (eds.), *Evolutionary Anatomy of the Primate Cerebral Cortex*. Cambridge: Cambridge University Press, pp. xiii–xvii.

Gould, S. J. and Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society London B*, **205**: 581–98.

Gowlett, J. A. J. (2006). The elements of design form in Acheulian bifaces: modes, modalities, rules and language. In Goren-Inbar, N. and Sharon, G. (eds.), *Axe Age: Acheulian Tool-making from Quarry to Discard*. London: Equinox, pp. 50–67.

Green, R. E., Krause, J., Briggs, A. W. *et al.* (2010). A draft sequence of the Neandertal genome. *Science*, **328**: 710–22.

Grün, R., Beaumont, P., Tobias, P. and Eggins, S. (2003). On the age of Border Cave 5 human mandible. *Journal of Human Evolution*, **45**: 155–67.

Hawks, J. and Cochran, G. (2006). Dynamics of adaptive introgression from archaic to modern humans. *PaleoAnthropology*, **2006**: 101–15.

Henshilwood, C., D'Errico, F., Vanhaeren, M. *et al.* (2004). Middle Stone Age shell beads from South Africa. *Science*, **304**: 404.

Henshilwood, C. S., d'Errico, F. and Watts, I. (2009). Engraved ochres from the Middle Stone Age levels at Blombos Cave, South Africa. *Journal of Human Evolution*, **57**: 27–47.

Herries, A. I. R., Curnoe, D. and Adams, J. W. (2009). A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa. *Quaternary International*, **202**(1–2), 14–28.

Holloway, R. L, Clarke, R. J. and Tobias, P. V. (2004). Posterior lunate sulcus in *Australopithecus africanus*: was Dart right? *Comptes Rendus Palevol*., **3**: 287–93.

Hopley, P. J. and Maslin, M. A. (2010). Climate-averaging of terrestrial faunas: an example from the Plio-Pleistocene of South Africa. *Paleobiology*, **36**(1): 32–50.

Hughes, A. R. and Tobias, P. V. (1977). A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. *Nature*, **265**: 310–12.

Keyser, A. W., Menter, C. G., Moggi-Cecchi, J. *et al.* (2000). Drimolen: a new hominid-bearing site in Gauteng, South Africa. *South African Journal of Science*, **96**: 193–7.

Kibii, J. M. (2004). Comparative taxonomic, taphonomic and palaeoenvironmental analysis of 4–2.3 million year old australopithecine cave infills at Sterkfontein. PhD thesis, University of the Witwatersrand.

Krause, J., Lalueza-Fox, C., Orlando, L. *et al.* (2007). The derived *FOXP2* variant of modern humans was shared with Neandertals. *Current Biology*, **17**: 1–5.

Kuman, K. (1994). The archaeology of Sterkfontein: past and present. *Journal of Human Evolution*, **27**: 471–95.

Kuman, K. and Clarke, R. J. (2000). Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *Journal of Human Evolution*, **38**: 827–47.

Leakey, R. E. F. (1974). Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. *Nature*, **248**, 653–6.

Leakey, L. S. B., Tobias, P. V. and Napier, J. R. (1964). A new species of the genus *Homo* from Olduvai Gorge. *Nature*, **202**: 7–9.

Leakey, M. G., Spoor, F., Brown, F. H. *et al.* (2001). New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature*, **410**: 433–40.

Levin, D. (2002). Hybridization and extinction. *American Scientist*, **90**: 254–61.

Lockwood, C. A. and Tobias, P. V. (2002). Morphology and affinities of new hominin cranial remains from Member 4 of the Sterkfontein Formation, Gauteng Province, South Africa. *Journal of Human Evolution*, **42**: 389–450.

Lockwood, C. A., Menter, C. G., Moggi-Cecci, J. *et al.* (2007). Extended male growth in a fossil hominin species. *Science*, **318**: 1443–6.

McHenry, H. M. and Corruccini, R. S. (1976). Fossil hominid femora and the evolution of walking. *Nature*, **259**: 657–8.

(1978).The femur in early human evolution. *American Journal of Physical Anthropology*, **49**: 473–88.

McBrearty, S. (2001). The Middle Pleistocene of East Africa. In Barham, L. and Robson-Brown, K. (eds.), *Human Roots – Africa and Asia in the Middle Pleistocene*. Bristol, England: Western Academic & Specialist Press Limited, pp. 81–98.

McBrearty, S. and Brooks, A. S. (2000). The revolution that wasn't: a new interpretation of the origin of modern human behavior. *Journal of Human Evolution*, **39**: 453–563.

Menter, C., Kuykendall, K. L., Keyser, A. W. *et al.* (1999). First record of hominid teeth from the Plio-Pleistocene site of Gondolin, South Africa. *Journal of Human Evolution*, **37**: 299–307.

Mercader, J., Barton, H., Gillespie, J. *et al.* (2007). 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences* **104**(9): 3043–8.

Moggi-Cecchi, J., Grine, F. E. and Tobias, P. V. (2006). Early hominid dental remains from Members 4 and 5 of the Sterkfontein Formation (1966–1996 excavations): catalogue, individual associations, morphological descriptions and initial metric analyses. *Journal of Human Evolution*, **50**: 239–328.

Morwood, M. J., Soejono, R. P., Roberts, R. G. *et al.* (2004). Archaeology and age of a new hominin from Flores in eastern Indonesia. *Nature*, **431**: 1087–91.

O'Regan, H. J. and Reynolds, S. C. (2009). An ecological reassessment of the southern African carnivore guild: a case study from Member 4, Sterkfontein, South Africa. *Journal of Human Evolution*, **57**: 212–22.

Panger, M. A., Brooks, A. S., Richmond, B. G. *et al.* (2002). Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evolutionary Anthropology*, **11**: 235–45.

Partridge, T. C., Shaw, J., Heslop, D. and Clarke, R. J. (1999). The new hominid skeleton from Sterkfontein, South Africa: age and preliminary assessment. *Journal of Quaternary Science*, **14**(4): 293–8.

Pickford, M. and Senut, B. (2005). Hominoid teeth with chimpanzee- and gorilla-like features from the Miocene of Kenya: implications for the chronology of the ape–human divergence and biogeography of Miocene hominoids. *Anthropological Science*, **113**: 95–102.

Pickford, M., Senut, B., Gommery, D. *et al.* (2002). Bipedalism in *Orrorin tugenensis* revealed by its femora. *Comptes Rendus Palevol*, **1**: 191–203.

Pickering, T. R. (1999). Taphonomic interpretations of the Sterkfontein early hominid site (Gauteng, South Africa) reconsidered in light of recent evidence. PhD thesis, University of Wisconsin, Madison. University Microfilms, Ann Arbor, Michigan.

Pickering, T. R., White, T. D. and Toth, N. (2000). Cutmarks on a Plio-Pleistocene hominid from Sterkfontein, South Africa. *American Journal of Physical Anthropology* **111**: 579–84.

Scott, R. S., Ungar P. S., Bergstrom, T. S. *et al.* (2005). Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature*, **436**: 693–5.

Senut, B., Pickford, M., Gommery, D. *et al.* (2001). First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus de l'Académie des Sciences*, **332**: 137–44.

Senut, B. and Pickford, M. (2004). La dichotomie grands singes – homme revisitée. *Comptes Rendus Palevol*, **3**: 265–76.

Shennan, S. (2001). Demography and cultural innovation: a model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal*, **11**: 5–16.

Smith, F. (1993). Models and realities in modern human origins: the African fossil evidence. In Aitken, M., Stringer, C. & Mellars, P. (eds.), *The Origins of Modern Humans and the Impact of Chronometric Dating*. Princeton: Princeton University Press, pp. 234–48.

(2002). Migrations, radiations, and continuity: patterns in the evolution of Middle and Late Pleistocene humans. In Hartwig, W. (ed). *The Primate Fossil Record*. Cambridge: Cambridge University Press, pp. 437–56.

Sponheimer, M., Passey, B. H., de Ruiter, D. J. *et al.* (2006). Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. *Science*, **314**, 980–2.

Reynolds, S. C., Clarke, R. J. and Kuman, K. (2007). The view from the Lincoln Cave: mid- to late Pleistocene fossil deposits from Sterkfontein hominid site, South Africa. *Journal of Human Evolution*, **53**(3): 260–71.

Reynolds, S. C., Bailey, G. and King, G. C. P. (2011). Landscapes and their relation to hominin habitats: case studies from *Australopithecus* sites in eastern and southern Africa. *Journal of Human Evolution*, **60**(3): 281–98.

Richmond, B. G. and Jungers, W. L. (2008). *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science*, **319**: 662–1665.

Taylor, R. C. and Rowntree, V. J. (1973). Running on two or four legs: which consumes more energy? *Science*, **179**: 186–7.

Tobias, P. V. (1967). *Olduvai Gorge Volume 2: the Cranium and Maxilliary Dentition of* Australopithecus (Zinjanthropus) boisei. Cambridge: Cambridge University Press.

(1979). The Silberberg Grotto, Sterkfontein, Transvaal, and its importance in palaeo-anthropological research. *South African Journal of Science*, **75**: 161–4.

(1991). *Olduvai Gorge Volume 4: the Skulls, Teeth and Endocasts of* Homo habilis. Cambridge: Cambridge University Press.

van der Merwe, N. J., Thackeray, J. F., Lee-Thorp, J. A. and Luyt, J. (2003). The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. *Journal of Human Evolution*, **44**, 581–97.

Vekua, A., Lordkipanidze, D., Rightmire, G. P. *et al.* (2002). A new skull of early *Homo* from Dmanisi, Georgia. *Science*, **297**(5578): 85–9.

Wadley, L. (2007). Announcing a Still Bay Industry at Sibudu Cave, *Journal of Human Evolution*, **52**: 681–9.

Walker, J., Cliff, R. A. and Latham, A. G. (2006). U-Pb isotopic age of the StW 573 hominid from Sterkfontein, *South Africa. Science*, **314**: 1592–4.

Weber, G. W., Schäfer, K., Prossinger, H. *et al.* (2001). Virtual anthropology: the digital evolution in anthropological sciences. *Journal of Physiological Anthropology and Applied Human Sciences*, **20**: 69–80.

White, T. D., Ambrose, S. H., Suwa, G. *et al.* (2009). Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus. Science*, **326**: 87–93.

Wood, B. A. (1991). *Koobi Fora Research Project. Volume 4. Hominid Cranial Remains*. Oxford: Clarendon Press.

2 *Academic genealogy*

PETER S. UNGAR AND
PHILLIP V. TOBIAS

Time, the Refreshing River:[1] an academic genealogy extending more than half a millennium.

We are like dwarfs on the shoulders of giants, so that we can see more than they, and things at a greater distance…not by virtue of any sharpness of sight on our part, or any physical distinction…but because we are carried high and raised up by their giant size.

(John of Salisbury, 1159 quoting Bernard of Chartres)[2]

Introduction

Palaeoanthropologists often justify the study of human evolution as important to our understanding of where we as a species have been, where we are today, and where we will go in the future. Following the same logic, palaeoanthropologists should be better able to understand their own intellectual traditions with an appreciation of their academic genealogies. The history of palaeoanthropology and the personalities of its practitioners have had a profound impact on our field and the way we have phrased hypotheses, gathered data and interpreted our results (Cartmill *et al.* 1986; Landau 1991).

It may in this light come as a surprise that little formal work has been published on academic genealogies of palaeoanthropologists. Academic lineages have been well documented and detailed for a number of disciplines. The Mathematics Genealogy Project at North Dakota State University, for example, has been recognised by the *Chronicle of Higher Education*, *Science* magazine and other media outlets. This well funded, web-based project now boasts an academic tree listing more than one

[1] This phrase, from a poem by W. H. Auden, was used by Joseph Needham as the title of one of his books of essays (1943).

[2] Quoted in Rees (2006).

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hundred thousand individuals with roots dating back hundreds of years. Similar web-based genealogy databases are available for chemistry, physics, linguistics, computer science, neuroscience, philosophy, and other disciplines.

So why not palaeoanthropology? Our field is relatively young, but its intellectual roots span back through the centuries to the great medical schools of the European Renaissance. Surely we could benefit from, take comfort in, or at least gain some wry amusement out of, an understanding of our academic pedigrees. This chapter presents an academic genealogy of intellectual ancestry and descent shared to varying degrees by many palaeoanthropologists. It works backward from one of us (PVT), and reaches across four continents and more than five hundred years (Figure 2.1).

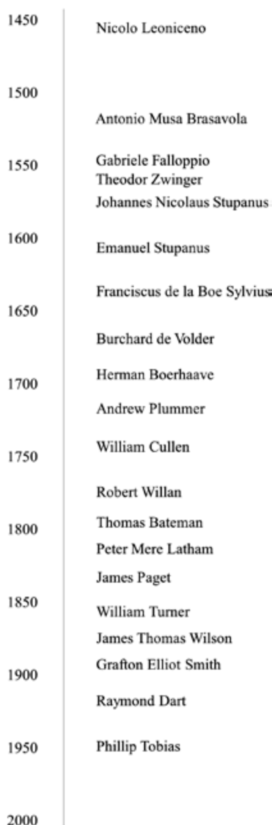

Figure 2.1. Academic lineage described in this chapter. Individuals are placed according to the dates of their highest relevant degrees.

Approaches to this genealogy

This exercise is by its nature an oversimplification. To be sure, no individual academic is influenced by only one mentor. In this sense, a genealogical plexus of blood vessels is probably a reasonable analogy, especially for the academic pedigree of an anatomical scientist! Our intellectual family tree more closely resembles a tangle of lianas connecting back and forth in seeming indecipherable chaos. Add to this the fact that ancestors came from many different academic traditions and that some individuals are better documented than others, and the task of tracing an academic genealogy becomes a formidable undertaking.

First and foremost, we must carefully define 'mentor' to make sense out of any academic genealogy. For this chapter, we identify a mentor as the individual who had the most documented influence on the student in the discipline of palaeoanthropology, or before the advent of palaeoanthropology, in the academic field for which that student became best known. This could be a teacher, a doctoral dissertation, research or clinical advisor, or a graduate or postdoctoral mentor. Academic genealogy is not an exact science. Some student and mentor relationships are obvious, whereas others are more difficult to establish and must be selected as 'best choice' among several possibilities.

Most of the individuals in this genealogy are well known from biographies, published or unpublished letters, detailed obituaries and other documents. This is fortunate, as the strength of a chain is only as good as its weakest link. Relationships between each mentor–student pair and facts about each individual were gathered from the primary literature and confirmed with demonstrably independent sources whenever possible. Rationales for ascribing relationships for less obvious links are offered as necessary.

Information on each individual is presented in a separate section. These sections provide only basic biographic facts because the emphasis here is on the linkages between mentor and student. Details provided include formal education and degrees, academic positions held and major contributions in research and teaching. Occasional anecdotes and quotations are also offered to give the reader a sense of these academicians as 'real people'. References to more detailed biographic information are presented at the end of each section.

Phillip Vallentine Tobias (1925–)

Mentor: Raymond Arthur Dart

Phillip Tobias was born in Durban, South Africa in 1925. His university education began at the University of the Witwatersrand in 1942, where he earned BSc and BSc Honours degrees (1946, 1947), the medical degrees MB, BCh

(1950) and a PhD (1953) for a thesis entitled *Chromosomes, Sex-Cells and Evolution in the Gerbil*. He was awarded a DSc degree for his works on hominid evolution in 1967. Tobias mentions Raymond Dart first among the 'veritable *Senatus Academicus*' that helped shape his academic career (Tobias, 2005). While Joseph Gillman advised Tobias on his cytogenetics doctoral thesis, Dart was clearly his mentor in palaeoanthropology – from the classroom to the laboratory and into the field.

Tobias was appointed demonstrator and instructor in histology and physiology at the University of the Witwatersrand in 1945. He served as lecturer (1951–2), senior lecturer (1953–8), professor and chair (1959–90) of anatomy, and as dean of the Faculty of Medicine (1980–2) at the University of the Witwatersrand, Johannesburg. He remains today professor emeritus and honorary professorial research fellow at that institution. Tobias is a captivating and respected teacher and lecturer, as well as a caring and diligent mentor. One of Tobias's academic protégés, Frederick Grine (1990), wrote of his 'extraordinarily thorough, painstaking and incisive comments, suggestions and criticisms', noting that his 'unfailing encouragement and wise counsel have truly been inspirational'. Tobias has had many academic descendants to date, spanning at this point at least four academic generations. These include the first author of this article, Peter Ungar, who was Frederick Grine's student. Ungar himself has now mentored several students, who today are in the process of training their own. And so it continues.

Phillip Tobias is best known for his landmark descriptions of early hominins. He has authored over 1150 works to date, spanning a dizzying variety of topics from genetics to human evolution, and anatomy, growth and development, to the history and philosophy of science. He has received numerous awards and honorary degrees, including three Nobel Prize nominations. He is a Fellow of the Royal Society (London) and a Foreign Associate of the National Academy of Sciences of the USA, Commander of the Order of Merit of France and Commander of the National Order of Merit of Italy. He has maintained an inspiring stance against apartheid from 1949 onward.

References: Sperber, 1990; Tobias, 2005; Koenig, 2005.

Raymond Arthur Dart (1893–1988)

Mentor: Grafton Elliot Smith, but see also
James Thomas Wilson

Raymond Dart was born in Toowong, Brisbane, Australia in 1893. His university education began in 1910 at the University of Queensland, where he

received a BSc in 1913 and MSc in 1914. He enrolled in the University of Sydney in 1913, where he received his MB and ChM in 1917 and MD in 1927. Dart studied anatomy under James Thomas Wilson and served as his assistant between 1914 and 1917. He wrote more than four decades later that Wilson's influence on him was 'so great that even today, I find myself guided by the standards he implanted in my young mind' (Dart, 1959).

Following brief military service, Dart was appointed senior demonstrator under Grafton Elliot Smith at University College, London. In 1919 he continued his studies of neuroanatomy. Smith had a tremendous influence on Dart's interests in palaeoanthropology and thus may be considered Dart's primary mentor for this genealogy. Dart left London at the end of 1922 to accept a post as professor of anatomy in the Medical School at the University of the Witwatersrand, Johannesburg, South Africa. He served as professor and head of the Department of Anatomy from 1923 to 1958. Concurrently he was dean of the Faculty of Medicine from 1925 to 1943. Dart was a 'brilliant, gifted teacher who brought all the passion and conviction of a missionary preacher to his classes' (Fagan, 1989). Raymond Dart's best known accomplishment is his recognition of the human-like qualities in the famous Taung child skull discovered in 1924 and assigned by him to a new genus and species, *Australopithecus africanus*. His claim flew in the face of the prevailing paradigm, that mankind had evolved in Asia. He doggedly championed his view that it represented a species whose members have taken steps in a human direction and from the middle of the twentieth century saw its almost universal acceptance. He and his team recovered from the site of Makapansgat some 300 km north of Johannesburg further remains of *Australopithecus*, but his association with that site generated another revolutionary claim, namely that the thousands of broken bones had been artificially smashed and shaped by the australopithecines. Although his claim for a bone, tooth and horn culture has not been supported, the impact of that work catalysed the development of the field of taphonomy. Dart pioneered studies on the evolution of the human upright posture and made many contributions in southern African archaeology. It has been said of him that he was 'a maker of men' and this is perhaps his most lasting contribution. Raymond Dart played a major role in building up the infant Medical School of the University of the Witwatersrand, Johannesburg, including the establishment of the Witwatersrand Medical Library (now the Health Sciences Library), university courses for physiotherapists, occupational therapists and nurses, and the Medical BSc and honours degrees, which laid a foundation for many of the distinguished graduates of this School.

References: Dart, 1959; Wheelhouse, 1983; Tobias, 1984; Tobias, 1989; Fagan, 1989; Wheelhouse and Smithford, 2001.

Grafton Elliot Smith (1871–1937)

Mentor: James Thomas Wilson

Grafton Elliot Smith was born in Grafton, New South Wales, Australia in 1871. He entered the University of Sydney in 1888 to study medicine, and graduated as MB and ChM in 1893. He received an MD in 1895 for his dissertation on the anatomy and histology of the non-placental mammal brain. Smith served as a demonstrator of anatomy under his mentor James Thomas Wilson from 1894–6. He continued his research at Cambridge until 1900.

Elliot Smith's first professorship was the chair of anatomy at the University of Cairo from 1900 to 1909. During that time he continued to develop his research on neuroanatomy, but added Egyptian bioarchaeology, human evolution and the origin and spread of civilisation to his repertoire of interests. He accepted the chair of anatomy at the Victoria University of Manchester, where he served until 1919. He then filled the chair of anatomy at University College, London until his retirement in 1936. Smith mentored many students and staff during his career, and more than twenty went on to fill chairs of anatomy. He must have been an inspiring lecturer, as Raymond Dart recounted after hearing him speak for the first time, 'I fell under his spell that night and prayed that at some time I would be allowed to work under him' (Dart, 1959).

Elliot Smith was a remarkably prolific researcher with some 434 works to his credit, including eight books. He is perhaps best known for his work on the infamous Piltdown man and on hyperdiffusionism, but he published on an amazing assortment of topics, from mammalian comparative neuroanatomy to many aspects of human evolution, and the bioarchaeology of Dynastic Egypt. Elliot Smith received many accolades, including a Knighthood in 1934, and Cross of the French Legion of Honour in 1936.

References: Wilson, 1938; Dart, 1959; Elkin and MacIntosh, 1974; Blunt, 1988; Morison, 1997.

James Thomas Wilson (1861–1945)

Mentor: William Turner

James Thomas Wilson was born in 1861 at Moniaive, Dumfriesshire, Scotland. He began his medical training at the University of Edinburgh in 1879 and received his BM degree there in 1883. After a surgical rotation at the Royal Infirmary in Edinburgh and a year as a surgeon on a cargo ship at sea, he returned to the University of Edinburgh as demonstrator of anatomy under William Turner for two winter sessions. Of his mentor, Wilson later wrote

'I cannot omit a special reference to the Edinburgh School of Anatomy in which I received not only my early anatomical instruction, but my later training as a teacher of anatomy under my old chief Sir William Turner, to whom as in private duty bound, I must pay tribute' (Morison, 1997).

Wilson began his career as demonstrator of anatomy in the Medical School at the University of Sydney in 1887. He remained in Sydney for more than three decades, later serving as professor of anatomy and as dean of the Faculty of Medicine. He also served as director of the Prince Alfred Hospital and held numerous other appointments. Wilson returned to Britain in 1920 to fill the chair of anatomy at Cambridge University, a position he held until his retirement in 1934. Wilson was evidently not the most exciting of lecturers. His pupil, Elliot Smith, once wrote that his boring osteology lectures 'rapidly killed all interest in the subject' (Morison, 1997). Nevertheless, he was an excellent research mentor, 'advising, criticizing, and above all, encouraging, all with great vehemence' (Morison, 1997).

Wilson's best known publications involve the anatomy, physiology and embryology of native Australian mammals, but he also published on other subjects, including human anatomy. Like his mentor before him, Wilson took an active role in military affairs, ascending through the ranks to Lieutenant-Colonel in the Australian Intelligence Corps and Honorary Colonel in the Censorship Service.

References: Hill, 1949; Smith, 1950; Morison, 1997.

Sir William Turner (1832–1916)

Mentor: Sir James Paget

William Turner was born in Lancaster, England in 1832. He began his medical training as an apprentice to a local general practitioner in 1848 and his formal education two years later when he enrolled in St. Bartholomew's Hospital Medical School to work under James Paget. Turner was qualified to practise by the Royal College of Surgeons and took honours in chemistry at the London University in 1853. He became the favourite pupil of Paget, who recommended him for the post of demonstrator at the University of Edinburgh in 1853.

Turner served the University of Edinburgh from 1854 to his death in 1916, first as demonstrator, then as professor, dean of the Faculty, and finally principal and vice-chancellor. He took a great interest in his students and trained, encouraged and guided them. It should come as no surprise then that, according to Hill (1949), 'round about the turn of the century, the vast majority of professors of anatomy in the [British] Empire had been pupils of William Turner'. Turner had a distinguished career in the Volunteer Service, becoming

a decorated Lieutenant Colonel. He was knighted in 1886 and created Knight Commander of the Order of Bath in 1901.

Turner was Britain's leading anatomist for much of the nineteenth century, and had a diverse portfolio of interests. He published more than 200 works on topics ranging from human craniology to mammalian placentation. William Turner advised Charles Darwin during the development of natural selection theory, and was among the first researchers to look to comparative anatomy for evidence of evolution.

References: Keith, 1916; M. A. (anon), 1917; Morison, 1997; Anon, 2002; Magee, 2003.

Sir James Paget (1814–1899)

Mentor: Peter Mere Latham

James Paget was born in Great Yarmouth, Norfolk, England in 1814. His medical education began in 1830 with apprenticeship to a general practitioner-surgeon in Great Yarmouth. In 1834, he moved to London and became a student at St. Bartholomew's Hospital. Paget spent much of his time attending the ward rounds of Peter Mere Latham, and served under Latham as clinical clerk between 1835 and 1836, when he was qualified to practise by the Royal College of Surgeons.

Paget's teaching, research and clinical appointments, and accomplishments are too many to list here. He spent most of his career at St. Bartholomew's Hospital Medical School, where he served first as the curator of the anatomy and pathology museum, then as demonstrator, lecturer, warden and, ultimately, surgeon. He also served as professor at the Royal College of Surgeons and ran a very busy private practice, seeing up to 200 patients a day at the hospital! He was appointed Surgeon Extraordinary to Queen Victoria in 1858, Surgeon-in-Ordinary to the Prince of Wales in 1863 and was conferred a baronetcy in 1871. He resigned from St. Bartholomew's Hospital that year, but continued to practise medicine and hold various appointments, including that of President of the Royal College of Surgeons and Vice-Chancellor of the University of London.

Paget is best known as one of the founding fathers of scientific medical pathology, and his name is associated with Paget's disease of the bone and nipple. His works include *Lectures on Tumours* (1851) and *Lectures on Surgical Pathology* (1853) and numerous papers on cancer, syphilis and typhoid. Despite all this, teaching remained important to Paget. He wrote to

his pupil William Turner 'I can feel with and for you the immense pleasure of lecturing to full benches of attentive men. Many and great as have been the pleasures that I have derived from my profession, none has been as great as this' (Paget, 1901).

References: Paget, 1901; Roberts, 1989; Coppes-Zantinga and Coppes, 2000; Royal College of Physicians, 2006a.

Peter Mere Latham (1789–1875)

Mentor: Thomas Bateman

Peter Mere Latham was born in London, England in 1789. After taking a BA at Brasenose College in Oxford in 1810, he began medical studies at St. Bartholomew's Hospital and at the Carey Street Dispensary under the tutelage of Thomas Bateman. He earned an MA in 1813, MB in 1814 and MD from St. Bartholomew's Hospital in 1816.

Latham worked as a physician at the Middlesex Hospital between 1815 and 1824, and then at St. Bartholomew's Hospital until ill health forced him to resign in 1841 (though he maintained a small private practice until 1865). Latham had a decorated clinical career, including an appointment as Physician Extraordinary to Queen Victoria from 1837 to his death in 1875. Latham became a lecturer in medicine at St. Bartholomew's Hospital Medical School in 1836, and taught students there for many years. He was a very dedicated teacher and he wrote passionately on medical education reform. As for his teaching, his pupil James Paget wrote, 'I think there were none who did not thoroughly admire him, and imitate him in his mode of study, and very gratefully remember his teachings' (Paget, 1901). On his lecturing style, however, Paget added curiously 'he was very pompous; sometimes almost laughably so, especially if he had to speak of general rules relating either to personal conduct or to modes of study; but this only helped the memory of his hearers' (Paget, 1901).

Latham is remembered for his descriptions of clinical symptoms and physical findings in cardiology as presented in his *Essays on Some Diseases of the Heart* (1828) and *Lectures on Clinical Medicine Comprising Diseases of the Heart* (1845). He is also remembered for his pioneering work on auscultation and percussion, published in *Lectures on Subjects Connected with Clinical Medicine* in 1836.

References: Munk, 1878; Paget, 1901; Spaulding, 1971; Fleming, 1997; Royal College of Physicians, 2006b.

Thomas Bateman (1778–1821)

Mentor: Robert Willan

Thomas Bateman was born in Whitby, Yorkshire, England in 1778. His early medical training began with an apprenticeship to an apothecary in Whitby. Bateman's formal studies began in 1797 at the Windmill Street School of Anatomy and St. George's Hospital in London. He then matriculated at the University of Edinburgh in 1798, and received an MD in 1801 for a thesis on *Haemorrhoea Petechialis.* He returned to London that year and began training under Robert Willan. Bateman quickly became Willan's disciple, championing his mentor's works (and gratefully acknowledging his indebtedness to Willan) for many years.

Bateman began work as a physician at both the Fever Institution and the Carey Street Dispensary in 1804. He continued practising until ill health forced his resignation from the institution in 1818 and from the dispensary the following year. He died in 1821 at the age of 42. He evidently mentored several young physicians during his years at the dispensary, and was a serious and intense teacher. Rumsey (1827) wrote 'the simplicity of his language and conscientious fidelity of his whole mind to his office, were admirably calculated to fix the attention and attachment of a scholar. No levity unworthy of his learning or his subject ever dishonoured either'.

Bateman is known for continuing Willan's work to describe skin diseases and standardise dermatology nomenclature. His *Practical Synopsis of Cutaneous Diseases According to the Arrangement of Dr. Willan* in 1813 and *Delineations of Cutaneous Diseases, Exhibiting the Characteristic Appearances of the Principal Genera and Species, Comprised in the Classification of Willan* in 1817 are considered to have been the most influential textbooks of dermatology in the nineteenth century. Bateman is credited with identifying and describing several skin diseases, among them *Herpes iris* of Bateman and eczema. He published a collection of papers as the *Reports on the Diseases of London and the State of the Weather* that drew much attention, as well as other works based on his practice at the Fever Institution.

References: Bateman, 1812; Rumsey, 1827; Booth, 1999; Levell, 2000; J. R. (anon), 2006; Royal College of Physicians, 2006c.

Robert Willan (1757–1812)

Mentor: William Cullen

Robert Willan was born at The Hill, near Sedbergh in Yorkshire, England in 1757. He began his medical training in Edinburgh in 1777, studying medicine

under William Cullen and other teachers at the university. Cullen's influence is evidenced in Willan's later work classifying skin lesions, which followed his mentor's efforts to categorise diseases using the Linnaean system (see below), just as Erasmus Darwin was to do. Willan received his MD in Edinburgh in 1780 for a thesis on inflammation of the liver.

After two years of private practice in Darlington, Willan moved to London. He was appointed physician to the newly established Carey Street Dispensary in 1783, where he treated patients and mentored some forty young physicians during his tenure. Such dispensaries catered for the poor, disheveled masses, providing Willan with a 'dermatological goldmine' (Booth, 1999) upon which to base the research for which he became best known. He resigned from the dispensary in 1783, but continued to practise medicine until he became ill in 1811. Willan died in 1812.

Willan is recognised for bringing order to the discipline of dermatology with his classifications and descriptions of skin lesions. These he codified in his very successful treatise *On Cutaneous Diseases*. He has been called the father of modern dermatology, and his name remains attached to *lupus vulgaris* (Willan's lupus) and *psoriasis vulgaris* (Willan's lepra). He also wrote on a host of other medical topics ranging from the history of leprosy to the advantages of vaccination.

References: Bateman, 1812; Beswick, 1957; Hare, 1973; Sharma, 1983; Doig *et al.*, 1993; Booth, 1999.

William Cullen (1710–1790)

Mentor: Andrew Plummer

William Cullen was born in Hamilton, Lanarkshire, Scotland in 1710. His early medical training was informal, involving apprenticeships in Glasgow and London. He began his formal medical education by attending winter classes in 1734–5 and 1735–6 at the University of Edinburgh. While he earned his MD in Glasgow in 1740, genealogists consider Andrew Plummer to have been his principal mentor, as Cullen was evidently greatly influenced by Plummer and his lectures in Edinburgh (Kerker, 1955; Gaffney and Marley, 2002).

Cullen began lecturing on medicine at the University of Glasgow in 1744, and was appointed to its first lectureship in chemistry three years later. He taught chemistry and medicine in Glasgow until 1755, when he returned to Edinburgh to share a professorship with Plummer until his mentor died the following year. Cullen continued at Edinburgh until 1789, and died the following year. William Cullen is best remembered as a teacher and mentor. He was, by all accounts, a lucid and enthusiastic lecturer, more concerned with getting

his points across than with formality. In one famous quotation, he referred to Carolus Linnaeus's writings as 'the most uncouth jargon and minute pedantry' he had ever seen!

He is, nevertheless, well known for applying the Linnaean system to classify diseases by symptom. Cullen wrote many popular medical textbooks widely used throughout Europe and North America during the late eighteenth and early nineteenth centuries. His *First Lines of the Practice of Physic* and *A Treatise of the Materia Medica*, for example, set the standard for decades. In fact, it was in these works that he coined the term 'neurosis'. On the other hand, while he is best known as a founding father of chemistry in Britain, he wrote only one research paper related to this field – an examination of the cooling effects of evaporating fluids.

References: Thomson, 1832; Wightman, 1955; Kerker, 1955; Doig *et al.*, 1993; Gaffney and Marley, 2002; Doyle, 2005b.

Andrew Plummer (1697–1756)

Mentor: Herman Boerhaave

Andrew Plummer was born in Edinburgh, Scotland, in 1697. He began his university studies in the arts at the University of Edinburgh from 1712 to 1717, but then switched to medicine, matriculating at the University of Leiden in 1720 under the direction of Herman Boerhaave. Of Boerhaave's impact on Plummer, Kerker (1955: 38) wrote that Plummer 'could not have failed to succumb to his influence'. Plummer graduated MD in 1722 for a thesis *De phthisi pulmonali a catarrho orto*. He then returned to Scotland in 1724 and passed the licentiate examination of the Royal College of Physicians of Edinburgh permitting him to practise medicine.

Plummer and three other Leiden alumni began teaching medicine and chemistry at the new Edinburgh Dispensary in 1725, 'according to the method of the celebrated Herman Boerhaave' (Doyle, 2005a). The four were appointed professors, without salary, at the University of Edinburgh the following year, effectively founding the medical school. Plummer continued his private practice, taught chemistry and helped develop and run the group's pharmaceutical laboratory. He continued this work until his death in 1756. Plummer was evidently a better chemist than teacher, as one student, Oliver Goldsmith wrote, 'Plumer [sic] professor of chymistry understands his busines [sic] well but delivers himself so ill that he is but little regarded' (Doyle, 2005a). John Fothergill later recounted 'had not a native diffidence veil'd his talents as a praelector he would have been among the foremost in the pupils' esteem' (Doyle, 2005a).

Plummer published papers on clinical medicine and chemistry, including *Remarks on chemical solutions and precipitations* and *Experiments on neutral salts, compounded of different acid liquors, and alcaline salts, fixt and volatile*. He is best known for formulating Plummer's pills – a preparation of calomel, antimony sulfide and mercuric acid used, rather ineffectively, for more than a century as a panacea for numerous ailments.

References: Kerker, 1955; Underwood, 1977; Gaffney and Marley, 2002; Doyle, 2005a.

Herman Boerhaave (1668–1738)

Mentor: Burchard de Volder

Herman Boerhaave was born in 1668 in the parsonage at Voorhout near Leiden, the Netherlands. He entered the University of Leiden in 1684, and attended the lectures and demonstrations of Burchard de Volder. Boerhaave earned a doctorate in philosophy in 1690, after which De Volder promoted him to magister. Boerhaave later edited De Volder's *Oratio de novis et antique*. The pupil's respect for his mentor is clear in the preface, where he praises De Volder's 'sharpness of mind (*acerrimam ingenii aciem*), by which he exceeded everyone else' (Knoeff, 2002). Boerhaave also earned an MD from Harderwyck in 1693.

Boerhaave practised as a physician in Leiden for some years, and then was appointed to teach medicine at the University of Leiden in 1701. He worked at Leiden until his death in 1738, much of the time holding simultaneous chairs in botany, clinical medicine and chemistry. Boerhaave has been called one of the great teachers of all time (Kerker, 1955), and was named *communis Europae praeceptor* (the common teacher of Europe) by Albrecht von Haller (Underwood, 1977). Many of Boerhaave's students, such as Carl Linnaeus and Andrew Plummer, became some of the most influential academicians in the world.

Boerhaave wrote the medical textbooks *Institutiones medicae* and *Aphorismi de cognoscendis et curandis morbis*, and his *Elementa Chemiae* was among the most influential texts of the eighteenth century. He is considered the father of physical chemistry, with contributions including the introduction of exact measurements to chemistry, demonstration that water is a product of combustion, proof that heat is weightless and performance of the first calorimetric studies.

References: Kerker, 1955; Lindeboom, 1968; Underwood, 1977; Luyendijk-Elshout, 1998; Kidd and Modlin, 1999; Knoeff, 2002.

Burchard de Volder (1643–1709)

Mentor: Franciscus Sylvius

Burchard de Volder was born in Amsterdam, the Netherlands in 1643. He began to study medicine and philosophy in Amsterdam, and took an MA at Utrecht in 1660. He continued his education in Leiden, falling under the influence of Franciscus Sylvius. He earned an MD in 1664, with a dissertation *Theses de la Nature, très opposes aux idées Péripateticiennes*. De Volder then went back to Amsterdam to establish a medical practice, but returned to Leiden in 1670 following an offer of the chair of logic. During his time in Leiden, De Volder served also as professor of mathematics. He was appointed rector by William of Orange (then also the King of England) in 1697. De Volder taught the classics, mathematics and physics in Leiden, but resigned from his professorship due to illness in 1705.

Burchard de Volder did not produce a great volume of works, but his contributions were influential. His work reflected the ideas of his mentor Sylvius, and offers insights on some of De Volder's contemporaries including Spinoza, Descartes, Newton, Huygens and Boyle. De Volder argued for the integration of mathematics and physics in his *Oratio de conjungendis philosophicis et mathematicis disciplinis* (1682) and later for the integration of these with medicine in *De rationis viribus et usu in scientiis* (1698). He published studies on the weight of air and invented an air pump. He set up the first physics laboratory in Leiden and his lectures and demonstrations on gases and the atmosphere had a clear impact, especially on his most renowned student, Herman Boerhaave.

References: Partington, 1961; Klever, 1988; Gaffney and Marley, 2002; Knoeff, 2002.

Franciscus Sylvius (1614–1672)

Mentor: Emanuel Stupanus

Franciscus Sylvius (François Dubois or De le Boë) was born in Hanau, Germany, in 1614. He began his formal education with courses in Sedan and at other universities in Germany and France, ultimately receiving his MB at the University of Leiden in 1634. Sylvius obtained his MD in Basel in 1637 for this thesis, *Disputatio medica de animale motu einsque laesionibus*, under the direction of Emanuel Stupanus. The strong Paracelsian tradition at Basel clearly exerted an influence on Sylvius, as is evident in his later works.

Sylvius practised for a short time in Hanau, and then returned to Leiden to give private lectures on anatomy. He started a lucrative practice in Amsterdam in 1641, but was drawn back to Leiden by an appointment as professor of medicine in 1658. Sylvius remained at the University of Leiden, ultimately becoming *rector magnificus* from 1669–70. Sylvius was evidently a great teacher, and 'his clear, elegant and sometimes eloquent speech, slow enough to be followed by even somewhat dull intellects, drew around his chair an immense concourse of pupils who regarded him with strong affection' (Baker, 1909). He himself wrote 'I have endeavoured with all my might to make sure that my auditors should profit as much as possible from my industry and labor and go out as excellent physicians' (Baker, 1909). Indeed, Sylvius drew students from all over Europe, teaching them anatomy, chemistry and clinical medicine.

Sylvius conducted research on anatomy, physiology and pathology. He was a leading proponent of the school of Iatrochemistry, a doctrine that held that life and disease processes are based on chemical actions, and that medicine could be understood in terms of universal rules of physics and chemistry. The basic idea was a good one, but it fell apart quickly when Sylvius tried to unite the Galenic notions of humoral medicine with seventeeth-century chemistry. Much of this work is laid out in *Praxeos medicae idea nova* published in 1671. We know the name of Franciscus Sylvius today by his research on the structure of the brain, and particularly by his recognition of the 'Sylvian fissure' (lateral sulcus) as described in *Disputationes Medicae* (1663), 'Sylvian ventricle' (cave of septum pellucidum), 'Sylvian fossa' (lateral cerebral fossa) and a number of other eponymously designated entities. However, the 'Sylvian aqueduct' (cerebral aqueduct) owes its name to Jacobus Sylvius (1478–1555).

References: Baker, 1909; Baumann, 1949; Gubster, 1966; Underwood, 1972; van Gijn, 2001.

Emanuel Stupanus (1587–1664)

Mentor: Johannes Nicolaus Stupanus

Emanuel Stupanus (Emanuele Stupano) was born in Basel, Switzerland, in 1587. His formal education began in Geneva under Esaïe Colladone and Caspar Laurentius, and he attended classes at various universities in Germany, France and Italy. Stupanus returned to the University of Basel to earn his MD with highest honours conferred by mathematics professor Petrus Ryffius (Peter Ryff), who studied under Theodor Zwinger (see below) in 1613. Emanuel served an apprenticeship under his father, Johannes Nicolaus, until 1620 when he replaced the older Stupanus as professor of theoretical medicine. We know

little about Emanuel's teaching prowess, though Baumann (1949) reported that 'as promoter he seems not to have been unattractive'.

Emanuel Stupanus was a very active scholar, producing dozens of works spanning a career of more than forty years. His known works include *Vere' Aureorum Aphorismorum Hippocratis enarrationes & commentaria aphoristica Nova Methodo eiusmodiin ordinem digesta* (1615) and his translation and completion of Bartholomew Castelli's *Lexicon Medicum Graeco-Latinum* (1628). He published on a broad range of medical subjects.

References: Hofmann, 1698; Burckhardt, 1917; Baumann, 1949.

Johannes Nicolaus Stupanus (1542–1621)

Mentor: Theodor Zwinger

Johannes Nicolaus Stupanus (Juan Nicolás Stupano) was born in 1542 in Chiavenna, Italy. He took his formal education at the University of Basel, receiving his BA in 1563, MA in 1565 and MD in 1569 under the direction of Theodor Zwinger. Stupanus began teaching as professor of logic and rhetoric at the Basel Academy in 1560, and was appointed professor of theoretical medicine at the University of Basel in 1589, where he replaced Zwinger in 1589. He resigned from the University of Basel in 1620.

Stupanus senior was a prolific researcher and writer, publishing many works on physiology, pathology and diagnostic medicine. He was evidently a fervent advocate of the Paracelsian approach that presaged Sylvius's Iatrochemical School. Johannes Nicolaus Stupanus translated many works from Italian into Latin. These included texts on astronomy, the works of Machiavelli (*Prince, Discorsi*) and histories (including a history of Naples by Pandulphis). He is best known for his treatise *Medicina Theorica* (1614).

References: Hofmann, 1698; Koelbing, 1970.

Theodor Zwinger (1533–1588)

Mentor: Gabriele Falloppio

Theodor Zwinger (Theodoro Zuingero) was born in 1533 in Basel, Switzerland. He studied in Basel, Lyon and Paris, where he attended the lectures of Petrus Ramus. Zwinger then studied anatomy at the University of Padua, perhaps the most renowned Medical School of the European Renaissance. He received his medical degree in 1559 at the University of Padua under the direction of Gabriele Falloppio. Zwinger took a faculty position in the medical school at

the University of Basel in 1559, and was elected chair of Greek in 1565, ethics in 1571 and theoretical medicine in 1580.

Zwinger was an accomplished physician and philosopher known for his contributions in many fields. He is best remembered for his *Theatrum vitae humanae*, first published in 1565. This work is said to be 'the most comprehensive compilation of knowledge ever achieved by a single human being in the Early Modern Period' (Zedelmaier, 2008). As for his teaching and mentoring, little is known, though Blair (2008) does refer to a letter from the medical students at the University of Basel asking him to speak more slowly because of difficulty keeping up with him.

References: Herzog, 1778; Haeser, 1881; Dufournier, 1936; Kolb, 1951; Karcher, 1956; Bietenholz, 1971; Portmann, 1988; Blair, 2008; Zedelmaier, 2008.

Gabriele Falloppio (1523–1562)

Mentor: Antonio Musa Brasavola

Gabriele Falloppio (Gabriel Fallopius, Gabriello Falloppio) was born in Modena, Italy in 1523. He began his studies in anatomy in 1544 in Modena with Niccolo Machella, and is said to have spent some time at the University of Padua with Ratteo Realdo Colombo. He evidently completed his education at the University of Ferrara in 1548, under the direction of Antonio Musa Brasavola and Giovanni Battista Canano. Academic genealogists consider Brasavola to have been his mentor. Falloppio briefly taught pharmacy at Ferrara, but became professor of anatomy at the University of Pisa in 1549 and, in 1551, chair of anatomy and surgery at the University of Padua, where he also held a professorship in botany.

Falloppio was an outstanding teacher and anatomist. Hamilton (1831) reported that his lectures both at Pisa and Padua 'attracted crowds of auditors', and that he was 'most methodical in teaching'. According to O'Malley (2008), Falloppio 'lectured and demonstrated with such success as to attract a number of later to be distinguished students'. While several works are attributed to him, only *Observations anatomica* (1561) was published during his lifetime. This important book includes a series of commentaries and criticisms on Vesalius's *De humane corporis fabricate*. Falloppio is perhaps best known for his meticulous dissections and his descriptions of the vestibulococclear system, deciduous teeth and female reproductive tract, including the tubes that now bear his name.

References: Hamilton, 1831; Walsh, 1913; Sanchez, 2009.

Antonio Musa Brasavola (1500–1555)

Mentor: Nicolo Leoniceno

Antonio Musa Brasavola (Brassavola, Brasavoli) was born in 1500 in Ferrara. He attended universities in Padua, Bologna and Paris before returning to Ferrara, where he studied medicine under Nicholas Leoniceno and Giovanni Manardi. Brasavola's biography of Leoniceno, entitled *Praeceptor meus* (*My teacher*) makes the student–mentor relationship clear. Brasavola received his medical degree in 1521, though began lecturing in logic at Ferrara in 1519. While his tenure at Ferrara was interrupted periodically by breaks for private practice, Brasavola taught logic there until 1527, natural philosophy until 1536 and medicine until his death in 1555.

Brasavola was evidently a dedicated teacher. Thorndike (1941) tells of Brasavola being informed whilst lecturing that his house was on fire, and of his instance on finishing the lecture before leaving! He was also a well respected medical doctor, and served as court physician for Ercolo II, the Duke of Este, and for a time attended Pope Paul III in Rome. Brasavola also consulted for King Francis I of France, Kaiser Charles V of Germany and King Henry VIII of England, and treated patients from all walks of life. His principal research interests were in botany and pharmacology, and he is known for performing the first recorded successful tracheostomy. Brasavola was a prolific author, with more than forty major works to his credit. Some of the best know are *Examen omnium simplicium medicamentorum, quorum in officinis usus est* (1537), a witty imaginary conversation in which he introduced several new pharmaceuticals, and his commentaries on Hippocrates and Galen, *In octo libros aphorismorum Hippocratis & Galeni commentaria & annotationes* (1541), *In libros de ratione victus in morbis acutis Hippocratis & Galeni commentaria & annotationes* (1546) and *Index refertissimus in omnes Galeni libros* (1556).

References: Panoucke, 1820; Hamilton, 1831; Bottoni, 1892; Garrison, 1913; Thorndike, 1941; Nutton, 1997.

Nicolo Leoniceno (1428–1524)

Nicolo Leoniceno (Nicolaus Leoninus, Nicolo da Lonigo) was born in Lonigo in 1428. He studied Latin and Greek under Ognibene da Lonigo in Vicenza, but moved to Padua in 1446. He completed his education in philosophy and medicine at the University of Padua in 1453. Most academic genealogies list Pelope, or Pietro, Roccabonella as Leoniceno's primary mentor, but we have been unable to find confirmation in either case. Pietro Roccabonella, for

example, evidently did not become professor of medicine at Padua until 1465. It is possible that Pietro's grandfather, Niccolo Roccabonella, was Leoniceno's mentor, as Niccolo also taught medicine at Padua, but more research is needed to evaluate this possibility. Leoniceno taught philosophy and medicine at the University of Ferrara for an extraordinary 60 years, from 1464 until his death in 1524, with sabbaticals to teach at Bologna in 1483 and 1508–9. He was also an accomplished clinician.

Leoniceno saw himself as an educator first, his motto being *Plus ago docens omnes medicos* (Nutton, 1997). He is best remembered for his translations of ancient Greek texts by Galen, Hippocrates and others. Among his many works, two stand out: his criticism of Pliny, Avicenna, Serapio and others in *De Plinii et plurium aliorum in medicina erroribus liber ad doct. Virum Angelum Politianum* (1492) and the documentation of a syphilis pandemic that spread across Europe in the late 1400s in *Libellus de epidemia, quam vulgo morbum gallicum vocant* (1497).

References: Castigloni, 1941; Major, 1954; Pepe, 1986; Nutton, 1997.

Discussion

The twists and turns of research focus and interests presented in this genealogy are a product of the personalities of the individuals involved and the historical contexts in which they lived. Linnaean taxonomy led Willan to his classification of skin lesions, and Darwinian Natural Selection led Turner to comparative anatomy. While their styles varied from 'diffident' (Plummer) to 'pompous' (Latham), most of the men in this genealogy shared a remarkable drive and enthusiasm for teaching and research. Some, such as Falloppio, Sylvius, Boerhaave and Cullen, were excellent teachers, whereas others, such as Elliot Smith and Paget, are best remembered for their scientific contributions. Several, including Plummer, Wilson and Dart laboured to establish new departments modelled on their own almae matres, demonstrating yet again how the kernels of academic thought can be passed from mentor to pupil over centuries.

In the end, it is likely that none of these men would have been the academicians they turned out to be without the contributions of their mentors.

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References

Anon (2002). *Sir William Turner, 1832–1916. Surgeon's News 1.* Edinburgh.

Baker, F. (1909). The two Sylviuses. An historical study. *Johns Hopkins Hospital Bulletin*, **20**: 329–39.

Bateman, T. A. (1812). A biographical memoir of the late Dr. Willan. *Edinburgh Medical and Surgical Journal*, **8**: 502–12.

Baumann, E. D. (1949). *Francois dele Boë, Sylvius*. Leiden: Brill.

Beswick, T. S. (1957). Robert Willan: the solution to a ninety-year-old mystery. *Journal of the History of Medicine and Allied Sciences*, **12**: 349–65.

Bietenholz, P. G. (1971). *Basle and France in the Sixteenth Century. The Basle Humanists and Printers in their Contacts with Francophone Culture*. Toronto-Buffalo and Geneva: University of Toronto Press and Libraire Droz.

Blair, A. (2008). Student manuscripts and the textbook. In Campi, E., De Angelis, S. and Groeing, A.-S. (eds.), *Scholarly Knowledge: Textbooks in Early Modern Europe*. Geneva: Libraire Droz S.A, pp. 39–74.

Blunt, M. (1988). Sir Grafton Elliot Smith (1871–1937). In Ritchie, J. (ed), *Australian Dictionary of Biography*, Volume 12. Melbourne: Melbourne University Press. pp. 645–6.

Booth, C. C. (1999). Robert Willan MD FRS (1757–1812): Dermatologist of the millennium. *Journal of the Royal Society of Medicine*, **92**: 313–18.

Bottoni, A. (1892). *Cinque Secoli d'Universita a Ferrara, MCCCXCI-MDCCCXCI.* Bologna: Stabilimento Tip, Ramorani E. Albertazzi.

Burckhardt, A. (1917). *Geschichte der Medizinischen Fakultaet zu Basel, 1460–1900*. Basel: Reinhardt.

Cartmill, M., Pilbeam, D. and Isaac, G. (1986). One hundred years of paleoanthropology. *American Scientist*, **74**: 410–20.

Castiglioni, A. (1941). *A History of Medicine*. New York: Alfred A. Knopf.

Coppes-Zantinga, A. R. and Coppes, M. J. (2000). Sir James Paget (1814–1889): a great academic Victorian. *Journal of the American College of Surgeons*, **191**: 70–4.

Dart, R. A. (1959). *Adventures with the Missing Link*. New York: Harper and Brothers.

Doig, A., Ferguson, J. P. S., Milne, I. A. and Passmore, R. (1993). *William Cullen and the Eighteenth Century Medical World.* Edinburgh: Edinburgh University Press.

Doyle, W. P. (2005a). *Andrew Plummer (1697–1756). http://www.chem.ed.ac.uk/about/professors/plummer.html*. Edinburgh: Chemistry Webmaster, School of Chemistry, University of Edinburgh.

(2005b). *William Cullen (1710–1790). http://www.chem.ed.ac.uk/about/professors/cullen.html*. Edinburgh: Chemistry Webmaster, School of Chemistry, University of Edinburgh.

Dufournier, B. (1936). Th. Zwinger de bale et la scolastique de l'histoire au XVIe siecle. *Revue d'Histoire Moderne*, **11**: 323–35.

Elkin, A. P. and MacIntosh, N. W. G. (1974). *Grafton Elliot Smith: the Man and his Work*. Sydney: Sydney University Press.

Fagan, B. (1989). The passion of Raymond Dart. *Archaeology*, **42**: 18–&.

Fleming, P. R. (1997). *A Short History of Cardiology*. Amsterdam: Rodopi.

Gaffney, J. S. and Marley, N. A. (2002). Chemical genealogy of an atmospheric chemist: James N. Pitts, Jr., a case study. *Fourth Conference on Atmospheric Chemistry Symposium: Urban, Regional, and Global-Scale Impacts of Air Pollutants 82nd American Meteorological Society National Meeting, Orlando, FL 2002, Proceedings Volume, Paper* P1.3: 181–6.

Garrison, F. H. (1913). *An Introduction to the History of Medicine.* Philadelphia: W. B. Saunders.

Grine, F. E. (1990). Deciduous dental features of the Kalahari San: comparison of non-metrical traits. In Sperber, G.H. (ed.), *From Apes to Angels: Essays in Anthropology in Honor of Phillip V. Tobias*. New York: Wiley-Liss, pp. 153–70.

Gubster, A. (1966). The positiones variae medicae of Franciscus Sylvius. *Bulletin of the History of Medicine*, **40**: 72–80.

Haeser, H. (1881) *Lehrbuch der Geschichte der Medicin: Geschichte der Medicin in der neuren zeit.* Jena: Verlag Von Gustav Fischer.

Hamilton, W. (1831). *The History of Medicine, Surgery, and Anatomy, from the Creation of the World, to the Commencement of the Nineteenth Century.* London: Henry Colburn and Richard Bentley.

Hare, P. J. (1973). A note on Robert Willan's Edinburgh days. *British Journal of Dermatology*, **88**: 615.

Herzog (1778). *Athenae Rauricae. Sive Gatalogus Professorum Academiae Basiliensis Ab A. MCCCCLX ad A. MDCCLXXVII Cum Brevi Singulorum Biographia. Adiecta Est Recensio Omnium Eiusdem Academiae Rectorum.* Basel: Car. Aug. Serini.

Hill, J. P. (1949). James Thomas Wilson. *Obituary Notices of Fellows of the Royal Society*, **6**: 18.

Hofmann, J. J. (1698). *Lexicon Universale, Historiam Sacram*. Leiden: Jacob Hackius, Cornel. Boutesteyn, Petr. Vander Aa., & Jord. Luchtmans.

J. R. (anon) (2006). *The Life of Thomas Bateman*. London: Longman, Hurst, Reese, Orme and Brown.

Karcher, J. (1956). *Theodor Zwinger und sein Zeitgenossen. Episode aus dem Ringen der Basler Arzte um die Grandlehren der Medizin im Zeitalter des barocks. Studien zur Geschichte der Wissenschaften in Basel, III.* Basel: Helbing und Lichtenhahn.

Keith, A. (1916). Sir William Turner, K.C.B., F.R.S. *Man*, **16**: 65–71.

Kerker, M. (1955). Herman Boerhaave and the development of pneumatic chemistry. *Isis*, **46**: 36–49.

Kidd, M. and Modlin, I. M. (1999). The luminati of Leiden: from Bintius to Boerhaave. *World Journal of Surgery*, **23**: 1307–14.

Klever, W. N. A. (1988). Burchard De Volder (1643–1709), a Crypto-Spinozist on a Leiden Cathedra. *Lias*, **15**: 191–240.

Knoeff, R. (2002). *Herman Boerhaave (1668–1738). Calvinist Chemist and Physican.* Amsterdam.

Koelbing, H. M. (1970). Johannes Nicolaus Stupanus, Rhaetus (1542–1621). In *Äskulap in Graubünden*. pp. 628–46.

Koenig, R. (2005). South Africa's bone man: 80 and still digging into the past. *Science*, **310**: 608–9.

Kolb, W. (1951). *Geschichte des anatomischen Unterrichtes an der Universität zu Basel, 1460–1900.* Basel: B. Schwabe.

Landau, M. (1991). *Narratives of Human Evolution*. New Haven: Yale University Press.

Levell, N. J. (2000). Thomas Bateman MD FLS 1778–1821. *British Journal of Dermatology*, **143**: 9–15.

Lindeboom, G. A. (1968). *Herman Boerhaave: the Man and his Work.* London: Methuen Press.

Luyendijk-Elshout, A. M. (1998). Herman Boerhaave. *Journal of the History of the Neurosciences*, **7**: 52–4.

M. A. (anon) (1917). Sir William Turner. *Proceedings of the Royal Society of London Series B*, **89**: 622.

Magee, R. (2003). Sir William Turner and his studies on the mammalian placenta. *ANZ Journal of Surgery*, **73**: 449–52.

Major, R. H. (1954). *A History of Medicine*. Springfield, IL: Charles C. Thomas.

Morison, P. (1997). *J. T. Wilson and the Fraternity of Duckmaloi*. Amsterdam: Rodopi Press.

Munk, W. (1878). *The Role of the Royal College of Physicans of London*, Volume 3. London: Royal College of Physicians.

Nutton, V. (1997). The rise of medical humanism: Ferrara, 1464–1555. *Renaissance Studies*, **11**: 2–19.

O'Malley, C. D. (2008). Falloppio, Gabriele. In *Complete Dictionary of Scientific Biography*, Vol. 4. Detroit: Charles Scribner's Sons. pp. 519–21.

Paget, S. (1901). *Memoirs and Letters of Sir James Paget*, 2nd edn. London: Longmans, Green and Company.

Panckoucke, C. L. F. (1820–1822). *Dictionare des Sciences Medicales Biographie Medicale*. Paris: C.L.F. Panckoucke.

Partington, J. R. (1961). *A History of Chemistry.* Volume 2. New York: St. Martins Press.

Pepe, L. (1986). Scienziati e stabilimenti scientifici a Ferrara. *Museologia Scientifica*, **3**:113–19.

Portmann, M.-L. (1988). Theodor Zwinger (1533–1588), ein Basler Humanistenarzt. *Schweizerische Rundschau fur Medizin Praxis*, **77**: 1110–13.

Rees, N. (2006). *Brewer's Famous Quotations*. London: Weidenfeld and Nicolson.

Roberts, S. (1989). *Sir James Paget: the Rise of Clinical Surgery*. London: Royal Society of Medicine.

Royal College of Physicians (2006a). *A biography of Sir James Paget*. Published online at www.aim25.ac.uk: The National Archives.

(2006b). *Latham, Peter Mere (1789–1875)*. Published online at www.aim25.ac.uk: The National Archives.

(2006c). *A Biography of Thomas Bateman.* Published online at www.aim25.ac.uk: The National Archives.
Rumsey, J. (1827). *Some Account of the Life and Character of the Late Thomas Bateman*. London: Longman, Rees, Orme, Brown and Green.
Sanchez, O. F. (2009). Curiosidades en Medicina: Gabrielle Falloppio. *Revisita Medica de Rosario*, **75**:112–13.
Sharma, O. P. (1983). Robert Willan remembered. *Journal of the American Academy of Dermatology*, **9**: 971–6.
Smith, S. A. (1950). The life and work of James Thomas Wilson. *Bulletin of the Post-Graduate Committee in Medicine, University of Sydney*, **6**: 1–12.
Spaulding, W. B. (1971). Peter Mere Latham (1789–1875): a great medical educator. *Canadian Medical Association Journal*, **104**: 1109–14.
Sperber, G. H. (1990). *From Apes to Angels: Essays in Anthropology in Honor of Phillip V. Tobias.* New York: Wiley-Liss.
Thomson, J. (1832). *Account of the Life, Lectures, and Writings of William Cullen.* Volume 1. Edinburgh: Blackwood Press.
Thorndike, L. (1941). *A History of Magic and Experimental Science, VI*. New York: MacMillan.
Tobias, P. V. (1984). *Dart, Taung, and the Missing Link: An Essay on the Life and Work of Emeritus Professor Raymond Dart, Based on a Tribute to Professor Dart on His 90th Birthday, Delivered at the University of the Witwatersrand, Johannesburg, on 22 June 1983*. Johannesburg: Witwatersrand University Press.
(1989). Dart, Raymond Arthur (1893–1988). *Nature*, **337**: 211.
(2005). *Into the Past: A Memoir*. Johannesburg: Picador Africa.
Underwood, E. A. (1972). Fransciscus Sylvius and his Iatrochemical School. *Endeavor*, **31**: 73–6.
(1977). *Boerhaave's Men at Leyden and After*. Edinburgh: Edinburgh University Press.
van Gijn, J. (2001). Franciscus Sylvius (1614–1672). *Journal of Neurology*, **248**: 915–16.
Walsh, J. J. (1913). Fallopio, Gabriello, anatomist. In Herbermann, C. G., Pace, E. A., Pallen, C. B., Shahan, T. J. and Wynne, J. J. (eds.), *The Catholic Encyclopedia: An International Work of Reference on the Constitution, Doctrine, Discipline, and History of the Catholic Church*. New York: The Encyclopedia Press, p. 722.
Wheelhouse, F. (1983). *Raymond Arthur Dart*. Sydney: Transpareon Press.
Wheelhouse, F. and Smithford, K. S. (2001). *Dart: Scientist and Man of Grit*. Sydney: Transpareon Press.
Wightman, W. P. D. (1955). William Cullen and the teaching of Chemistry. *Annals of Science* **11**: 154–65.
Wilson, J. T. (1938). Sir Grafton Elliot Smith (1871–1937). *Obituary Notices of the Fellows of the Royal Society*, **2**: 322–33.
Zedelmaier, H. (2008). Navigieren im Text-Universum. Theodor Zwingers *Theatrum Vitae Humanae*. *Metaphorik*, **14**: 113–35.