

HUMAN EVOLUTION FROM AN
AFRICAN PERSPECTIVE

WITH REFERENCE TO CHARLES DARWIN PALAEOCLIMATE
AND THE PROBLEM OF DEFINING A SPECIES

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(1868-1945)

INTRODUCTION

In 1836, Charles Darwin visited South Africa during his travels around the world on the ship called *The Beagle*. In 1837 he was already thinking about evolutionary development. He chose to use barnacles to study the concept of species, but realized that boundaries between species were not clear. This problem was expressed in two substantial volumes on barnacles published in 1851 and 1854. There were several reasons why Darwin (1859) delayed the publication of *The Origin of Species*, in which he recognized the need to quantify the “amount” of difference when species are considered. One way to assess the degree of difference between specimens is to use least squares linear regression analysis of measurements of pairs of specimens. This approach can lead to a statistical (probabilistic) definition of a species, and is useful for assessing the degree of difference between hominid specimens from Africa, recognizing that there is no clear boundary between *Australopithecus* and *Homo* in the context of palaeoclimatic change between about 1.8 and 2.5 million years ago.

CHARLES DARWIN

Charles Darwin was born just over 200 years ago in England. His connections with South Africa began at an early age, because there is a famous portrait of him, painted when he was only seven years old. He is shown holding a flower pot, which was part of his father’s collection of plants from around the world. This particular plant held by the young Darwin has recently been identified as *Lachenalia*, the Cape Cowslip, a plant which is part of the South African Fynbos Floral Kingdom.

As a young man, after a spell at Edinburgh University in Scotland, and at Cambridge University in England, Charles Darwin boarded *The Beagle* and sailed around the world in five years. He was appointed as a naturalist, and collected animals, plants and fossils from many countries. It is not commonly known that



Fig. 1 Charles Darwin, aged 7, with a pot in which Lachenalia from South Africa is growing. Drawn by Rolinda Sharples. Wikipedia.

Darwin visited South Africa for three weeks in the Cape winter of 1836. The Beagle docked at Simonstown, and almost immediately Darwin set off by horse to explore the Cape Flats. What he saw was seemingly boring sandy veld, with very little in the way of big animals.

Previously Dutch explorers, who had visited South Africa in the 17th century, had described African animals in dramatic ways. For example, J.G. Gravenbroek gave the following account in 1695:

“The number of animals here, on earth and in air and in water, is so prodigious that it is like living in a zoo. As a rule, the genera of these animals each split up into four or more species, and I am astonished to perceive that these are for the most part unknown to the Europeans and unrecognized by the naturalists. I do not want to suppose that I am straying from the truth”.

Gravenbroek (1695) was right in stating that some of the animals were new to European naturalists. For example, in parts of South Africa there were extensive herds of *Equus quagga*, partially striped zebras, as well as the “blaaubok”, *Hippotragus leucophaeus*, with long curved horns. The quagga and the blaaubok became extinct in historic times, but fortunately there are mounted skins of these animals in the excellent Naturalis Museum in Leiden in The Netherlands.

When Darwin travelled across the sandy Cape Flats a short distance from Cape Town, without going into the interior of the country, he was not impressed. He wrote in his diary:

“I never saw a much less interesting country”.

However, he returned to Cape Town and met Adam Smith, a naturalist who was familiar with the large herds of animals that could be seen if one travelled over the Hottentot's-Holland mountains beyond the Cape Flats. Smith reported that there were great herds of wildebeest, hartebeest, springbok, quagga, eland as



Fig. 2. (a) Marechal's drawing of the partially striped zebra, Equus quagga (above), and (b) La Vaillant's painting of the "Blaauwbok", Hippotragus leucophaeus (below). Wikipedia.

well as rhinoceros, elephants, lions and leopards on the other side of the mountains.

Darwin's departure from Cape Town was delayed because of winter, and during the time while he was obliged to stay in the

Cape, he continued to write chapters for his book called *Voyages of the Beagle*. In this book he completely changed his initial views about South Africa and its fauna. Instead of saying that it was an uninteresting country, he stated that "with regard to the number of large quadrupeds, there certainly exists no quarter of the globe which will bear comparison with southern Africa" He was referring to the kind of evidence presented to him by explorers such as Adam Smith from England, and J.G. Gravenbroek from Holland, who had described large herds of wild animals in the interior of South Africa.

While in the Cape in 1836, Darwin met scientists such as the astronomer John Herschel, who had an interest in botany as well as in astronomy. As Professor Brian Warner (University of Cape Town) has recognized, it is probable that when Darwin and Herschel met in South Africa, both of them were beginning to think about long term changes through evolutionary time. In the case of stars, it was Herschel who had seen that certain stars change in brightness in the course of their evolution. In fact, in 1836, a star called Eta Carinae essentially exploded and became one of the brightest stars in the southern sky. This was a supernova, going through a dramatic part of its stellar evolution. Eta Carinae continues to show changes in brightness, and may explode again in the near future. Astronomers in the southern hemisphere are monitoring its evolution even today, using telescopes such as the Southern African Large Telescope (SALT) which is situated at Sutherland in the Cape Karoo, where the night sky is exceptionally clear and brilliant.

Herschel had a collection of Cape bulbs from the Fynbos, and he wondered about the diversity that could be seen in their spatial distribution. Both Darwin and Herschel appreciated that the granitic rocks at Paarl or at Sea Point near Cape Town must have related to geological changes through long periods of time. Thus Darwin and Herschel were interested in the process of evolutionary change, going back more than the biblical 6,000 years suggested by Bishop Ussher in about 1600 AD. Both Darwin and

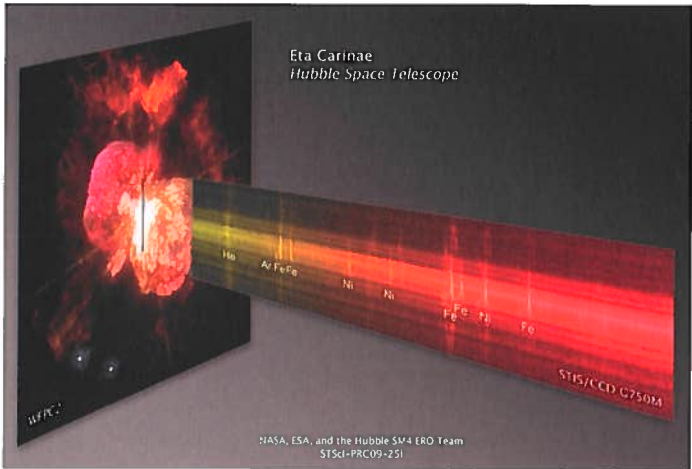


Fig. 3. Image of a supernova, an exploding star called Eta Carinae, with a spectrum showing its chemical composition (Hubble Space Telescope, NASA, ESA). Darwin would have seen this star when it exploded in 1836 when he was in Cape Town where he met the astronomer John Herschel.

Herschel referred to the evolutionary process as “The mystery of mysteries”.

Darwin returned to England after his visit to South Africa in 1836. In 1837, in one of his notebooks, there is a sketch of his first evolutionary tree, referring to the evolution of genera and the emergence of distinct species, A, B, C and D, differing in their degree of proximity on the evolutionary tree. I have had the privilege of seeing this drawing when it was on display at the Natural History Museum in London at the time of the bicentennial anniversary of Darwin’s birth. The notebook was exhibited together with objects that Darwin had collected from many parts of the world, including insects from South Africa. When I saw the notebook and its evolutionary tree, I was emotionally moved. Scientists have feelings.

Darwin had had the opportunity to see the great diversity of living plants and animals across the world. Before Darwin published *The Origin of Species* in 1859, he spent a great deal of time studying barnacles, to test the concept of a species. He described many of these animals (arthropods with calcareous shells) in two substantial volumes in 1851 and 1854. But he encountered a problem. He realized that as the number of his barnacle specimens increased in his collections, the very boundaries between species began to break down. It was initially easy to distinguish between a specimen of Species A from a specimen of species B, but as he began to increase the numbers of specimens of species A and B, the boundaries between the two species began to become blurred, to the extent that he experienced great difficulty in classifying barnacle species. He is known to have torn up pages of the barnacle books before they were eventually published in 1851 and 1854. The main problem was that he was forced to think about variation within a species ("varieties" of a species). This is very interesting, because it relates to the kind of problem that we have now, when more and more hominid fossils such as *Australopithecus africanus*, or early *Homo*, are discovered in the Cradle of Humankind and elsewhere in Africa.

Darwin spent many years delaying the publication of *The Origin of Species*. I suspect that one of the reasons for this related to his difficulty in recognizing clear boundaries between species. But he was encouraged to get down to writing by an old Scottish woman, Jessie Brodie, who served as the nurse for Charles Darwin's young children. Brodie had formerly been the nurse for William Makepeace Thackeray, the novelist who wrote *Vanity Fair* and other novels, in installments. William Thackeray always had to complete each installment on time, and Jessie Brodie was evidently impressed by Thackeray's sense of urgency and the importance of meeting deadlines. When Jessie Brodie moved to the Darwin family, she scolded Charles Darwin for not progressing faster with his writing. She told Darwin: "I wish you would do what Mr Thackeray does, and get down to the writing". So perhaps it was partly thanks to the nurse that Darwin eventually completed *The*

Origin of Species in 1859, spurred on of course by the independent recognition of evolution as a process by Alfred Russell Wallace.

Charles Darwin makes almost no reference to human evolution in *The Origin of Species*, except to mention that “new light will be shed on the origin of man”. Later, in 1871, he dared to write a book called *The Descent of Man*. In this book he recognizes Africa as the continent from which humanity evolved. However, this conclusion was not based on fossils. Instead it was based on comparative anatomy. He had looked at the skeletons of chimpanzees, gorillas, humans, monkeys and a great diversity of living primates. He recognized that of all the living primates, it was the chimp and the gorilla that were most similar in terms of anatomy. He went further to recognize that chimps and gorilla are distributed only in Africa. On this basis he suggested, very cautiously, that the “progenitors” for humans must have had an African origin. His view was that living chimps and humans must have had a common ancestor that lived in Africa, some time ago.

Hominid fossils from Africa

Fossils from Africa have indeed confirmed Darwin's views on human evolution. In 1925, Professor Raymond Dart described a new primate species as *Australopithecus africanus*. This description was based on the discovery of the so-called Taung Child from the site of Buxton in the North West Province. The fossil is about 2.5 million years old, from the late Pliocene. More australopithecine fossils were discovered in the Cradle of Humankind (Broom, 1938; Broom and Robinson, 1949, 1950; Broom and Schepers, 1946).

Dart claimed that the Taung Child was a distant relative of all humanity, in line with Darwin's prediction that Africa was the Cradle of Humankind. Dart was an anatomist at the University of the Witwatersrand, and his description of the Taung Child made both the University and himself world famous.



*Fig. 4. The “Taung Child”, the type specimen of *Australopithecus africanus*, from South Africa, described by Raymond Dart (1925). University of the Witwatersrand.*

Additional fossils from the Cradle of Humankind (Fig. 5) have been found by other scientists associated with Wits University. Ron Clarke (1998), Nkwane Molefe and Stephen Motsumi all contributed to the discovery of the skeleton nicknamed “Little Foot”, an extraordinary australopithecine fossil that may be as old



Fig. 5. Map of southern Africa, showing the Cradle of Humankind world heritage sites, including Taung, Makapansgat as well as Sterkfontein and other caves near Pretoria and Johannesburg.



Fig. 6. Professor Ron Clarke with the fossil of "Little Foot", a skeleton of a species of Australopithecus. Photograph by Francis Thackeray, University of the Witwatersrand.

as 3 million years old, from Sterkfontein, where the late Professor Phillip Tobias directed excavations for many years since 1966.

Professor Lee Berger (2010) and his team have found two extraordinary hominid skeletons, about 2 million years old, from the site of Malapa in the Cradle of Humankind.

Dr Bob Brain has discovered many hominid fossils from the cave of Swartkrans, together with evidence for the controlled use of fire, more than one million years ago (Brain and Sillen, 1988).

With a French team (including Jose Braga, Dominique Gommery, Frank Senegas, Sandrine Prat and Vincent Balter), and with scientists from the Ditsong National Museum of Natural History (formerly Transvaal Museum, including Lazarus Kgasi, Stephany Potze and the late Lawrence Radebe), Francis Thackeray has found fossils from Bolts Farm (including a site 4 – 4.5 million



Fig. 7. The skull of *Australopithecus sediba*, part of a skeleton discovered by Professor Lee Berger and his son Matthew at the site of Malapa in the Cradle of Humankind, South Africa. University of the Witwatersrand.

years old) and fossils of early *Homo* and *Paranthropus robustus* from Kromdraai (between 1.5 and 2 million years old) adjacent Sterkfontein in the Cradle of Humankind World Heritage Site.

Piltdown

The hominid fossils from the Cradle of Humankind confirm Darwin's view that Africa is the continent from which humanity evolved. However, when we look at the history of palaeoanthropology, we recognize that there was a serious problem that emerged with the announcement of a curious fossil from England in 1912, from a site called Piltdown in Sussex. Almost exactly a century ago, the British Museum of Natural History announced what they considered to be an important fossil that related to human evolution in the Pleistocene. The fossil was called *Eoanthropus* ("Early Man" or "Dawn Man"). It was announced with

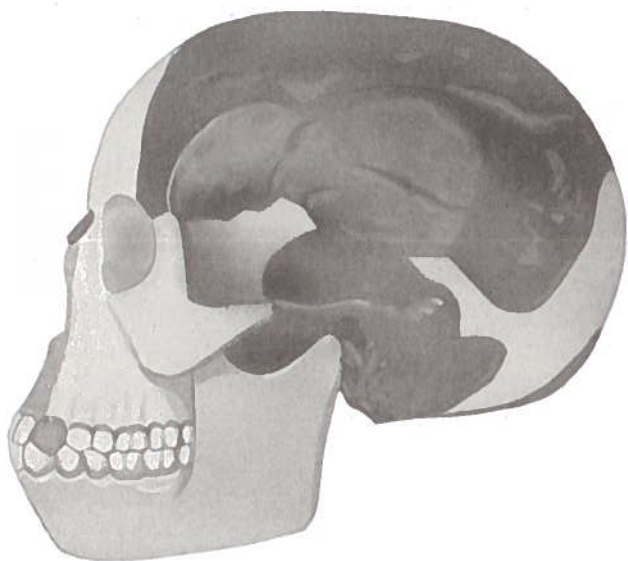


Fig. 8. A reconstruction of "Piltdown Man", including a human skull and a jaw of an ape. Wikipedia.

great fanfare at Burlington House in London, and was accepted as an extraordinary fossil that showed an apparent combination of features of apes and humans, in one individual. The jaw looked ape-like, but the skull looked human. The skull was found with artefacts and fossils that dated to the Pleistocene, indicating an apparent age of at least one million years for the skull and jaw.

100 years ago, most palaeontologists accepted the discovery of Piltdown Man but many scientists were puzzled by the fact that it did not fit in comfortably with discoveries of other fossils, such as "*Sinanthropus*" or *Homo erectus* studied by, among others, Gustav Heinrich Ralph von Koenigswald, who spent many years in The Netherlands after discovering hominid fossils in Java. A specimen of *Homo erectus* is to this day curated at the Naturalis Museum in Leiden.



Fig. 9. Gustav Heinrich Ralph von Koenigswald with a specimen of Homo erectus. Wikipedia.

We now recognize that Piltdown Man was actually a hoax or joke. It had the jaw of an orangutan, combined with a human skull, and both had been stained brown to make them look old. The hoax was not revealed until about 1953 when Dr Joe Weiner, a South African anatomist, as well as Dr Kenneth Oakley, a British chemist, recognized a forgery. The mystery is that we don't know exactly who was involved in the joke or hoax.

Within the last 60 years, the Piltdown investigation has continued. Many people think that a local Sussex lawyer, Charles Dawson, was the prime suspect. Other people have suspected Sir Arthur Keith and Sir Grafton Eliot Smith, famous anatomists who were interested in human evolution. Others have suspected Martin Hinton, an assistant at the British Museum of Natural History. Remarkably even Sir Arthur Conan Doyle has been sus-

pected. Conan Doyle was of course the author who created the character of Sherlock Holmes, but not many people today regard Doyle as a likely suspect.

There is one individual whom I have been investigating with a great deal of interest. His name is Pierre Teilhard de Chardin, a French Jesuit priest, philosopher and palaeontologist. He was based in Sussex for four years, between 1908 and 1912, during which time he was trained as a Jesuit priest at a seminary not very far from the site of Piltown. He was allowed to collect fossils in his spare time, and was invited to participate in excavations at Piltown after human remains had been discovered.

Piltown Man was officially announced on December 18, 1912, in London. By that time Teilhard de Chardin was back in Paris, ready to begin studies in palaeontology with Professor Marcellin Boule at the Institute for Human Palaeontology. In Paris Teilhard learnt that English palaeontologists had accepted Piltown Man as a genuine fossil. Perhaps he was horrified, because on January 1st 1913, he immediately wrote from Paris to his friend Felix Pel-

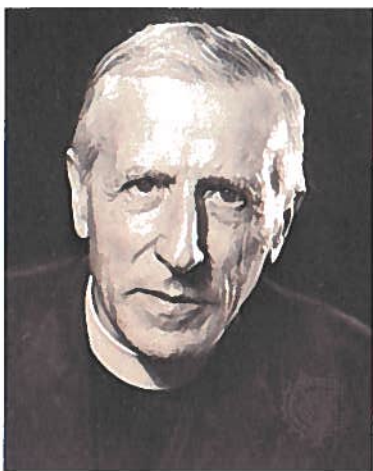


Fig. 10. Pierre Teilhard de Chardin, a French palaeontologist and Jesuit priest. He was based in Sussex in England between the years 1908 – 1912, during which time fossils were discovered at Piltown. Teilhard discovered the canine of “Piltown Man” in August 1913. The canine was painted a Van Dyke brown. Teilhard was perhaps part of a “Piltown joke”. Wikipedia.

letier, with whom he had collected fossils in Sussex. He wrote to Felix saying “We must wait for the criticisms that will follow”. He went on to say that his French supervisor, Marcellin Boule, would not be easily “taken in – especially if the finds are English”.

In my investigations (Thackeray, 2011, 2012), I have found that Teilhard de Chardin then wrote an essay on the current understanding of human evolution in Europe. The essay is dated January 5th 1913. The essay refers to the work published by Professor Hugo Obermaier, a respected German palaeoscientist who was temporarily based in Paris, at the Institute for Human Palaeontology, together with Professor Marcellin Boule. But remarkably, Teilhard de Chardin makes absolutely no mention of Piltdown at all in his essay on European prehistory. This is extraordinary, especially as he certainly knew of the recent announcement (December 18, 1912) of Piltdown Man as a new species from Sussex in England.

If we look at the first sentence of his essay, we become even more suspicious. Teilhard writes “Palaeontology deserved to be suspect, and Palaeontology deserved to be the subject of jokes”. This is very suspicious, especially since I know from the late Professor Phillip Tobias that Teilhard de Chardin was “something of a joker”.

I have learnt something else that is very interesting: among Jesuits, it was allowed to lie, providing it was a joke. Perhaps Teilhard de Chardin was part of a Piltdown joke, one that went seriously wrong (Thackeray, 2012).

There is another item of interest that makes one suspicious of Teilhard de Chardin. It is the fact that in August 1913, he was invited back to Piltdown to continue excavations. He came over from France, and remarkably found a canine tooth of so-called “Piltdown Man” in an area that had already been thoroughly searched. There was something different about this tooth. It was painted a reddish-brown, apparently Van Dyke brown. I suspect that Teilhard had actually wanted the English palaeontologists to

recognize the tooth as a joke. But the British scientists were taken in, even though the canine tooth was painted a reddish brown, as if to speak from the grave, to say “Look, *voilà*, this is not a real fossil, the whole thing is a joke, and it must stop immediately”. But instead, Smith Woodward, an expert on fossil fish at the British Museum, accepted the Piltdown tooth as genuine.

Thereafter, Teilhard de Chardin said very little if anything about Piltdown Man.

In my investigations, I have discovered that before he died, Teilhard wrote a letter about Piltdown, and deposited the letter in a bank with instructions that it should be opened after he had died, and only after others associated with Piltdown were also dead. Unfortunately we have not been able to find Teilhard’s letter (Thackeray, 2012).

In searching for Teilhard’s letter, which may have been a confession after his death, I have discovered that his bank details were destroyed after his death. Perhaps that letter is still sitting a bank somewhere in France or New York, or even in the Vatican, waiting to be opened.

The Piltdown case was an unfortunate incident in the history of palaeoanthropology, adversely affecting the acceptance of the discovery of the Taung Child (*Australopithecus africanus*) from South Africa, described by Raymond Dart in 1925. It also adversely affected the acceptance of the discovery of small-brained fossils from Kromdraai and Sterkfontein, as well as elsewhere. But the science of anthropology, of the kind involved with Lee Berger’s discovery of *Australopithecus sediba*, and Ron Clarke’s Little Foot, is sufficiently strong today that we can be assured that there never will be another Piltdown, and we can rest assured that Darwin was right in indicating that Africa is the Cradle of Humankind. The Cradle certainly never was at Piltdown in Sussex. Perhaps Teilhard de Chardin continues to laugh in his grave, about a joke that was eventually exposed.

HOMINID TAXONOMY

Hominid fossils have been found not only in South Africa but also in East Africa. Leakey et al. (2012) describe three new early Pleistocene hominin fossils from Koobi Fora in Kenya. Wood (2012) uses the word “compelling” to refer to evidence for at least two species of the genus *Homo* in the period between 1.8 and 2 million years ago (Mya). Such specimens may be classified by some as *H. habilis* and *H. rudolfensis*. However, Leakey et al (2012) and Wood (2012) focus on East African specimens without taking into account complexity when South African specimens are also assessed, including material from the sites of Sterkfontein, Swartkrans and Kromdraai where both early *Homo* and *Paranthropus* (a robust australopithecine) are represented in pene-contemporary deposits.

Leakey et al. (2012, supplementary material, page 1) admit that *Paranthropus* “largely overlaps with early *Homo* in temporal and geographic distribution, and distinguishing the two genera is not always equivocal”. Indeed, it should be noted that mesiodistal (MD) length relative to buccolingual (BL) diameter of the lower M1 of the new hominin specimen KNM-ER 60000 is similar not only to that of OH 7 (type specimen of *Homo habilis*) from Olduvai Gorge in Tanzania, but also to that of the type specimen of *Paranthropus robustus* (TM 1517) from Kromdraai in South Africa.

Other examples of similarity between specimens attributed to early *Homo* and *Paranthropus* are the following. In mid-sagittal plane, the inner cranial wall of KNM-ER 1470 (attributed by some to *H. rudolfensis* or *H. habilis*) matches very closely the outer mid-sagittal contour of a natural endocast of *P. robustus* (SK 1585) from Swartkrans in South Africa (Fig. 11). In addition, the dental arcade of SK 83 (attributed to *P. robustus*) matches that of KNM-ER 1470 (Fig. 11), and both have broad flat faces like robust australopithecines (Thackeray, 2001). Furthermore, the mean MD length of first lower molars attributed to *H. rudolfensis* is 14.4 +/- 0.8 mm (n=5), which corresponds closely to the MD

Photo: Francis Thackeray

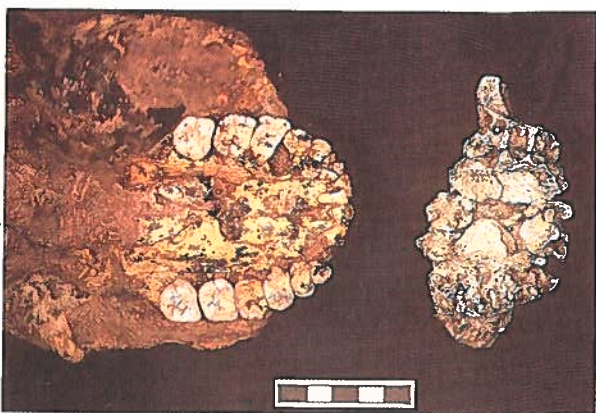


Photo: Francis Thackeray

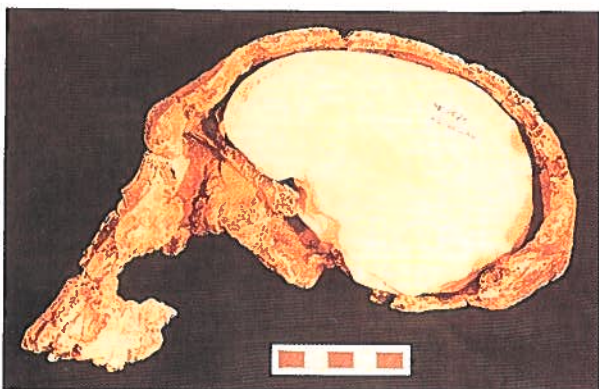


Fig. 11 (a) Upper photograph (left) show the maxilla of SK 83 (attributed to *Paranthropus robustus* from Swartkrans, South Africa), compared to (upper right) a cast of the maxilla of KNM-ER 1470 (attributed to *Homo rudolfensis* from East Turkana, Kenya). The two maxillae reflect similar size and shape of the maxillary tooth rows. (b) Replica of the right side of the cranium of KNM-ER 1470 (attributed to *Homo rudolfensis*), comfortably enclosing the white endocast (brain impression) of a specimen from Swartkrans in South Africa (SK 1585) attributed to *Paranthropus robustus*. (Thackeray, 2001, p. 107).

length of lower first lower molars for *P. robustus* (mean MD length = 14.7 +/- 0.7 mm, n=31; Thackeray et al, 2005).

The coefficient of variation for cranial capacities of “robust” australopithecines is unusually small. The question arises as to whether some specimens attributed to *Paranthropus* (including SK 83), and some specimens attributed to early *Homo* (including KNM-1470 and KNM-ER 62000), are conspecific, belonging to a taxon in which cranial capacities range from about 500 to 800 cc. If this is the case, perhaps KNM-ER 1470 and SK 83 could be seen as conspecific male hominids, differing in cranial capacity, with KNM-ER1470 having a sufficiently large cranial capacity to preclude the need for a sagittal crest, contrasting with SK 83, a male hominid having a smaller cranial capacity and requiring a sagittal crest to increase the surface area for the attachment of temporalis muscles. KNM-ER 62000 might be seen as a smaller (female) specimen of the same species.

In terms of lower first molar MD/BL diameter ratios, the differences between some “robust” australopithecines and some specimens of early *Homo* are comparable to the differences in these ratios found for male and female specimens of modern *H. sapiens* (Thackeray et al., 2005). The question that arises from this observation is whether sexual dimorphism accounts to some extent for differences in at least some specimens attributed to early *Homo* and *Paranthropus*.

The discovery of three new early Pleistocene African hominins (Leakey et al., 2012) confirms the fact that there are not necessarily clear boundaries between early Pleistocene hominid taxa, at the genus or species level. As in the case of Darwin’s studies of barnacles (Thackeray, 2001), the limits between taxa become blurred as sample sizes increase.

Darwin (1859) emphasized the need to quantify the “amount” of variability in a species. This has been attempted in the context of a statistical (probabilistic) definition of a species (Thackeray,

2007), using an approach which has been applied to early Pleistocene hominids from both East and South Africa, leading to the recognition of a spectrum of diversity in hominids attributed to early *Homo*, *Paranthropus* and *Australopithecus* within the period between about 1.8 and 2.5 Mya, changing in ecological space and evolutionary time, associated with the concept of “palaeospectroscopy” (Thackeray and Odes, in press).

In view of the lack of consensus regarding the taxonomy and phylogeny of specimens attributed to hominid genera, there clearly is a need for a species definition that can be applied in palaeontological contexts. Thackeray’s (2007) statistical (probabilistic) definition of a species is based on least squares linear regression analysis of pairs of modern specimens of the same species, and is outlined below.

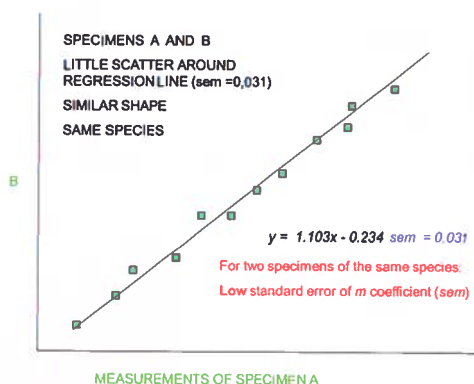


Fig. 12 Pair-wise comparison of measurements obtained from skulls of two specimens of the same species. There is little scatter around the regression line of the form $y = mx + c$ where m is the slope of the regression line obtained from least squares linear regression analysis. The standard error of the slope is designated se_m . A low se_m value is associated with similarity in shape between the two specimens of the same species.

A statistical (probabilistic) definition of a species (Thackeray, 2007) is associated with the degree of scatter around the regression line, quantifiable by means of the se_m statistic which is the standard error the m -coefficient related to equations of the form $y = mx + c$ (Fig. 12). In the case of many pair-wise comparisons of measurements obtained from extant vertebrate (mammals, birds, reptiles) and invertebrate (Lepidoptera and Coleoptera) species, it has been found that log transformed se_m statistics display a normal distribution (Thackeray, 1997; Thackeray et al, 1997; Aiello et al, 2000), now known to show central tendency around a mean value of -1.61 (± 0.23 , $n=1424$ specimens) (Thackeray, 2007) (Fig. 13). It has been suggested that the value of -1.61 approximates a biological species constant (T) for species across evolutionary time and geographical space (Thackeray, 2007). The standard deviation (± 0.23) around the mean value of -1.61

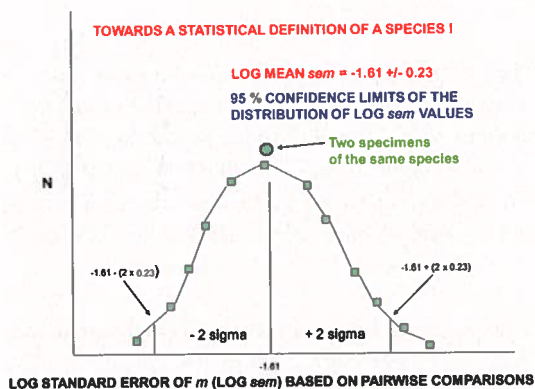


Fig 13. A log-normal distribution of the standard error of the m coefficient (se_m), obtained from pair-wise comparisons of specimens of extant vertebrate and invertebrate species. The mean $\log se_m$ value of -1.61 (± 0.23) constitutes a statistical (probabilistic) definition of a species (Thackeray, 2007).

allows one to make comparisons with data obtained from fossil hominid specimens.

Log se_m statistics have been obtained from early Pleistocene adult hominid specimens in order to try to identify patterns in the degree of similarity between specimens. For example, measurements of hominid crania published by Wood (1991) and Berger et al (2010) are used for purposes of least squares linear regression analysis in pair-wise comparisons. A low degree of scatter around a regression line, associated with the general equation $y = mx + c$, reflects a high degree of morphological similarity between pairs of specimens. The degree of scatter, quantified in terms of the standard error of the m coefficient (se_m), reflects variability in shape, whereas the m -coefficient is a reflection of size. This technique has been applied to extinct hominin specimens attributed to *Australopithecus africanus*, *A. sediba*, *Homo habilis*, *H. rudolfensis*, *H. erectus* or *H. ergaster* as well as to robust australopithecines *Paranthropus boisei* and *Paranthropus boisei*.

A list of hominid cranial specimens included in this study is given in Fig. 14 which is a matrix of log se_m values obtained from pairwise comparisons of these specimens. The results, reflecting degrees of similarity in shape and controlling for variability in size, are colour-coded in a spectrum such that red reflects a high degree of similarity, whereas violet reflects a low degree of similarity between specimens.

The highest degrees of similarity are obtained for comparisons between KNM-ER 1813 and KNM-ER 3733, despite the fact these specimens have been attributed to *H. habilis* and *H. ergaster*, respectively. High degrees of similarity are also obtained between KNM-ER 1813 and KNM-ER 1470. The latter has been attributed to *Homo rudolfensis*.

Sts 5 ("Mrs Ples"), a cranium from Sterkfontein, represents *Australopithecus africanus*, a little over 2 million years old (Fig. 15). It was discovered by Robert Broom and John Robinson in 1947.

PAIR-WISE COMPARISON OF EARLY PLEISTOCENE FOSSILS

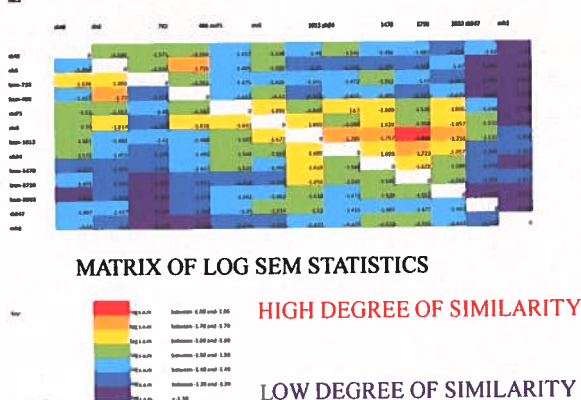


Fig.14 A matrix of $\log se_m$ statistics that reflect the degree of similarity between pairs of hominid specimens (Thackeray and Odes, 2012). The results are colour-coded to indicate high degrees of similarity (red and orange) through to lower degrees of similarity (violet).

Sts 71 is another cranium from Sterkfontein and was originally placed in the species *A. africanus*, but Prof Ron Clarke regards it as a different australopithecine species. Do the two specimens represent different species? This question can be addressed in the light of $\log se_m$ statistics. When the two specimens are compared, $\log se_m$ values are close to -1.6. In the light of these results, based on comparisons of more than 50 measurements, it can be concluded that Sts 5 and Sts 71 have a high probability of conspecificity, and may represent the same species, *A. africanus*. This conclusion differs from a previous result based on fewer numbers of measurements of the two crania.

Australopithecus sediba (Fig. 7) has recently been described as a new hominid species with Homo-like characters (Berger et al., 2010). The species is represented by two skeletons, MH1 and



*Fig.15. "Mrs Ples", a fossil from Sterkfontein, South Africa, classified as *Australopithecus africanus*, discovered by Robert Broom and John Robinson (Transvaal Museum) in 1947. Ditsong National Museum of Natural History, Pretoria.*

MH2, a little younger than 2 million years old (Mya) (Dirks et al., 2010; Pickering et al., 2011). In terms of log se_m statistics, MH1 (the type specimen of *A. sediba*) is different from other specimens, but is most similar to KNM-ER 3733, KNM-ER 1813 and OH 24 which have been placed in the genus *Homo* although KNM-ER 1813 and OH 24 have been considered by some to be better placed in *Australopithecus* (Wood and Collard, 1999). MH1, incorporating a mosaic of characters found in specimens attributed to *Australopithecus* and *Homo*, reflects the lack of a clear boundary between the two genera. If MH1 and MH2 were to be placed in a distinct hominin genus, one might consider *Australomo*, in the same way that *Velindastus* (including *V. thackerayi*) was described as a new coleopteran genus, intermediate between the genera *Velinda* and *Astastus* (Schule and Lorenz, 2008).

CLIMATIC CHANGE

It is essential to consider hominid evolution in the context of past changes in climate (notably temperature and rainfall), which affects changes in habitat, in turn contributing to changes in the distribution and abundance of animals (including hominids), leading in turn to changes in gene pools of populations, and thereby to anatomical variability in species. Changes in climate can be examined by using multivariate analysis (principal component or factor analysis) of relative abundance of fauna such as rodents and insectivores (Thackeray, 1987) or pollen spectra (Scott and Thackeray, 1987) or foraminifera (Imbrie and Kipp, 1971). Changes in palaeotemperature indices for southern Africa can be correlated with changes in temperature reflected by variation in deuterium isotope ratios in ice cores from Antarctica (Thackeray, 1990), and by variation in oxygen isotope data from deep sea cores (Shackleton 1995).

Coppens (1975, 1988), Brain (1981), Vrba (1976, 1995) and deMenocal (2004, 2011) have all recognized the importance of environmental change in relation to the origin of the genus *Homo*. One of the most important challenges in palaeo-environmental studies is not only the identification of climatic change, but also its quantification.

FACTOR ANALYSES AND QUANTIFICATION OF PAL- AEOCLIMATIC CHANGE

Three examples of factor analysis are given to demonstrate how climatic indices for temperature or other parameters can be quantified. The first is based on a multivariate analysis of a data matrix of percentages of a set of rodents and insectivores from the Late Pleistocene and Holocene sequences from southern Africa (Thackeray, 1987). The second is based on factor analysis of Late Quaternary pollen spectra from the site of Wonderkrater in the interior of South Africa (Scott and Thackeray, 1987). The third

is a factor analysis of a set of data of foraminiferal species from the Atlantic, including a Late Quaternary sequence (Thackeray, 1987; Imbrie and Kipp, 1971). The results of the three exploratory factor analyses have one striking thing in common. The first factor (F1, or Principal Component), which accounts for the greatest variance in all three examples, relates to a dichotomy between two sets of taxa: (a), those that have high loadings on F1 and which are today associated with warm local environments, and (b) those taxa that have low loadings on F1 and which are today associated with relatively cold or cool local environments. Thackeray (1987) demonstrated how the "Factor Loadings" for each species can be used to generate a temperature index for sequences through time, by summing the products of Factor Loadings for any species ($a_1, a_2, a_3 \dots a_n$) and the relative abundances of those species. The temperature indices are summary statistics (SS) based on Factor 1. These SSF1 temperatures indices can be expressed on an arbitrary scale between 0 (representing the coldest assemblage) and 100 (the warmest assemblage) in any sequence or set of assemblages.

In the case of the Late Quaternary rodents and insectivores from southern Africa, *Saccostomus campestris* (the pouched mouse) and *Crocidura hirta* (the lesser red musk shrew) are the species with the highest F1 loadings (represented today in relatively warm woodland savanna regions of the African subcontinent). By contrast, *Otomys saundersae* (Saunders' vlei rat) has the lowest loading on F1 and is today distributed only at extreme southerly latitudes and high altitudes (in the southern mountains of the Cape Fold Belt where it is able to tolerate cold conditions).

In the case of Late Quaternary pollen spectra from Wonderkrater in the interior of South Africa, the dichotomy on F1 relates to warm-temperature Combretaceae and Capparaceae having extreme loadings on the First Factor, in contrast to *Stoebe* and *Tulbaghia* types (today distributed primarily in cool environments at more southerly latitudes), with F1 loadings at the other extreme of this First Factor.

In the case of a Late Quaternary foraminiferal sequence from a Caribbean core VS 12-122 (Imbrie and Kipp, 1971), *Globorotalia menardii* has high loadings on F1, and this species is today distributed in warm equatorial regions of the Atlantic ocean. By contrast, *Globorotalia inflata* has low loadings on F1 and is today distributed in cold waters such as those of the Benguela current associated with upwelling from the Antarctic on the west coast of southern Africa (Thackeray, 1987).

An implication of these factor analyses (applied to Late Quaternary assemblages of rodents and insectivores from southern Africa; to Late Quaternary assemblages of pollen representing a diversity of plants in a southern African core from Wonderkrater; and to Late Quaternary foraminifera from an Atlantic core) is that temperature is probably one of the most important environmental variables (if not the most important variable) that influenced changes in the abundance of fauna or flora through evolutionary time in the Quaternary.

The factor analyses of Late Quaternary rodent and insectivore sequences from South Africa (Thackeray, 1987) also provide a moisture index (the Summary Statistic based on F3, or SSF3). The importance of the SSF3 moisture indices, in relation to the SSF1 temperature indices, is that there is not a linear relationship between temperature and moisture (*cf.* rainfall) indices for the Late Pleistocene and Holocene (Fig. 16).

From the factor analysis of mammalian microfauna from Late Quaternary sites in southern Africa, conditions were cold (SSF1 = 0 to 10) and dry (SSF3 = 0 to 25) about 18,000 years ago during the so-called "Last Glacial Maximum", to use an expression used for contemporary northern hemisphere climates. Around 40,000 years ago, parts of southern Africa were associated with cool and moist conditions (SSF1 *circa* 35, SSF3 *circa* 90), but in parts of the Holocene, notably in interior areas of South Africa, conditions were warm (SSF1 > 80) and dry (SSF3 < 20) (Thackeray, 1987).

Fig. 16 is based on factor analysis of Late Quaternary micromammalian assemblages from southern Africa, indicating that there is a positive correlation between SSF1 and SSF3 for cold to cool conditions (SSF1 > 0 but < 35), when SSF3 ranges between 0 (dry) to 100 (moist, with high rainfall). By contrast, there is a negative correlation between SSF1 and SSF3 for cool to warm conditions when SSF1 > 60 but < 100, and when SSF3 ranges between 0 (dry) to 90 (moist) (Thackeray, 1988).

An example of how summary statistics based on F1 can be used as temperature indices in southern Africa is given by Thackeray

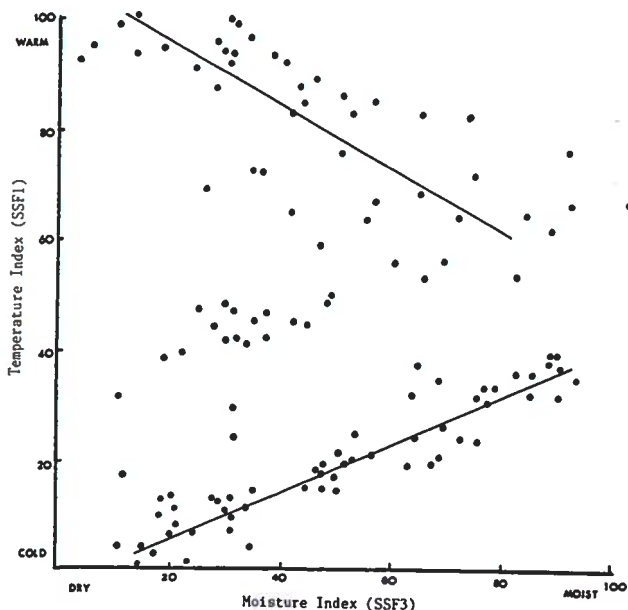


Fig. 16. Relationships between temperature (SSF1) and moisture (SSF3) indices generated from multivariate (factor) analysis of rodent and insectivore from Late Quaternary assemblages in southern Africa (Thackeray, 1988)

and Scott (2006) for the Wonderkrater Late Quaternary pollen sequence from about 16,000 BP to the present (Fig. 17). Temperatures rise after the period of the Last Glacial Maximum, as expected, but a cool episode occurs circa 12,000 BP. This is identified here with the “Younger Dryas” for the South African Wonderwerk sequence. A mid Holocene “hyperthermal” of warm conditions is dated between circa 7,000 and 9,000 years BP. This is when temperatures were warmer than present conditions, by at least one degree Celsius in terms of mean annual temperature (Thackeray, 1999). The warm Holocene interval at Wonderkrater appears to be correlated with dry conditions (Scott and Thackeray, 1987), corresponding to independent data from Wonderwerk cave (Thackeray, 1987).

Oxygen isotope data from foraminifera in marine cores (Shackleton, 1995) can be related to indices of ungulate biomass for periods within the last 3 million years in the interior of southern Africa (Thackeray and Reynolds, 1997). The ungulate biomass records can be associated with habitats, rainfall and mean annual temperature, based on modern African ecosystems (Thackeray,

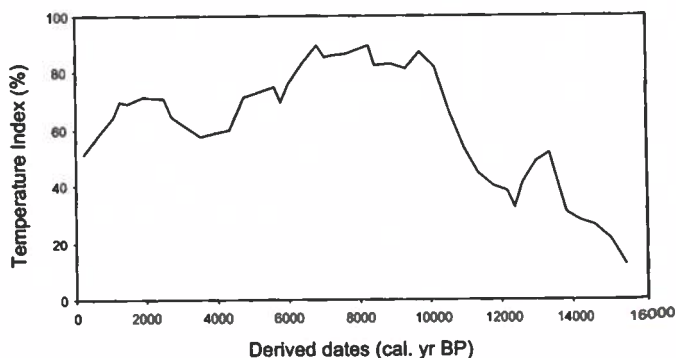


Fig. 17. Temperature indices for the Wonderkrater sequence in South Africa, based on Factor Analysis of Late Quaternary pollen spectra (Thackeray and Scott, 2006).

1995). High ungulate biomass is associated with mixed grassland savanna habitats, whereas low ungulate biomass is associated with forest or woodland environments. The changes through time (Fig. 18, based in part on oxygen isotope data) reflect variation in habitat, from forest or woodland circa 3 million years ago (corresponding to warm and wet conditions), to episodic changes between woodland savanna and more open grassland between 2.5 and 1.8 million years ago, when conditions became episodically cooler and drier. It is within the latter period that the genus *Homo* is thought to have originated.

General changes in temperature related to the transition between *Australopithecus* and *Homo* are shown in Fig. 19. A point to be made is that there is not necessarily a clear boundary between *Australopithecus* and *Homo* in response to changes in gene pools that

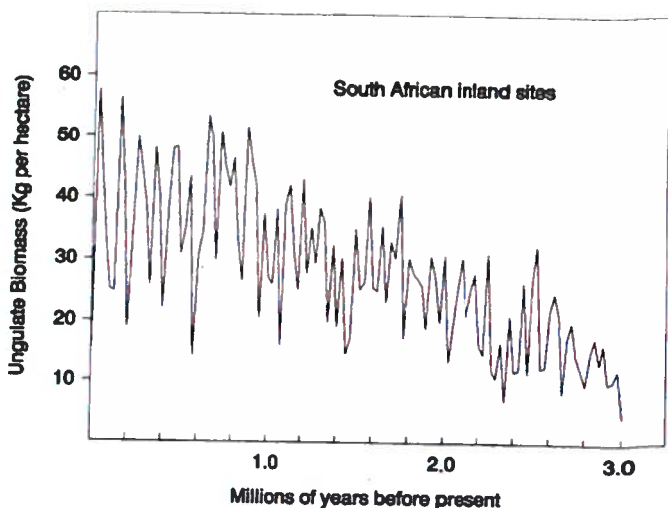


Fig. 18. Estimated ungulate biomass (kg per hectare) for interior regions of southern Africa. Fluctuations in ungulate biomass relate in part to changes in habitat, associated with variability in temperature and rainfall (Thackeray and Reynolds, 1997; Thackeray, 1995).

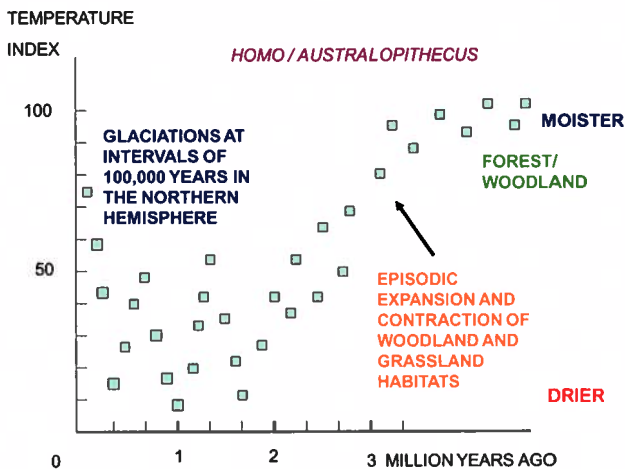


Fig. 19. A generalized graph of changes in palaeotemperature within the last 4 million years in southern Africa, affecting habitats, which in turn affect the distribution and abundance of animals (including hominids), thereby influencing gene pools which ultimately lead to variation in anatomy and the emergence of new species or genera. There is not necessarily a clear boundary between Australopithecus and Homo within the period between 1.8 and 2.5 million years ago.

are influenced by variation in habitats which are in turn affected by variation in temperature and rainfall.

CONCLUSION

The results of recent research (Thackeray and Odes, 2012) confirm that there are no clear boundaries between African early Pleistocene hominin species or even genera. In the context of these results, it is pertinent to quote Buffon (1749) who noted that variation may occur “from one species to another, and often from one genus to another, with imperceptible nuances” (p.150

of the first English translation of *Premier Discours of Histoire Naturelle*). Further, one may assess the results of this study in the context of a statement by Locke who stated the following in 1689: “The boundaries of the species, whereby men sort them, are made by men” (Locke’s Essay, Book III, part vi); see also Cain (1997).

Taken together, the data in the matrix presented in Fig. 14 can be regarded as a first attempt to address the concept of a chrono-species using $\log se_m$ values, recognizing that there are no clear boundaries between Early Pleistocene hominin taxa in the context of palaeoclimatic variation which affected habitats and the distribution and abundance of hominids and other fauna, in turn influencing gene pools and thus also anatomical (morphological) variability.

The morphometric approach outlined here can be regarded as “palaeo-spectroscopy”. I appeal for its application to address the problem of morphological changes through evolutionary time, associated with anagenesis, without relying strictly on the Linnaean binomial system of nomenclature.

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