

Opinion Paper

Recommendations for taxonomic submissions to *Hydrobiologia*

Stanley I. Dodson* & Carol Eunmi Lee

Department of Zoology, University of Wisconsin, 430 Lincoln Drive, Madison, WI, 53706, USA
(*Author for correspondence: E-mail: sidodson@wisc.edu)

Received 6 January 2005; in revised form 23 March 2005; accepted 12 April 2005

Key words: new species, taxonomy, morphology, phylogeny

Dr. Stanley Dodson received his PhD from the Zoology Department, University of Washington, USA, in 1970, on the interaction of size-selective predator–prey interactions and zooplankton community structure. He is a Zoology professor at the University of Wisconsin, Madison, USA, doing research in the area of freshwater ecology, especially zooplankton ecology. Current research topics include effects of productivity and land use (agricultural, urban) on zooplankton community structure, the pattern of morphological variation in *Diatomus*, and the ecology and evolution of the *Acanthocyclops vernalis* species group. He advises graduate students, teaches summer limnology and ecology courses, directs an undergraduate ecology internship program, and chairs the Biological Aspects of Conservation Program (about 90 majors).

Carol Eunmi Lee completed her bachelor's and master's degrees at Stanford University and her PhD at the University of Washington. Her work focuses on the evolution of physiological mechanisms that allow species to breach boundaries barriers between habitats. She uses genomic tools to determine characteristics that are exclusive of invasive populations. In addition, links between colonization and speciation have led her to examine patterns of reproductive isolation and incipient speciation following geographic separation. Her lab focuses on some of the most pervasive invaders in aquatic ecosystems, such as the copepod *Eurytemora affinis* and zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis*).



Abstract

Morphological taxonomy is a critical component of all aspects of aquatic biology. *Hydrobiologia* receives many manuscripts that focus on descriptions of new species of aquatic organisms. We offer suggestions for how these papers can better conform to the stated aims and scope of *Hydrobiologia*, which read, in part: ‘*Hydrobiologia* publishes original articles...of interest to a broad and international audience. Purely descriptive work...will be considered if it is firmly embedded in a larger biological framework’. In our opinion, taxonomic studies that classify new species are more likely to meet these aims if they state the species concept being used, and include additional experimental, analytical or conceptual analyses. For example, we recommend that studies that use morphological taxonomy also include independent tests of species boundaries, such as multivariate analyses, molecular genetic analyses, and/or tests of reproductive isolation. Given the constraints under which many taxonomists operate, collaboration might be the most effective strategy for achieving these goals.

Introduction

The journal *Hydrobiologia* has a long tradition of publishing taxonomic descriptions of aquatic organisms (Schram, 2004). We are writing this essay, as our own opinions, with the purpose of encouraging and assisting prospective authors of taxonomic papers who would like to continue this tradition in *Hydrobiologia*. We will focus on papers that treat microcrustacean taxonomy, which is our area of expertise.

Advances in theories of speciation, systematics, morphometrics statistical analyses, multivariate analyses, and molecular markers have changed the face of taxonomy profoundly (Mayr, 1963; Wiens, 2000; Avise, 2004; Coyne & Orr, 2004). Since the 1950s, taxonomists have known that species are fascinating and slippery creatures, prone to allometry, heritable polymorphisms, geographic variation, phenotypic plasticity, or morphological stasis. The integration of an analysis of one or more of these problems into a taxonomic treatment of a group has the potential to greatly increase its relevance, as well as its impact.

New directions

A description of a new species (or a higher taxon) that makes a larger and more general contribution to the scientific community can be built on the foundation of a traditional taxonomy paper by making one or more of several possible additions.

First, an essential element of a modern taxonomy paper is an explicit statement of the species

concept used in the paper. There are many species concepts, such as biological, morphological, or phylogenetic, and it is important that the readers know what an author means by ‘species’ (Knowlton & Weigt, 1997; Freeman & Herron, 2004). An important point to keep in mind is that species categories are projections of the human desire to neatly classify the world (Darwin, 1859). In reality, species boundaries are often indeterminate, reflecting the jagged and idiosyncratic manner in which speciation occurs. Thus, the use of multiple measures (morphology, molecular genetic, reproductive isolation) to define species boundaries is ideal, but could yield discordant results (Knowlton & Weigt, 1997). For example, for the copepod *Eurytemora affinis*, rates of morphological evolution, molecular evolution, and reproductive isolation were not congruent (Lee & Frost, 2002). Large genetic divergences and reproductive isolation were found among morphologically indistinguishable clades, and the one morphologically distinct group was no more genetically distant from the others (Lee & Frost, 2002). In such cases, rather than designate species boundaries, it would be preferable to describe the group as a ‘species complex,’ or as ‘sibling species’ (Knowlton, 1993).

Second, morphological characters are affected by many factors, such as heritable polymorphisms, allometry, phenotypic plasticity (in response to seasonal, geographic, latitudinal, and climatic variation), and morphological stasis. The reader of a taxonomic paper might be interested in knowing whether the author accounted for these factors, and if so, how the potential problems were addressed. For example, common-garden

experiments assist in identifying traits that are subject to phenotypic plasticity and reveal true heritable differences in morphology among species. In such experiments, different morphotypes are reared under identical laboratory conditions to determine whether the apparent differences are a result of phenotypic plasticity. Woltereck (1909) used laboratory cultures of several forms of *Daphnia* to show that they were actually morphological variants ('cyclomorphosis') of one basic morphological form (Dodson, 1989). Laboratory cultures revealed that the major morphological character used to distinguish two *Daphnia* species was induced by predaceous Chaoborus larvae (Krueger & Dodson, 1981), and that the major morphological character used to distinguish two *Acanthocyclops* species were in fact variants of a single morphological form induced in response to temperature (and subject to phenotypic plasticity) (Dodson et al., 2003). Lee & Frost (2002) found that morphological variance (Q_{ST}) was much greater among wild-caught populations of the copepod *Eurytemora affinis* than among those reared in common-garden in the laboratory. Their results indicate that the morphological characters used to distinguish *Eurytemora* species are prone to environmentally-induced plasticity.

Small sample size is an issue that can lead to misinterpretation of morphological data. Large scale studies (using large sample sizes and multiple characters) are often an antidote for this kind of misinterpretation (Böttger-Schnack & Huys, 2004). Reviews of multiple species, such as those by Halse & McRae (2004), Short (2004) and Rogers (2002) could generate the larger sample sizes that improve the generality of a taxonomy paper. Comparative morphological analyses of traits among multiple species, even qualitative comparisons, also add value to a taxonomic paper (for example: Martens, 2003). A clear and user-friendly identification key also increases the general utility of a taxonomic paper.

When describing a species based on morphological criteria, independent evaluation of the characters is particularly desirable. Molecular markers are often independent of macro-morphological characters (Burton, 1996). Molecular markers could suggest the presence of cryptic species or morphological stasis (Avisé, 2004), and could clarify phylogenetic relationships (Thum,

2004). For instance, the use of molecular markers have revealed that populations that differ morphologically could actually be genetically indistinguishable (Lee, 2000). Conversely, other studies have used molecular markers to detect cryptic species (Knowlton, 1993, 2000; Lee and Frost, 2002).

Third, quantitative analyses would help provide a means to use morphological characters in an objective manner. Multivariate analysis of many characters can provide insight into which characters are most independent and useful for separating morphological forms. In *Hydrobiologia*, multivariate techniques (ordination, classification) are used by ecologists (Derry et al., 2003; Steinarsdottir et al., 2003; Pinel-Alloul et al., 2004), but could also be used by taxonomists (Schram, 2004). Paggi (2001) used a two-dimensional graphical analysis to evaluate two characters at a time; there are much more powerful techniques available. For example, Petrussek et al. (2004) used multivariate analysis of molecular data to better understand the classification of *Moina* species, and Gili et al. (2004) used multivariate techniques to distinguish morphologically-similar *Daphnia* clones. The software PC-Ord (McCune & Mefford, 1999) and the companion text (McCune & Grace, 2002) provide an introduction to multivariate techniques.

Phylogenetic analyses are a class of multivariate techniques developed especially for the exploration of evolutionary relationships among taxa, and could employ both morphometric and molecular data (Knowlton, 2000; Wiens, 2000, Lee & Frost, 2002). Several phylogenetic approaches use shared derived characters to identify new groupings or to test traditional classification schemes (Thum, 2004). Several software packages, such as PAUP (Swofford, 1998) and PHYLIP (Felsenstein, 2004), are used for phylogenetic analyses. Fourier analysis and landmark analyses are useful for quantifying continuous morphometric traits (e.g., Baltanas et al., 2000). A good resource for references, software, and courses on morphometric analysis is available at the SUNY-Stony Brook website (<http://life.bio.sunysb.edu/morph/>) and in Judd et al. (2002).

Fourth, the use of mating experiments for sexual species to test for reproductive isolation between putative species is highly encouraged.

Reproductive compatibility or isolation would add an independent measure of speciation that is likely to be more informative than morphology, and in some cases, molecular phylogenies. The biological species concept is still considered a valid standard for defining species boundaries for sexual species (Mayr, 1963; Knowlton, 2000; Coyne & Orr, 2004), especially for animals, and is sometimes the most sensitive measure of speciation (Lee, 2000; Lee & Frost, 2002). Such tests could include analyses of behavioral (pre-mating) isolation, and F1 and F2 hybrid sterility and/or inviability (post-mating isolation). Cicchino et al. (2001) used laboratory experiments to show that diaptomid copepod males and females, which had been described as different species, were actually able to mate and produce offspring. Cryptic (reproductively isolated but morphologically indistinguishable) species are frequently revealed by mating experiments (Knowlton, 2000; Lee & Frost, 2002; Dodson et al., 2003; Avise, 2004). Careful morphological analysis of cryptic species can sometimes reveal morphological differences among cryptic species, once the (biological) species have been revealed using mating experiments (Knowlton, 2000; Dodson et al., 2003).

Final words

Clearly, taxonomists working with limited resources will sometimes find it difficult or impossible to augment their studies with additional techniques. One possible solution is collaboration. By selecting animal or plant groups for taxonomic revision that have (almost) immediate application in other studies (phylogeny, biodiversity, environmental monitoring, ecotoxicology, to suggest a few) the *Hydrobiologia* requirement of a ‘... broad international audience ...’ is almost immediately fulfilled. Many scientists across the world support *Hydrobiologia*’s commitment to supporting aquatic ecology in places where resources are limited.

Acknowledgements

Our opinions on taxonomic publications were refined through fascinating conversations with a

number of colleagues, all of whom provided insight into this complex issue. Special thanks are due to Jenny Boughman, Nancy Knowlton, Frank Ferrari, Koen Martens, Christopher Rogers, Marcelo Silva-Briano, Piet Spaak, and Grace Wyngaard.

References

- Avise, J. C., 2004. Molecular Markers, Natural History, and Evolution. 2004 (2nd ed.). Sinauer Associates, Sunderland, MA. USA.
- Baltanas, A., M. Otero, L. Arqueros, G. Rossetti & V. Rossi, 2000. Ontogenetic changes in the carapace shape of the non-marine ostracod *Eucypris virens* (Jurine). *Hydrobiologia* 419: 65–72.
- Böttger-Schnack, R. & R. Huys, 2004. Size polymorphism in *Oncaea venusta* Philippi, 1843 and the validity of *O. frosti* Heron 2002: a commentary. *Hydrobiologia* 513: 1–5.
- Burton, R. S., 1996. Molecular tools in marine ecology. *Journal of Experimental Marine Biology Ecology* 200: 85–101.
- Cicchino, G., E. N. S. Silva & B. Robertson, 2001. A new species of *Notodiaptomus* Kiefer, 1936 (Copepoda, Diaptomidae) from the Amazon and Orinoco River Basins. *Hydrobiologia* 453: 539–548.
- Coyne, J. A. H. & A. Orr, 2004. Speciation. Sinauer Associates, Sunderland, MA. USA.
- Darwin, C., 1859. On the Origin of Species by Means of Natural Selection, or, the Preservation of Favoured Races in the Struggle for Life. J. Murray, London.
- Derry, A. M., E. E. Prepas & D. P. N. Hebert, 2003. A comparison of zooplankton communities in saline lakewater with variable anion composition. *Hydrobiologia* 505: 199–215.
- Dodson, S. I., 1989. Predator-induced reaction norms. *Bioscience* 39: 447–452.
- Dodson, S. I., A. K. Grishanin, K. Gross & G. A. Wyngaard, 2003. Morphological analysis of some cryptic species in the *Acanthocyclops vernalis* species complex from North America. *Hydrobiologia* 500: 131–143.
- Felsenstein J., 2004. PHYLIP. Distributed free on the internet.
- Freeman, S. & J. C. Herron, 2004. Evolutionary Analysis (3rd ed.). Pearson/Prentice Hall, Saddle River, NJ. USA.
- Ganz, H. H. & R. S. Burton, 1995. Genetic differentiation and reproductive incompatibility among Baja-California populations of the copepod *Tigriopus californicus*. *Marine Biology* 123: 821–827.
- Gili, M., M. T. Monaghan & P. Spaak, 2004. Amplified fragment length polymorphism (AFLP) reveals species-specific markers in the *Daphnia galeata-hyalina* species complex. *Hydrobiologia* 526: 63–71.
- Halse, S. A. & J. M. McRae, 2004. New genera and species of ‘giant’ ostracods (Crustacea: Cyprididae) from Australia. *Hydrobiologia* 524: 1–52.
- Judd, W. S., C. S. Campbell, E. A. Kellogg, P. F. Stevens & M. J. Donoghue, 2002. Plant Systematics: A Phylogenetic Approach (2nd ed.). Sinauer Associates, Sunderland, MA. USA.

- Knowlton, N., 1993. Sibling species in the sea. *Annual Review of Ecology Systematics* 24: 189–216.
- Knowlton, N., 2000. Molecular genetic analyses of species boundaries in the sea. *Hydrobiologia* 420: 73–99.
- Knowlton, N. & Weigt L. A., 1997. In M. F., Dawah, H. A. Wilson, M. R. (eds.), *Species: The Units of Biodiversity* by Claridge, Chapman and Hall, New York: 199–219.
- Krueger, D. A. & S. I. Dodson, 1981. Embryological induction and predation ecology in *Daphnia pulex*. *Limnology and Oceanography* 26: 212–223.
- Lee, C. E., 2000. Global phylogeography of a cryptic copepod species complex and reproductive isolation between genetically proximate ‘populations’. *Evolution* 54: 2014–2027.
- Lee, C. E. & B. W. Frost, 2002. Morphological stasis in the *Eurytemora affinis* species complex (Copepoda: Temoridae). *Hydrobiologia* 480: 111–128.
- Martens, K., 2003. On the evolution of Gomphocythere (Crustacea, Ostracoda) in Lake Nyassa/Malawi (East Africa), with the description of five new species. *Hydrobiologia* 497: 121–144.
- Mayr, E., 1963. *Animal Species & Evolution*. Harvard University Press, Cambridge, MA. USA.
- McCune, B. & J. B. Grace, 2002. *Analysis of Ecological Communities*. MjM Press, Gleneden Beach, OR. USA.
- McCune, B. & M. J. Mefford, 1999. *PC-ORD. Multivariate Analysis of Ecological Data, Version 4*. MjM Software Design. Gleneden Beach, OR. USA.
- Paggi, J. C., 2001. Clarification of the taxonomic status of *Notodiptomus anisitsi* (Daday, 1905) and related species, with description of a new species from Argentina. *Hydrobiologia* 453: 549–564.
- Petrusek, A., M. Černý & E. Audenaer, 2004. Large intercontinental differentiation of *Moina micrura* (Crustacea: Anomopoda): one less cosmopolitan cladoceran?. *Hydrobiologia* 526: 73–81.
- Pinel-Alloul, B., G. Méthot & N. Z. Malinsky-Rushansky, 2004. A short-term study of vertical and horizontal distribution of zooplankton during thermal stratification in Lake Kinneret, Israel. *Hydrobiologia* 526: 85–98.
- Rogers, D. C., 2002. The amplexial morphology of selected Anostraca. *Hydrobiologia* 486: 1–18.
- Schram, F. R., 2004. The truly new systematics – megascience in the information age. *Hydrobiologia* 519: 1–7.
- Short, J.W., 2004. A revision of Australian river prawns, *Macrobrachium* (Crustacea : Decapoda: Palaemonidae). *Hydrobiologia* 525: 1–100.
- Steinarsdottir, M. B., A. Ingólfsson & E. Ólafsson, 2003. Seasonality of harpacticoids (Crustacea, Copepoda) in a tidal pool in subarctic south-western Iceland. *Hydrobiologia* 503: 211–221.
- Swofford, D., 1998. *PAUP 4.0 – Phylogenetic Analysis Using Parsimony*. Sinauer Associates, New York.
- Thum, R. A., 2004. Using 18S rDNA to resolve diaptomid copepod (Copepoda: Calanoida: Diaptomidae) phylogeny: an example with the North American genera. *Hydrobiologia* 519: 135–141.
- Wiens, J. J., 2000. *Phylogenetic Analysis of Morphological Data*. Smithsonian Institution Press, D.C. USA.
- Woltereck, R., 1909. Weitere experimentelle Untersuchungen über das Wesen quantitativer Artunterschiede bei Daphniden. *Verhandlungen der Deutschen Zoologischen Gesellschaft*. 19: 110–172.