Duke of Edinburgh Prize to:

Gen Suwa
Professor and Director, The University Museum,
The University of Tokyo

for "Human Origins and Evolution: from *Ardipithecus ramidus* to *Homo sapiens*"

Outline of the work:

Prof. Gen Suwa is a biological anthropologist and paleoanthropologist who has considerably contributed to the understanding of human evolution through the discovery and analysis of fossil human remains and associated contextual evidence. His most notable contribution is the elucidation of the earliest stages of human ancestry via the discovery and analysis of the 4.4 million-year (Ma)-old *Ardipithecus ramidus* and the nearly 6-Ma-old but more fragmentary *Ardipithecus kadabba* fossils. Other major works include the discovery and naming of the 8-Ma-old African great ape *Chororapithecus abyssinicus*, the establishment of the timing of the split between the *Homo* and the robust *Australopithecus* lineages, the dating of the earliest Acheulean stone tools to 1.75 Ma, and various studies on more recent Pleistocene and Holocene fossil and skeletal materials.

Between the 1980s and 1990s, Prof. Suwa has led the comparative analysis of *Australopithecus* and early *Homo*, particularly regarding dental fossil records spanning a period between 4 and 1 Ma. Importantly, his work is internationally recognized as the standard for the period between 3 and 2 Ma, which is crucial for the understanding of the emergence of the genus *Homo* and its subsequent evolutionary trajectories. Suwa's work on the dentition contributed significantly to the elucidation of the evolution of the earliest *Australopithecus* species from the more primitive *Ardipithecus ramidus* by 4.2 Ma, which then largely evolved as a lineage with considerable populational variation and finally split into two clades just after 3 Ma. His work identified the earliest definitive record of the specialized robust *Australopithecus* clade at 2.7 Ma. His work demonstrated that the lineage ancestral to the genus *Homo* can be traced back to 2.7–2.8 Ma but did not exhibit the derived features characteristic of the genus (associated with the increased neurocranial size or a trend toward reduced masticatory apparatus) until after 2.4 Ma. Considering the period after 2.3 Ma, Prof. Suwa has consistently supported the hypothesis that the transition from the early *Homo* species to *Homo erectus* occurred largely in a unilineal mode between 2 and 1.6 Ma ago.

In the early 1990s, by surveying Ethiopian rift valley, Suwa and his colleagues discovered a new paleoanthropological research area, unknown until that moment (Nature, 1992). They named the fossiliferous sediments the Konso Formation and found it rich in fossils and artifacts belonging to a period between 2 and 1 Ma ago. This site is now recognized as one of the most informative sites about Africa from this period. Based on the systematic annual field and laboratory investigations, particularly between 1993 and 2003, Prof. Suwa and his colleagues established a detailed chronological sequence of the Konso Formation and the co-occurrence of *Australopithecus boisei* and *H. erectus* species at 1.4 Ma (Nature, 1997). Most importantly, they documented the emergence and development of the Acheulean lithic technology (hand axes and related

stone tools) and the associated patterns of faunal change and paleoclimatic indicators. Contrary to previous assumptions, Suwa's research demonstrated that the Acheulean extends back to 1.75 Ma, which is broadly simultaneous with the transition from *H. habilis sensu lato* to *H. erectus* (PNAS, 2013). This suggests that a major change in subsistence and adaptive strategies occurred during this transition and was accompanied or driven by technological innovation. They also documented the tempo and mode of lithic technological development between 1.75 Ma and less than 1 Ma ago and revealed that a second event of technological innovation occurred prior to 0.8–0.9 Ma, which is relevant to the transition from *H. erectus* to *H. heidelbergensis sensu lato*. His work on the early Acheulean is recognized as significant for the understanding of the coevolution of tool use/manufacture, language/symbolic capacities, and neurological function.

Between 1990 and 1992, Suwa participated in field research at the Middle Awash area (field research led by Berhane Asfaw and Tim D. White) and discovered the first fossil that was later named as *Ardipithecus ramidus*, arguably one of the major breakthroughs in the history of paleoanthropology. Prof. Suwa's field discovery led to further discoveries of a total of 17 specimens by 1993/94, based on which a new genus and species, *Ardipithecus ramidus*, was named (Nature, 1994). This was the oldest known species of the human ancestor at the time and was suggested to be substantially more primitive than any known *Australopithecus* fossil or other human ancestors. In the Middle Awash area, following the discovery and naming of *Ardipithecus ramidus*, other important fossils were discovered and reported. Prof. Suwa was one of the primary researchers that undertook the comparative analysis and interpretations of these fossils, which included the following, in order of publication:

2.5-Ma-old new species, *Australopithecus garhi*, a candidate ancestor of *Homo* (Science, 1999); 160,000-year-old, earliest important fossil cranium of *Homo sapiens* from Herto (Nature, 2003); nearly 6-Ma-old teeth of *Ardipithecus kadabba* (Science, 2004); and the earliest *Australopithecus* fossils, *Australopithecus anamensis*, considered to be 4.2 Ma old (Nature, 2006).

Prof. Suwa's most notable contribution to paleoanthropology is his extensive and thorough comparative analysis of *Ardipithecus ramidus*, which resulted in a series of papers on the paleobiology of the species (eight of nine papers designated the "breakthrough of the year;" Science, 2009). Prof. Suwa performed the bulk of the analysis of the dentition and skull of *Ardipithecus ramidus* as well as of the key aspects of the postcranial skeleton, particularly involving micro-CT data. Most importantly, Prof. Suwa and his colleagues revealed that *Ardipithecus* represents a novel step in the human evolution, distinctly primitive compared with *Australopithecus* (and *Homo*) characteristics. *Ardipithecus ramidus* was shown to be a forest- to woodland-adapted species that combined considerable arboreal capacities with a transitional form of terrestrial bipedality. It had a more omnivorous and probably search-intensive dietary adaptation, which was not observed in modern apes. With low levels of body and canine size dimorphisms indicative of reduced male aggression, *Ardipithecus ramidus* is inferred to have had a reproductive strategy and social structure that was unique among modern apes. Furthermore, despite the comparatively small genomic differences between chimpanzees and humans, *Ardipithecus ramidus* was found *not* to converge phenetically toward the chimpanzees or other modern apes. This suggests that the common ancestor of humans and apes was unlike any of the modern apes, in contradistinction to the perception of a chimpanzee-like ancestry. These insights have led to the hypothesis that, from an ancestral ape species more generalized than any modern form, the gorilla, chimpanzee/bonobo, and human lineages each specialized in their own ways, with the human lineage acquiring terrestrial bipedality and reduced male canines and aggression prior to 6–7 Ma.

The hypothesis of a non-modern-ape-like common ancestor in turn leads to the deep divergence

hypothesis of human and modern ape developments. Although these conclusions should be further tested by examining 12- to 7-Ma-old fossil records from Africa, such fossil assemblages have been, to date, extremely scarce. Prof. Suwa has significantly contributed to bridging this gap in our knowledge by discovering and analyzing the 8-Ma-old *C. abyssinicus* and associated fauna (Nature, 2007 and 2016). Prof. Suwa considers *Chororapithecus* a primitive member of the gorilla clade, and his ongoing work is recognized as the only sub-Saharan African project that directly addresses the hypothesized period of the human and chimpanzee split.

Prof. Suwa has also contributed to the understanding of more recent phases of human evolution, particularly regarding the relationships and skeletal biology of the Late Pleistocene and Holocene populations of the Japanese archipelago. His findings clarified some aspects of the chronology and morphology of the Latest Pleistocene Minatogawa skeletal remains from Okinawa Island. He has also promoted new field work and discoveries at Okinawa Island, showing the establishment of maritime adaptation in the Japanese archipelago as early as about 30,000 years ago (PNAS, 2016). Suwa has also performed important studies examining the skeletal growth series of the Holocene Jomon people and participated in the first collaborative study on the nuclear DNA of the Jomon people.

List of Main Publications (*: the most significant papers)

White TD and **Suwa G** (1987) Hominid footprints at Laetoli: Facts and interpretations. ***Am. J. Phys. Anthropol. 72: 485–514***.

Suwa G (1988) Evolution of the "robust" australopithecines in the Omo succession: Evidence from mandibular premolar morphology. In: Grine FE (Ed.) *Evolutionary History of the Robust Australopithecines*. ***Aldine de Gruyter, New York, pp. 199–222***.

Suwa G (1989) The premolar of KNM-WT 17000 and relative anterior to posterior dental size. ***J. Human Evol. 18: 795–799***.

Asfaw B, Beyene Y, **Suwa G**, Walter RC, White TD, WoldeGabriel G and Yemane T (1992) The earliest Acheulean from Konso-Gardula. ***Nature 360: 732–735***.

*White TD, **Suwa G** and Asfaw B (1994) *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. ***Nature 371: 306–312***.

Suwa G, Wood BA and White TD (1994) Further analysis of mandibular molar crown and cusp areas in Pliocene and early Pleistocene hominids. ***Am. J. Phys. Anthropol. 93: 407–426***.

Suwa G (1996) Serial allocations of isolated mandibular molars of unknown taxonomic affinities from the Shungura and Usno Formations, Ethiopia, a combined method approach. ***Human Evol. 11: 269–282***.

Suwa G**, White TD and Howell FC (1996) Mandibular postcanine dentition from the Shungura Formation, Ethiopia: Crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. ***Am. J. Phys. Anthropol. 101: 247–282.

Suwa G**, Asfaw B, Beyene Y, White TD, Katoh S, Nagaoka S, Nakaya H, Uzawa K, Renne P and WoldeGabriel G (1997) The first skull of *Australopithecus boisei*. ***Nature 389: 489–492.

Suwa G and Kono-Takeuchi R (1998) A refined method of measuring basal crown and cusp areas by use of a three-dimensional digitizing system. ***Anthropol. Sci. 106: 95–105***.

Asfaw B, White TD, Lovejoy CO, Latimer B, Simpson SW and **Suwa G** (1999) *Australopithecus garhi*: A new species of early hominid from Ethiopia. ***Science 284: 629–635***.

White TD, **Suwa G**, Simpson SW and Asfaw B (2000) Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. ***Am. J. Phys. Anthropol. 111: 45–68***.

Katoh S, Nagaoka S, WoldeGabriel G, Renne P, Snow MG, Beyene Y and **Suwa G** (2000) Chronostratigraphy and correlation of the Plio-Pleistocene tephra layers of the Konso Formation, southern Main Ethiopian rift, Ethiopia. ***Quat. Sci. Rev. 19: 1305–1317***.

Kono RT, **Suwa G** and Tanijiri T (2002) A three-dimensional analysis of enamel distribution patterns in human permanent first molars. ***Arch. Oral. Biol. 47: 867–875***.

Baba H, Aziz F, Kaifu Y, **Suwa G**, Kono RT and Jacob T (2003) *Homo erectus* calvarium from the Pleistocene of Java. ***Science 299: 1384–1388***.

White TD, Asfaw B, DeGusta D, Gilbert H, Richards GD, **Suwa G** and Howell FC (2003) Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. ***Nature 423: 742–747***.

Suwa G, Nakaya H, Asfaw B, Saegusa H, Amzaye A, Kono RT, Beyene Y and Katoh S (2003) Plio-Pleistocene terrestrial mammal assemblage from Konso, southern Ethiopia. ***J. Vertebr. Paleontol. 23: 901–916***.

*Haile-Selassie Y, **Suwa G** and White TD (2004) Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. ***Science 303: 1503–1505.***

Suwa G and Kono RT (2005) A micro-CT based study of linear enamel thickness in the mesial cusp section of human molars: reevaluation of methodology and assessment of within-tooth, serial, and individual variation. ***Anthropol. Sci. 113: 273–289***.

Nagaoka S, Katoh S, WoldeGabriel G, Sato H, Nakaya H, Beyene Y and **Suwa G** (2005) Lithostratigraphy and sedimentary environments of the hominid-bearing Pliocene–Pleistocene Konso Formation in the southern Main Ethiopian Rift, Ethiopia. ***Palaeogeogr. Palaeoclimatol. Palaeoecol. 216: 333–357***.

WoldeGabriel G, Hart WK, Katoh S, Beyene Y and **Suwa G** (2005) Correlation of Plio-Pleistocene tephra in Ethiopian and Kenyan rift basins: Temporal calibration of geological features and hominid fossil records. ***J. Volcanol. Geotherm. Res. 147: 81–108***.

White TD, WoldeGabriel G, Asfaw B, Ambrose SH, Beyene Y, Bernor RL, Boisserie J-R, Currie B, Gilbert H, Haile-Selassie Y, Hart WK, Hlusko LJ, Howell FC, Kono RT, Lehmann T, Louchart A, Lovejoy CO, Renne PR, Saegusa H, Vrba ES, Wesselman H and **Suwa G** (2006) Asa Issie, Aramis and the origin of *Australopithecus.* ***Nature 440: 883–889***.

Suwa G, Asfaw B, Haile-Selassie Y, White TD, Katoh S, WoldeGabriel G, Hart WK, Nakaya H and Beyene Y (2007) Early Pleistocene *Homo erectus* fossils from Konso, southern Ethiopia. ***Anthropol. Sci. 115: 133–151***.

Suwa G**, Kono RT, Katoh S, Asfaw B and Beyene Y (2007) A new species of great ape from the late Miocene epoch in Ethiopia. ***Nature 448: 921–924.

Kono RT and **Suwa G** (2008) Enamel distribution patterns of extant human and hominoid molars: Occlusal versus lateral enamel thickness. ***Bull. Natl. Mus. Nat. Sci., Ser. D 34: 1–9.***

Kubo D, Kono RT, Saso A, Mizushima S and **Suwa G** (2008) Accuracy and precision of CT-based endocranial capacity estimations: a comparison with the conventional millet seed method and application to the Minatogawa 1 skull. ***Anthropol. Sci. 116: 77–85***.

Fukase H and **Suwa G** (2008) Growth-related changes in prehistoric Jomon and modern Japanese mandibles with emphasis on cortical bone distribution. ***Am. J. Phys. Anthropol. 136: 441–454***.

Haile-Selassie Y, **Suwa G** and White TD (2009) Hominidae. In: Haile-Selassie Y and WoldeGabriel G (Eds.) *Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash, Ethiopia*. ***University of California Press, Berkeley, pp. 159–236***.

*White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, **Suwa G** and WoldeGabriel G (2009) *Ardipithecus ramidus* and the paleobiology of early hominids. ***Science 326: 64–86.***

*White TD, Ambrose SH, **Suwa G**, Su DF, DeGusta D, Bernor RL, Boisserie J-R, Brunet M, Delson E, Frost

S, Garcia N, Giaourtsakis IX, Haile-Selassie Y, Howell FC, Lehmann T, Likius A, Pehlevan C, Saegusa H, Semprebon G, Teaford M and Vrba ES (2009) Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. ***Science 326: 67–93***.

*Suwa G, Asfaw B, Kono RT, Kubo D, Lovejoy CO and White TD (2009) The *Ardipithecus ramidus* skull and its implications for hominid origins. ***Science 326: 68–68e7***.

*Suwa G, Kono RT, Simpson SW, Asfaw B, Lovejoy CO and White TD (2009) Paleobiological implications of the *Ardipithecus ramidus* dentition. ***Science 326: 69–99***.

*Lovejoy CO, Suwa G, Spurlock L, Asfaw B and White TD (2009) The pelvis and femur of *Ardipithecus ramidus*: The emergence of upright walking. ***Science 326: 71–71e6***.

*Lovejoy CO, Suwa G, Simpson SW, Matternes JH and White TD (2009) The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. ***Science 326: 73–106***.

Lovejoy CO, Simpson SW, White TD, Asfaw B and Suwa G (2009) Careful climbing in the Miocene: The forelimbs of *Ardipithecus ramidus* and humans are primitive. ***Science 326: 70–70e8***.

Lovejoy CO, Latimer B, Suwa G, Asfaw B and White TD (2009) Combining prehension and propulsion: The foot of *Ardipithecus ramidus*. ***Science 326: 72–72e8***.

Saso A, Matsukawa S and Suwa G (2011) Comparative analysis of the glabellar region morphology of the late Pleistocene Minatogawa crania: a three-dimensional approach. ***Anthropol. Sci. 119: 113–121***.

Suwa G, Fukase H, Kono RT, Kubo D and Fujita M (2011) Mandibular tooth root size in modern Japanese, prehistoric Jomon, and Late Pleistocene Minatogawa human fossils. ***Anthropol. Sci. 119: 159–171***.

Suwa G, Fujita M, Yamasaki S, Oshiro I, Baba H, Shinzato N, Kinjo T, Kaifu Y and Matsu'ura S (2011) New insights on the excavation and chronological status of the Late Pleistocene Minatogawa human fossils from Okinawa Prefecture. ***Anthropol. Sci. (Jpn. Ser.) 119: 125–136 (in Japanese)***.

Suwa G, Lovejoy CO, Asfaw B and White TD (2012) Proximal femoral musculoskeletal morphology of chimpanzees and its evolutionary significance: a critique of Morimoto et al. (2011) ***Anat. Rec. 295: 2039–2044***.

*Beyene Y, Katoh S, WoldeGabriel G, Hart WK, Uto K, Sudo M, Kondo M, Hyodo M, Renne PR, Suwa G and Asfaw B (2013) The characteristics and chronology of the earliest Acheulean at Konso, Ethiopia. ***Proc. Natl. Acad. Sci. USA 110: 1584–1591***.

Suwa G, Beyene Y and Asfaw B (Eds.) (2014) Konso-Gardula Research Project Volume 1. Paleonotological Collections: Background and Fossil Aves, Cercopithecidae, and Suidae. ***The University Museum***, ***The University of Tokyo, Bulletin 47, 125 pp***.

Suwa G and Ambrose SH (2014) Reply to Cerling et al. ***Curr. Anthropol. 55: 473–474***.

Kimbel WH, Suwa G, Asfaw B, Rak Y and White TD (2014) *Ardipithecus ramidus* and the evolution of the human cranial base. ***Proc. Natl. Acad. Sci. USA 111: 948–953***.

*White TD, Lovejoy CO, Asfaw B, Carlson JP and Suwa G (2015) Neither chimpanzee nor human, *Ardipithecus* reveals the surprising ancestry of both. ***Proc. Natl. Acad. Sci. USA 112: 4877–4884***.

Beyene Y, Asfaw B, Sano K and Suwa G (Eds.) (2015) Konso-Gardula Research Project Volume 2. Archaeological Collections: Background and the Early Acheulean Assemblages. ***The University Museum, The University of Tokyo, Bulletin 48, 103 pp***.

Suwa G, Beyene Y, Nakaya H, Bernor RL, Boisserie J-R, Bibi F, Ambrose SH, Sano K, Katoh S and Asfaw B (2015) Newly discovered cercopithecid, equid and other mammalian fossils from the Chorora Formation, Ethiopia. ***Anthropol. Sci. 123: 19–39***.

Fujita M, Yamasaki S, Katagiri C, Oshiro I, Sano K, Kurozumi T, Sugawara H, Kunikita D, Matsuzaki H, Kano A, Okumura T, Sone T, Fujita H, Kobayashi S, Naruse T, Kondo M, Matsu'ura S, Suwa G and Kaifu Y (2016) Advanced maritime adaptation in the western Pacific coastal region extends back to 35,000–

30,000 years before present. ***Proc. Natl. Acad. Sci. USA 113: 11184–11189***.

Mizushima S, **Suwa G** and Hirata K (2016) A comparative analysis of fetal to subadult femoral midshaft bone distribution of prehistoric Jomon hunter-gatherers and modern Japanese. ***Anthropol. Sci. 124: 1–15***.

*Katoh S, Beyene Y, Itaya T, Hyodo H, Hyodo M, Yagi K, Gouzu C, WoldeGabriel G, Hart WK, Ambrose SH, Nakaya H, Bernor RL, Boisserie J-R, Bibi F, Saegusa H, Sasaki T, Sano K, Asfaw B and **Suwa G** (2016) New geological and palaeontological age constraint for the gorilla–human lineage split. ***Nature 530: 215–218***.

Suwa G, Kunimatsu Y, Mirzaie Ataabadi M, Orak Z, Sasaki T and Fortelius M (2016) The first hominoid from the Maragheh Formation, Iran. ***Palaeobiodiv. Palaeoenviron. 96: 373–381***.

Kanzawa-Kiriyama H, Kryukov K, Jinam TA, Hosomichi K, Saso A, **Suwa G**, Ueda S, Yoneda M, Tajima A, Shinoda K, Inoue I and Saitou N (2017) A partial nuclear genome of the Jomons who lived 3000 years ago in Fukushima, Japan. ***J. Human Genet. 62: 213–221***.

Boisserie J-R, **Suwa G**, Asfaw B, Lihoreau F, Bernor RL, Katoh S and Beyene Y (2017) Basal hippopotamines from the upper Miocene of Chorora, Ethiopia. ***J. Vertebr. Paleontol. 37: e1297718***.

Suwa G, Asfaw B, Nakaya H, Katoh S and Beyene Y. Early Pleistocene fauna and palaeoenvironments at Konso, Ethiopia. In: Reynolds S and Bobe R (Eds.) *African Palaeoecology and Human Evolution*. ***Cambridge University Press, Cambridge (in press)***.