

From *Purgatorius ceratops* to *Homo sapiens*

2. Human Evolution

Sindhu Radhakrishna

For establishing our bearings through time, we obviously owe an incalculable debt to vanished and endangered species...

John McPhee

The second part of this article on the evolution of the primate order, deals with the final part of the tale, that of the evolution of the human lineage. Before we launch into the origin and evolution of the human species, it is a useful exercise to take a brief look at what distinguishes humans from other primates. Most of the anatomical differences between humans and other primates are simply an extension of the morphological differences between primates and other mammals (see Part 1¹). For example, the trends towards increased brain size, delayed maturational periods and specialization of the hand for object manipulation, already present in non-human primates, reach the apex of development in modern humans.

Human Characteristics

In an interesting discussion on 'what makes us human?' Harvard anthropologist David Pilbeam points out some of the more distinctive characteristics that give us our unique stamp. To briefly enumerate, in terms of population size and distribution, human beings are found in virtually every environment on earth. Such an enormous range extension, in comparison to nonhuman primates, is due to the fact that human individuals carry a 'microenvironment' with them, in the form of clothes and shelters, wherever they travel. Another striking difference is that, compared to nonhuman primates, humans are a genetically uniform species. Even if all human populations, save one, went



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¹ Primate Evolutionary History, *Resonance*, Vol.11, No.7, 2006.

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Bipedal locomotion, increase in brain size and decrease in teeth, jaws and chewing muscles are some of the major anatomical distinctions between humans and other primates.

extinct, three-quarters of the total human genetic diversity would still be preserved. The human species is also distinctive in its eclectic feeding habits. Nonhuman primates do have fairly generalized diets in comparison to other mammals, but viewed against the omnivorous diets of human beings, their dietary preferences are specialized. Bipedal locomotion, increase in brain size and decrease in teeth, jaws and chewing muscles are some of the major anatomical distinctions between humans and other primates. Apart from these, humans are also marked by delayed life-history schedules, such as longer gestation periods, longer life spans, prolonged periods of infant dependency, delayed sexual maturation and longer post-reproductive phase. But the most distinctive characteristics of the human species are our dependence on material culture and the evolution of language. Language underlies and makes possible much of our social behaviour and interactions: “its most essential feature is that it allows human behaviour to be governed by the complex and subtle rules that together make up human culture”.

The anatomical and behavioural differences between humans and other primates are interesting, when analysed in retrospect, so to say, 100,000 years after the emergence of the first modern humans. Tracing the evolution of these differences as they slowly emerged over the years, offers a fascinating perspective into the forces of evolution and the adaptability of the primate order. Evolution of the human species passed through three main phases – the prehuman ape phase, the early hominid² phase and the emergence of the genus *Homo* (Figure 1).

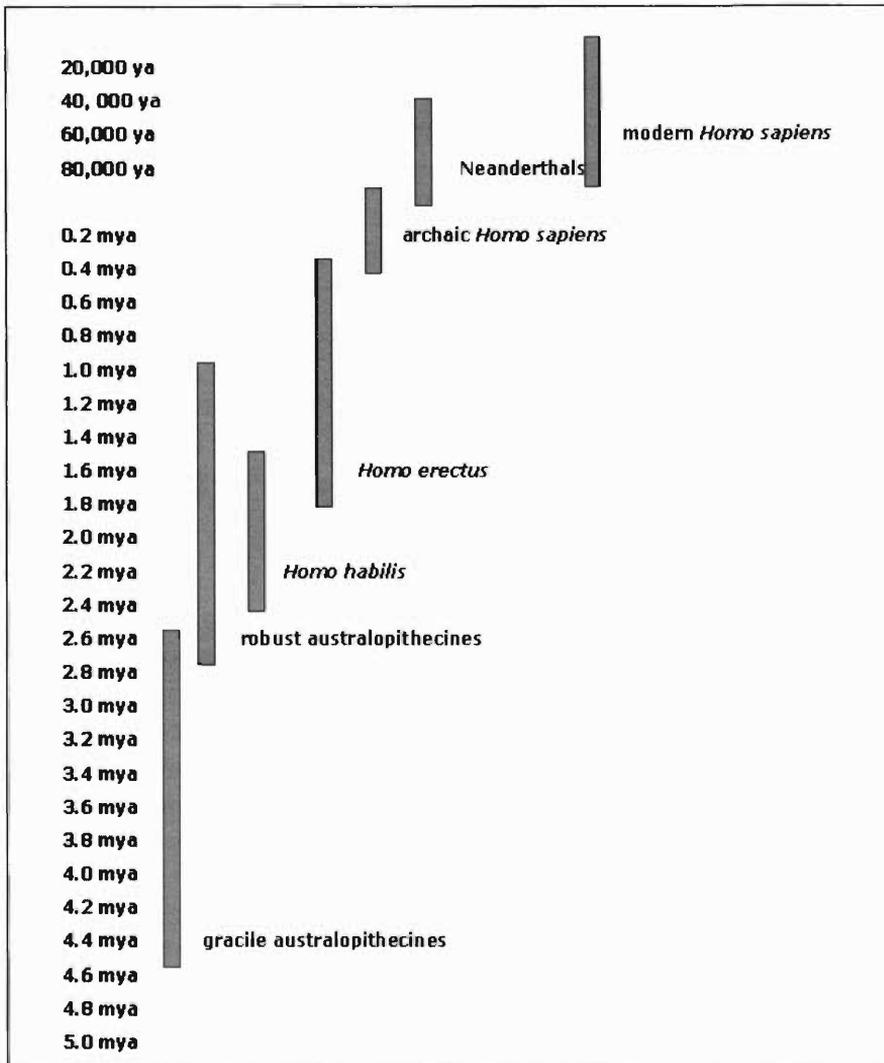
The Prehuman Apes

Although evolution of the human lineage occurred largely in the Pliocene (5 - 1.8 mya) and Pleistocene Epochs (1.8 -0.012 mya), it is in the fossils of the Miocene Epoch (22 - 5 mya) that we find the first signs of human origins. Three distinct groups of hominoids³ are recognised from this period – (i) dryomorphs, the early and middle Miocene hominoids of East Africa and Eurasia, characterised by thin enamel on the molar teeth ; (ii) ramamorphs,

² Lesser apes (gibbons and siamangs), great apes (orangutans, chimpanzees and gorillas) and humans

³ Humans and their immediate fossil relatives, but not living or fossil apes.





the middle Miocene hominoids of East Africa and Eurasia, with thickened enamel on the molar teeth and (iii) pliomorphs, early and middle Miocene hominoids of Eurasia that share many primitive catarrhine features. Early Miocene hominoid fossils show a mosaic of monkey-like and ape-like morphological features. As a group, early Miocene hominoid forms can be clearly distinguished from middle Miocene hominoid forms, and it is generally accepted that human origins can be traced back to one of the thick-enamelled African middle Miocene groups.

Figure 1. Simplified representation of hominid evolution.



Early Hominids

Bipedal hominids first make their appearance in East Africa around 5 mya and in southern Africa around 3 mya. These early hominids called australopithecines, were smaller than modern humans (they have been estimated to weigh about 28-53 kg), but had brain sizes almost three times larger than the Miocene hominoids (*Box 1*). The first australopithecine fossil to be discovered was that of a young child from Taung in the northern Cape Province of Africa in 1924. This Taung skull was brought to Raymond Dart, a professor of anatomy at the University of Witwatersrand in Johannesburg. Dart analysed the skull, and in his article, published in *Nature* in 1925, described the specimen

Box 1. Hominid Encephalization

The steady increase in brain size in the hominid lineage – from 420 cc in *Australopithecus afarensis* to 1500 cc in *Homo sapiens* – is a remarkable evolutionary change. It cannot be argued away as a simple relation to increase in body size, for brain size increased from 1050 cc in *Homo erectus* to 1500 cc in *Homo sapiens*, without any apparent change in body size. Early evolutionists postulated that evolution of the human brain occurred after many human features, including bipedalism, had been established. Evidence from the hominid fossil record confirm this view and add unexpected details to information about the pattern of human encephalization (increase in brain size during the evolution of a species, with no concomitant increase in body size). It is now accepted that brain expansion was not an early trend in human evolution, but that this phenomenon confines itself to the last two million years of human evolution. Warfare, language, tools and labour, hunting, heat stress, population structure and culture have been listed as some of the prime movers behind encephalization of the human brain. Though all these factors may have played important roles, currently, it is believed that language was the prime mover behind this evolutionary change. (See also S Rajappa, *Resonance*, Vol.10, pp.8-14, 2005)

Apart from the increase in size, an important feature of hominid encephalization is the reorganization of different areas in the brain. A significant difference between the hominid brain pattern and the pongid/great apes brain pattern lies in the sulcal patterns of the brain. In the pongid brain, the lunate sulcus (a small semilunar furrow on the lateral surface of the occipital lobe of the cerebrum) conspicuously marks the parietal/occipital boundary, whereas the hominid brain is characterized by the absence of an observable lunate sulcus and a neural junction of the parietal, occipital and temporal association cortices. In a stimulating paper on brain evolution and neurolinguistic preconditions, Wendy Wilkins and Jennie Wakefield [1] argue that development of the POT (parieto-occipito-temporal junction) was directly preadaptive for language processing and that *Homo habilis* was the first hominid to evolve this neuroanatomical configuration.



as a man-like ape and named it *Australopithecus africanus* (southern ape of Africa). Dart's views were not well received; Victorian paleoanthropologists believed that early hominids must have had large brains, and that they must have evolved in Europe or Asia but surely not in the 'Dark Continent' of Africa. It wasn't until the 1930s and 1940s when adult australopithecine fossils were found in other southern African sites, that australopithecines gained recognition as early hominids.

Traditionally, two forms have been recognised among the australopithecines – a lighter, smaller-toothed gracile form (*Australopithecus afarensis*, *Australopithecus africanus*, *Australopithecus ramidus*, *Australopithecus anamensis*) and a heavier, larger-toothed robust form (*Australopithecus robustus*, *Australopithecus boisei*, *Australopithecus aethiopicus*) – though recent studies suggest that this dichotomy may not be strict. For e.g., fossil specimens allocated to a gracile form like *Australopithecus africanus* may actually have larger teeth than specimens allocated to a robust form like *Australopithecus robustus*. In general, robust australopithecines appear to succeed gracile australopithecines, though early forms of a robust australopithecine evidently coexisted with the later forms of a gracile australopithecine.

One of the better-known australopithecine specimens is 'Lucy', the most complete adult skeleton of a female. Limb proportions of Lucy suggest that gracile australopithecines may have used some form of bipedal locomotion, though it was not identical to the gait of modern humans. The crucial difference lies in the length of the hind limbs. Although the forelimb proportions of Lucy are similar to those of modern humans, her hind limbs are much shorter and more akin to those of the African apes. This implies that the relative energy cost of walking must have been greater in the gracile australopithecines than in later hominids. Gracile australopithecines also appear to have retained arboreal adaptations for movement in trees. In conclusion, it can be said that though there are many ape-like retentions in Lucy, many of the morphological changes are in the direction of bipedalism (*Box 2*).

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Box 2. The Laetoli Footprints

Discovered in 1978 by members of Mary Leakey's team, in Laetoli, Tanzania, the Laetoli footprints are a remarkable trail of fossilized footprints of three or four bipedal hominids. Preserved in volcanic ashfall, they are dated at 3.6 mya and provide unequivocal support for the hypothesis that australopithecine hominids practised bipedal locomotion. The footprints at Laetoli appear indistinguishable from the footprints of modern humans – the great toe is aligned with the lateral toes and a medial longitudinal arch is present as in modern humans. However, interestingly enough, foot bones recovered from australopithecine specimens do not appear to fit in with the shape of the footprints seen in Laetoli.

The origin of bipedalism and causes that led to the adoption of a bipedal mode of locomotion has always been an intensely debated topic in anthropology. Some of the earlier theories advanced to explain the evolution of bipedalism hypothesised that the new form of locomotion freed the hands for tool use, allowed carrying food or infants, improved new feeding adaptations etc. The traditional view postulates that climatic fluctuations in the Miocene resulted in receding forests and more open grassland. Australopithecines would thus have had to travel greater distances to harvest the now widely dispersed food sources, and hence evolved bipedal walking in order to improve efficiency of travel. This view has been challenged by the notion that bipedal locomotion could not have naturally evolved, because in comparison to mammalian quadrupedalism, it is energetically inefficient and causes reduction in speed and agility. In an interesting examination of 'bipedal theories' H M McHenry [2] quotes Taylor and Rowntree's examination of energetic efficiency in chimpanzees, and points out that hominid bipedalism is as efficient as average mammalian quadrupedalism at normal speeds. Hence the adoption of bipedal locomotion by australopithecines could have been a natural progression of events.

Apart from bipedalism, australopithecines are also noted for the first signs of tool-use. Since early species of *Homo* are also found in many of the tool sites where australopithecines were found, it cannot be definitively said that australopithecines made the stone tools. However it does seem clear that early australopithecines were using simple opportunistic tools like sticks, bones

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and stones, for collecting plant food and insects, and killing and scavenging small animals (Box 3).

Genus *Homo*

Fossil specimens belonging to the genus *Homo*, first appear in the palaeontology record of Africa around 2.4-2 mya. Traditionally the genus has been divided into three chronospecies, or time-successive species – *Homo habilis*, *Homo erectus* and *Homo sapiens*.

Box 3. Culture and Tool Traditions

Evolution of tool-use among humans has always attracted considerable attention, because of its importance as a cultural behaviour. Although non-human primates, like chimpanzees, have been observed to make and use tools, tool-use in hominids is significant for its complexity and the role it plays in hominid survival. The earliest examples of stone tool use, between 2.0 to 1.5 mya, are referred to as the Oldowan tradition, and include an assortment of choppers, hammerstones and flake scrapers. The Developed Oldowan Tradition continues the flake and chopper industry, but also includes proto-handaxes and crude bifacial forms. The Acheulian Tradition (1.5 mya – 60,000 ya) is characterised by true handaxes and cleavers and is the most widespread and longest lived cultural tradition. The Oldowan Tradition is usually associated with *Homo habilis*, though, due to the presence of australopithecine and *Homo erectus* fossils in the same area, it cannot be definitely said that *Homo habilis* was the sole maker of these tools. Similarly, the Acheulian Tradition is usually associated with *Homo erectus*, though again, this association cannot be definitively confirmed. The tool tradition of the Neanderthals is referred to as the Mousterian industry and is marked by reduction in the use of large core tools and increase in specialised flake tools, like knives, scrapers and spear points. The Middle (1000,000 – 40,000 ya) and Late Stone (40,000 ya -) Ages are associated exclusively with *Homo sapiens* and characterized by carefully prepared stone cores for the production of flake tools and a predominance of blade tools and microliths.



a) Oldowan choppers

b) Acheulian handaxe

c) Mousterian tool scrapers

Courtesy: a) James Harrod (www.origins.net.org). Artifacts at National Museums of Kenya, b) <http://hoopermuseum.earthsci.carleton.ca>, c) <http://hoopermuseum.earthsci.carleton.ca>

Homo habilis, or Handyman as this species is called, was discovered in 1959 at Olduvai in East Africa by Louis Leakey and his colleagues (Box 4). Analyses of the fossil fragments showed that that this new kind of species was distinctly different from australopithecines and “showed hominizing tendencies in its teeth...a more hominized brain-size”. Though his co-authors suggested that *Homo habilis* was a phyletic link between *Australopithecus* and *H. erectus*, Leakey went one step ahead to propose that *H. habilis* should not be regarded as a form between *Australopithecus* and *H. erectus*, but rather as directly ancestral to *Homo sapiens*. Morphologically, *H. habilis* showed a mosaic of australopithecine and *Homo* like features, with clear evidence for bipedality and hands capable of grasping.

Homo erectus, interestingly enough, was discovered earlier than *Homo habilis* – in 1890 by Eugene Dubois in Trinil, central Java

Box 4. The Leakeys

Popularly referred to as the first family of paleontology, Louis Leakey, his wife Mary and son Richard are credited with some of the most groundbreaking discoveries in anthropology. A dynamic and flamboyant personality, with wide-ranging interests in wildlife conservation, primate behaviour, human evolution and African natural history, Louis Seymour Bazett Leakey wrote himself into the annals of history with his multiple human fossil and stone tool discoveries. L S B's biggest contribution lay in his promotion of the theory that Africa is the cradle of humanity. Although some of his theories with respect to fossil dating and human lineage have been disproved, Louis Leakey's work undeniably influenced future generations of paleoanthropologists. L S B is also remembered for his role in encouraging and supporting three unique and definitive studies on great apes in the wild – ‘Leakey's Angels’ Dian Fossey and Jane Goodall studied gorillas and chimpanzees in Africa, while Birute Galadikas studied orangutans in Indonesia.

A renowned paleoanthropologist, Mary Leakey is credited with some of the most significant fossil finds in the field of human evolution. Together with Louis Leakey, her findings at the Olduvai Gorge in Africa, particularly those of *Proconsul africanus*, and *Australopithecus boisei* redefined existing concepts on the timeline of human evolution. Richard Leakey began his professional career with an avowed disinterest in paleoanthropology, but went on to make some very exciting fossil findings, note worthily that of a *Homo erectus* skeleton called Turkana Boy. Former Director of the National Museums of Kenya and the Kenya Wildlife Service, Richard Leakey is a tireless crusader in his efforts to preserve Kenyan wildlife and culture. Currently the Leakey legacy is being continued by Louise Leakey, Richard and Meave Leakey's daughter. Her work in the Turkana Basin has resulted in the discovery of hominid fossils that are believed to belong to a new branch of early hominids, named *Kenyanthropus platyops*.



– though Dubois published his discovery only 33 years later. Even more ironical, Dubois was ridiculed for his discovery of the “missing link” (turning him into a scientific recluse) and it was only in 1936, with von Koenigswald’s discovery of a skull fragment in Modjokerto, that paleontological interest was rekindled in *H. erectus*. Subsequently, *H. erectus* fossil specimens have been reported from China, Africa, Germany and central Europe, giving the species an enormous geographical range, extending far outside Africa. *H. erectus* seems to have been the first hominid to migrate from Africa, and this migration appears to have occurred fairly early on, about 1.5 mya. The species also persisted in Asia far longer than in Africa. Brain and body size is slightly bigger in *H. erectus* in comparison to *H. habilis*, and the species is characterised by robust skulls and prominent brow ridges. *H. erectus* is associated with the Acheulian tool tradition, and is also thought to have used fire.

Towards the end of the documented history of *Homo erectus*, about 400,000 years ago, a varied group of hominids make their appearance in the fossil records. These hominids do not have the typical morphological features associated with modern *H. sapiens*, and hence are grouped together as ‘archaic *H. sapiens*’. Archaic *H. sapiens* are associated with the Developed Oldowan/Acheulian tool traditions and are known from sites in Africa, Europe and Asia. One group of archaic humans that has received special attention is the Neanderthal. Recovered from fossil sites in Europe and dated to have existed about 150,000-30,000 ya, Neanderthals are typified by pronounced facial prognathism (protruding jaw), large brain sizes and robust, heavy bodies. They are associated with the Mousterian tool tradition and (despite the prevalent notion that they were incapable of culture or art) there is clear archaeological evidence that Neanderthals practised religious and symbolic behaviours and achieved high levels of social caring.

Anatomically modern humans have a relatively recent origin, about 130,000 years ago. At this stage, the species is morphologically similar to present-day humans with less prominent brow-

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ridges, modern-type hip joints and shorter, more rounded skulls. The best known of these are the Cro-Magnons, the oldest anatomically modern human populations of Europe. One of the more contentious issues in paleoanthropology is that of the relationship of Neanderthals to succeeding human populations. According to some of the more influential and contending hypotheses: (a) Neanderthals were genetically isolated from modern human populations and are peripheral to mainstream human evolution; (b) Human evolution went through a worldwide Neanderthal stage; hence there is evolutionary continuity between Neanderthals and modern humans; (c) Neanderthals went extinct without issue; hence there is no evolutionary continuity with modern humans. To date, the subject of Neanderthal phylogeny has not been satisfactorily resolved; hence their taxonomy also remains a matter of some debate. Some paleontologists consider them a separate species, thus *Homo neanderthalensis*; while others define them as intrinsic to modern human evolution, and closely related to modern humans, hence *Homo sapiens neanderthalensis*. According to the latter interpretation, modern humans are recognised as another subspecies, *Homo sapiens sapiens*.

Directly related to the ongoing debate about Neanderthal phylogeny is the controversy regarding the evolution of modern humans. Two main competing theories are the Multiregional Continuity Model and the Replacement Hypothesis. According to the Multiregional Continuity model, best represented by the views of Milford Wolpoff and Alan Templeton, *H. erectus* evolved slowly throughout its range into the various early *H. sapiens* forms, thus producing the distribution of modern humans. Hence, this model argues that there was substantial gene flow between the various groups of early *H. sapiens*. The Replacement Hypothesis, propounded by authors like Chris Stringer and Ian Tattersall, argues that modern humans evolved once in Africa and migrated out from there to displace the other early human populations with little or no gene mixing between these populations.



Both models have many variants, and have been examined for supporting evidence in the form of genetic, fossil and archeological data, but neither model completely explains existing data. In a very elegant paper published in *Current Anthropology* in 2002, Vinayak Eswaran [3] proposes that the anatomically modern human form arose due to a 'diffusive wave' out of Africa. Eswaran clarifies that this diffusion is not migration, and instead defines it as "a continuous expansion of modern populations by small random movements, hybridization and natural selection favoring the modern genotype". Eswaran's Diffusion Wave model is a variant of the Multiregional Continuity model in that its basic premise is introgression⁴ between archaic and modern humans. However it also adopts elements of the Replacement Hypothesis, as it supports the view that modern *Homo sapiens* arose in Africa. An intriguing study by Reed *et al* in 2004 [4], attempted to infer human evolutionary history from the evolutionary history of their parasites. The authors reconstructed the evolutionary history of head/body lice *Pediculus humanus* using both morphological and molecular data, and then used the results to check which model of human origins best fits the louse lineage data. The study concluded that the Diffusion Wave theory offered the best fit to the lice data, and that although louse evolutionary history does not offer evidence for introgression between archaic and modern humans, it definitely supports direct physical contact between the two groups.

⁴ The movement of genes from one population into another through hybridization followed by backcrossing.

The last word in this tale definitely belongs to the most significant anthropological find in recent years – a discovery that has been dubbed the Little Lady of Flores. Excavations at Liang Bua, a limestone cave on the island of Flores in Indonesia, in 2003, yielded hominid fossils that were sufficiently distinct anatomically to be assigned to a new species *Homo floresiensis*. Anthropologists involved in the study have concluded that *H. floresiensis* were little people, less than a metre tall that lived on Flores, possibly from 38,000 years ago to 18,000 years ago. The 'Flores people' probably descended from *Homo erectus* who first arrived on Flores about 900,000 years ago, and in a classic case of



endemic dwarfing, grew smaller and smaller, until they were transformed into the new species.

The discovery of *H. floresiensis* is momentous for the Pandora's Box it opens on the subject of human diversity. The complacency with which we have lived for eons, that we are the only human species inhabiting the planet, comes with a baggage of species-superiority and non-accountability to the rest of the natural world. The knowledge that another human species existed alongside us unnoticed, for several thousands of years, is disquieting for the insinuation it carries that perhaps it is time we changed our understanding of our history and ourselves.

Suggested Reading

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Beauty of Maths!

$1 \times 8 + 1 = 9$
 $12 \times 8 + 2 = 98$
 $123 \times 8 + 3 = 987$
 $1234 \times 8 + 4 = 9876$
 $12345 \times 8 + 5 = 98765$
 $123456 \times 8 + 6 = 987654$
 $1234567 \times 8 + 7 = 9876543$
 $12345678 \times 8 + 8 = 98765432$
 $123456789 \times 8 + 9 = 987654321$

$1 \times 9 + 2 = 11$
 $12 \times 9 + 3 = 111$
 $123 \times 9 + 4 = 1111$
 $1234 \times 9 + 5 = 11111$
 $12345 \times 9 + 6 = 111111$
 $123456 \times 9 + 7 = 1111111$
 $1234567 \times 9 + 8 = 11111111$
 $12345678 \times 9 + 9 = 111111111$
 $123456789 \times 9 + 10 = 1111111111$

$9 \times 9 + 7 = 88$
 $98 \times 9 + 6 = 888$
 $987 \times 9 + 5 = 8888$
 $9876 \times 9 + 4 = 88888$
 $98765 \times 9 + 3 = 888888$
 $987654 \times 9 + 2 = 8888888$
 $9876543 \times 9 + 1 = 88888888$
 $98765432 \times 9 + 0 = 888888888$

Brilliant, isn't it?