J. Mar. Biol. Ass. U.K. (2007), **87**, 1629–1633
Printed in the United Kingdom
doi: 10.1017/S0025315407058274

DNA taxonomy of sponges—progress and perspectives

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Sponges (Phylum Porifera) are among the most ancestral metazoans and are frequently difficult to identify, even by taxonomic experts, due to their lack of complex morphological characters. However, poriferans are highly diverse, ecologically important and of significant importance to pharmaceutical and biomaterials industries. Therefore, means of unambiguous identification are urgently needed. A DNA taxonomic system, and in particular sponge DNA barcodes, will provide a set of indispensable tools to aid taxonomists and ecologists in the rapid identification of sponge species, which will enhance the discovery of drug-producing species. Here, we will argue for the implementation of a DNA supported taxonomic system and introduce the Sponge Barcoding Project.

INTRODUCTION

(A plea for a DNA taxonomy of sponges)

Correct identification of species as entities is a pivotal and mandatory first step in biodiversity and ecological surveys as well as other biological researches, but this process is frequently underestimated or even ignored, often leading to the accumulation of erroneous data for analyses. Correct taxonomic identification and description of new species by non-taxonomic experts is relatively slow and tedious for some organismal groups, partially also because taxonomists frequently developed their own specialized nomenclature which is difficult to understand and use for non-experts, and often relies on only marginally detectable literature. Conventional morphological taxonomy, which often relies on years of specialized taxonomic experience, clearly is at its limit with the task of distinguishing closely related but evolutionary distinct lineages, especially in character poor taxa such as the sponges, and with the workload required in large scale biodiversity surveys.

Fortunately, recent advances in DNA sequencing technologies have promoted the advent of DNA signature sequence-based identification systems, called DNA barcoding (Hebert et al., 2003), and have led to the proposition to establish a DNA-based taxonomy (Hebert & Gregory, 2005; Vogler & Monaghan, 2006). The utilization of those signature DNA sequences as additional characters with a morphological taxonomic system provides an opportunity to overcome the shortcomings outlined above. DNA barcoding in combination with the molecular systematic methods of DNA taxonomy provide powerful tools to aid in more comprehensive species discoveries and deeper understanding of evolutionary relationships and speciation.

Crucial pitfalls of DNA barcoding have been criticized and are widely acknowledged (e.g. Moritz & Cicero, 2004; Meyer & Paulay, 2005; Hickerson et al., 2006; Solé-Cava & Wörheide, 2007), but cannot diminish the fact that alternative non-morphological characters are necessary to complement traditional morphological characters to facilitate species identification and discovery. Especially in sponges, where certain groups of supra-specific taxa such as halichondrids, 'Keratosa' and most Calcarea have a depauperate suite of morphological characters and/or are plagued by morphological homoplasies (e.g. Dohrmann et al., 2006), additional non-morphological characters for identification are in demand. However, many taxonomists fear that sponges will be defined by a string of DNA only in the future and criticize that species identities cannot be 'reduced' to a DNA sequence of a single locus. There are two important facts that are ignored by this criticism: first, species will not solely be defined by a sequence string, but DNA signature sequences will be added to the species description. Secondly, for example, many arthropod species are distinguished by features of disputable evolutionary value (such as the number of hairs on their legs), and it appears at least equally sophisticated to use DNA sequences, the point of natural selection, to aid species distinction. Why should 21st Century researchers keep on studying the phenotype alone if the genotype, the focal point of evolution, is (almost) readily accessible?

DNA barcoding is a tool, whose basic techniques like DNA extraction, PCR, sequencing, comparing with databases, etc. are nowadays taught in most undergraduate genetics practical courses. Virtually every scientist with such basic molecular skills can obtain the DNA signature of a specimen, without year-long experience of the taxonomy of a special group. In any case, a sponge DNA (assisted) taxonomy is intended to go further and beyond the pure use of DNA barcodes for distance-based species identification, in that it also takes into account evolutionary and phylogenetic relationships that shape species for their delimitation

Figure 1. Screenshot of the Sponge Barcoding Project's website at www.spongebarcoding.org. Accessed on 30 April 2007.

and identification (see e.g. Pons et al., 2006). However, DNA signature sequences shall be regarded as additional characters to describe morphological (and biochemical) features, and morphological information must still be used for the reference database, the backbone of sponge DNA-taxonomy, on whose correctness the user wishes to rely.

Why should the sponge scientist bother? Sponges are abundant in nearly every aquatic habitat and play numerous important ecological roles, e.g. in nutrient cycling (Lesser, 2006) or as bioeroding organisms in coral reefs (Lopez-Victoria & Zea, 2005). Their significant commercial importance to the pharmaceutical and biomaterials industry has been recognized for decades, e.g. as producers of highly potent secondary metabolites (reviewed in e.g. Faulkner, 2002) and useful for drug development (Munro et al., 1994). Sponges are highly diverse, but frequently do not display definable morphological autapomorphies and as a result, most sponge species are well known for their difficult identification by the non-expert. Consequently, sponges discovered in large-scale biodiversity surveys often remain undescribed (Hooper & Ekins, 2005) because the few taxonomic experts, mostly specialized on certain supra-specific taxa cannot (or do not want to) cope with large amounts of material to be identified. But correct identification of reproductively isolated and evolutionary distinct lineages of sponges is the pivotal first step for understanding a broad range of subjects such as marine ecology, biodiversity, dispersal, (cryptic) speciation, animal evolution and discovery of pharmaceutically/biotechnologically valuable taxa (see Wörheide et al., 2007, for further examples). However, sponge taxonomy still is an expert's task and will remain an obstacle for many promising downstream projects unless it becomes more accessible. A further advantage of a DNA assisted taxonomic system is that DNA characters are (relatively) constant and cannot mislead the DNA taxonomist under varying environmental conditions. Some morphological characters in sponges are prone to such variations, i.e. the silica content of seawater has the potential to modulate the phenotypic expression of various spicule types (Maldonado et al., 1999; see also Fromont & Bergquist, 1990; Schönberg & Barthel, 1997).

A philosophical (and practical) problem certainly is the definition of what a (sponge) species actually is. (Sponge) taxonomists still mostly use fixed 'diagnostic' characters (e.g. spicules and architecture) derived from comparative morphology to diagnose and separate species, not necessarily adhering to the biological species concept or any other than a typological one. While this is practical and has served reasonably well to catalogue diversity, it remains contentious whether it reflects the real biological diversity of sponges, considering that so-called 'cosmopolitan' sponge species, often only possessing a small number of morphological characters, are most likely a set of sibling (cryptic) species with different and divergent evolutionary histories, as uncovered by numerous genetic studies (e.g. Klautau et al., 1999). The existing morphological alpha-taxonomy of sponges is a rather artificial system solely based on morphological differences without considering evolutionary history and/or reproductive isolation.

Admittedly, there are technical aspects of DNA taxonomy that need careful consideration before application, especially in sponges. First of all, contamination by the numerous microbial and/or metazoan commensals or symbionts is an acknowledged issue. Designing sponge-specific primers for DNA-taxonomic markers should circumvent this problem, however, sequences obtained will have to be verified by phylogenetic tests, which should be the usual procedure in any laboratory anyway. Paralogy, horizontal gene transfer and introgression on the other hand, can and will only be detected by phylogenetic tests once sufficient comparative data are accumulated. This is identical to morphological classification systems, in which only after careful comparisons with many taxa or ontogenetic stages over the decades (spectacular) homoplasies have been observed.

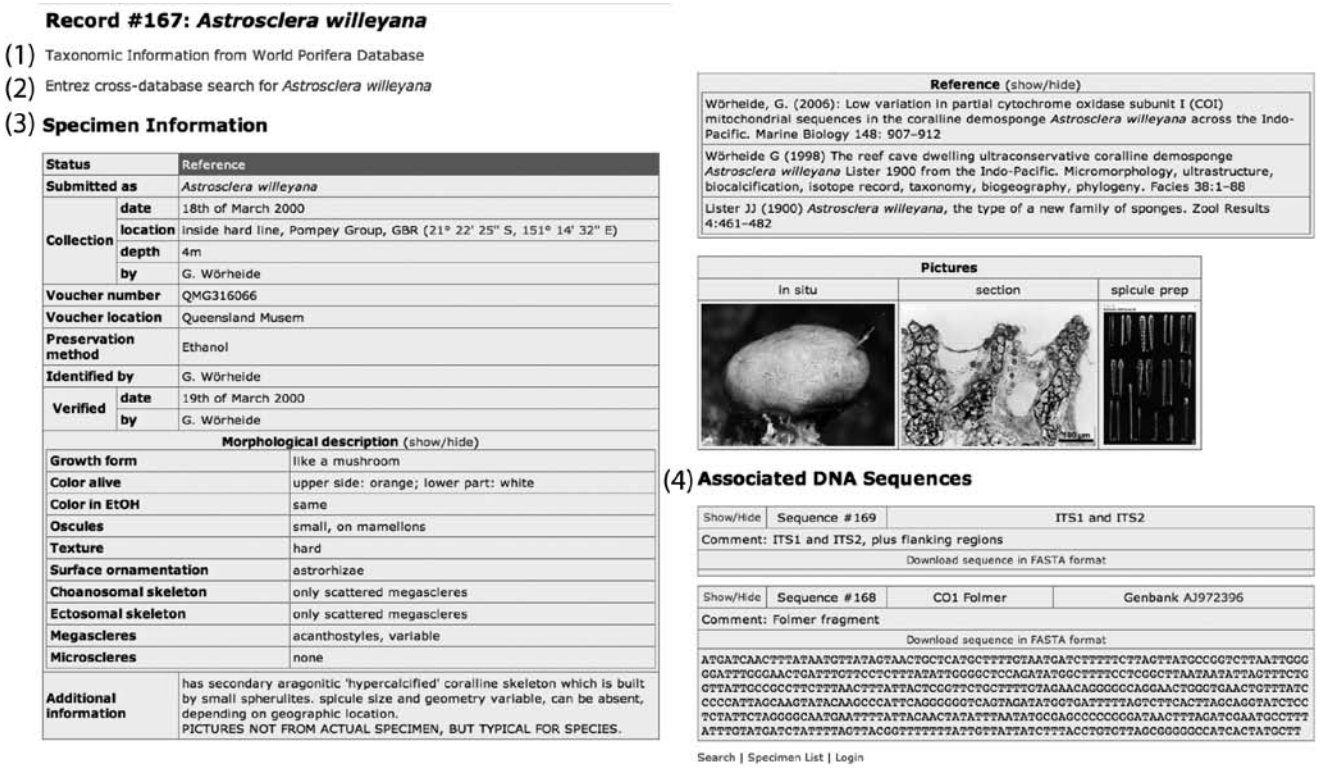
All the above-mentioned pitfalls are in no way greater than the problems of the traditional morphological system and should be no obstacle when opening up the exciting new possibilities in applied sponge science. In our opinion sponge sciences need to capitalize on the new potential of scientific and financial opportunities and resources that DNA taxonomy and the DNA barcoding movement creates and use them to further mutual benefit.

MATERIALS AND METHODS

(The Sponge Barcoding Project)

To our knowledge, the first CO1 DNA barcoding campaign had been attempted by the Smithsonian Institution in Fort Pierce (USA), which designed a preliminary sponge barcoding database (Duran, Rützler & Paul: 'DNATaxPor', first presented at the workshop at the Smithsonian Tropical Research Institute (STRI) on Barcoding and Molecular Ecology in September 2005). The currently most comprehensive approach undertaken to date to establish a DNA taxonomy of sponges is the Sponge Barcoding Project (SBP, www.spongebarcoding.org, Figure 1). It originated out of an international steering group with the aim to set up a comprehensive database of sponge DNA signature sequences facilitating the unambiguous identification of

https://doi.org/10.1017/S0025315407058274 Published online by Cambridge University Press



Record #167: *Astrosclera willeyana*

(1) Taxonomic Information from World Porifera Database

(2) Entrez cross-database search for *Astrosclera willeyana*

(3) **Specimen Information**

Status		Reference
Submitted as		*Astrosclera willeyana*
Collection	date	18th of March 2000
	location	inside hard line, Pompey Group, GBR (21° 22' 25" S, 151° 14' 32" E)
	depth	4m
	by	G. Wörheide
Voucher number		QMG316066
Voucher location		Queensland Musem
Preservation method		Ethanol
Identified by		G. Wörheide
Verified	date	19th of March 2000
	by	G. Wörheide

Morphological description (show/hide)

Growth form	like a mushroom
Color alive	upper side: orange; lower part: white
Color in EtOH	same
Oscules	small, on mamellons
Texture	hard
Surface ornamentation	astrorhizae
Choanosomal skeleton	only scattered megascleres
Ectosomal skeleton	only scattered megascleres
Megascleres	acanthostyles, variable
Microscleres	none
Additional information	has secondary aragonitic 'hypercalcified' coralline skeleton which is built by small spherulites. spicule size and geometry variable, can be absent, depending on geographic location. PICTURES NOT FROM ACTUAL SPECIMEN, BUT TYPICAL FOR SPECIES.

Reference (show/hide)

Wörheide, G. (2006): Low variation in partial cytochrome oxidase subunit I (COI) mitochondrial sequences in the coralline demosponge *Astrosclera willeyana* across the Indo-Pacific. Marine Biology 148: 907–912

Wörheide G (1998) The reef cave dwelling ultraconservative coralline demosponge *Astrosclera willeyana* Lister 1900 from the Indo-Pacific. Micromorphology, ultrastructure, biocalcification, isotope record, taxonomy, biogeography, phylogeny. Facies 38:1–88

Lister JJ (1900) *Astrosclera willeyana*, the type of a new family of sponges. Zool Results 4:461–482

Pictures

in situ | section | spicule prep

(4) **Associated DNA Sequences**

Show/Hide	Sequence #169	ITS1 and ITS2
Comment: ITS1 and ITS2, plus flanking regions		
Download sequence in FASTA format		

Show/Hide	Sequence #168	CO1 Folmer	Genbank AJ972396
Comment: Folmer fragment			
Download sequence in FASTA format			

ATGATCAACTTTATAATGTTATAGTAACTGCTCATGCTTTTGTAATGATCTTTTTCTTAGTTATGCCGGTCTTAATTGGG
GGATTTGGGAACTGATTTGTTCCTCTTTATATTGGGGCTCCAGATATGGCTTTTCCTCGGCTTAATAATATTAGTTTCTG
GTTATTGCCGCCTTCTTTAACTTTATTACTCGGTTCTGCTTTTGTAGAACAGGGGCCAGGAACTGGGTGAACTGTTTATC
CCCCATTAGCAAGTATACAAGCCCATTCAGGGGGGTCAGTAGATATGGTGATTTTTAGTCTTCACTTAGCAGGTATCTCC
TCTATTCTAGGGGCAATGAATTTTATTACAACTATATTTAATATGCGAGCCCCCGGATAACTTTAGATCGAATGCCTTT
ATTTGTATGATCTATTTTAGTTACGGTTTTTTTATTGTTATTATCTTTACCTGTGTTAGCGGGGGCCATCACTATGCTT

Search | Specimen List | Login

Figure 2. Screenshot of a reference record in the Sponge Barcoding Database (accessed on 30 April 2007 via 'Data' button at www.spongebarcoding.org). Records are directly linked to taxonomic information at the World Porifera Database (1) via a unique identifier, as well as to entries in Genbank (2). Specimen information (3) includes collection data (with location linked to maps.google.com), voucher numbers and voucher location and taxonomic verification data. A brief morphological description is presented, with the option to show or hide, as well as relevant references for the species, images *in situ*, from a typical histological section and a spicule preparation. Associated DNA signature sequences (4) can be viewed and/or downloaded in FASTA format and are linked to their corresponding Genbank entries.

sponge species. It will work towards covering species from all sponge taxa of the three extant classes Demospongiae, Hexactinellida, and Calcarea, and ranging in habitat from the marine intertidal to the deep-sea, as well as freshwater. Its core element, the recently launched Sponge Barcoding Database (SBD, Figure 2) is not only intended as a collection of sponge DNA sequences and morphological specimen descriptions, it also provides a vital interface between the two most important data servers for sponge DNA taxonomy: Genbank (www.ncbi.nlm.nih.gov) and the World Porifera Database (www.vliz.be/vmdcdata/porifera) and updates directly to the Barcode of Life Database (BOLD; www.boldsystems.org). A more detailed description of the Sponge Barcoding Project and the Sponge Barcoding Database is forthcoming in Wörheide et al. (2007) and is available from its website (www.spongebarcoding.org).

RESULTS

(Progress and application of sponge DNA taxonomy)

The data content of the Sponge Barcoding Database will rapidly be increasing by addition of data from ongoing current studies that we are aware of (e.g. Duran et al.; Itskovich et al.; Wörheide et al.; Moorea Biocode Project [http://moorea.berkeley.edu/research/biotic/moorea/]). Exponential growth in data mining is expected in the coming years, when results of purpose-funded barcoding projects are gathered (e.g. Erpenbeck et al.; Wörheide et al.). This, and the consequent provision of morphological data and determination of the samples by recognized taxonomists, support its function and status as the prime reference database.

As an example, DNA taxonomy in sponges is currently applied in in collaboration with the Queensland Museum (Brisbane, Australia), which harbours the largest sponge collection of the southern hemisphere. The Indo-Pacific is a hotspot for sponges and in particular for the character-poor 'keratose' sponges. Different (and assumed) sponge species are registered and recorded in so-called 'mudmaps', which contain brief morphological descriptions and specimen photographs *in situ*, on deck and microscopic slides. The overwhelming amount of sponge material does not admit the thorough time-consuming comparison with assumed congenerics and conspecifics, and the description of new species. Therefore, all assumed newly discovered species are registered under unique species numbers. Currently CO1 and rDNA sequences are generated to verify species and genus entities for several taxa of the keratose sponge collection. By doing so, identification and mislabelling of species is easily detected and corrected. Once verified, data will be transferred to the Sponge Barcoding Database.

There are currently further applications of DNA barcodes in sponge DNA taxonomy. Van Soest et al. (2006) recruited DNA markers (Erpenbeck et al., 2007) to verify that the Hadromerida (incertae sedis) Sollasellidae are in fact Raspailiidae (order Poecilosclerida). Wörheide et al. (2006, unpublished data) used a multi-locus approach to

https://doi.org/10.1017/S0025315407058274 Published online by Cambridge University Press

estimate the placement of the coralline sponge *Vaceletia* in the Dictyoceratida and distinguish several species within the genus, and Duran & Rützler (2006) presented a nice example of the use of CO1 for DNA taxonomy to help to untangle ecological processes leading to speciation in Caribbean sponges. Data from the Sponge Barcoding Project have been used to gain further insight in the phylogenetic relationships of Demospongiae (see Erpenbeck et al., this volume).

DISCUSSION

(or the perspective of DNA taxonomy in sponges)

DNA signature sequences (DNA barcodes, here not limited to the standard fragment of the mitochondrial cytochrome oxidase subunit 1 [COI] gene), in combination with conventional morphological characters, will revolutionize sponge taxonomy and downstream applications in systematics and ecology in the near future. DNA taxonomic studies around DNA barcodes will provide multiple exciting opportunities for sponge research, e.g. to increase our knowledge and understanding of principles of molecular evolution, speciation processes, community ecology and species delimitation. A DNA sequence-supported taxonomic system for sponges, providing the means to quickly and unequivocally identify taxa, significantly decreases the workload of taxonomic service provided by the few experts in the field to pharmaceutical and ecology researchers, who need timely identification of their target taxa. DNA barcoding will open up a new dimension and quality in biodiversity research and will become of vital importance for the survival and acknowledgement of sponge taxonomy and increase its reputation over the coming decades. It would be a serious disadvantage to disregard the opportunities that molecular approaches bring to the field.

DNA barcoding resources will be vital to actually get the work done when attempting to identify relatively recently collected (<20 years) and/or appropriately preserved taxa in large collections that exist in various museums around the world in a reasonable timeframe (i.e. before retirement and with a respectable publication list)—otherwise we will never create interest among young scientists to endeavour in sponge taxonomic research. A good example is the large collection of the Great Barrier Reef Seabed Biodiversity mapping project (www.reef.crc.org.au/resprogram/programC/seabed/index.htm), coordinated by the Australian Institute of Marine Science, which is attempting to document the sessile epibenthic fauna in the inter-reefal areas of the Great Barrier Reef. Thousands of samples have been collected, but without additional funding from DNA barcoding initiatives (or pharmaceutical companies for that matter), taxonomic work on such large collections will only proceed very, very slowly.

The few examples presented here clearly show that DNA taxonomy is not only aiding in obtaining reliable species information in the shortest time, it will also be of great use in unravelling the evolutionary history of species and species complexes. A larger amount of DNA data from denser taxon sampling, gathered with barcoding projects and subsequently used for phylogenetic analyses, will result in better-resolved gene trees (Hillis et al., 2003) and aids in identifying clades in need of further deeper investigation (see Erpenbeck et al., this volume). Increasingly sophisticated algorithms are currently being developed that place species distinction in a phylogenetic context (e.g. Pons et al., 2006), and from such gene trees, the true species trees can be approximated after sufficient data, e.g. from multiple loci, is gathered (Edwards et al., 2007). However, more research is needed to evaluate the potential of various molecular markers for such a task alongside the standard COI barcoding fragment and to refine existing algorithms to enable correct species delimitation and identification of sponges, preferably in a probabilistic framework. Sponge phylogenetic relationships can be resolved and with it many relevant questions on biogeography, dispersal, character evolution, secondary metabolite evolution etc. Clearly, molecular phylogenies are not new to sponge science, but a comprehensive DNA taxonomical approach e.g. the Sponge Barcoding Database with DNA barcodes consequently sampled for (almost) all sponge species will provide every researcher with the possibility to test their relevant hypotheses immediately and without the need of collecting comparative material (with uncertain taxonomy) and time consuming data generation.

G.W. acknowledges funding from the German Research Foundation (DFG). D.E. acknowledges financial support of the European Union under a Marie-Curie outgoing fellowship (MOIF-CT-2004 Contract no. 2882).

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Submitted 30 April 2007. Accepted 14 August 2007.