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REVIEW

The application of "-omics" technologies for the classification and identification of animals

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Abstract The correct classification of organisms based on specific rules is essential in biological sciences. Traditionally, morphological characteristics such as size, shape, color, and anatomical structures have been used to identify and classify species. However, as consequence of the tremendous advances in molecular technologies during the last years, new approaches have become available for taxonomic research. Various modern high-throughput technologies allow the detailed characterization of the genome, proteome, metabolome as well as the morphology of an organism. Furthermore, the open access storage of such comprehensive data sets as part of an uprising digital cybertaxonomy enables highly fascinating digital dimensions for modern taxonomy, including the buildup of virtual collections as well as data sets for 3D printing techniques that can be used to replicate complete voucher specimens or at least important diagnostic characters. As a result of these advances, we are now able to document, describe, and identify species much more comprehensively than just a few years ago. In this review we provide an overview about the technical advances in taxonomic research in recent years and discuss their power and limitations.

Introduction

Taxonomy, derived from Greek *taxis* (ταξις), meaning "arrangement or division," and *nomos* (νομία), meaning "law," the science of describing and classifying living things, represents the backbone of biological sciences and can be understood as "laws of arrangement and division" (Enghoff 2009). Despite all the efforts of describing organisms in the past centuries, there are still many species to be discovered and described. To date, taxonomy represents a very active and dynamic field with taxonomists describing 15,000–20,000 new species per year (Polaszek et al. 2005; IISE 2011). Interestingly, new species descriptions do not only include arthropods but also large-bodied mammals (e.g., Roos et al. 2008; Thinh et al. 2010; Cozzuol et al. 2013; Hrbek et al. 2014). Current estimates suggest that only about two million of the expected ca. 10 million eukaryotes on Earth have been described so far (May and Harvey 2009; Mora et al. 2011). In order to provide more accurate species descriptions, an integrative approach is preferred which combines morphological features that were used since the beginning of taxonomic research more than 200 years ago with additional biochemical, molecular, behavioral, ecological, and/or geographical data (e.g., Dayrat 2005; Padial et al. 2010; Schlick-Steiner et al. 2010).

The tremendous technological advances in molecular biology have significantly revolutionized biological sciences during the last decade. New technologies have become available for the complete acquisition of molecular biological information, such as genes, proteins, or small metabolites, and are

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named by appending the common suffix "-omics" (Greek: −ομική), as in the term "genomics" for the acquisition of the complete genetic information of an organism or "proteomics" for proteins. With these high-throughput methods, it is possible to generate huge amounts of data in a short period of time and at substantially lower costs than methods applied just some few years ago. Generated data are stored in databases and can be analyzed using advanced bioinformatics tools (Schneider and Orchard 2011). In particular, various lower priced high-throughput sequencing technologies make deep transcriptome sequencing and quantification as well as whole genome sequencing and resequencing available to many researchers and projects than ever before (e.g., Kircher and Kelso 2010; Mardis 2013; van Dijk et al. 2014). Other high-throughput technologies allow a fast and comprehensive analysis of the proteome or metabolome of an organism (Fig. 1). For taxonomic research, the application of such high-throughput technologies improved the quality and expanded the amount of data that can be applied now as part of species descriptions (e.g., Stoev et al. 2013; Puillandre et al. 2014). Since molecular data will become more and more popular in modern biodiversity studies (e.g., Ji et al. 2013; Cristescu 2014; Orgiazzi et al. 2015), these methods likewise offer new perspectives in accelerating a correct identification of specimens, as it is required in ecology (e.g., Leray and Knowlton 2015; Tang et al. 2015), pest biology (e.g., Nicholson and Puterka 2014; Villar et al. 2014; Sherwin et al. 2015), and many other biological fields.
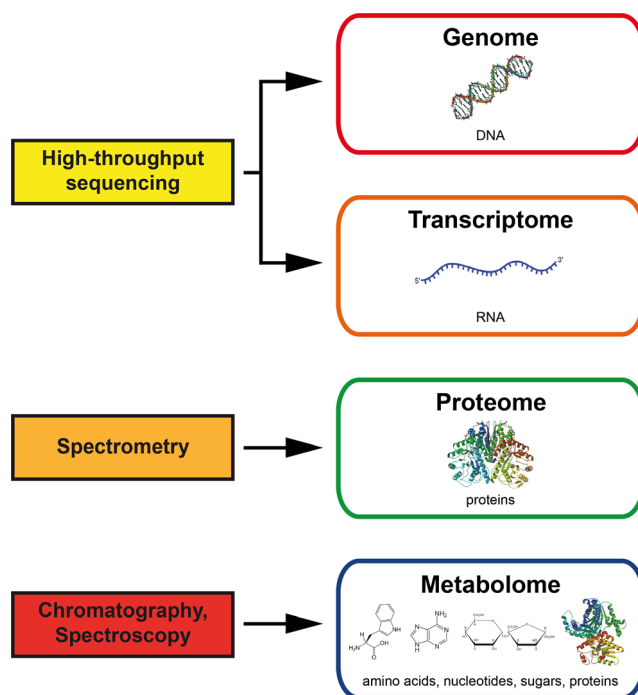

Fig. 1 Modern analytical -omics technologies (*left*) that allow a characterization of the genome, transcriptome, proteome, and metabolome of an organism

In this article we provide an overview about current advances and trends in using high-throughput technologies for compiling molecular as well as morphological data in modern taxonomic research and discuss their suitability and limitations to identify specimens as part of an applied taxonomy, with a focus on metazoans. Furthermore, we highlight various aspects of the ongoing digitalization of taxonomic data.

From single genetic markers to genomes

With the rise of DNA sequencing technologies in the early 1990ths, the utilization of DNA sequence data has become popular as supplementary markers for species description, identification, and classification. This is particularly true for DNA barcoding which represents the most prominent approach in this context. Here, an app. 650 base-pair fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene was proposed as global standard for the identification of unknown animal specimens in terms of a given classification (Hebert et al. 2003a, 2003b). In spite of the fact that DNA barcoding has been criticized from its beginning (e.g., Will et al. 2005; Cameron et al. 2006; Taylor and Harris 2012) and various problems may affect the use of mitochondrial DNA, e.g., recent speciation events, heteroplasmy, incomplete lineage sorting, (introgressive) hybridization as well as the presence of mitochondrial pseudogenes, DNA barcoding has been successfully applied in a vast number of taxa (e.g., Bucklin et al. 2011; Spelda et al. 2011; Nagy et al. 2012; Hausmann et al. 2013; Raupach et al. 2014; Hendrich et al. 2015). Consequently, many recently published species descriptions include barcode sequence data (e.g., Chang et al. 2014; Khalaji-Pirbalouty and Raupach 2014; Soldati et al. 2014; Weis et al. 2014). Based on such studies, the so-called turbo-taxonomy combines DNA barcodes, concise morphological descriptions by an expert taxonomist, geographical information, and high-resolution digital imaging in order to standardize and accelerate the formal description of a large number of new species (Butcher et al. 2012; Summers et al. 2014). A further improvement of this approach joins open access web publication and an automated content transfer from a journal into a fully versioned and dynamic wiki-framework (Riedel et al. 2013a, b), where descriptions can be continuously updated or even fully modified (Riedel et al. 2013b). The applications of DNA barcoding are manifold and have been already adapted in different fields of biological science including food quality analysis (e.g., Haye et al. 2012; Rasmussen et al. 2013), forensics (e.g., Nelson et al. 2007; Schilthuizen et al. 2011), invasive species biology (e.g., Pilgrim and Darling 2010; Chen et al. 2013; Shipway et al. 2014), pest biology (Engstrand et al. 2010; Blacket et al. 2012; Correa et al. 2012), as well as wildlife monitoring and conservation biology (e.g., Eaton et al. 2010; Yan et al. 2013;

Gonçalves et al. 2015). Further, the Food and Drug Administration (FDA) of the USA accepted DNA barcoding as official method for seafood identification.

DNA barcodes act also as central element of metabarcoding studies using high-throughput sequencing technologies (Valentini et al. 2009). Metabarcoding can be applied to DNA from any environment or organism and is gaining increasing prominence in modern biodiversity studies (e.g., Ji et al. 2013; Cristescu 2014; Leray and Knowlton 2015; Orgiazzi et al. 2015). Whereas such approaches are routinely used to characterize microbial communities, its application is now being extended more and more on eukaryotic organisms and opens new perspectives in biodiversity assessment studies (e.g., Orgiazzi et al. 2015; Leray and Knowlton 2015).

As already mentioned, the application of DNA barcodes and mitochondrial DNA in general can be limited by various phenomena, including closely related or introgressing species (Zinner et al. 2009a, 2009b; Haus et al. 2013). In such cases, a number of studies clearly favor a combined multi-locus approach of mitochondrial and nuclear sequence data (Yang and Rannala 2010; Roos et al. 2011; Dupuis et al. 2012; Fujita et al. 2012; Carstens et al. 2013). Based on the massive transcriptome and/or genome sequence data that will become available in the near future, new markers, e.g., taxon-specific single copy nuclear genes or introns, can be easily identified and applied to delineate even closely related species where currently applied markers fail (e.g., Perelman et al. 2011; Wang et al. 2012). In addition to analyzing genes or gene fragments, other genome-based approaches can become suitable tools for species delimitation and specimen identification as well. Whereas restriction site-associated DNA tag sequencing (RAD tag, see Baird et al. 2008) is typically applied to analyze gene flow and population connectivity within a species, first studies also demonstrate its potential in species delineation (e.g., Nadeau et al. 2013; Leaché et al. 2014; Pante et al. 2015). Likewise, single nucleotide polymorphisms (SNPs) can be suitable markers, particularly for population or species delineation (e.g., Ferguson et al. 2007).

Since steadily sinking sequencing costs will make the analysis of complete genomes increasingly attractive, multi-locus approaches will probably be used only temporarily. The incorporation of genome size and complete genome sequence data into taxonomy and systematics has already taken place for bacteria and archaea (Richter and Rosselló-Móra 2009; Serrano et al. 2010; Thompson et al. 2014; Chun and Rainey 2014) and obviously will follow for eukaryotes in the near future, even if the large genome size within some taxa (e.g., of some crustaceans and orthopterans within the Arthropoda) represents a challenging task (Dufresne and Jeffery 2011). For animals, a first study combining genomic data with phylogenetic and taxonomic aspects of the Darwin finches of Galapagos was recently published (Lamichhaney et al.

2015). The presented genomic data reveal significant discrepancies with the phenotype-based taxonomy for some species, recommending a revision for the sharp-beaked ground finch species *Geospiza difficilis* Gould, 1837 and the large cactus finch *Geospiza conirostris* Ridgway, 1890 (Lamichhaney et al. 2015).

However, the analysis of whole genomes is not restricted to single specimens. Some pioneering studies demonstrate the possibility to recover and assembly partial or full mitochondrial or even nuclear genomes from a bulk of samples as part of biodiversity studies (Zhou et al. 2013; Tang et al. 2014, 2015; Andújar et al. 2015; Crampton-Platt et al. 2015). Such so-called genome skimming approaches show that high-throughput sequencing analysis provide a solid phylogenetic framework to estimate species diversity. Whereas additional developments in bioinformatics and molecular biology are required, metagenome skimming constitutes a powerful application of high-throughput sequencing technologies for modern community ecology (Papadopoulou et al. 2015).

Transcriptomics

As long as assembling full genomes remains a difficult task, transcriptome sequencing constitutes an attractive alternative for the characterization of non-model species (Pop and Salzberg 2008; Riesgo et al. 2012). In spite of the fact that the transcriptome of an organism is subject to change as a result of its environment, life stage, and/or lifestyle, transcriptomic data have been successfully applied to comparative genomics (e.g., Romiguier et al. 2014), studies of gene expression (e.g., Eichner et al. 2011; Costa-da-Silva et al. 2014; Schunter et al. 2014), venom evolution (Rendón-Anaya et al. 2012; von Reumont et al. 2014), phylogenetics (e.g., Dunn et al. 2008; Struck et al. 2011; Oakley et al. 2012; von Reumont et al. 2012; Misof et al. 2014), and others during the last few years. Transcriptome data might be even fundamental when DNA information alone does not help to differentiate among taxa. In a population genomics study on crows it was recently demonstrated that small differences in gene expression are sufficient to maintain the phenotypic differences between carrion and hooded crows, although there is some gene flow between the two taxa still given (Poelstra et al. 2014).

Until now, the application of transcriptomes in taxonomic studies is almost absent. However, a first pioneering study combining transcriptomic data, DNA barcodes, and micro-computed tomography (micro-CT) images as part of a eukaryotic species description has been published recently (Stoev et al. 2013). Transcriptomes may represent a time and cost-effective substitute to whole genome sequencing for non-model organisms with a lack of reference genomes, producing large amounts of gene sequence data that can be applied as

taxonomic traits (Stoev et al. 2013). In our view, it is evident that as a result of the continuous improvement of high-throughput sequencing technologies transcriptome data will become an important and extending element in taxonomic studies of eukaryotes in the near future.

Proteomics

The proteome is the complete set of proteins expressed by a genome in a cell, tissue, or an organism at a specific point of time, linking the genotype with the phenotype of a specimen (Diz et al. 2012). In the past, 1D and 2D gel electrophoreses were routinely employed methods for the characterization of the proteome of an organism. Today, modern gel-free mass spectrometric approaches (MS) revolutionized the field of proteomics and offer a much higher sensitivity, speed, quantitative dynamic range, and ease of use in which hundreds of proteins from a tissue are analyzed in parallel (e.g., Sehrawat and Gakhar 2014). Moreover, new imaging technologies allow a 3D molecular analysis of a tissue sample or entire organ (Oetjen et al. 2015). Modern mass spectrometry can be also applied to taxonomic questions, being able to investigate even century-old tissue samples. In combination with morphological and ancient DNA analysis, high-throughput proteomics based on MS revealed that a widely accepted syntype of the Asian elephant *Elephas maximus* Linnaeus, 1758, which represents one of the most iconic and well-known mammalian species, is actually an African elephant of the genus *Loxodonta* (Cappelini et al. 2014).

In terms of species identification and classification in microbiology, the matrix-assisted laser desorption/ionization time-of-flight (MALDI-TOF)-MS has emerged as routinely applied high-throughput technique to characterize bacteria based on species-specific proteome fingerprints (e.g., Welker and Moore 2011; De Bruyne et al. 2011; Fournier et al. 2013). In MALDI-TOF-MS analyses, samples are spotted onto a target plate with a suitable matrix (Karas and Hillenkamp 1988). Afterwards a brief laser impulse irradiates a spot on the sample, resulting in ablation of a small volume of the matrix and desorption of the embedded analyte molecules (Sauer and Kliem 2010). The ionized molecules are accelerated and drift along a vacuum tube, surrounded by a strong electrical field. Based on the flight time, the different molecule masses which typically range between 1000 and 20,000 Dalton are represented as spectra. The advantages of MALDI-TOF-MS are rapidity, low costs, accuracy, and its suitability for high-throughput studies. Various pioneering studies demonstrate the capability of MALDI-TOF-MS as an efficient and a fast identification system for non-microorganisms, e.g., various insect species (Cvačka et al. 2006; Feltens et al. 2010; Kaufmann et al. 2011), crustaceans (e.g., Riccardi et al. 2012; Laakmann et al. 2013), mollusks (Puillandre et al. 2014), and fish (Mazzeo et al.

2008; Volta et al. 2012). In the case of marine calanoid copepods, the analyzed proteome fingerprints of whole animals were accurate for species clusters irrespective of a high intraspecific variability of mitochondrial sequence data (COI), including significant differences between early developmental stages as well as adults (Laakmann et al. 2013).

So far, studying the proteome has played a less prominent role in evolutionary and ecological analysis compared to genome and transcriptome data (Karr 2008; Gotelli et al. 2012; Diz et al. 2012). However, proteomic spectra represent valuable data for the taxonomic analysis of a vast number of specimens, in particular small insects, midges, crustaceans, or others as part of comprehensive surveys. Considering that different life stages of an organism as well as tissues express different proteomes, analysis protocols have to be standardized to guarantee comparable proteome spectra for larger animals. This is also true for data banks storing these spectra sets. Nevertheless, proteome fingerprints can become valuable traits for species descriptions and accelerated specimen identification upon the scientific community manages to buildup reference databases that are based on commonly accepted protocols.

Metabolomics

In addition to the favored high-throughput sequencing-based approaches, other, so far less applied molecular fingerprinting methods may become more important in animal taxonomy in the near future, for example the chromatographic analysis of secondary metabolites of a specimen. In this context, high-performance liquid chromatography (HPLC) represents a popular method of choice. Finding its origin in analytical chemistry, HPLC is a technique that focuses on the separation, quantification, and identification of known organic molecules and ions within a sample which is forced to pass a column with a solid absorbent material at high pressure. Due to the fact that each component in the sample interacts somewhat differently with the absorbent material, components can be separated by different flow rates as they leave the column (e.g., Hanai 1999; Skoog et al. 2006). Whereas HPLC and related approaches are routinely applied to differentiate plants and fungi (e.g., Zapata et al. 2004; Lu et al. 2005; Frisvad et al. 2008), taxonomic studies focusing on animals are still limited but promising (e.g., Wilson and Alewood 2006; Ivanisĕvić et al. 2011; Erpenbeck et al. 2012; Wilson et al. 2013).

Coupled gas chromatography-mass spectrometry (GC-MS) represents another, more frequently used technique to characterize the metabolome of an organism. Here, the analysis of species-specific cuticular hydrocarbons (CHCs) using GC-MS is increasingly applied to delimit insect species (see review of Kather and Martin 2012). CHCs are expressed on an insect's cuticle and are one of the major factors allowing insects to identify members of their own species. In terms of taxonomic

research, many cryptic species can be identified by their unique CHC profiles despite of being morphologically indistinguishable (e.g., Martin et al. 2008; Guillem et al. 2012).

Finally, the automated usage of spectroscopic methods based on the interaction of matter and radiated energy becomes more and more attractive for species identification and taxonomy. For the Metazoa, non-invasive near-infrared spectroscopy (NIRS) has been utilized for the identification of a variety of insect species during the last years (see review in Rodríguez-Fernández et al. 2011). NIRS is based on the measurement of the wavelength and intensity of absorption of near-infrared light (800 nm–2.5 μm) by a sample (Pasquini 2003). Typically, it is employed for the quantitative measurement of functional organic groups, such as O–H, N–H, or C=O bonds. In the case of insects, each species has a unique absorbance characteristic of its cuticular layers, representing a "metabolomic fingerprint" (Lockey 1988). This allows a correct identification even of closely related species as it has been demonstrated for various insects (see review in Rodríguez-Fernández et al. 2011).

Like any metabolite composition, the cuticular signature of individuals can depend on nutrition, gender, age, and sexual maturity, leading to intraspecies variations in CHC profiles (Kather and Martin 2012) and NIRS fingerprints (e.g., Mayagaya et al. 2009). As a consequence, taxonomists need to be aware of that specimens varying in their CHCs do not necessarily belong to different species (e.g., Liang and Silverman 2000; Arienti et al. 2010; Frentiu and Chenoweth 2010; Kather et al. 2011). Similar to other molecular methods, it is impossible to define a universal threshold for species delineation. Moreover, a number of technical problems can limit the use of CHCs as taxonomic tool, for example the co-evolution of compounds that belong to the same chemical family and have the same chain length but differ in the position of their double bounds (Kather and Martin 2012).

Still, these methods represent highly innovative high-throughput approaches for species identification and description with a focus on small organisms, e.g., most arthropod species, whereas its efficiency for many larger animals, e.g., mammals, birds, or reptiles, may be limited. Nevertheless, zoologists should feel motivated and stimulated to test chromatographic and spectroscopic approaches as part of their taxonomic studies. We doubt, however, that metabolic fingerprinting in taxonomy will ever achieve the wide applications of nucleic acid and/or protein-based sequencing approaches, not the least since extraction/analysis protocols and reference databases will likely always be specialized for particular groups of organisms.

Analyzing the phenotype: imaging and tomography

Until recently, the description of a new animal species has typically been based on drawings that show characteristic morphological traits in detail. However, a morphological description of a new species does not have to rely on drawings only. Improvements in resolution, suitability, and quality of modern imaging techniques, among them the confocal laser scanning microscopy (CLSM) (Fig. 2), magnetic resonance imaging (MRI), and micro-CT, have led to a remarkable increase in morphological studies that buildup massive amounts of digital raw data during the last years (see reviews in Ziegler et al. 2010; Boistel et al. 2011; Faulwetter et al. 2013; Sombke et al. 2015). Such new high-throughput analyses allow the digitalization of complete biological specimens or specific diagnostic structures (Handschuh et al. 2013; Lenihan et al. 2014, Ziegler et al. 2014; Akkari et al. 2015), acting as supplementary traits and making morphological descriptions of a species significantly more comprehensive and the identification of individuals easier. To meet the requirements of the digital era, these data have to be deposited in public online data banks, building up a virtual collection of type material as "cybertypes" (Brooker et al. 2012; Faulwetter et al. 2013; Akkari et al. 2015). Such data may also act as matrix for 3D printing of specific characteristic structures or even whole specimens, allowing scientists to assemble a comprehensive collection of models without loaning highly valuable museum-stored vouchers (Fig. 3). Furthermore, state-of-the-art automated 2D mass imaging technologies can provide the basis to create a virtual global natural "metacollection" of high-resolution digital images that allow an automated image analysis (Balke et al. 2013).

Becoming digital: the perspectives of cybertaxonomy

Cyber-enabled taxonomy, or cybertaxonomy, aims to use the latest cyber and digital tools to accelerate descriptive taxonomy, preserving the best of its traditional practices while improving its efficiency (Wheeler and Valdecasas 2010). Today, we are still in early days of cybertaxonomy. Data portals like the

0.1mm

Fig. 2 Lateral view of the harpacticoid copepod *Evansula pygmaea* (Scott, 1903) based on confocal laser scanning microscopy (CLSM)

Fig. 3 Dorsal 3D print of a serolid isopod (Crustacea, Peracarida)

Encyclopedia of Life (EOL; www.eol.org), the Biodiversity Heritage Library (BHL; www.biodiversitylibrary.org), the Global Biodiversity Information Facility (GBIF; www.gbif.org) as well as the current push in several countries to digitize museum specimens are foreshadows of what is soon to come. Beyond open access digital archives, it is now possible to access rare and type specimens remotely (Wheeler et al. 2012). Other initiatives link specimen images and DNA barcodes from ecological structured species inventories (Miller et al. 2014). However, this is only the beginning (e.g., Rosenberg 2012). The aim, to be reached within a few years, should be to seamlessly link all natural history museums and taxonomists in a cyber-enabled "species observatory," including software that meets the special needs of revisionary taxonomy and other aspects. In this process, taxonomists must explore how to shift taxonomy from the centuries-old single-scholar producing a monograph once every few decades to an online knowledge base that is a living, dynamic monograph reflecting moment to moment advances in theories of species and apomorphies (e.g., Miller et al. 2012; Riedel et al. 2013b). Even our best hypotheses about homology, apomorphy, species status, and phylogeny are subject to repeated testing and refutation. Unless species and characters are constantly critically tested through additional specimens and evidence, they become rigid artifacts of past ideas rather than the theories required of good science. This vision of efficient and dynamic e-monographies and reviews can be built, aside from certain software requirements, from off-the-shelf components almost instantly given the will power of the scientific community and modest funding.

With a modernization of taxonomy, we can simultaneously accelerate the inventory of our world's species and populate a database of adaptations that can be tapped by inventors, engineers, and entrepreneurs to solve countless problems as part of an applied taxonomy. Here, natural selection has done the hard work of weeding out the bad and preserving the good ideas. But, this vast library of options and opportunities remains unopened to us if we continue to do a simplified, only morphological-based taxonomy.

Conclusion and outlook

The now available technologies will allow taxonomy to enter a new era of quality. The rise of efficient high-throughput methods, web-based technologies as well as comprehensive open access data bases have already and will further affect species descriptions in the near future dramatically. First, pioneering taxonomic studies clearly demonstrate this revolution in species descriptions (e.g., Stoev et al. 2013). However, although such comprehensive species descriptions are desirable, the right balance between fast and exhaustive descriptions needs to be found. As a consequence of the tremendous developments, the rules of nomenclature have to be adapted to the new requirements of the digital era (Minelli 2013). First steps have been made already. For example, with the new amendment of the International Code of Zoological Nomenclature in September 2012, it is now possible to publish new names in online-only studies which have to be registered with ZooBank (Minelli 2013). Nevertheless, more rigorous changes, e.g., the acceptance of cybertypes (Faulwetter et al. 2013), will become necessary to come up with the rapid technological advances. Similar to the obligatory deposition of nucleotide sequence data in open access databases as GenBank (NCBI; www.ncbi.nlm.nih.gov), the European Molecular Biology Laboratory (EMBL; www.ebi.ac.uk/embl), or the DNA Data Bank of Japan (DDBJ; www.ddbj.nig.ac.jp) (but see also Cochrane et al. 2012), it is also essential to guarantee an efficient long-term storage of tissue samples and DNA extracts (Savolainen and Reeves 2004; Corthals and DeSalle 2005; Astrin et al. 2013). Although nowadays, a mass of data can easily be generated with high-throughput technologies, there is an increasing demand for bioinformatic tools, workflows, and statistical methods that can be applied to manage and analyze huge large data sets. The buildup of powerful computer facilities as well as the development of advanced but also user-friendly software represents one of the most challenging and essential tasks in the near future. Of course, the main limiting factor for taxonomic research is still the lack of available funding. However, we hope that the application of such new technologies as part of species description and their use for the accelerated identification of specimen will promote taxonomic research in the future.

Our review demonstrates that modern taxonomy is integrating a broad array of genotypic and phenotypic methods and data that allow the analysis and characterization of a species in a multifaceted way (Fig. 4). Taxonomy should not be restricted to certain types of data (Cook et al. 2010), yet also utilize more specialized approaches where necessary. This could include, e.g., flow cytometry (Kron et al. 2007), wing inference (Shevtsova et al. 2011), or hyperspectral imaging (Pettersen et al. 2014) as well as Raman spectroscopy (e.g., Ashton et al. 2011), Fourier transform infrared spectroscopy

(FTIR; e.g., Wenning and Scherer 2013), PCR electrospray ionization mass spectrometry (PCR-ESI-MS) (e.g., Sauer and Kliem 2010), and other methods. Of course, not all approaches and technologies are useful for all taxa. Whereas NIRS can be advantageous for the routine identification of insects and other arthropods, this method may fail analyzing annelids and others. As consequence, the possible application of each approach has to be independently evaluated according to the taxa of focus. Yet, we foresee that beside the phenotype, the genome, transcriptome, and possibly proteome will become core traits for the description of taxa, facilitating comparisons beyond the boundaries of narrow groups.

It is also obvious that the application of these new technologies should not be restricted on the description of new species. Depending on the quality of specimens, some techniques can be also applied to analyze and revise collection material of natural history museums (Rowe et al. 2011). Whereas DNA barcodes have been already successfully generated from old collection material (e.g., van Houdt et al. 2010; Strutzenberger et al. 2013; Hebert et al. 2013), high-throughput sequencing technologies allow the analysis of complete mitochondrial

genomes (Guschanski et al. 2013; Liedigk et al. 2015), nuclear DNA fragments (Asher and Hofreiter 2006; Bi et al. 2013), or even complete nuclear genomes (Jónsson et al. 2014). All these pioneering studies show that museum-preserved samples constitute an extraordinarily rich source for DNA studies using modern sequencing technologies.

However, it is important that the taxonomy of the twenty-first century is not carried away by the fascination intrinsic to ever-increasing array of methods and the sheer amount of data. The traditional aims of taxonomy are unchanged and include, e.g., (i) detailed high-quality descriptions and delimitation of species, (ii) a classification that reflects evolution, (iii) a dynamic nomenclature, and (iv) fast and reliable identification tools. Although all these new high-throughput technologies are available now and certainly they are able to provide additional information for a species, not all these technologies can be routinely applied due to cost and time intensity. Hence, the scientific community needs to standardize and simplify species descriptions with the aim to balance between cost/time and the additional value high-throughput technologies can bring. It should be also kept in mind that the access to such approaches is generally limited to academics. For various taxa (e.g., insects), numerous taxonomic studies are typically performed by amateurs that have no access to such technologies. This is also true for most taxonomists in developing countries. As a consequence, scientists of research institutes who have the chance to use such technologies should be motivated to cooperate with them more than in the past. However, in spite of the fact that the number of taxonomic works using -omics technologies will steadily increase in the future, many studies will still be performed applying classical "non-omics" methods. Anyway, the success of integrative taxonomy will ultimately be charged qualitatively and quantitatively with respect to the previously mentioned aims.
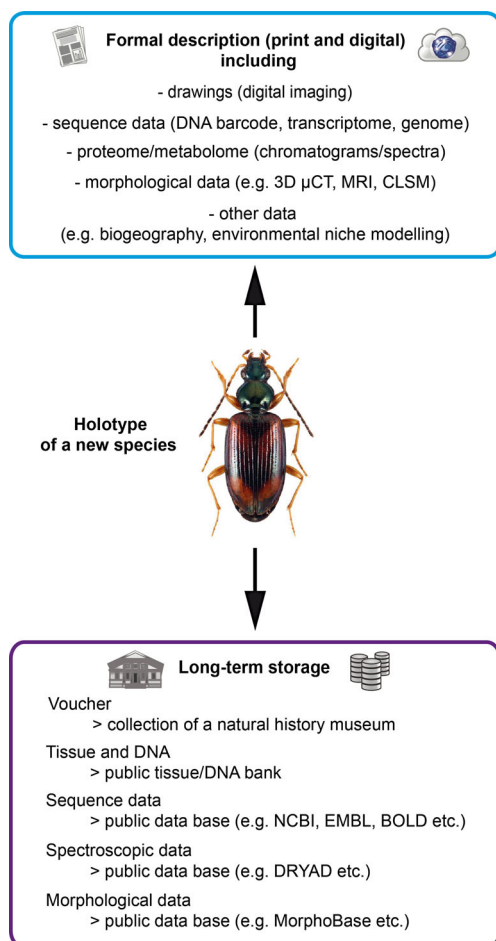

Formal description (print and digital) including

- drawings (digital imaging)

- sequence data (DNA barcode, transcriptome, genome)

- proteome/metabolome (chromatograms/spectra)

- morphological data (e.g. 3D μCT, MRI, CLSM)

- other data
(e.g. biogeography, environmental niche modelling)

Holotype of a new species

Long-term storage

Voucher
> collection of a natural history museum

Tissue and DNA
> public tissue/DNA bank

Sequence data
> public data base (e.g. NCBI, EMBL, BOLD etc.)

Spectroscopic data
> public data base (e.g. DRYAD etc.)

Morphological data
> public data base (e.g. MorphoBase etc.)

Fig. 4 Aspects of an idealized species description using morphological, genomic, proteomic, and metabolomic data sets as part of an integrative cybertaxonomic approach

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