Abstract

Hominin fossils are the most important materials for exploring questions about human origins and evolution. Because human fossils are very rare, it is impossible to use highly destructive techniques in order to study their morphology. Traditional analyses can only rely on the information gained from the study of the external morphology of specimens, and these approaches limited the study of human evolution. The application of computed tomography (CT) has facilitated major developments in paleoanthropology. To date, few studies on Chinese hominin fossils have used CT scanning methodology, but this is rapidly changing. In order to better understand the application of CT methodology in paleoanthropology, we review the applications of CT scanning on hominin fossils throughout the world. Studies examined include virtual fossil reconstruction, the use of endocasts to elucidate brain morphology, biomechanical analyses of bone distribution, imaging of mummies and research on early human health, and skeletal and dental microanatomical research.

Keywords: Paleoanthropology; Hominin fossil; CT; 3D reconstruction; Virtual anatomy

1. Introduction

Paleoanthropology is the study of human origins and evolution. Based on the analysis of ancient human skeletons, teeth and living people, paleoanthropologists elucidate the variation of human physical characteristics and model human behavior and phylogenetic relationships. As most hominin fossils are incomplete, distorted, or filled with calcified matrices, it is difficult or often impossible to clean or reconstruct specimens without destroying them. Morphological study is often restricted to the exterior surface features. Accordingly, traditional methods limited any further research on hominin fossils.

In 1895, the German physicist Wilhelm Röntgen first indicated that X-rays could be used to image internal structures. This “new light” soon was put to use identifying fractures and locating bullets in gunshot wounds [1]. In 1905, X-rays were applied on a Neanderthal fossil collection and revealed some health issues affecting early hominins dating 130,000 years ago. These radiographs yielded several important results: identification of one of the earliest benign bone tumors ever found, the possibility that one individual may have had a surgical amputation of his hand, and recognition that several individuals had osteoarthritis [2]. X-ray technology initiated a new era for diagnosis and disease management, however, the use of conventional radiography for the study of human skeletons has limitations. For instance, images produced by X-rays are two-dimensional plane films; all structures in the path of the X-ray beams are superimposed in the image and cannot be distinguished. Another problem is that conventional radiography cannot be used to detect mineralization or the presence of the sedimentary matrix because of its low resolution. Additionally, excessive radiation poses dangers to the human body [3].

Computed tomography (CT) was invented in 1972 by the British engineer Godfrey Hounsfield [4]. In CT scan-
The resolution of industrial CT is about 30–200 μm. With high radiation sources, industrial CT technology is capable of generating very high-resolution images of bone, tooth and biomaterial samples [12,13].

3. Applications and recent advances in the use of CT on hominin fossils

3.1. Virtual fossil reconstruction

Because of the destructive processes that occur during fossilization, hominin fossils are usually fragmented, distorted, or filled with heavily calcified matrix when they are unearthed from sediments. Traditional preparation involves physically separating the fossil from the surrounding matrix and then repairing the missing parts with plaster or silica. Reconstruction is a highly invasive and potentially destructive process that is often irreversible; it is also highly subjective and dependent upon the skills of the preparator.

One of the first, and most important, steps in virtual fossil reconstruction is to free fossil fragments from the surrounding matrix. Because the burial environment of hominin fossils is variable, bone density and the density of the adhering sediment also vary. CT technology can be used to distinguish between the two materials although scanning parameters used in modern skeletons are usually unsuitable for hominin fossils. Specific adjustment is necessary for each specimen. The window setting of the computer graphic tools must be calibrated based on the mean values of the fossilized bone and on the threshold effects so as to identify the density difference among the cranial cavities, bones and the surrounding matrix. Then the boundary between bone and sediment in each two-dimensional slice can be manually outlined in a virtual reality to separate the two components [14].

The second step in virtual fossil reconstruction is to reconstruct the missing parts of the fossil. This is illustrated by the work on a Neanderthal fossil skull. The St. Césaire 1 Neanderthal partial skeleton, dated to 30,000 years ago, is fragmented and the left side of the braincase is almost entirely missing. In 2002, Zollikofer et al. [15] made a CT scan of St. Césaire. As described above, all the fossil fragments were isolated electronically from the matrix and then recomposed on the computer screen. The missing parts were rebuilt using mirror imaging of the preserved antimeres or corresponding structures. A rather complete virtual object was reconstructed in a noninvasive way (Fig. 1(a)).

Another example is the virtual work on the nearly 7-million-year-old early hominin skull, Toumai (Sahelanthropus tchadensis), from the Djurab Desert of northern Chad. Although largely complete, the Toumai skull had been crushed under a sand dune, with some distortion caused by the expansion of the matrix. The discoverers suggested that the fossil displays a unique mosaic of primitive and derived characters, and that Toumai is the oldest known hominin or representative of the lineage that includes...
humans but not other apes. Critics soon argued that it looked more like a gorilla ancestor than a human [16]. A critical component of the disagreements hinged upon the evaluation of the cranial evidence for bipedal locomotion and head positioning. In 2005, Zollikofer and Ponce de Leon [17] created a digital representation of the Toumai cranium using high-resolution computed tomography. The distortion was corrected by the use of 3D graphic tools (Fig. 1(b) and (c)). The new reconstruction revealed that the angle between the bottom of Toumai’s eye orbit and the base of the skull is much smaller than what is observed in quadruped apes. This would indicate that the Toumai head was positioned directly atop a vertical spine, as would be expected in an upright biped.

In summary, CT is now used to acquire serial cross-sectional image data from fossil specimens in a noninvasive way. Using 3D visualization software, for instance, Amira (http://www.amiravis.com), 3D Slicer (http://www.slicer.org) or Mimics (http://www.materialise.com), the fossil fragments are separated from the surrounding matrix with computer tools, the missing parts are replaced by mirror-imaging preserved antimeres, and the distortions are corrected. CT scans transform a real fossil into a virtual object and make it possible for paleoanthropologists to extend the study of fossil specimens from the exterior to the interior so that reconstructions are models that can be discussed within the scientific community and revised when new information becomes available.

Additionally, CT techniques can also be used for the 3D facial reconstruction of human fossil ancestors. Facial reconstruction refers to rebuilding a face from skeletal remains in order to create the physiognomy of the living individual. Traditional facial modeling methods use plasticulture to build up the depth of muscle and skin on the skull (or a cast of the skull) using tissue thickness standards derived from living individuals and cadavers. While these methods can produce useful reconstructions, they are extremely time consuming and subtle details such as wrinkles and skin folds are difficult to include. Computerized methods of 3D facial reconstruction transform scanned 3D skull images into faces that can be easily rebuilt to incorporate different details. Aside from the applications for ancient human reconstructions that are invaluable educational tools, 3D facial reconstruction has obvious importance for forensic investigations.

3.2. Virtual endocast and brain morphology studies in paleoanthropology

An endocast is the impression taken from the inside of a cranium that retains the surface features of the brain. Endocasts supply the most direct evidence for studies of human brain evolution. Analyses of fossil hominin endocasts allow paleoanthropologists to make inferences about functional anatomy, physiology, and phylogenetic relationships [18]. Endocasts can be produced naturally during fossilization, but this kind of natural “fossil brain” is very rare. The specimens used in human brain evolution research are mostly artificial endocasts that are manually produced with plaster, latex, or other materials. Because most hominin fossils are incomplete or filled with heavy calcified matrix, it is difficult to reconstruct the endocast in a real fossil without destroying it. CT and virtual imaging have greatly facilitated developments in paleoneurology. Virtual skulls and endocasts can be used together to facilitate study of the brain/cranial interface.

Overall brain size increase is one of the most important trends documented during human evolution. It is, therefore, very important to get accurate brain size to judge the taxonomic affinities of hominin fossils. 3D graphic measuring tools can be used to accurately determine the size, angles, areas and volumes of virtual endocasts. Cranial capacity estimations based on the CT data are more precise than those determined using the conventional millet seed volumetric method [6,19].

Several early hominin cranial capacities have been re-examined using CT technology. In 1990, Conroy et al. [9] used medical CT scanning to study the Australopithecus MLD 37/38 specimen from Makapansgat, South Africa. This partial cranium contains a heavily calcified, solid matrix. The frontal part of the endocranium and most of the face are missing. Virtual 3D reconstructions were created for the ectocranium and endocranium, and the missing portions of the frontal lobes, occipital lobes, right temporal lobe, and most of the left temporal lobe were modeled. A 425 cm$^3$ cranial capacity was computed for this virtual cranium. This estimate is lower than the previous calculations of 480 cm$^3$ [20] and 435 cm$^3$ [21] based on the ectocranial measurements. In 1998, the partial and distorted Australopithecus Stw505 cranium was virtually reconstructed by Conroy et al., and a cranial capacity estimate of 515 cm$^3$ was obtained from the CT data [9]. In 2007, Falk et al. [22] reconstructed the Australopithecus...
africanus child from Taung, South Africa. The Taung fossil includes a natural endocast that reproduces the external morphology of the right cerebral hemisphere. Previously, the total endocranial capacity of Taung had been estimated at 440 cm³ [23]. Using CT scanning, a new cranial capacity estimate of 382 cm³ and a projected adult capacity of 406 cm³ were determined [22].

Virtual endocasts constructed using CT techniques retain the surface features of the brain and these aspects of brain morphology are important data for paleoneurology studies. In 2005, Balzeau et al. [24] used CT to study the endocranial features of the Mojokerto child, a Homo erectus fossil from Indonesia. The CT images show that Mojokerto has a long and low brain with flat frontal lobes. This is different from the morphology of modern children whose brains are round and high.

In 2003, a new hominin species dating to as recently as 18,000 years ago was found on the Indonesian island of Flores. The type specimen of Homo floresiensis, LB1, is less than one meter tall and has a brain size of 400 cm³. Some researchers suggested that LB1 is a microcephalic or pygmy modern human. In 2005, Falk et al. [25] reconstructed the virtual endocast of LB1 (Fig. 2), and found that the brain shape and the sulcal patterns resembled those of H. erectus. LB1 also has an enlarged left Broca’s area and big temporal lobes – features that are associated with complex cognition and language in modern humans. Although the brain size of LB1 is similar to that of a microcephalic, LB1’s brain morphology resembles that of a normal human in many respects. Comparing the virtual endocast of LB1 with endocasts from H. erectus, H. sapiens, a human pygmy, and a human microcephalic, Falk et al. suggested that H. floresiensis is not a microcephalic or pygmy, and that its morphology reflects capabilities for higher cognitive and language processing.

3.3. Biomechanical analysis of the human skeleton

The bones of modern humans are the hard, rigid supports of the body that protect and house the brain and vital organs. The modern human skeleton represents an end point of several million years of adaptation since our divergence into an independent evolutionary lineage. Early humans had a wide range of morphological and behavioral variations, and analysis of their skeletons provides a temporal context for interpreting living human variation [26].

Early hominins, for example, the Australopithecines, developed massive faces and jaws with large teeth; in modern humans, teeth are smaller and the facial structures and masticatory apparatus are gracile. The reasons for skull variation are not entirely understood. Some scholars suggest that masticatory characters are highly prone to homoplasy and that some aspects of the primate facial skeleton, teeth, and mandible are designed to resist biomechanical loads imposed by chewing [27]. Mavropoulos et al. [28] investigated the structural adaptation of the mandibular bone when subjected to different masticatory functional and mechanical demands during the growth of young rats. The results show that mandibular bone mineral density and trabecular bone structure relate to masticatory function. Soft diets and the consequent reduced forces applied to the mandible resulted in the reduction of bone mineral density as well as reduced volume and thickness of the trabecular bone. In 1991, Daegling and Grine used CT scanning to examine the biomechanical properties of the postcanine mandibular corpus of extant great apes, modern humans, and fossil hominins. He found that the mechanical properties of A. africanus and P. robustus jaws are different in terms of their cortical area and bone distribution. A. africanus utilized less cortical bone than P. robustus [29]. More recently, Fukase [30] demonstrated with micro-CT scans that there are potential relationships between local stress patterns and the external morphology of the mandibular symphysis. Cortical bone was significantly thicker on the lingual than on the labial aspect of the symphysis at all super to inferior levels. Bone is concentrated particularly at the lower lingual aspect of the symphysis, which is thought to experience high concentrations of tensile stress during mastication.

In 1985, the famous early Homo juvenile male skeleton (the ‘‘Nariokotome boy’’ KNM-WT 15000) dating to about 1.5 million years ago was found in West Turkana, Kenya. In 1994, Ruff et al. [31] analyzed his femoral strength using CT. The 3D image showed that the ‘‘Nariokotome boy’’ has less robust cortical bone and a small medullary cavity compared to contemporaneous adult early Homo specimens that are more similar to modern human adults. These observations have implications regarding growth and development, including the prediction of adult skeletal strength from subadult measurements and the expected effects of environmental factors on bone morphology during different periods of growth.

In 2000, the ‘‘Millennium Man’’ fossils dated to 6 million years ago were found in Kenya’s Tugen Hills. In order to reconstruct the locomotory posture, Galik et al. [32] scanned the three proximal femurs and reconstructed the virtual images. Although the ‘‘Millennium Man’’ fossils are similar in size to Pan troglodytes, CT scans of the fem-

Fig. 2. CT virtual anatomy of St. Césaire 1 Neanderthal cranial vault injury. (a) Showing the site of trauma (+) and a healed fracture (Δ) [15]; (b) 3D reconstruction of a Norris Farms site tibia showing the triangular and bifacial arrowhead through the bone layer [37].
oral neck-shaft junction reveal that the cortex is markedly thinner superiorly than inferiorly. This differs from the nearly equal cortical thicknesses observed in living African apes. It is more similar to the structure seen in later hominins and suggests that “Millennium Man” was bipedal.

Recently, CT techniques and finite-element analysis have been employed to evaluate the relationship between anatomical structures and the biomechanical characters of modern primate skeletons [33]. On the computer, a finite-element model was assigned the elastic properties of facial bone and loaded with muscle forces corresponding to the moment of centric occlusion during mastication. In this way, it is possible to develop models for living primates to test relative muscle forces and the physical properties of connective tissues. The goal is to use the same methods on extinct species.

3.4. Mummy and early human health studies

Mummies provide excellent opportunities for research in the fields of bioarchaeology and the history of disease [34]. The first CT scan of an Egyptian mummy was conducted in 1977. Using 3D imaging software, scanned mummies can be repeatedly “virtually” unwrapped and dissected, which allows for accurate and detailed documentation of the virtual skin, skeleton, and other contents. The application of CT techniques allows researchers to assess the sex, to estimate stature and age, to verify anatomical abnormalities or pathologies, and to identify artifacts and other foreign objects without having to unwrap and, in the process, destroy the mummy [34].

The life conditions of ancient humans were frequently harsh. Some experiences, such as trauma from violence or accidents, nutritional deficiencies, hormonal abnormalities and diseases, are often imprinted on the human remains. High-resolution CT can clearly display the microanatomy of external and internal structures of hominin fossil skeletons and it is, therefore, a valuable tool for investigating ancient health. In 1998, Spoor et al. [35] scanned the Singa fossil calvaria from the Sudan (dated to 130,000 years ago), to explore the possibility that the unusually shaped cranium was pathologically deformed. The scans revealed that the right temporal bone lacks the bony labyrinth structures of the inner ear. As a result, the Singa individual experienced considerable impairment. In 2002, Zollikofer et al. [15] studied the cranial vault of the St. Césaire 1 Neanderthal. 3D images revealed a healed fracture where the external lamina of the bone is rounded toward the medial wound margin, and the diploic region is covered with cortical bone, and the dislocated parts of the internal lamina were fixated, probably through the formation of connective tissue in the diploic region (Fig. 2(a)). The authors argue that St. Césaire 1 survived at least some months after the injury. It is possible that the cranial injury was inflicted with a stone tool during an act of violence between social groups.

In 2005, Ryan and Milner [37] reconstructed a chert arrowhead lodged inside the tibia by using a high-resolution CT scan (Fig. 2(b)). The arrowhead is triangular and bifacial worked. 3D reconstruction shows the arrow’s probable trajectory through the bone and that the bony layer surrounding the arrowhead shows signs of bone remodeling. This person did not experience any great disability after the injury healed. Most recently, in 2008 Shang et al. [38] analyzed the internal structure of the frontal and parietal bones of the Homo erectus cranium from Lantian. 3D images show that the superficial irregularities of the specimen are due to postmortem taphonomic alterations of the bone and not pathological processes.

3.5. Skeletal and dental microanatomical structures

High-resolution CT scanners can clearly display skeletal and dental microanatomical structures. They are particularly useful tools for studying the delicate internal features of structures such as the paranasal sinuses (Fig. 3(a)), the bony labyrinth of the ear (Fig. 3(b)), and the microanatomy of teeth (Fig. 3(c), (d)).

The paranasal sinuses are internal bony cavities surrounding the large nasal cavity and are located within the frontal, ethmoid, maxillary and sphenoid bones. Variations in the size and form of these sinuses have proven to have evolutionary and clinical significance. In 2001, Manzi et al. [39] analyzed the frontal sinus of the Saccopastore 1 Neanderthal skull using CT methodology. They found that the development of the sinus was related to the postorbital bar in fossils antedating Homo sapiens. Further research showed that maxillary sinus size correlates well with craniofacial size in all primates, including humans [40,41]. In 2003, Prossinger et al. [42] virtually reconstructed the frontal and sphenoid sinuses of three Middle Pleistocene crania from Steinheim, Petralona and Kabwe (Broken Hill). The 3D images show that the paranasal sinuses of early humans vary by geographical region. The sinuses of the European (Steinheim and Petralona) and African (Kabwe or Broken Hill) specimens differ in the degree of pneumatization. The frontal sinuses of the two European fossils extend laterally beyond the orbital rims.
At their outermost extension, they are separated by two very thin compact surfaces of the sphenoid and frontal bones from the sphenoid sinuses, which also extend far laterally (Fig. 3(a)).

The bony semicircular canals of the inner ear are a separate sense organ of balance and relate to locomotor behavior. High-resolution CT enables researchers to visualize the structures of the inner ear in detail. Comparisons of this morphology in different species can provide potential clues regarding the emergence of new locomotor behaviors. In 1994, Spoor et al. [43] reconstructed the inner ear structures of *Australopithecus* and *Homo erectus*. The 3D images show that the morphology of the bony labyrinth in *Australopithecus* is close to that of great apes, and the semicircular canal dimensions in *Homo erectus* are similar to those seen in modern humans. Studies of the Neanderthal bony labyrinth (Fig. 3(b)) revealed that it is different from European Upper Paleolithic and early modern humans [44,45]. Compared with recent humans the bony labyrinth of Neanderthals has an anterior semicircular canal arc which is smaller in absolute and relative size, is relatively narrow, and has more torsion. The posterior semicircular canal arc is smaller in absolute and relative size as well, it is more circular in shape, and it is positioned more inferiorly relative to the lateral canal plane. The European Upper Paleolithic and early modern humans are most similar in their morphologies. The functionally important arc sizes of the Neanderthal semicircular canals may reflect a pattern of head movements different from those of modern humans. The difference may possibly relate to aspects of locomotion and the kinematic properties of the Neanderthal head and neck [44].

Tooth enamel thickness has long been considered to be an important characteristic for distinguishing humans and apes. In 1991, Grine et al. [50] used CT to delineate clear boundaries between the enamel and the dentine in fossil teeth and to accurately measure enamel thickness in living primates. Later studies used micro-CT scanning to compare the enamel thicknesses of hominoid fossils [51–53].

### 4. Recent CT applications in China

In the 1980s, CT scanning was first applied to aid medical examinations in China. Currently, the CT technique is widely used in many fields, including pathology, archaeology, medicolegal cases, aviation, the automobile and steel industries, petroleum geology, paleontology, and security.

In the early 1990s, medical CT was first used for paleontology research in China. In 1994, Zhang et al. [54] used medical CT to study the brain endocasts of *Sinoconodon youngi* and *Dusungaripterus weii*, and they were able to find the sieve plate between the cranial and nasal cavities. Later, the CT technique was applied to the study of vertebrate fossils [55,56]. Zuo et al. [57] measured a dinosaur egg using CT, and obtained data on the egg cell, egg white, yolk and blastodisc. Zhou et al. [58] presented 3D images of the palatal structures of a psittacosaur specimen. In recent years, researchers expanded the application of CT in Chinese paleontology. By combining CT with 3D imaging software, the internal morphologies of some important fossils were reconstructed [59].

Currently, the use of CT on human subjects mainly focuses on modern humans. In addition to CT use for clinical examination and cranial reconstruction, as mentioned above, some research institutes are conducting studies of digitized visible humans, facial reconstruction, and mandi-
ble and tooth finite-element analysis [60–63]. The digitized visible human is also called the “virtual human”. Using CT scanning, cross-sectional images of a complete human cadaver were the basis of a 3D reconstructed human model. This highly accurate model is used to describe and study the anatomy and functioning of the human body [60]. In 2003, Pang et al. [61] reconstructed the 3D head and neck region of the first Chinese visible human. The nose, lips, ears, foramen ovale, foramen spinosum, pituitary gland, brain stem, cervical marrow, sphenoid sinus, and nasopharynx could be displayed in detail in the 3D reconstruction. Some researchers used CT scanning to do facial reconstruction on unclaimed bodies or skeletons from archeological tombs to aid in forensic case studies or to create visualizations of eminent historical people [62]. Compared with some other countries, the use of CT technology in paleoanthropology came later in China. In 2004, a Chinese–French team [64] used medical CT to scan and reconstruct the Yunxian 2 Homo erectus cranium. They estimated the cranial capacity to be 1065 cm$^3$. Limited by the resolution of medical CT, the brain endocast of the fossil was not clearly imaged. In 2007, the first author of the paper, and her colleagues [65] studied the Liujiang Homo fossil cranium with high-resolution industrial CT and obtained clear images of the exterior and interior structures (Fig. 4). More information pertaining to the phyletic position of Liujiang was derived from this new research.

5. Questions and future perspectives

The use of CT technology to conduct research on hominin fossils is just beginning in China. Many fundamental projects still need to be done. For instance, there are distorted fossils that await virtual correction and repair of missing portions, and studies of microanatomical structures that can only be achieved through CT analysis.

In recent years, many Chinese hospitals and research institutes purchased CT scanning equipment. These include Beijing 301 hospital, Capital Normal University, the Institute of High Energy Physics of the Chinese Academy of Sciences, and the Beijing University of Aeronautics and Astronautics. These CT facilities are mainly used for the examination of hospital patients or for industrial productions. The suitability of medical CT for the study of hominin fossils is limited by its low X-ray dosage that is unable to penetrate highly mineralized and matrix-filled specimens. The advantage of industrial CT is that the resolution is very high, but the scanning speed is slow. It is, therefore, a very long process to completely scan a fossil. The Institute of High Energy Physics, the Institute of Automation, and the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences are collaborating on a series of CT scans for paleontology studies. The equipment employed for this project has high space and density resolution with two different X-rays: one has a strong X-ray source for big fossils, and the other one has a tiny X-ray source for small fossils. The CT scans are scheduled for the end of 2008.

Compared with most other countries, the hominin fossil record of China is very rich. In the past 80 years since Pei Wenzhong found the first Zhoukoudian Homo erectus cranium in 1929, more than 100 Paleolithic sites were found in China. Many of these have yielded rather complete human cranial fossils; hominins were discovered at Yuanmou, Lantian, Hexian, Tangshan, Yunxian, Dali, Jinniushan, Maba, Xujiauao, Dingcun, Huanglong, Shandingdong, and Ziyang. Although CT has been used to examine fossils since the early 1980s, it has been rarely used to investigate those found in China. Currently, the morphological studies of these fossils are mostly restricted to the exterior of the specimens. With CT scanning and 3D visualization techniques now available to reconstruct virtual specimens, it is possible for Chinese hominin paleontologists to collect more information about our national treasures. CT techniques will undoubtedly have significant influence on future Chinese paleoanthropological research.

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