Sober, E. 2004. The contest between parsimony and likelihood. Syst. Biol. 53:644–653.
Swofford, D. L., G. J. Olsen, P. J. Waddell, and D. M. Hillis. 1996. Phylogenetic inference. Pages 407–514 *in* Molecular systematics (D. M. Hillis, C. Moritz, and B. Mable, eds.). Sinauer Associates, Sunderland, Massachusetts.
Urbach, P. 1991. Bayesian methodology: Some criticisms answered. Ratio (New Series) IV:170–184.

First submitted 24 March 2004; reviews returned 19 May 2004; final acceptance 22 February 2005
Associate Editor: Paul Lewis

Syst. Biol. 54(5):841–844, 2005

ISSN: 1063-5157 print / 1076-836X online
DOI: 10.1080/10635150500354894

DNA Barcoding: Perspectives from a "Partnerships for Enhancing Expertise in Taxonomy" (PEET) Debate

VINCENT S. SMITH

Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, USA; E-mail: vsmith@inhs.uiuc.edu

Responding to a decade of scientific and political discussion during the 1980s, the United States, under the auspices of the U.S. National Science Foundation (NSF), initiated a series of programs that would directly impact taxonomic research. The Biotic Surveys and Inventories program and PEET (Partnerships for Enhancing Expertise in Taxonomy) were the first of several program announcements of particular relevance. Of these, PEET warrants particular attention, because it has been championed by some as a model for the future of taxonomic research (Rodman and Cody, 2003). Focusing on training and building electronic infrastructure in the context of taxonomic revisions and monographs, PEET provided a vital infusion of cash into a field of research that had been starved of resources. Crucially, PEET along with related programs supporting systematic biology, gave United States–based institutions the confidence to hire permanent staff to support these efforts. Almost a decade on from the first PEET awards, Rodman and Cody (2003) proclaimed that the "taxonomic impediment" (Taylor, 1983) had been overcome, advocating PEET and related programs as a model to redress the recent global decline of taxonomic research. Yet despite PEET and a handful of similar initiatives worldwide, many of the underlying problems for taxonomic research programs persist (Godfray and Knapp, 2004), and an increasingly vocal group of taxonomists are not shy in pointing this out.

The pace of change in the molecular and phylogenetic communities is so fast that traditional taxonomic practice is struggling to keep up. From the inception of the GenBank genetic database back in 1982 until the close of 2004, over 40 million genetic sequences for 125,063 species have been deposited (NCBI, 2005). Of these, about 90% of the sequences have been added in the last 5 years. By contrast, circa 1.7 million species have been described by traditional taxonomic means to date, and at present rates this list is accruing about 10,000 additional taxa per year (May, 2004). However, it has taken traditional taxonomy about 250 years to get this far, and still only accounts for somewhere between 10% and 50% of the estimated global species diversity. Crude comparisons such as this are unfair, belittling the fact that each of these 1.7 million described species is a tested hypothesis, but they underscore the scale of a problem that the taxonomic community must face. Good biological taxonomy fundamentally benefits science and ultimately society, but as fresh demands are placed on the taxonomic community, it is not certain that taxonomy as practiced today can fulfil these needs. For some biologists the solution is not a modernized resurgence of traditional taxonomy as envisioned by PEET. It has been argued that such initiatives, even on a global scale, would still be woefully inadequate to keep pace with the demand for taxonomic data. For some, a more radical solution is required and amongst the possibilities one concept in particular has captured the imagination of the biological community.

DNA barcoding, a concept so profound it can be expressed in just two words has created a storm of controversy that fills the pages of many leading science journals (e.g., Blaxter, 2003; Pennisi, 2003; Tautz et al., 2003). Put simply, advocates of barcoding propose to use a small fragment of DNA to describe and discriminate between all life on earth (Hebert et al., 2003). In their eyes this would free biologists from the task of routine identifications, revitalize the role of biological collections, and leave taxonomists to get on with the task of collecting and discovering the world's biodiversity. The concept has gained broad acceptance by those working on the least morphologically tractable groups, such as viruses, bacteria, protists, and some fungi. However, its wider application to all taxa is deeply controversial (Holmes, 2004). Many take objection to the name, emphasizing that biological species are not analogous to the unique barcodes of the commercial world. However, concerns

run deeper than this, and are entrenched in political, sociological, and scientific arguments on the desirability and practicalities of such a plan (Pennisi, 2003). At one extreme some taxonomists view DNA barcoding as an Orwellian nightmare that would distil taxonomy to a clustering algorithm viewed through the distorted prism of phenetics. In their eyes this would essentially kill the science of taxonomic research. To others, DNA barcoding will save taxonomy, servicing the rising demands of the molecular and phylogenetics community, whilst instilling new life into an aging institution. For them DNA barcoding would leave a legacy that outlives any single taxonomist and remove the uncertainty that besets traditional taxonomy. Doubtless, many will take issue with the way I have characterized the debate. In truth a spectrum of positions exist between these extremes, but they serve to underline the fundamental disagreement amongst many taxonomists.

Central to the arguments over DNA barcoding is a growing tension within the taxonomic community between those that stress taxonomy's value as a science, and those that emphasize its value as a service (Lipscomb et al., 2003). To most practicing taxonomists it is self-evident that taxonomy is clearly both. However, there has been a tendency by both DNA barcoding advocates and dissenters to disproportionately focus on one or the other of these values, perhaps in tune to the demographic of their respective audiences. Barcoding advocates are typically (but not exclusively) drawn from the service side of the discussion. They are often end users of taxonomic data, frustrated with the deficiencies of the present system (Gotelli, 2004) and keen to talk up barcoding's potential. Dissenters are invariably practicing taxonomists in the traditional sense. These scientists are all too familiar with the inherent risks of single-character taxonomy, and have been stung by accusations that their science is just a service to other biologists. The different research backgrounds of these communities has polarized debate and is not helped by suggestions that barcoding might usurp traditional taxonomy. Barcoding advocates (at least recently) stress integration, noting that their methods will compliment existing taxonomic practice (Schindel and Miller, 2005), but this was not the way barcoding was originally sold (Anonymous, 2003; Nicholls, 2003). Some protagonists did envisage a radically different molecular future for taxonomy (perhaps they still do) and advocates for the PEET approach to taxonomy are keen to point this out. However, extreme positions are not just the purview of barcoding activists. Some traditionalists are similarly intransigent in their reluctance to accept any role for molecular data in taxonomic practice, predicting the demise of taxonomy if such a situation were to arise.

The rarefied atmosphere in which discussion on the merits of DNA barcoding has largely taken place has not helped the quality of debate. Indeed, it is fair to say this has created confusion and mistrust on both sides. In an effort to engage these issues head-on, a special debate was convened as part of the fifth PEET conference hosted by the University of Illinois in Champaign-Urbana (http://www.conferences.uiuc.edu/peet/). This biennial meeting funded by NSF is dedicated toward furthering the goals of the PEET initiative and included representation from the 41 active PEET projects throughout the United States. Central to this debate was a series of questions solicited in advance by the session chair (V.S.) from taxonomists worldwide. An advocate for DNA barcoding (Paul Hebert) and another for the PEET taxonomic model (Kipling Will) were invited to discuss these issues in front of this audience. Debate was structured around two propositions fundamental to DNA barcoding and its role in taxonomic research, which were:

(i) Should we devote resources toward sequencing a reference collection of specimens for the development of a DNA barcoding system?
(ii) Should DNA sequences play a primary role in the discovery of new species?

To gauge opinion on the merits of the speaker's arguments, the audience was balloted on these propositions before and after the debate. For the remainder of this article, I briefly provide a précis of some key events at the PEET DNA barcoding symposium.

Hebert and colleagues vision for DNA barcoding is deeply seductive. Based on a principal that is easy to understand, and with an immutable goal that encompasses all life on earth, it is hard not to be carried away with fanciful notions of handheld Star Trek–like devices, capable of delivering instant species identifications. New technologies enabling the sequencing of single DNA molecules (Kurosawa and Washizu, 2004) and constant temperature DNA amplification (Vincent et al., 2004) are on the horizon. If (perhaps that should be "when") successful, these techniques might enable the science fiction fantasy of a Star Trek "tricorder" to become reality. But for the moment, while DNA sequencing is still confined to the laboratory, taxonomists are apt to ask, "What can DNA barcoding do for us?"

Kipling Will's presentation suggested that although identification tools may be a product of taxonomy, they are not the purpose of the discipline. According to Will, identification is just one element of what taxonomists do and to focus on this goal undermines the intellectual content of taxonomy. These remarks echo comments by many leading systematists, not least NSF official and plant systematist James Rodman who was among the audience and is on record as stating "it's not research," (Pennisi, 2003:1697), with respect to DNA barcoding. Hebert tackled this criticism head on, emphasizing barcoding's utility beyond species identification. Species discovery emphatically is research, and in citing examples from his recent Public Library of Science (PLoS) paper (Hebert et al., 2004), Hebert demonstrated how DNA barcoding was used to "discover" several new North American bird species. In this case, not only are the DNA profiles of the 260 sampled birds distinct and identifiable, but they highlight four taxa that might putatively be described as new species. Subsequent to the publication of Hebert

et al.'s PLoS paper, it had emerged that these "new species" have long been suspected by ornithologists as likely new taxa, supporting the case of barcoding role in species discovery. However, one might legitimately ask that if we already knew these were new taxa, did we really need to go to the trouble of screening all these DNA profiles in the first place. Indeed, it has been argued that DNA barcodes are most likely to fail in precisely those cases where they would be most useful—closely related species that are hard to diagnose with other characters (Moritz and Cicero, 2004).

Focusing on methods of taxon identification, a practical demonstration was organized midway through the session to illustrate some of the pitfalls and potential of molecular and traditional methods. Confronted with no more than a networked computer and five unlabeled text files containing DNA sequences, Paul Hebert and a handful of students were tasked with the challenge of identifying each sequence to species. Likewise, the PEET audience, comprising about 100 mainly United States–based taxonomists, was provided with five whole specimens whose identity matched those of Hebert's sequences. They were similarly tasked to identify each specimen, but in this case by somewhat more conventional means. Taxa were carefully chosen by V.S. in advance to match the anticipated taxonomic expertise amongst the audience, but more importantly were selected to illustrate various principals. Among the specimens were an extinct subfossil, for which there was obviously no corresponding DNA; a purposely contaminated DNA sequence to highlight the importance of specimen vouchers; and various other taxa that were either devoid of diagnostic characters, unknown from the United States, and/or were sparsely represented in NCBI's GenBank database. In admittedly difficult circumstances both traditional and barcoding methods performed equally well, each correctly identifying three of the five taxa to the rank of species. Only in one case (that of the European May bug, *Melolontha melolontha* [Linné, 1758]) were both techniques successful, underlining the point that both methods have something distinct to offer when it comes to taxon identification. However, some might be disturbed to note that without any specific training and with minimal resources, the DNA barcoding approach performed as well as that of an audience that have dedicated much of their working life to taxonomy.

At the close of this session, the audience was given the chance to deliver their verdict on the merits of Will and Hebert's arguments by voting for a second time on the two propositions outlined earlier. Notwithstanding minor variation in the apparent number of votes cast, the results (Fig. 1) are in at least one respect surprising. Both the pre- and postdebate ballot delivered a "no" vote to DNA barcoding, reflecting the considerable hostility to barcoding among the PEET audience that persisted throughout the debate. However, the significant rise in the number of abstentions reflected a considerable softening in this stance. On the question of whether resources should be devoted toward sequencing a reference collection of specimens for DNA barcoding, almost a quarter of the audience that originally voted no, switched to abstaining by the end of the debate. Less than one third were left voting against this proposition at the sessions close. A more dramatic switch occurred on the question of whether DNA barcoding should play a primary role in species discovery. By the second vote a small majority (53%) still rejected this proposition, down from almost 70% initially. However, there was a threefold rise in the number of abstentions and almost a quarter of the audience left the room in favor of this proposition. So why the switch? Why did an audience of PEET-funded taxonomists soften their stance on barcoding? I will let you decide. In the Points of View articles

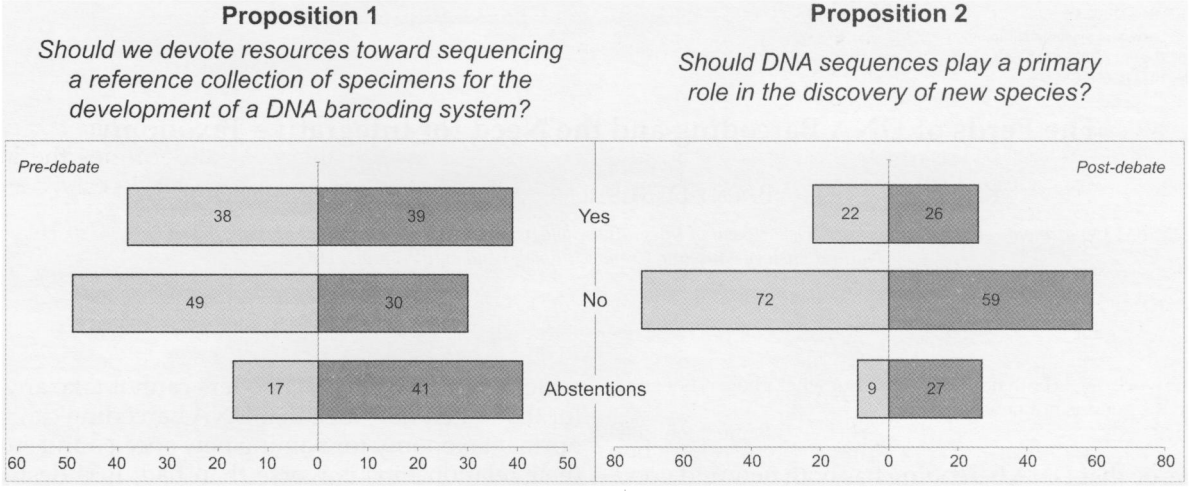

FIGURE 1. Results of the pre- and postdebate votes from the DNA barcoding session at the fifth biennial PEET conference hosted by the University of Illinois in Champaign-Urbana, 20–23 September, 2004. Ballot was by show of hand and the counts include minor discrepancies due to inconsistencies in the votes cast (±3) and size of the pre- and postdebate audience, which gained between six to nine members by the final vote.

that accompany this article, Will and Hebert respond to 10 questions selected by V.S. to reflect the balance of issues raised by the PEET audience (Hebert and Gregory, 2005; Will et al., 2005). Alternatively, you can follow the original debate as all 2 hours of the complete symposium are available to watch as a streaming video from http://streamer.cen.uiuc.edu/seminars/peet/peet2-3-4.wmv (Windows Media Player required).

ACKNOWLEDGEMENTS

I thank Kipling Will and Paul Hebert for taking part in the debate, Mike Irwin and Gail Kampmeier for organizing the fifth biennial PEET conference, and the National Science Foundation for financially supporting this meeting. Kevin Cummings, Martin Hauser, Andrew Miller, Mark Wetzle, and Kazunori Yoshizawa provided specimens and in some cases unpublished DNA sequences that were used during the species identification demonstration in this session. Martin Hauser, Mathys Meyer, Floyd Shockley, Daniela Takiya, and Jamie Zahniser assisted in the running of the debate. The symposium video was filmed and edited by Ritch Strom on behalf of the office of continuing education at the University of Illinois. Rasplus Jean-Yves, Kevin Johnson, Rod Page, Diana Percy, Vincent Savolainen, Jason Weckstein, and an anonymous reviewer provided comments on an earlier (and considerably different) version of this manuscript. This work was supported by a grant from the National Science Foundation (DEB-0107891).

REFERENCES

Anonymous. 2003. What's in a name? Economist 366:62.

Blaxter, M. 2003. Counting angels with DNA. Nature 421:122–124.

Godfray, H. C. J., and S. Knapp. 2004. Introduction [to a theme issue 'Taxonomy for the twenty-first century']. Phil. Trans. R. Soc. Lond. B 359:559–569.

Gotelli, N. J. 2004. A taxonomic wish-list for community ecology. Phil. Trans. R. Soc. Lond. B 359:585–597.

Hebert, P. D. N., A. Cywinska, S. L. Ball, and J. R. deWaard. 2003. Biological identifications through DNA barcodes. Proc. R. Soc. Lond. B 270:313–322.

Hebert, P. D. N., and T. R. Gregory. 2005. The promise of DNA barcoding for taxonomy. Syst. Biol. 54:852–859.

Hebert, P. D. N., M. Y. Stoeckle, T. S. Zemlak, and C. M. Francis. 2004. Identification of birds through DNA barcodes. PLoS Biol. 2:1657–1663.

Holmes, B. 2004. Barcode me. New Scientist 182:32–35.

Kurosawa, O., and M. Washizu. 2004. Acquisition and amplification of targeted position of electrostatically stretched DNA. J. Inst. Electrostat. Jpn. 28:59–64.

Lipscomb, D. L., N. Platnick, and Q. D. Wheeler. 2003. The intellectual content of taxonomy: a comment on DNA taxonomy. TREE 18:65–66.

May, R. M. 2004. Tomorrow's taxonomy: Collecting new species in the field will remain the rate-limiting step. Phil. Trans. R. Soc. Lond. B 359:733–734.

Moritz, C., and C. Cicero. 2004. DNA barcoding: Promise and pitfalls. PLoS Biol. 2:1529–1531.

NCBI. 2005. National Center for Biological Information. GenBank statistics available at http://www.ncbi.nlm.nih.gov/About/tools/restable_stat.html.

Nicholls, H. 2003. DNA: The barcode of life? Originally published on behalf of Elsevier by BioMedNet. Now available at http://www.uoguelph.ca/~phebert/media/BioMedNet%20News%20article.pdf.

Pennisi, E. 2003. Modernizing the tree of life. Science 300:1692–1697.

Rodman, J. E., and J. H. Cody. 2003. The taxonomic impediment overcome: NSF's Partnerships for Enhancing Expertise in Taxonomy (PEET) as a model. Syst. Biol. 52:428–435.

Schindel, D. E., and S. E. Miller. 2005. DNA barcoding a useful tool for taxonomists. Nature 435:17.

Tautz, D., P. Arctander, A. Minelli, R. H. Thomas, and A. P. Vogler. 2003. A plea for DNA taxonomy. TREE 18:70–74.

Taylor, R. W. 1983. Descriptive taxonomy: Past, present, and future. Pages 93–134 *in* Australian systematic entomology: A bicentenary perspective (E. Highley, and R. W. Taylor, eds.). CSIRO, Canberra.

Vincent, M., Y. Xu, and H. Kong. 2004. Helicase-dependent isothermal DNA amplification. EMBO Rep. 5:795–800.

Will, K. W., B. D. Mishler, and Q. D. Wheeler. 2005. The perils of DNA barcoding and the need for integrative taxonomy. Syst. Biol. 54:844–851.

First submitted 23 March 2005; reviews returned 9 June 2005; final acceptance 12 July 2005
Associate Editor: Vincent Savolainen

Syst. Biol. 54(5):844–851, 2005

ISSN: 1063-5157 print / 1076-836X online
DOI: 10.1080/10635150500354878

The Perils of DNA Barcoding and the Need for Integrative Taxonomy

KIPLING W. WILL,[1] BRENT D. MISHLER,[2] AND QUENTIN D. WHEELER[3]

[1]*ESPM Department—Insect Biology and* [2]*Department of Integrative Biology, University of California, Berkeley, California 94720, USA*
[3]*Natural History Museum, Cromwell Road, London, SW7 5BD, UK*

"Your work, Sir, is both new and good, but what's new is not good and what's good is not new."

Samuel Johnson

We argue that DNA barcoding has both new and good elements, but unfortunately no elements that are both. We are strongly in favor of the good idea of using DNA for identification, but that is old hat—the use of DNA for identification goes back to the beginning of molecular systematics. The DNA barcoders cannot take any credit for that. Their new idea that DNA barcoding can replace normal taxonomy for naming new species and studying their relationships is worse than bad, it is destructive. Statements by some barcoding proponents suggest an inevitable replacement of taxonomic research rather than augmentation of technology to taxonomic science, e.g., "a COI-based identification system will undoubtedly