

1. Introduction

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The study of the external tooth morphology can be undertaken in a non-destructive and relatively inexpensive manner. All one needs are good eyes (or a good hand lens), a decent set of calipers and a good single-lens reflex (SLR) or digital camera to keep a permanent record. As such, gross morphology (including size and shape) has long been a subject of interest to paleoanthropologists. Measurements also have a long-standing role in assessing human evolution (Wolpoff, 1971; Frayer, 1977; Brace et al., 1987; e.g., Bermúdez de Castro and Nicolás, 1996). The assessment of metric variation in living modern humans has also been applied to questions of modern populations (Hanihara and Ishida, 2005). Simple measurements of tooth length and breadth can be used to obtain broad morphological characterizations (e.g., crown indices and crown areas). However, tooth size does not discriminate well between closely related hominin species and appears to be under greater environmental influence than crown morphology (Townsend and Brown, 1978). Consequently, it may be

less useful for addressing hominin evolutionary relationships.

The bumps and grooves that make up the tooth surface are more challenging to quantify than are dental metrics. Attempts to quantify morphological variation include the study of relative cusp areas (Wood and Abbott, 1983; Wood and Uytterschaut, 1987; Wood and Engleman, 1988; Bailey et al., 2004; Moggi-Cecchi and Boccone, 2007), cusp angles (Morris, 1986; Bailey, 2004), crest lengths (Pilbrow, 2003; 2007), as well as non-metric traits. Discrete, non-metric traits (e.g., shovel-shaped incisors, Carabelli's cusp) have a long history of use in characterizing modern human populations (Hrdlička, 1920; Pedersen, 1949; Turner and Scott, 1977). They have also played an important role in human evolutionary studies (Hrdlička, 1911; Weidenreich, 1937; Robinson, 1954; Grine, 1985; Suwa et al., 1996). However, the systematic study and application of dental non-metric traits to questions of human evolution has grown since standards were developed (Dahlberg,

1956) and made readily available to the public (Turner et al., 1991). These standards have helped to ensure that researchers are all talking about the same thing, facilitating comparative studies of contemporary (Lukacs, 1984; Turner, 1985; Sofaer et al., 1986; Hanihara, 1989; Irish and Turner, 1990; Turner, 1990; Turner, 1992; Irish, 1994; Hawkey, 1998) and fossil (Crummett, 1994; Bailey, 2002b; Irish and Guatelli-Steinberg, 2003) humans.

Some of the issues of interest in human evolutionary studies include assessing intra- and inter-specific variability, identifying and diagnosing taxa, and working out phylogenetic relationships among extinct fossil species. The application of dental morphology to these questions has come a long way since the days when the primary focus was on shovel-shaped incisors and taurodont molars. Researchers have accumulated large quantities of data on many non-metric trait frequencies in living modern humans. There is less information, however, on the morphometric variation among and within extant ape species (Uchida, 1996; Uchida, 1998a; Uchida, 1998b; Pilbrow, 2006). Assessing variation within and between species of extant apes is important if we are to successfully use dental morphology to identify the number of species represented in a particular fossil collection. Here, Pilbrow uses dental morphometrics (length, breadth and crest lengths) as a proxy for morphological variation to examine variation in extant apes. This marks a significant step forward in understanding intra- and inter-specific variation in our closest living relatives, and in making predictions about what we might expect to find in early hominins.

In the 1980s Wood and colleagues investigated dental morphological variation in early (Plio-Pleistocene) hominins using cusp areas and a limited number of morphological traits (Wood and Abbott, 1983; Wood et al., 1983; Wood and Uytterschaut, 1987; Wood and Engleman, 1988). Since then, technological advances (e.g., digital imaging and image

analysis) have made the collection and manipulation of large amounts of data more feasible. In addition, many new fossils from this time period have been uncovered.

Bailey and Wood move beyond previous studies of Plio-Pleistocene dental morphology that relied solely on modern human standards (Irish, 1998; Irish and Guatelli-Steinberg, 2003), and incorporate several new traits in their analysis of dental evolution within the hominin clade. They conclude that some of the dental trends (e.g., morphological simplification) said to be characteristic of *Homo* appear relatively late in human evolution. However, a more accurate assessment of hominin dental evolution will come only after scoring standards that incorporate variation observed in Plio-Pleistocene hominins are developed.

Moggi-Cecchi and Boccone use new digital imaging and analysis techniques to assess upper molar morphometric variation of the expanded South African Pliocene fossil hominin record. Their results support trends and characterizations suggested previously by Wood and colleagues, but they also note a great deal of size variability in the expanded *A. africanus* sample. Studies in inter- and intra-specific variation in extant apes (e.g., Pilbrow, 2007) may ultimately help work out the significance of this variation.

The dentition has traditionally played a less prominent role in studies of later human evolution (Middle and Late Pleistocene) than it has in earlier human evolution. This may be because later hominins (e.g., Neandertals) have been assumed to have teeth that are indistinguishable from our own. Recent studies showing that teeth are important tools in assessing later human evolution (e.g., Bailey, 2002a, 2004, 2006; Bailey and Lynch, 2005), as well as the discovery of large samples of well-preserved European Early and Middle Pleistocene fossil hominins have led to a renewed interest in dental variation during this important time period. Here, Martínón-