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Species concepts: leeches versus bacteria

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With 2 figures

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Practising taxonomists largely ignore the continuing debate about the definition of species. In this contribution I will summarize recent discussions about the validity of the biological species concept with reference to microorganisms, which form ecotypes rather than true species. It is concluded that a bio-morpho-eco species definition is implicitly used by most modern leech scientists and other zoologists. This integrative species concept is discussed.

1 Introduction

It is a matter of considerable concern that after two centuries of scientific taxonomy there is no general consensus amongst naturalists as to which species definition to adopt (Bock 2004). Most taxonomists regard the biological species concept (BSC) – the view that species are reproductively isolated population systems in sexually reproducing organisms – as the most useful definition. In this *Essay*, which is dedicated to Prof. Ernst Mayr on the occasion of his 100th birthday (July 5, 2004) I will review some controversial discussions on this topic with special reference to leeches and bacteria.

2 Species definitions of Alfred R. Wallace and Ernst Mayr

In a recent "News and Views"-report published in the journal *Nature,* Eriksson (2004) claimed that the biological species concept cannot generally be true for many reasons, the most obvious being that some organisms, such as bacteria, reproduce clonally and "yet have species". In the same volume of *Nature* Axel Meyer (2004) pointed out that the "Darwin of our time", Ernst Mayr, defined what species are and how they arise. As a practising leech taxonomist and physiologist/evolutionist I would like to comment on these statements as follows.

In contrast to Charles Darwin, who did not distinguish between varieties and species (Kutschera 2001, 2003), natural selection's co-discover, Alfred Russel Wallace, published two tentative species definitions and one final version: "A species ... is a group of living organisms, separated from all other such groups by a set of distinctive character(istic)s, having relations to the environ-

ment not identical with those of any other group of organisms, and having the power of continuously reproducing its like" (Wallace 1895, Kutschera 2003). Similarly, Ernst Mayr, the principal father of the modern BSC, published throughout his long career several definitions. The first one appeared six decades ago (Mayr 1942) and the most recent is as follows: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups". Mayr (1996, 2001) agrees with his critics that the BSC does not apply to asexual (uniparental) organisms such as bacteria. In several recent interviews and a new book (Mayr 2001), he stated that bacteria do not form biological species, but pointed out that this has no bearing on the validity of the BSC, which is essentially restricted to animals and plants.

For instance, the medicinal leech *Hirudo verbana* Carena, 1820 (Fig. 1 A) , which is similar in size and morphology to the closely related *H. medicinalis* Linnaeus, 1758, represents a separate biospecies (Fig. 2) (Nesemann and Neubert 1999). To my knowledge, in aquatic ecosystems throughout Europe, where both species have been recorded, no intermediate forms have ever been found.

In addition, in freshwater aquaria, where both species have been maintained together over several generations, no hybrids (*H. verbana x H. medicinalis*) have been observed (U. Kutschera & C. Grosser, unpublished results). It follows that the taxon *H. verbana* represents reproductively isolated populations of leeches that are distinct from the "true" medicinal leech *H. medicinalis*, as described by Linnaeus in 1758. Both leech species have been used in medicine, *H. verbana* sometimes under the synonym *H. officinalis*. Sawyer (1986) did not distinguish between the taxa *H. verbana* (syn. *H. officinalis*) and *H. medicinalis*. This view is no longer valid, i. e., in European freshwater ecosystems at least two *Hirudo*-species occur, sometimes in the same pond (Nesemann & Neubert 1999).

3 Bacterial ecotypes

It is well known that microbial systematists have not yet reached a consensus on a species definition in the bacterial world. However, it has recently been pointed out that there is an appropriate species concept for bacteria: ecotypes. These are defined as populations of microbes that occupy the same ecological niche, whose divergence is purged recurrently by natural selection (Cohan 2002). Bacterial ecotypes can be identified as DNA-sequence clusters and are more like a genus than a (bio)species. In microbial systematics no "type specimens" are defined and deposited. Instead, certain bacterial strains are maintained in collections such as the *Deutsche Sammlung von Mikroorganismen und*

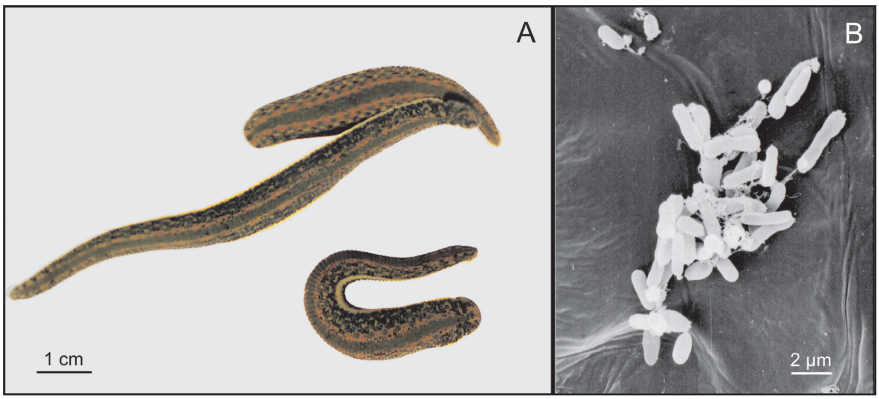

Fig. 1: Leeches (*Hirudo verbana*) in an aquarium (A) and epiphytic bacteria (*Methylobacterium mesophilicum*) on a sunflower leaf (B): biospecies vs. ecotypes

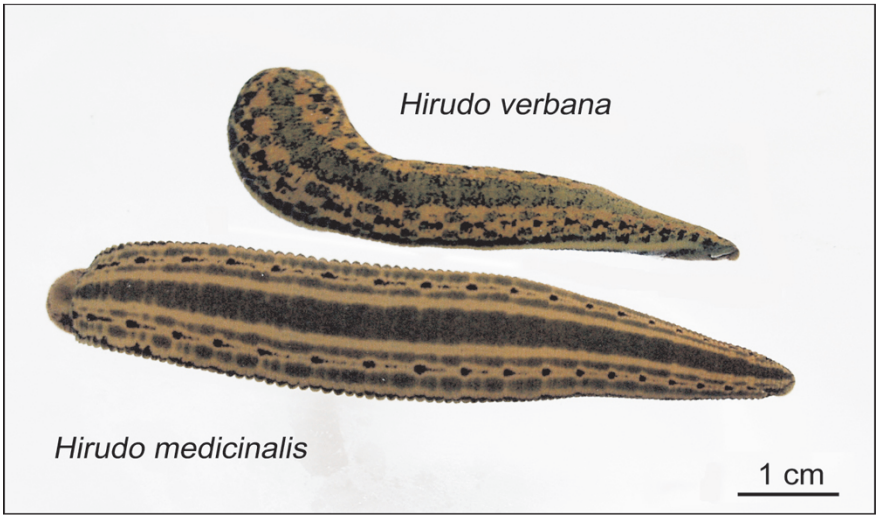

Fig. 2: The closely related medicinal leeches *Hirudo verbana* Carena, 1820 and *H. medicinalis* Linnaeus, 1758 can be distinguished by morphological characteristics (dorsal and ventral colour patterns, respectively). In addition, they do not interbreed. These taxa represent true biospecies

Zellkulturen (Braunschweig, Germany). For instance, the laboratory strain *Methylobacterium mesophilicum* ATCC 29983 (Fig. 1 B) can be purchased from this supplier and used as a reference for identification of other, related *Methylobacterium*-"species". These "pink-pigmented facultative methylotrophic bacteria" have been isolated from lake sediments, soils and the cuticle of leaves,

where they utilize methanol and related organic substances (Hornschuh et al. 2002). The BSC and the concept of ecotypes used by microbiologists can both be traced back to the "general" species definition of A. R. Wallace cited above. In the asexual world of bacteria, the resources of the microhabitat determine which populations can survive and spread, whereas in eukaryotic macroorganisms (animals, plants) the ability to interbreed and produce fertile offspring is the defining criterion in phylogenetic taxonomy.

4 Conclusions

Most evolutionary biologists agree that Ernst Mayr's BSC is alive and well, in spite of the fact that microbes form ecotypes rather than biospecies (Cohan 2002, Kutschera 2001, 2003, Mayr 2001). However, it should be noted that the BSC, which developed from population-level thinking of the modern synthesis (Kutschera & Niklas 2004) has not been adopted by taxonomists who study microbial eukaryotes (for instance, unicellular algae such as *Chlorella* and related taxa, which belong to the Protists i.e., kingdom Protoctista). Finlay (2004) pointed out that most free-living protozoan species are defined by their body form (morphology). Like prokaryotic microorganisms (bacteria), these morphospecies are to a large extent defined by the ecological niche that the protozoon-population occupies under natural conditions.

Leech taxonomists and other practising zoologists have adopted a combined species concept: Ernst Mayr's BSC, supplemented by a careful description of the morphology (phenotype) of the organism and information on the natural habitat (ecological niche) of the population. These "bio-morpho-eco species", represented by the type specimens deposited in museum collections, are the "basic units" of our knowledge of extant biodiversity in all four kingdoms of eukaryotic organisms (Protoctista, Fungi, Animalia, Plantae). Bacteria, which represent the oldest branch of life forms and the "unseen majority" in the biosphere (Kutschera & Niklas 2004) are different: they are classified as ecotypes and there are no dead "type specimens" deposited in taxonomic collections around the world.

It should be mentioned that the medicinal leech *H. medicinalis* (Fig. 2) carries in its digestive tract a pure culture of one "species" of bacteria (*Aeromonas veronii*). The exact role of these extracellular symbionts is unknown; however, a beneficial function of the microbes for their host is likely (Sawyer 1986, Graf 2000).

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Forschungsberichte

Kerschbaumer, G., E. Lorenz & M. Konar (2004): **Fischökologische Untersuchung der Lieser und ihrer Hauptzubringer**. 65 Abb., 20 Lit.- Veröffentlichungen des Kärntner Instituts für Seenforschung o. Nr., 104 pp., Klagenfurt
Schlagwörter: Pisces, Drau, Donau, Kärnten, Österreich, Ökologie, Durchgängigkeit, Wanderungshinderniss

Untersuchung der Fischfauna im gesamten Einzugsgebiet im Hinblick auf die zahlreichen Wanderungshindernisse durch Wasserkraftanlagen und auf die Gewässergüte (pendelt zwischen Güteklasse I und II).

Kärntner Institut für Seenforschung (2004): **Kärntner Seenbericht 2004**. 58 Abb., 54 Tab., Glossar.- Veröffentlichungen des Kärntner Instituts für Seenforschung 18, 102 pp., Klagenfurt
Schlagwörter: Kärnten, Österreich, See, Badegewässer, Gewässergüte, Hygiene

Übersicht über den aktuellen Zustand der Seen in Kärnten im Hinblick auf Limnologie und Hygiene.

Kärtner Institut für Seenforschung (2004): **Der Wörthersee - Limnologische Langzeitentwicklung 1970-2002**. 75 Abb., 8 Tab., 51 Lit., 1 Kt., Anh.- Veröffentlichungen des Kärntner Instituts für Seenforschung o. Nr. 71 pp., Klagenfurt
Schlagwörter: Planktothrix, Cyanobacteria, Plankton, Wörthersee, Kärnten, Österreich, See, Chemismus, Trophie, Reoligotrophierung, Zirkulation

Die Ergebnisse des mit 20 km² größten Sees Kärntens zeigen ausgehend vom Höhepunkt der Eutrophierung eine ständige Verbesserung, die sich in der Struktur des Phyto- und Zooplanktons abbildet. Eine Besonderheit bildet die Planktothrix rubescens Population als Ausdruck der Oligotrophie und ihr Einfluss auf die Nahrungskette.

Dettinger-Klemm, P.-M., A. (2003): **Chironomids (Diptera, Nematocera) of temporary pools - an ecological study**. 96 Abb., 74 Tab., 365 Lit., 13 Anh.- 371 pp.- Dissertation Fachbereich Biologie der Phillips-Universität Marburg. Bezug: Über den Autor, Plattenhof, D-64560 Riedstadt
Schlagwörter: Limnophyes, Chironomidae, Diptera, Insecta, Hessen, Deutschland, Temporärgewässer, Tümpel, Morphologie, Taxonomie, Bestimmung, Austrocknungstoleranz, Ökologie, Emergenz, Parthenogenese, Lebenszyklus, Temperatur

Langjährige, breit angelegte Untersuchung der Überlebensstrategien von Chironomiden temporärer Tümpel an Hand von Emergenzstudien und Besiedlungsversuchen im Freiland mit Chironomus dorsalis und über Laborversuche zum Einfluss von Temperatur, Photoperiode und Besiedlungsdichte auf Wachstum und Entwicklung sowie zur Austrocknungstoleranz und zur Parthenogenese. Im Labor beobachtet wurden vor allem typische Arten temporärer Tümpel: Limnophyes asquamatus, Paralimnophyes hydrophilus, Chironomus dorsalis und Polypedilum tritum unter Einschluss morphologisch-taxonomischer Untersuchungen, dabei auch ein Bestimmungsschlüssel für die Larven und Puppen der Gattung Limnophyes.

Wichtiger Beitrag zur Ökologie der Chironomiden-Gesellschaften extremer Biotope sowie zur Taxonomie, zur Autökologie und zum Lebenszyklus der untersuchten Arten und ebenso in methodischer Hinsicht.

Herausgeber