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BARCODING METHODOLOGY AND APPLICATIONS

DNA barcoding and the mediocrity of morphology

LAURENCE PACKER,* JASON GIBBS,* CORY SHEFFIELD* and ROBERT HANNER†
**Department of Biology, York University, 4700 Keele Street, Toronto, Ontario, Canada M3J 1P3, †Biodiversity Institute of Ontario and Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1*

Abstract

A small but vocal community of critics has questioned the epistemological value of DNA barcoding by suggesting that either it 'cannot work' for the identification or discovery of species or that it ignores the 'richness' inherent in traditional approaches. We re-examine these arguments through a comparison of DNA barcoding and morphological taxonomy in terms of their accuracy and diversity of characters employed. We conclude that morphology often does not work and that it is often nowhere near as 'rich' as has been argued. Morphology is particularly poor in numerous important situations, such as the association of larvae with adults and discrimination among cryptic species. The vehemence of some of the criticisms is surprising given that morphology alone is known to be inadequate to the task of species-level identification in many instances.

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> 'Keys are written by those who don't need them for those who can't use them.' (Packer 2008)

But,

> 'Don't panic' (Adams 1979)

The recent history of taxonomy is one of almost continuous change. Any senior taxonomist attempting to keep abreast of the most recent developments in their field would have had to deal with the battles among classical, phenetic and cladistic schools (Hull 1988) and, more recently, the apparent ascendancy of Bayesian analysis. In parallel, there have been methodological advances associated with the way in which taxonomic data can be obtained: scanning electron microscopy, allozyme electrophoresis, DNA sequencing and now genomics. More recently, entirely new expectations have arisen; such as web-based interactive identification keys and global biodiversity mapping (Godfray 2002). The taxonomic community has not always welcomed these philosophical and methodological developments with open arms. Indeed, the field as a whole has had some difficulty shaking off the impression that it is the purview of old-fashioned eccentrics working away in dusty museums. The rancour of the debates has not always helped.

To those trained in more traditional approaches to taxonomy, the development of DNA barcoding must have seemed like the proverbial last straw. Back in the early days of computational biology, it was possible for a traditional taxonomist to be threatened by 'taxonomy by computer' (Hull 1988). But at least someone versed in morphology was required to decide upon identifications, characters to be coded and states to be scored. DNA barcoding now seems to some as even more of a threat because it has the potential to dissociate the morphological taxonomist from the entire process of organismal identification.

Since its inception, DNA barcoding has been met with scepticism and resistance from some quarters in the taxonomic community (e.g. Meyer & Paulay 2005; Wheeler 2005; Hickerson *et al*. 2006). Conversely, others have embraced the method from the outset as an additional and useful tool (Tautz *et al*. 2003; Schindel & Miller 2005). Beyond the common recital of theoretical limitations associated with barcoding (which have been openly acknowledged by barcoders), the more pejorative criticisms have: (i) suggested that DNA barcoding cannot do what it purports to do, that is, it cannot identify (let alone discover) species accurately, or (ii) compared the 'richness' of barcoding to that of traditional taxonomic practice and argued that it fares extremely poorly. Our objective in this study is to refute the argument that morphological approaches to taxonomy are necessarily more accurate or 'richer' than barcoding. Indeed, when the users of traditional taxonomic keys attempt the identification of specimens that do not conform to the referential standards

Correspondence: L. Packer, E-mail: bugsrus@yorku.ca

upon which morphological taxonomy is based (often adult males), barcoding outperforms morphology and this is similarly true for species that exist in cryptic complexes.

First, we examine these two major criticisms and then provide a brief description of traditional taxonomic practice. We then investigate the 'richness' of morphological taxonomy using an example from slime mold beetles. Lastly, we try to understand why some of the critics of DNA barcoding have been so vociferous.

Two major criticisms

1 Barcoding does not, or cannot, work for the identification of species or the discovery of new ones

It is well known that a barcoding 'panacea' for the identification of all life using a single gene target, does not work. For example, mtDNA is not a good source of automated identifications for plants because the nucleotide substitution rates are much less than that of animals (Wolfe *et al*. 1987; Kress *et al*. 2005). Nonetheless, analogous approaches, but using several different gene fragments in combination, are showing promise (Kress *et al*. 2005; Fazekas *et al*. 2008). Some other taxa are also proving recalcitrant to DNA barcoding methodologies, corals for example (Hellberg 2006). Nonetheless, the range of animal taxa for which the same fragment of COI works is impressively enormous. While larger or different regions of the same gene have been suggested to work even better in specific situations (e.g. Roe & Sperling 2007), the efficiency of using a minimalist, standard fragment approach wherever possible is obvious.

That barcoding can work for species identification has been demonstrated in most of the papers that have used the methodology. The utility of this approach for associating the sexes in dimorphic species (Sheffield *et al.* 2009), for associating larval and adult forms (Köhler 2007), or for the identification of fragmentary remains (Wong & Hanner 2008) is undeniable.

An important component of the 'it doesn't work' criticism concerns false positives and false negatives: barcoding discovers new species that are not real and/or it fails to detect differences among species that are discriminable by other means. For example, Meier *et al*. (2006) found examples of both false positives and false negatives using sequences for flies obtained from GenBank. They point out that the inaccuracies could have come from specimens that were misidentified but counter this with an argument that specimens used in producing the barcode database would have a similar rate of misidentification prior to sequencing. However, the accepted community data standard for barcoding (Hanner 2005; Hubert *et al*. 2008) requires reference to the actual specimens examined, such that any potential misidentification of an organism contributing to the reference sequence library can be traced and the specimen itself can be re-examined. GenBank has no such quality control and inferences about the accuracy of barcoding should not be based on data obtained from it as the errors contained therein are well documented (e.g. Harris 2003).

That DNA barcoding can work for the discovery of species is also obvious. For the better-known taxonomic groups, such as birds, surprisingly large sequence divergences within 'species' generally occur in situations where subspecific differentiation has been postulated or where previously differentiated species had been (incorrectly) synonymized by later workers (Kerr *et al*. 2007).

The classic example of *Astraptes fulgerator*, a skipper butterfly '10 species in one', is further evidence of the potential of DNA barcoding to differentiate among otherwise seemingly conspecific adult butterflies (Hebert *et al*. 2004). In this example, however, the term cryptic species would seem not to apply to the larvae as these are readily distinguishable based upon colour patterns (see their Figure 2) and thereby arguing against the conclusions of Brower (2006). But as insect taxonomists rarely pay close attention to larval forms; it is not surprising that such species-level diagnostic variation went undetected until the application of molecular approaches in combination with the unique mass-rearing of caterpillars undertaken by Dan Janzen's research operation in Guanacaste, Costa Rica (Janzen *et al*. 2005).

Our experience with barcoding bees (Sheffield *et al.* submitted; Gibbs 2009) demonstrates that new species can be readily discovered using barcoding as the detection of genetically discrete units, considerably facilitates the discovery of morphological differences among species that would likely have gone unrecognized for decades or more. Barcoding can be used as a first approximation to delimit taxa for which variation within species makes it difficult to discern subtle signal from the morphological noise. In these cases, deep divergences indicate a lack of genetic cohesion among reproductively isolated taxa for which morphological differentiation has not yet arisen, or has not developed sufficiently for easy recognition using traditional methods. Recent studies have demonstrated the utility of barcoding for species discovery on a massive scale (e.g. Smith *et al*. 2008).

2 Barcoding ignores the rich legacy of traditional taxonomy

Traditional taxonomic methods have been remarkably successful in describing the diversity of life on planet Earth. In the past 250 years, the number of known animal species has increased from about 4400 (Linnaeus 1758, as cited in Mayr 1982) to approximately 1.5 million (Chivian & Bernstein 2008); our understanding of the higher-level classification of this diversity is both impressive and fascinating. Nonetheless, even conservative estimates suggest that we have discovered perhaps 10% of the animal species on our planet, and unsurprisingly, the taxonomic make-up of the undiscovered contains a very high representation of organisms

that belong to taxonomically difficult groups such as insects, mites and nematodes (Chivian & Bernstein 2008). At current rates of progress, life may not be completely inventoried for several millennia, by which time human beings may, and certainly much of remaining biodiversity will, have become extinct. This biodiversity crisis has been recognized by traditional taxonomists and armies of newly trained experts have been called for (Wilson 2000). These calls have largely been ignored, although the barcoding enterprise is probably the best hope to rectify the situation, perhaps specifically through demonstrating the relevance of taxonomy by enhancing access to its application (see below).

Yet there are those that criticize DNA barcoding as being intellectually impoverished in comparison to the monumental richness of traditional morphological approaches. Certainly an organism's DNA barcode might be considered as simple compared to its entire morphology (although this is not so obviously true for many microbes, tapeworms, parasitic copepods and other organisms with simplified morphology). But, it brings an entirely independent set of data to bear on the study of organismal diversity and thereby helps to calibrate the level of taxonomic uncertainty in the existing system. This should be seen as being advantageous to the process surely?

But let us reverse this argument. What is the richness of traditional morphological approaches in the situation in which DNA barcoding is most useful — discriminating among species in difficult-to-identify species complexes or fragmentary specimens? We will return to a comparative analysis of the richness of morphological vs. DNA barcoding data in a later section, but first, a description of standard traditional taxonomic practices is in order. Space constraints preclude a more detailed presentation and the following account is, by necessity, considerably oversimplified. Furthermore, we concentrate on those aspects of traditional methods that permit others to use taxonomic knowledge, as this is the major aim of the barcoding enterprise. For a detailed account of traditional taxonomy, the interested reader is referred to Winston (1999).

Traditional taxonomic practice

The most important result of traditional taxonomic research is a species-level revisionary study. A taxonomic revision usually involves the researcher gathering together all of the specimens of a particular taxonomic group available from museums and other repositories for study. The revision may be global, or regional, in scope. Through use of available literature, previously identified specimens and the study of types, the amassed material is sorted into putatively different species-level units. At least since the advent of cladistics, the morphological variation observed among species is commonly coded into discrete character states and a data matrix constructed and analysed with appropriate computer programs and outgroups. The results of the phylogenetic analysis are used to construct a classification for the species under consideration. The published product of revisionary work typically includes a diagnosis and description of each of the species in the group, an identification key, a listing of specimens studied, distribution maps and summaries of non-taxonomic information available for the constituent species. The diagnoses, descriptions and keys are usually copiously illustrated.

Depending upon the size (both in terms of the number of species and number individuals available) of the group, these studies may take from a few weeks to several decades of full time research to complete. A good taxonomic revision or identification key may be in use for well over a century, yet such monographs will often be used by other researchers without citation. In this regard, it is perhaps no coincidence that the production of large-scale monographs declined after the concept of the citation index was introduced during the second half of the last century. Indeed, this metric of 'academic performance' may have contributed to the taxonomic impediment by suggesting that revisionary works, no matter their level of scientific excellence, lacked sufficient 'impact' to warrant support for their continued creation. In this respect, the web is considered an ideal medium for the reinvention of taxonomy (Godfray 2002; Zhang 2008).

As an indication of the coverage and longevity of taxonomic research, we assessed the status of traditional studies by using the bee family Colletidae as an example. We surveyed Michener (2007) for revisionary studies or keys omitting only monospecific higher-level categories and three taxa for which coverage was geographically complex but generally sparse. Of the 146 higher-level taxa/studies available for investigation, 44 (30%) had received no revisionary study and keys for the identification of their species (45% of the total) are simply not available. Thus, even assuming that all of the identification keys work and there are no undescribed taxa (neither of these assumptions being reasonable), at most, 55% of the species of Colletidae are readily identifiable. The average time since the revisions or keys were published was 26.3 years and only four taxa had received more than one revision. The length of time between the first and subsequent revision for these four taxa was 30, 59, 71 and 104 years (with one genus, *Scrapter*, receiving a third evaluation 9 years after the second revision and 80 years after the first detailed study).

This suggests that the taxonomic community considers re-revising a previously studied group to be an unnecessary duplication of effort. Thus, the results of a revisionary study are often not seriously checked by others for a long time. Nonetheless, when subsequent researchers re-examine a species or a group of species, they often make different decisions from those of earlier researchers. A common result is that the number of known species changes. The number may increase, either through splitting what was previously

considered a single species or through discovery of additional material. Or the number may decrease, what was previously considered to be more than one species become just a single species-level entity (for *Scrapter*, no fewer than 26 named species have been synonymized, so far). However, our own studies of bee taxonomy suggest that many synonymies have been made in error (Gibbs 2009 and in preparation).

That different individuals come to different conclusions about the number of species with the same material at hand is particularly worrying when one considers that whole large groups of taxa have often been revised by only one author. For example, for the colletid subfamily Euryglossinae, 32 of 33 revisions and/or keys to species within non-monotypic genera or subgenera were written by one person (the late E.M. Exley; Exley 1968a, b, c, d, e, 1969a, b, c, 1975, 1976, 1978, 1983, 2001, 2002) and the remaining paper concerns just four species and is over 80 years old (Cockerell 1926). This suggests that the idiosyncrasies of individual taxonomists are likely to have a large impact upon taxonomic decisions at the species level. Furthermore, the lack of reappraisal of most taxonomic works means that personal biases will have a large impact upon identifications. The independent data that barcoding provides is thus, at the very least, a useful calibration of the inherent taxonomic uncertainty in existing species-level taxonomic treatments.

The mediocrity of morphology

In this section, we turn the arguments used against barcoding's accuracy and effectiveness in identifying specimens and discovering new species on their head by critically evaluating the utility of traditional approaches to organismal identification. We must state at the outset that we are not decrying the procedures, principles and practices of morphological taxonomy. Neither are we criticizing the quality of work or dedication to duty evidenced in the construction of the often difficult-to-use keys or enormously time-consuming taxonomic revisions that taxonomists produce. Indeed, most of us spend as much of our research time as possible performing morphology-based taxonomic studies (see for example Sheffield & Westby 2007; Packer 2008; Gibbs 2009; Sheffield *et al*. submitted) or performing comparative morphological analyses upon which the character systems used by traditional taxonomy rely (Packer 2003, 2004, 2008). We do this work because we enjoy it; it is a marvellous thing to be able to do and it is this observation of specimens (in the field and in the laboratory), rather than the analysis of four nucleotide gene sequence data, that led us to become biologists in the first place. What we are decrying is the view that DNA barcoding is outrageously simplistic in comparison to traditional approaches: at the level of discrimination of very similar organisms, DNA barcoding often speaks loud and clear while morphology is mute. In other instances, morphology has something to say, but stating it in a key is often less elegant than with a good DNA sequence, especially now that a barcode sequences are becoming readily accessible to even the nonspecialist.

It has to be admitted that, in many situations, traditional approaches simply do not work: species-level identification of fish fillets for example (Wong & Hanner 2008). But even in situations where intact organisms are available, standard approaches often cannot provide identifications. For example, Stribling (2006) states that for freshwater benthic invertebrates, organisms that are very important for monitoring water quality, error rates of 10–15% are considered acceptable, *at the level of genus* and 45% error rates *at the level of genus* are sometimes found (italics ours). Many such organisms are juvenile insects for which species-level identification requires an adult. With barcoding, a fragment of one of these can be removed and sequenced and the rest of the animal raised to adulthood, thence becoming more easily identified. With such accurately identified voucher sequences with known voucher specimens, small portions of live animals can be removed, the animal returned to its habitat and an accurate identification obtained with barcoding. Under these circumstances, a 10–15% error rate at the level of genus would be turned into a 98% accuracy rate, or more, at the level of species. The level of accuracy DNA barcoding provides for these organisms is currently utterly impossible to achieve with traditional morphological methods.

There are numerous examples of molecular discrimination of morphologically monotonous species pairs or complexes. We provide one example: one of the commonest 'species' of bee in North America, *Halictus ligatus*. The first evidence that this 'species' was not one entity came from electrophoretic analysis of individuals from the southeastern USA; they had no fewer than eight fixed differences from specimens from elsewhere out of a total of 32 loci investigated (Carman & Packer 1996) yielding an enormous level of genetic differentiation at nuclear loci. These genetic differences are retained even in the Piedmont region of the Appalachians where males and virgin females of both species fly simultaneously in sympatry (Dunn *et al.* 1998). The two species possess unique and reciprocally monophyletic sequences for mitochondrial (Danforth *et al*. 1998) and nuclear DNA sequences (Danforth 1999). Current barcoding data suggest that there is at most 1.1% sequence divergence within species of this pair and 3.8% between them (C. Sheffield, J. Gibbs and L. Packer, unpublished). Morphological study has failed to yield any clear differences between the species; even multivariate morphometric analysis of male genitalia of genetically typed specimens gave no discrimination (L. Packer, unpublished). In this instance, the morphological equivalent of the 'barcode gap' is zero, the barcode gap is 3.8%. This is an impressive example of the failure of morphology, more impressive perhaps because of the high level of nuclear genetic differentiation between the two species and their sympatry in parts of their range.

But what of the use of traditional identification keys to aid in performing identifications? All authors of this study have attempted to use numerous identification keys written as parts of revisionary studies. It is evident that the quality of these works varies enormously. Some include couplets that are often simply impossible to use, not because of technical difficulties or characters being hard to see (such as microsculpture patterns on a hidden mouthpart) or difficult to comprehend (although some or all of these are often the case), but because of missing information. While a couplet that refers to the shape of the antennae is unlikely to be useful for the identification of a beheaded specimen, there are worse problems. Some keys for the identification of bees require knowledge of the species of flower that the bee was collected from [e.g. the large genus *Perdita* with 600+ species (Michener 2007) revised by Timberlake (1954, 1956, 1958, 1960, 1962, 1964, 1968, 1971, 1980)]. This makes specimens collected using passive traps impossible to identify. Some keys use geographical region of provenance as a character, and this remains an important feature in large-scale works. This is an important and usually accurately discriminating variable. However, the increasing number of exotic species introductions weakens the utility of geographically based identification characters. Even some whole subfamilies thought to be restricted to single continents have been found in the wild in entirely new ones. For example, the Euryglossinae are endemic to Australia, but one species has been introduced into South Africa (Michener 2007). Even family-level identification keys for bees are extremely difficult to use, for the simple reason that they often rely so heavily upon mouthpart characteristics that require relaxation and dissection if the individual bee did not die with the appropriate parts serendipitously on display.

The above examples may be thought of as 'low hanging fruit': we are comparing barcoding to bad taxonomy. But, given the scarcity of revisions, bad taxonomy is often all we have available. It is our view that even the best identification keys would benefit from the independent data that barcoding provides. Take the best large-scale, revision-associated, species-level identification key for bees known to us (McGinley 1986). Simply expressed, superbly illustrated with scanning electron microphotographs, this is a key that almost anyone can use and approach 100% success. Nonetheless, McGinley (1986) noted that there are some species in this group that exist in 'forms'. These may actually represent discrete species. Indeed, almost 10% of his species (five out of 51) occur in morphologically distinct 'forms' (interestingly, one pair exhibits geographical patterns almost identical to those of the two genetically discrete species previously lumped together as *Halictus ligatus* discussed above). Additional data, as can be most efficiently provided by DNA barcoding, will provide an additional line of evidence as to whether these 'forms' are separate species or not.

We now turn to the argument that barcoding ignores the richness of traditional taxonomy by evaluating just how rich morphology is as indicated by identification keys for difficult-to-identify taxa.

Anyone who has opened a tome on animal taxonomy will be under the impression that most zoologists are somewhat perverted in that they seem to spend all their time describing and illustrating intromittent organs (botanists similarly concentrate upon reproductive organs, but studying flowers seems less prone to suspicion). While there are good reasons for this (Eberhard 1996), the possibility that intraspecific genitalic variation causes trouble for identifications has received almost no attention, although such variation does exist (Jocque 2002; Mutanen & Kaitala 2006).

To assess the richness of morphology for species identification, we chose as our example the key to the species of the *Agathidium oniscoides* species group — the largest species group in this genus of slime mold beetles (Coleoptera: Leiodidae) in North and Central America (Miller & Wheeler 2005). A total of 52 couplets key five out the 37 species (or at least they do once the typo that makes it impossible to get to couplets five to 51 inclusive is corrected). Of all characteristics mentioned in any of the couplets, over one-half (53 out of 94 — if two or three structures are mentioned in a couplet, then two or three structures are included in the counts) are from the male genitalia. Almost half of the couplets deal with only genitalic characteristics (24 out of 52) and in instances where only one feature can be used to separate the species in the two halves of the couplet, over two-thirds (16 out of 23) of them deal only with one part of the genitalia. As figures 173 to 356 of Miller & Wheeler (2005) indicate, the structures of the genitalia that are so important for species identification in these beetles are relatively simple pieces of morphology and the differences used to separate species are often subtle. As is usually the case in standard morphology-based taxonomy, the range of intraspecific variation in these key characteristics is ignored entirely.

As this last example suggests, the morphological equivalent of the barcode gap that enables molecular identification of species cannot be calculated using traditional approaches, and the sample size of illustrations upon which measures of intraspecific variation might be estimated usually averages one per species with zero variance. The 'richness' of morphology seems somewhat illusory under these circumstances: if morphological variation in a single genitalic structure is necessary for the identification of a large proportion of species in a taxonomic group, is a 5% sequence divergence in a DNA barcode really that much simpler?

Discussion

In his *Hitchhiker's Guide to the Galaxy*, Douglas Adams (Adams 1979) describes a situation in which a computer,

named Deep Thought, has been designed to answer the question of life, the universe and everything. This causes trouble among members of the 'Amalgamated Union of Philosophers, Sages, Luminaries and other Professional Thinking Persons' who consider that this question falls entirely under their mandate. It seems that some taxonomists believe they are in a similar situation; while many are happy to have DNA barcodes assist them in specimen identification and species discovery, others attack the whole enterprise and some do so repeatedly.[1]

While an equivalent 'Amalgamated Union of Taxonomists, Systematists and other Professional Organism Identifying Persons' does not exist, as outlined at the beginning of this paper, there have been dramatic transformations in the ways taxonomists perform their work and an increased range of expectations for them. Fifty years ago, almost the entire enterprise was pursued by museum-based researchers who worked largely alone with their cabinets full of specimens. Becoming a global or regional expert on a particular taxonomic group was a lonely task as few others would become interested in the minutiae of the subtle differences among species that the individual taxonomist discovered as these are generally applicable only to their taxon of expertise. Add to this the widely divergent methods required to collect samples of different taxonomic groups (for example, dung-baited pitfall traps being preferred by some, shredding of dead trees by others) and it becomes clear that the entire culture of taxonomy can only have progressed as far as it has by being led by rugged individualists who did not care too much about what anyone else thought of them (being discovered placing a carrion-baited pitfall trap in a cemetery is not something relished by those of a sensitive nature; it happened to the senior author as a young taxonomist and may have precipitated a switch to the less malodorous study of bees). Nowadays, such isolated activities are becoming replaced by teams of researchers that include gel jockeys, computational wizards and, sometimes teams of traditionally trained taxonomists. It is not surprising that those of a traditional ilk are often uncomfortable with these new developments.

We have suggested that when DNA barcoding is compared to traditional taxonomy in the areas where barcoding is likely to be most useful—cryptic species recognition, it nearly always outperforms morphology which often simply does not work at all. In this respect, it is perhaps ironic that new species are readily described on the basis of subtle morphological variation, yet there is a general reluctance to describe species on the basis of genetic evidence alone, which suggests that data chauvinism (R. Mayden, personal communication) is alive and well within the taxonomic community.

For some, morphological taxonomy and its survival is a bread-and-butter issue: they fear that traditional approaches to taxonomy are going the way of the village potter in the age of plastic. But will DNA barcoding really make taxonomists obsolete? The answer is obviously no. When 10% of taxonomic diversity has been discovered in 250 years, no technological breakthrough is likely to make it possible for us to describe the remaining 90% in a shorter time period. But the technology of DNA barcoding will make it possible for us to identify species-level units most of the time, even if those units might have to wait a millennium for someone to have the time to describe and name them using the formal processes of traditional methods. Indeed, DNA barcoding promises to make the job of the traditional taxonomist easier while at the same time making the need for additional traditionally [or integratively (Dayrat 2005)] trained taxonomists even clearer.

We suspect that there are very few traditional taxonomists without hundreds, to tens of thousands of specimens in their taxonomic group awaiting study in their research facilities. The time taken up by routine identifications is enormous. Even the necessary genitalia preparation for a single lepidopteran identification can take a well-trained technician an hour (S. Miller, personal communication), and this does not include the time required to make the morphological comparisons necessary to put a name on the specimen from whence it came. Similarly, despite 33 years of work involving bee identification, the senior author can often spend over an hour *not* being able to identify a particular specimen for which an identification key is available. What taxonomist would not leap at the chance of having such routine identifications being made by machine, thus freeing up their time for the detailed taxonomic revisions that they can then produce in increasing numbers?

But taxonomic knowledge is more than a 'bread and butter' issue for large numbers of people on the planet. Correct identification can be a matter of life and death; for example, the identification of disease vectors. Bees are closer to the area of expertise of most of the authors, and thus, we will deal with the problem of pollinator identification.

We are in the midst of a food crisis, driven by numerous activities; prime among them our need to use agricultural products to fuel our obsession with driving and the need to heat or cool, drafty homes and workplaces. Africa is a part of the world where the food crisis is looming largest and it is an area where taxonomic understanding of the pollinators is poor (in comparison to Europe and North America). Farmers in Africa are not alone in not understanding the role of pollinators in crop production, but in some parts of this continent, where the domesticated honey bee is native, a study has shown that this species is responsible for a mere

[1] It matters not that the computer that so worried Magicthise and Vroomfondle, the leaders of the aforementioned union, came up with a nonsensical answer (42, Adams 1979) because the question itself was somewhat vague. In contrast, proponents of DNA barcoding have literally billions of precise questions; we want to be able to ask a biologically informed Deep Thought what species a particular sample belongs to.

1% of the yield of the crops that require pollination (Kasina *et al*. 2009). The relative importance of non-*Apis* pollinators is not much better understood than is their taxonomy. Unsurprisingly, crop yields have sometimes declined as a result of the loss of habitat that has destroyed the nest sites of the bees that nobody really understood the importance of and could not identify anyway.

This suggests the role of DNA barcoding in providing societally useful identifications that will free up traditional taxonomists to do what they alone are exquisitely qualified to do: perform taxonomic revisionary studies. Although some have balked at the notion of taxonomy existing as a 'service industry', we counter with the view that the role *of* science is to generate new knowledge, while the role *for* science is to serve humanity (e.g. Haller & Gerrie 2007). DNA barcoding thus promises to produce results in situations where traditional taxonomy often fails even if traditional taxonomists were willing to perform the task. A modern-day Vroomfondle has suggested that 'Taxonomy does not exist to answer the question "What species is this?" ' (Wheeler 2005), a statement to be disavowed by even the staunchest member of the Amalgamated Union of Taxonomists, Systematists and other Professional Organism Identifying Persons, at least when appealing to their research granting agencies for funds. Of course, we are not suggesting that taxonomy exists only to answer such questions, but surely, taxonomists should not be actively discouraged from providing them. Under these circumstances, the populace whose taxes provide the salaries of taxonomists that do not identify things will want to turn to an automated Deep Thought to provide identifications for them. Such 'ivory tower' attitudes might seem sensible in those that promote automated identification methodologies, but understanding why those that hold these views are against giving to a machine that part of their work that they decline to perform takes more consideration. Whence springs this taxonomic worldview that ignores the needs of humankind?

DNA barcoding promises to entirely democratize the taxonomic process: anyone (although they will need some funds, but perhaps no more than currently required to operate a cell phone) will be able to identify an organism from a mere fragment. It would seem possible that the most vociferous of barcode critics are not really afraid of the death of their discipline; rather perhaps they are more afraid of the loss of the privileges that results from their monopolization of knowledge.

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