Appendix 1. Relative enamel thickness, enamel volume, cuspal thickness, and estimated formation times of MSA fossil hominin teeth.

<table>
<thead>
<tr>
<th>Tooth code</th>
<th>Tooth</th>
<th>2D RET</th>
<th>Vol. (mm³)</th>
<th>Cusp</th>
<th>Thick. (µm)</th>
<th>Cusp time (days)</th>
<th>PK</th>
<th>CFT – 7 (days)</th>
<th>CFT – 8 (days)</th>
<th>CFT – 9 (days)</th>
<th>CFT – 8 (yr)</th>
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<tr>
<td>SAM-AP 6242</td>
<td>RLM1</td>
<td>16.29</td>
<td>195.0</td>
<td>mb 1100</td>
<td>355</td>
<td>93</td>
<td>1006</td>
<td>1099</td>
<td>1192</td>
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<tr>
<td></td>
<td>ml 800</td>
<td>273</td>
<td>80</td>
<td>833</td>
<td>913</td>
<td>993</td>
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<td></td>
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<td>1191</td>
<td>3.03</td>
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</tr>
<tr>
<td></td>
<td>dl 1200</td>
<td>381</td>
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<td>941</td>
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<td>SAM-AP 6277</td>
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<td>258.4</td>
<td>mb 1135</td>
<td>364</td>
<td>&gt; 88</td>
<td>938</td>
<td>1018</td>
<td>1098</td>
<td>2.79</td>
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<tr>
<td></td>
<td>ml 1190</td>
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<td>80</td>
<td>955</td>
<td>1036</td>
<td>1117</td>
<td>2.84</td>
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<td></td>
<td>db 1350</td>
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<td>&gt; 67</td>
<td>1060</td>
<td>1156</td>
<td>1252</td>
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</tr>
<tr>
<td></td>
<td>dl 1230</td>
<td>388</td>
<td>81</td>
<td>1198</td>
<td>1286</td>
<td>1374</td>
<td>3.52</td>
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<td>ml 1730</td>
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<td>&gt; 70</td>
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<td></td>
<td>dl 1990</td>
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<tr>
<td></td>
<td>ml –1350</td>
<td>417</td>
<td>&gt; 60</td>
<td>1198</td>
<td>1286</td>
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<td>1374</td>
<td>3.52</td>
<td></td>
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</tr>
</tbody>
</table>

Notes:
- Tooth code: given in primary references (see text). Tooth: RLM, right lower first molar; LLM, left lower first molar; RLM3, right lower third molar. 2D RET: relative enamel thickness, a scaled measure of enamel thickness derived from a plane across the mesial dentine horn tips; values are dimensionless. Vol.: enamel volume calculated from high-resolution mCT slices (see text). Cusp: the position on the tooth crown; mb, mesiobuccal cusp; ml, mesiolingual cusp; db, distobuccal cusp; dl, distolingual cusp. Thick.: cuspal thickness measured from mCT slices. Cusp time: cuspal formation time, calculated by entering the cuspal enamel thickness into a regression formula for modern human teeth. PK: Perikymata numbers, manifestations of long-period growth lines on the enamel surface counted from casts of the original teeth. CFT – 7: cuspal time plus the total number of perikymata multiplied by 7, the most common minimum periodicity value found in a large sample of modern humans. CFT – 8: cuspal time plus the total number of perikymata multiplied by 8, the mean periodicity value found in a large sample of modern humans. CFT – 9: cuspal time plus the total number of perikymata multiplied by 9, the most common maximum periodicity value found in a large sample of modern humans. *Grine had originally identified SAM-AP 6282 as a second molar, but this was changed during the current study due to lack of a distal facet and its slightly diminutive size.

**Taxonomy and barcoding: conflict or companions?**

Gideon F. Smith*, Jacobus P. Roux#, Krystal Tolley* and Ferozah Conrad

The technology of gene sequencing should be used to complement and enhance traditional taxonomic practices.

Many natural history museums, herbaria and other biodiversity organizations have a proud history of engagement in taxonomic work. The scientific output that has been and continues to be produced by taxonomists, much of it through the corporate publication series of their respective institutions, covers the entire range of stakeholder interests, from peer-reviewed scientific papers and books to popular articles. In this way, taxonomists serve a broad cross section of the communities among whom they operate. More recently, many taxonomists have started to embrace the possibilities offered by the internet and have contributed to the dissemination of biological information through websites that run and host electronic columns with biodiversity information, some including interactive identification tools.

Critical components of the core functions of taxonomists include conducting priority research, the identification of biological specimens, maintaining databases, curating scientific collections, and participating in corporate programmes such as the compilation of inventories of the biota of a country or region. Taxonomists are predominantly skilled natural historians and their knowledge is basic to numerous non-taxonomic projects.

At the South African National Biodiversity Institute (SANBI), taxonomy underpins projects and programmes involving climate change, seed and gene bank development, bioprospecting, horticulture, vegetation science, bioregional planning, systematics, Red Data Listing, and environmental education and outreach. As one example, almost 30% of the Southern African Red Data List assessments completed under the auspices of the Southern African Botanical Diversity Network (SABONET) were conducted by taxonomists. Collectively, therefore, taxonomists contribute fundamentally to virtually all of SANBI’s research and many associated endeavours.

Before the promulgation of the National Environmental Management: Biodiversity Act (No. 10 of 2004) on 1 September 2004, SANBI’s focus was primarily on plants. The new act, however, expanded the institute’s mandate to include all of South Africa’s rich biodiversity. To meet this mandate, SANBI is about to engage more actively those bodies that hold significant preserved and other collections of this biodiversity. SANBI is able to do this from a strong position, given its significant achievements in plant taxonomy. The institute is committed to maintaining and strengthening its taxonomic research while also exploring new initiatives, including the use of DNA sequences to refine existing classifications.

**Enter a new technology**

Taxonomy essentially describes, documents and classifies biodiversity, and is critically important to virtually all conservation efforts. During the past two decades, environmentalists have become acutely aware of the deterioration of the environment and the disturbing number of species that go extinct as a result of our unsustainable use of natural resources. This has sparked the need to document global biodiversity before it is too late and to set in train numerous taxonomic initiatives.

More recently, DNA ‘barcoding’ has been advocated as a way to catalogue biodiversity (e.g. ref. 1). In 2004, the Consortium for the Barcode of Life (CBOL) was established as an alliance of biodiversity research institutions including museums and herbaria, private sector
companies, NGOs and government departments. The aim of CBOL is to compile a comprehensive sequence database of all described species, preferably associated with voucher specimens with which sequences of sampled individuals can be compared.\(^2\) In February 2005, CBOL held its first international conference at the Natural History Museum, London, which brought together delegates from research institutions, NGOs and representatives from government departments to discuss ‘accelerating the development and application of barcoding technology’ (www.barcodinglife.org).

Taxonomists working with natural history and herbarium collections now feel obliged to consider involvement in the much publicized and sometimes severely criticized barcoding initiative. The central principal of barcoding involves creating a comprehensive, standardized database of DNA sequences of at least one reference gene (for instance, mitochondrial cytochrome c oxidase I, or COI) for every species. Thus, barcoding has come to mean devising a standardized COI catalogue for all species. As pointed out by Moritz and Cicero,\(^2\) ‘there is nothing fundamentally new in the DNA barcoding concept, except increased scale and proposed standardization.’ The purpose and uses of barcoding seem more nebulous, however, although its proponents have suggested it could be used for identifying species and for discovering new ones.\(^3,4\) Nevertheless, opponents view barcoding as technology-propelled rather than scientifically and taxonomically driven, and that it will further erode the already meagre financial and human resources available to taxonomy.\(^5,6\)

Some scientific journals have recently devoted pages to the debate (for example, Systematic Biology, Trends in Ecology and Evolution, and Proceedings of the Royal Society of London). The result has been thought-provoking but controversial commentaries either advocating the proposed uses (e.g. ref. 1) or pointing out their limitations, pitfalls, and abuses (e.g. refs 2, 6). We grant that DNA barcoding has limitations, but can we afford to ignore it? Using the barcoding technology for the sake of species identification seems too limited in scope. Furthermore, barcoding used alone for the identification and discovery of species based on a single DNA sequence would be irresponsible. Species concepts and the characters used for describing species are controversial enough, without trying to define, identify, and classify species based on a DNA sequence of a single gene. There are inherent dangers in this approach: a gene sequence is essentially a single taxonomic character, and can show ancestral polymorphism in two closely related species. Thus, a single gene sequence will not always have the resolution required to distinguish between two species. Most phylogenetic studies currently make use of several genes, often a combination of nuclear and mitochondrial genes to gain the resolution required to identify genetic lineages.

Despite the controversy surrounding barcoding, the practice has managed to build up momentum. Rather than trying to oppose the concept, perhaps the question to ask is how we can harness it for purposes that will advance taxonomy and systematics. In effect, should we not be putting our energy into integrating these large-scale sequence data sets with the more traditional taxonomic data to create comprehensive assessments of biodiversity? This method, termed ‘integrative taxonomy’,\(^7\) seems a responsible approach to using barcoding for taxonomic purposes. The aim is to use all characters and data available, including, but not limited to DNA sequences, to ‘… delimit, discover, and identify meaningful, natural species and taxa at all levels.’\(^7\)

Barcoding is not going away, given the resources already devoted to it. If the momentum it has created raises taxonomy’s scientific profile, this could be used to highlight the need for training taxonomists and supporting taxonomic research and natural history institutions. One way forward is to make a concerted effort among the scientific community for an integrated approach to taxonomy, but one that does not lose sight of the biology behind the DNA sequence.