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Comparing methods for estimating cranial capacity in incomplete human fossils using the Jingchuan 1 partial cranium as an example

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ABSTRACT

Cranial capacity is one of the most important features used in hominin taxonomic and morphological analyses. For complete or nearly complete modern human crania, the traditional methods of estimating cranial capacity include filling the vault with seeds, the water displacement method, and the use of regression formulae based on craniometrics. For incomplete human fossils, cranial capacities are estimated by reconstructing endocasts manually or virtually or by using existing modern human skull regression formulae; however, the accuracies of these methods are usually dubious. To find a more accurate way of estimating cranial capacity of partial skulls, seven different estimation methods are compared, including the manual reconstruction of the endocast, models built on skulls and models built on endocasts. We then estimated the cranial capacity of a fragmentary Late Pleistocene cranium, Jingchuan 1. The models are tested on 30 modern human skulls, three *Homo erectus* fossils and one Late Pleistocene *Homo sapiens* fossil. In terms of estimating the cranial capacity of the fossil humans, our results indicate that the cranial capacity estimates based on endocasts are more precise than those from exterior skull dimensions, that multivariate models are better than univariate ones, and that the new models using PCR and PLSR have the smallest errors (<50 ml). From the seven methods, the cranial capacity of Jingchuan 1 is estimated to be 1630 ml, 1505 ml, 1533 ml, 1468 ml, 1512 ml, 1470 ml, and 1457 ml, respectively. The most reliable results for the Jingchuan 1 cranial capacity are between 1470 and 1457 ml, and the average is 1464 ml. This study has direct applications to future studies of cranial capacity variation and brain evolution in fossil and modern humans.

1. Introduction

Cranial capacity, the volume of the cranium interior, is used to represent brain size in morphometric studies. Cranial capacity is one of the most important comparative features in human evolutionary research. For complete modern human skulls, the methods commonly used to estimate cranial capacities include various packing methods employing seeds or other small objects, water displacement or volume measurement (Morton, 1849; Stewart, 1934; Tildesley, 1948; Ricklan and Tobias, 1986) or regression formulae derived from modern skulls (Lee and Pearson, 1901; Olivier et al., 1978; Hwang et al., 1995).

In human fossils that are well-preserved and nearly complete, such as the Zhoukoudian *Homo erectus* specimens and the Liujiang 1 late Pleistocene *Homo sapiens* specimen, cranial capacities are estimated by reconstructing the endocasts manually or using CT technology (Weidenreich, 1936, 1937; Wu et al., 2008). However, for broken or incomplete specimens, the above methods are not useful, and many errors may be introduced due to poor preservation or the need to estimate landmarks. This often results in widely different estimates for the same specimen (Holloway, 2004, 1983, 1973). For example, the endocast of the australopithecine Stw-505 has been reconstructed many times, and its estimated cranial capacity ranges between 515 and 626 ml using different methods (Conroy et al., 1998; Lockwood, 1999). The 110-ml difference between the minimum and maximum estimates is >20% of the

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potential capacity. Clearly, there is a need for more precise methods of cranial capacity estimation, and many mathematical models have been proposed.

The basic mathematical models include the simple linear regression model (SLR) and the multiple linear regression model (MLR), based on exterior skull or endocranial cast measurements (Cameron, 1928; Jorgensen and Quaade, 1956; Wolpoff, 1981). Formulae derived from external cranial measurements were the most popular methods because of their convenience (Isserlis, 1914; Hwang et al., 1995; Manjunath, 2002), but special structures on the cranium, such as superciliary arches, external occipital protuberance, and bone thickness, can cause inevitable errors in estimating the cranial capacity. Models based on endocast or endocranial measurements can eliminate this problem to a certain extent. Anthropologists first developed this correction technique using roentgenograms to obtain the length, width and height of the internal cranium (Hoadley and Pearson, 1929; Haack and Meihoff, 1971; Kaufman and David, 1972). However, in doing so, specialized equipment is needed and only a few chord lengths can be measured. With the development of CT technology, virtual endocasts were reconstructed, and more details on the surface of the endocast that used to be difficult to obtain from traditional morphometrics were acquired (Weber et al., 2000; Bruner et al., 2003). Additionally, the surface area and the volume are now easily quantified using 3D software applications (Márquez and Laitman, 2008; Isaza et al., 2014).

Traditional linear models have a drawback involving the selection of the variables. When dealing with multi-collinearity, the situation where many measurements are correlated with each other, it is very difficult to choose which variables to use or to discard. A different selection of variables will make a difference in the ultimate prediction (Wold et al., 1984). To compensate for that issue, we also used Principal Component Regression (PCR) and Partial Least Squares Regression (PLSR) in building our models. PCR has many advantages over the traditional linear regression methods, including reducing the multi-collinearity, by analyzing more variables simultaneously. However, PCR only analyzes independent variables; thus, the extracted principle components may not truly reflect the relationship between the independent and dependent variables (Jolliffe, 1982; Carrascal et al., 2009). PLSR is quite similar to PCR, but it can offer further improvement for our purposes. PLSR is a relatively new multivariate statistical method that has developed rapidly in recent decades. This method was first developed in 1984 (Wold et al., 1984), and its principle basis is equivalent to principal component analysis and canonical correlation analysis (Geladi and Kowalski, 1986; Wang, 1999). As in canonical correlation analysis, PLSR also analyzes the relationship between the independent variables and the dependent variables. This means that the components extracted from the dependent variables are more related to the independent variable (Gil and Romera, 1998), i.e., cranial capacity in our study. Although PLSR has a short history, it has been used widely in many fields (Wold et al., 2001; Nguyen and Rocke, 2002; Liu et al., 2008). Its application to paleontology is rare, and this is the first trial use in paleoanthropology.

Jingchuan 1 is a partial human fossil cranium discovered in Niujiaogou, on the left bank of the Jingchuan river in Jingchuan County, Gansu Province (Liu et al., 1984). It was unearthed in dust-colored sandy clay associated with a typical Late Pleistocene mammalian fauna. The age of Jingchuan 1 is approximately 15 ka to

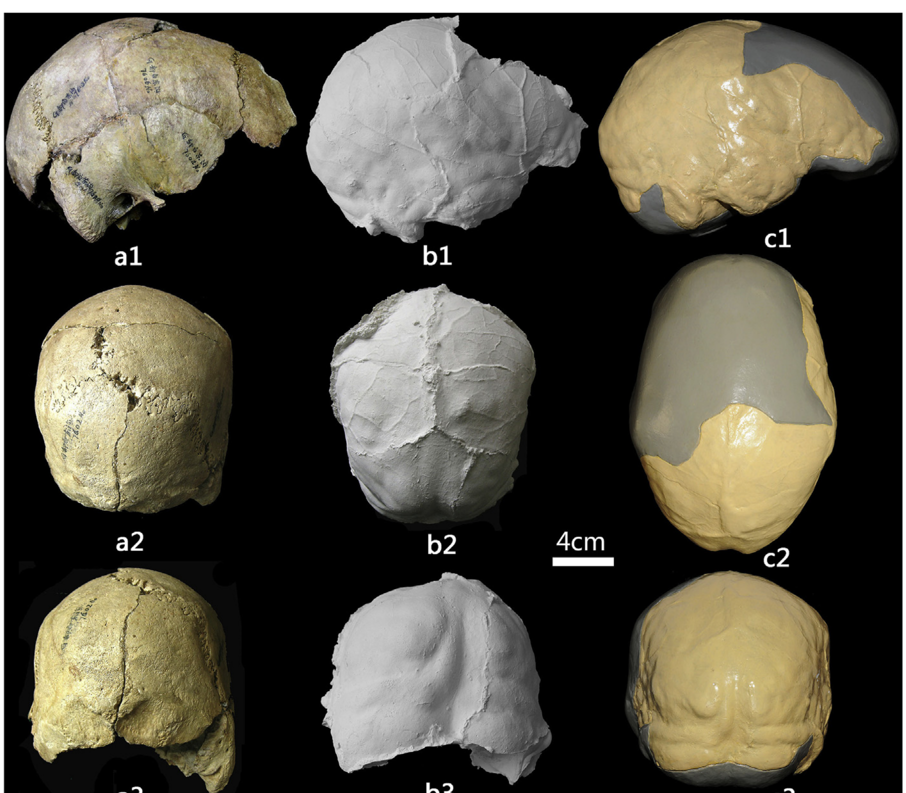

Fig. 1. The Jingchuan 1 cranium (a), the original endocast (b), and the full reconstructed endocast (c). a1, b1, c1: right lateral view; a2, b2, c2: posterior-superior view; a3, b3, c3: occipital view. The gray areas in c1–c3 are reconstruction.