

---

# The concept of species and practical taxonomy: what is in-between?

---

**Rimantas Rakauskas**

*Vilnius University,*

*M. K. Čiurlionio 21/27,*

*LT-2009 Vilnius, Lithuania.*

E-mail: rimantas.rakauskas@gf.vu.lt

The ecological approach considers the biological species as an ecological unit. This does not exclude recognition of biological species also as a genetic and morphological (*sensu lato*) unit. The article deals with the theoretical and practical aspects of such a treatment of the concept of biological species on the examples of aphid (Hemiptera, Sternorrhyncha: Aphididae) taxonomy.

**Key words:** species concepts, taxonomy, aphids

---

## INTRODUCTION

“Since the species are the units of evolution, and since they are the base units of biological systematics, a proper understanding of species is crucial for the success of evolutionary biology and biological systematics” (Ereshefski, 1992). Such or similar statements seem to be generally accepted among biologists. That is not the case when considering what the species really is. Numerous concepts and definitions of species are available, and none of them is widely accepted (Blackman, 1995; Grant, 1963; Klimaszewski et al., 1995; Mayr 1963; 1976; 1982; Matile et al., 1993; Завадский, 1968). Several papers appeared, propagating the understanding of biological species as an ecological unit, particularly addressing the aphid (Hemiptera, Sternorrhyncha: Aphididae) taxonomy (Shaposhnikov, 1981; 1987; Rakauskas, 1998). The aim of the present paper is to discuss such understanding of species from the point of view of practical taxonomic procedures, based on the examples from aphid biosystematic studies.

## BIOLOGICAL SPECIES AS AN ECOLOGICAL UNIT

Ecological methodology in the species-level taxonomy is based on the following ideas (Rakauskas, 1997; 1998; 2001). When describing the species as a general biological phenomenon, a more general biological approach is needed. It is often quoted that “in biology nothing makes sense except in the light of evolution” (Dobzhansky, 1970: 6). On the other hand, biological evolution is the process of adaptation of living things (Dobzhansky, 1970; Grant, 1963; Ridley, 1993; Северцов, 1987). Following this, one may consider that the main characteristic of the species is the role

performed by the species in nature. The following features seem to be characteristic of the biological species therefore.

1. A species is an ecological unit. A species is a system of related populations that are similarly adapted (Shaposhnikov, 1981; Blackman, 1995). All populations of the species have specific adaptations for surviving in the ecological niche of that species, and every population may have populational adaptations for surviving in its particular ecological subniche. Therefore the species is to be treated as an ecological unit. Species-specific adaptations are responsible for the specific role performed by a particular species in nature.

2. A species is a genetic unit. Species-specific adaptations must be fixed and inherited genetically. Thus, ecological specificity of the species is underlain by the genetic specificity. Forces responsible for the specificity and unity of the gene pool of the species are interpopulational gene flows (Dobzhansky, 1970; Mayr, 1982), specific mate recognition systems (Paterson, 1993), common selective regimes (Ehrlich et al., 1992). Selection might be treated as the most general force of maintaining or disturbing the unity of the gene pool of a particular species.

3. A species is a morphological (*sensu lato*) unit. Species-specific adaptations are provided due to species-specific morphological (*sensu stricto*), anatomical, physiological, cytogenetic, biochemical, immunological, etc. features, the inheritance of which is underlain by the specificity of the gene pool of the species. Species-specific adaptations need species-specific characters. An important practical conclusion that follows from understanding this fact is that real species can be recognized by their morphological characters. The so-called morphological species of early taxonomists are still valid in many cases therefore.

4. Treating species as a system of populations is useful for understanding the evolutionary processes. The idea of the complex nature of a species consisting of subspecific units having a potential to diverge (or, in other expression, forego its own evolutionary (tendencies) was present in Darwin's theory, and it is still actual in population-genetic modern synthesis (Вавилов, 1931; Dobzhansky, 1970; Mayr, 1982). There is no need to multiply species numbers by giving specific names to every "smallest diagnosable cluster of individual organisms" (Cracraft, 1992). It is population but not the species that is an elementary unit of evolution, the smallest group of individuals having a potential of independent evolution.

If any name for the above-mentioned understanding of species is needed, such a concept of species is to be called "biological species", because understanding species as a coadapted gene pool inhabiting a certain "adaptive peak" of "adaptive landscape" was already present in the concept of biological species (Dobzhansky, 1970: 26).

Having recognized the above-mentioned features of the biological species, what are the consequences for defining the species in taxonomy? When understanding the biological evolution (including speciation) as the history of adaptation of living things one might consider that the main feature of species is the role performed by it in nature. That is, the main characteristic of the species is its ecological niche. When solving the problem, is it one or two species, it is necessary to estimate the ecological specificity of the organisms studied.

Generally, all structural, physiological, biochemical, etc. characters of living things serve one purpose – successful existence in certain habitats. Morphology, anatomy, physiology, cytogenetics, biochemistry, etc. can provide valuable information when deciding whether the organisms under analysis are adapted to similar ecological niches (they belong to the same species in such case) or to different niches (the case of different species). Excellent understanding of the characters studied and successful intuition may result in a proper description of the species based on one or few criteria only. Morphospecies of early taxonomists are still valid in many cases therefore. Nevertheless, the probability of mistakes in such cases is much greater than when exploiting more criteria.

Concerning aphids, information on the life cycle and host specificity is supposed to be absolutely necessary for understanding their ecological specificity. Morphological analysis is necessary for a proper diagnosis of aphid species and constructing practical identification keys. Thus, when distinct differences in life cycles and host specificity correlated with clear morphological specificity and biogeographical evidence are available, sophisticated and expensive molecular techni-

ques (*e. g.*, allozymes or DNA analysis) seem to be not necessary. Cytogenetic and molecular methods are needed when ecological and morphological ones are insufficient on their own. Anyway, purely morphological, cytogenetic or molecular descriptions of aphid species, without any ecological data on new taxa, should be avoided. Information on the life cycles and host specificity is necessary in all cases. Let us see how this methodology works in practice.

## EXAMPLES FROM APHID TAXONOMY

### Aphid species of the genus *Aphis* L. living on currants and gooseberries (*Ribes* spp.) in the Palaearctics

Four species of the genus *Aphis* are reported as inhabiting currants and gooseberries (*Ribes* spp.) in the Palaearctics: *A. grossulariae* Kaltentbach, 1843, *A. schneideri* (Börner, 1940), *A. triglochinis* Theobald, 1926 and *A. popovi* Mordvilko, 1932. Numerous data concerning host specificity, life cycles and morphological features are available for the first three European species (for a wider review, see Rakauskas, 1998a). The fourth one is a Siberian species, closely related morphologically to the European *A. schneideri*; its entire life cycle is not known (Rakauskas, 1996). When treating a species as an ecological unit, one can justify the existence of three 'good' species inhabiting currants and gooseberries in Europe: the first is holocyclic monoecious on *Ribes* spp. (*A. schneideri*), the second is holocyclic facultatively heteroecious between *Ribes* spp. and Onagraceae (*A. grossulariae*), and the third one obligatorily alternates between *Ribes* spp. and various Brassicaceae, Boraginaceae, Asteraceae hosts (*A. triglochinis*). Nevertheless, the ecological niche of aphid species is not easy to define precisely, its boundaries remain uncertain. *E. g.*, monoecious holocyclic clones of *A. grossulariae* have been documented (Гусынина, 1963), making this species similar to *A. schneideri*. Resuming the available information on host specificity, life cycles, phenology and parasitoid-predatory species composition, only *A. triglochinis* seems to be a "good" species, whilst *A. grossulariae* and *A. schneideri* share many similar features (Rakauskas, 2000). Furthermore, successful interspecific crossing experiments were performed on these species, raising the question of the possibility of natural hybridisation (Rakauskas, 1999). Intermediate hybrid morphotypes appeared to be not so rare in natural conditions (Rakauskas, 2002). Additional ecological and morphological studies are needed to clarify the taxonomic status of *A. popovi* – it might be a sibling vicariant species to the European *A. schneideri* in Siberia, or just a Siberian representative (subspecies?) of *A. schneideri*. Molecular data seem to be necessary for the final decision on how many species of *Aphis* live on *Ribes* spp. in the Palaearctics.

DNA analysis techniques (*e. g.*, Sunnucks et al., 1997) seem to be most promising at the moment. Relations between the Palaearctic and Nearctic currant-inhabiting *Aphis* species also demand molecular techniques. That is, the Nearctic *A. neomexicana* – oenotherae complex is greatly similar to the Palaearctic *A. grossulariae* in its life cycle, host specificity and morphology (for a wider account, see Rakauskas, 2000). DNA sequencing and subsequent phylogenetic analysis (*e. g.*, Goto et al., 2001) might clarify the question whether Nearctic and Palearctic currant *Aphis* counterparts are the same species (which seems likely from ecological and morphological data), or they are vicariant sibling species that converged due to similar ecological niches being exploited on different continents.

#### **Aphid species of the genus *Macrosiphum* Pass. living on *Knautia* spp. in Europe**

Three species of the genus *Macrosiphum* are reported as inhabiting *Knautia* spp. (Dipsacaceae) in Europe. *M. rosae* (Linnaeus, 1758) is facultatively heteroecious between *Rosa* and various Dipsacaceae, Valerianaceae and Onagraceae hosts, the life cycle and host specificity being well documented from the very beginning of the last century (for a wider review, see (Ракаускас и др., 1983). *M. knautiae* Holman, 1972 and *M. silvaticum* Meier, 1985 are holocyclic monoecious on *Knautia* spp; that was proven experimentally for *M. knautiae* in Moravia (Holman, 1972) and *M. silvaticum* in Lithuania (Ракаускас, 1985). These two species utilize the same species of the genus *Knautia*, are sympatric in their distribution and resemble each other in their morphological features (Rakauskas, 2002). Ecological understanding of biological species suggests the existence of two *Knautia*-inhabiting *Macrosiphum* species in Europe. One is *M. rosae*. It is facultatively heteroecious between *Rosa* and various Dipsacaceae, Valerianaceae and Onagraceae hosts. Another species is oligophagous on *Knautia* spp. According to the Principle of Priority (International..., art. 23), a valid name for this species is *Macrosiphum knautiae* Holman, 1972, whilst *Macrosiphum silvaticum* Meier, 1985 is a younger synonym. This is justified, because *M. knautiae* and *M. silvaticum* have the same host specificity and life cycles, share a similar morphology and have the same distribution area. The idea of two subspecies inside *M. knautiae* (Holman, 1972) is not reasonable for the present understanding of biological species as an ecological unit and applying ecological thinking also to the subspecies level (Blackman et al., 1991; Rakauskas, 2001). Subspecies should be an ecological variant (subunit) of the species. The main characteristic of the aphid subspecies should be its ecological specificity. The ecological specificity of a certain aggregate of aphids, accompanied by the genetic and morphological specificity, is to be proven when

dignifying a new aphid subspecies. A formal description of a new subspecies urgently emphasizes the need of documenting the morphological differences between the subspecies, correlated with their ecological specificity. The subspecies of *Myzus cerasi* (F.) represent a good example of a proper subspecies (Gruppe, 1988; Müller, 1969). That is not the case with *M. knautiae*, where the evidence for different life cycle and/or host specificity modes, followed by distinct morphology, reproductive barriers and distribution peculiarities is lacking. Contrary to the above example of the currantdwelling *Aphis* species, molecular analysis of *Macrosiphum* species living on *Knautia* in Europe is not necessary. The available ecological, morphological and zoogeographical data are enough to justify the existence of only two *Macrosiphum* species inhabiting *Knautia* in Europe.

These examples show the ecological understanding of biological species to be not just a theoretical construction, but a useful tool for taxonomic practice as well. As concerns the aphid taxonomy, such understanding of species emphasizes the necessity to study aphid life cycles and host specificity, followed by the morphological analysis of ecologically different aphid clones. Valuable additional information can be supported by cytogenetic, biochemical characters (allozymes and DNA analysis) and hybridization experiments. Nevertheless, molecular data might appear necessary in certain cases. One must clearly recognise that life cycle and host specificity are not the only and maybe even not the most important characters of the aphid ecological niche. Different ecological features might indicate just different intraspecific units – host/life cycle races or subspecies. Similar life cycle and host specificity might be characteristic of different species (*e. g.*, vicariant species that can appear due to their different zoogeographical pathways). Host plant specificity is closely dependent on the taxonomy of host plants: the “same” plant species might in fact concern an aggregate of different sibling plant taxa having different environmental needs. For example, *Knautia arvensis* (L.) Coult. is sometimes treated as an aggregate of species (Štepanek, 1997). If this would be the case, the situation with *M. knautiae* in Europe should be also revised. So, aphidologists do not have the only, the main or the most important criterion for recognising the species, at least nowadays. Therefore the multidisciplinary approach (Blackman et al., 1995) seems to be the most relevant in taxonomic studies at present. Whatever methods exploited, the taxonomic evaluation of data should involve their ecological interpretation.

#### **CONCLUSIONS**

1. Following the general methodology of ecological thinking in biology, the biological species should be treated as an ecological unit.

2. Treating the biological species as an ecological unit does not exclude understanding the biological species also as a genetic and morphological (*sensu lato*) unit.

3. Ecological methodology stresses the need of ecological analysis in taxonomical practice. The results received when applying different methods of taxonomic analysis (morphometry, ethological, immunological, physiological analysis, cytogenetic and molecular methods, etc.) should be evaluated in the ecological context, concerning the specificity of the ecological niche of supposed species. Direct ecological analysis is highly appreciated.

4. When describing the aphid species, information on the life cycles and host specificity, followed by the morphological analysis of ecologically different clones, is absolutely necessary. Valuable additional information can be supported by cytogenetic, biochemical characters (allozymes and DNA analysis) and hybridization experiments.

#### References

- Blackman R. What's in a name? Species concepts and realities. *Bull. Ent. Res.* 1995. Vol. 85. P. 1–4.
- Blackman R. L., Brown P. A. Morphometric variation within and between populations of *Rhopalosiphum maidis* with a discussion of the taxonomic treatment of permanently parthenogenetic aphids (Homoptera: Aphididae). *Entomologia Generalis*. 1991. Vol. 16(2). P. 97–113.
- Blackman R., Watson G., Ready P. The identity of the African pine wooly aphid: a multidisciplinary approach. *Bulletin OEPP*. 1995. Vol. 25. P. 337–341.
- Cracraft J. Species Concepts and Speciation Analysis. *The Units of Evolution: Essays on the Nature of Species*. 1992. P. 93–120.
- Dobzhansky T. *Genetics of the Evolutionary Process*. New York: Columbia University Press. 1970. 505 p.
- Ehrlich P., Raven P. Differentiation of Populations. *The Units of evolution: Essays on the Nature of Species*. 1992. P. xiii.
- Ereshefsky M. *The Units of Evolution: Essays on the Nature of Species*. Cambridge, Mass.: The MIT Press. 1992. 405 p.
- Goto S. G., Kimura M. T. Phylogenetic utility of mitochondrial COI and nuclear Gpdh genes in *Drosophila*. *Molecular Phylogenetics and Evolution*. 2001. Vol. 18(3). P. 404–422.
- Grant V. *The Origin of Adaptations*. New York: Columbia University Press. 1963. 606 p.
- Grant V. Evolution of the Species Concept. *Biol. Zent. Bl.* 1994. Vol. 113. P. 401–415.
- Gruppe A. Electrophoretische Untersuchungen zur Unterscheidung der Subspecies von *Myzus cerasi* F. (Hom., Aphididae). *J. Appl. Ent.* 1988. Vol. 105. P. 460–465.
- Holman J. Description of *Macrosiphum knautiae* sp. n., with notes on the taxonomy of the *M. rosae* group (Homoptera, Aphididae). *Acta Ent. Bohemoslov.* 1972. Vol. 69. 175–185.
- International Code of Zoological Nomenclature. Fourth Edition*. London: The International Trust for Zoological Nomenclature. 1999. 306 p.
- Klimaszewski S., Wojciechowski W., Jedlička L. *Podstawy systematyki zoologicznej*. Katowice: Wydawnictwo UŚ. 1995. 92 p.
- Mayr E. *Animal species and evolution*. Cambridge, Mass.: Harvard University Press. 1963. 797 p.
- Mayr E. *Evolution and the diversity of Life*. Cambridge, Mass.: Harvard University Press. 1976. 758 p.
- Mayr E. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, Mass.: Harvard University Press. 1982. 974 p.
- Matile L., Tassy P., Goujet D. *Wstęp do systematyki zoologicznej*. Warszawa: PWN. 1993. 107 p.
- Müller F. P. Bastardierungsversuche zur Feststellung von Isolierungsmechanismen zwischen nahe verwandten Formen in der Gattung *Myzus passerini* (Homoptera: Aphididae). *Biol. Zbl.* 1969. Vol. 88. P. 147–164.
- Paterson H. *Evolution and the recognition concept of species: collected writings*. Baltimore: John Hopkins University Press. 1993. 234 p.
- Rakauskas R. Redescription of *Aphis popovi* and its relations with other Palaearctic species of the genus *Aphis* inhabiting *Ribes* (Hemiptera: Aphidoidea: Aphididae). *Eur. J. Entomol.* 1996. Vol. 93. P. 249–254.
- Rakauskas R. Biologinė rūšis kaip ekologinė sąvoka. *Ekologija* (Vilnius). 1997. Nr. 4. P. 58–62.
- Rakauskas R. What is the (aphid) species? Nieto Nafria J. M. & Dixon A. F. G. (Eds.) *Aphids in natural and managed ecosystems*. Leon: Universidad de Leon. 1998. P. 447–451.
- Rakauskas R. Morphometric analysis of European species of the genus *Aphis* (Sternorrhyncha: Aphididae) inhabiting *Ribes*. *Eur. J. Entomol.* 1998a. Vol. 95. P. 239–250.
- Rakauskas R. Hybridisation between *Aphis grossulariae* and *Aphis schneideri* (Sternorrhyncha: Aphididae): an experimental approach. *Eur. J. Entomol.* 1999. Vol. 96. P. 401–408.
- Rakauskas R. On the identity of *Aphis neomexicana* (W. P. and T. D. A. Cockerell, 1901). *Aphids and other Homopterous insects* (Warszawa). 2000. Vol. 7. P. 7–14.
- Rakauskas R. *Lietuvos amarų* (Hemiptera, Sternorrhyncha: Aphididae) biosistematiniai tyrimai. Vilnius: VU leidykla. 2000. 128 p.
- Rakauskas R. What is the (aphid) subspecies? *Materials of the Sixth International Symposium on Aphids*. Rennes (France), 3–7 September 2001 (in press).
- Rakauskas R. Natural hybridisation between *Aphis grossulariae* and *Aphis schneideri*: morphological evidence (Sternorrhyncha: Aphididae). *Eur. J. Entomol.* Submitted in March 2002.
- Rakauskas R. *Macrosiphum* on *Knautia* in Europe: biology, morphology and systematics, including new synonymy (Hemiptera: Aphididae). *Deutsche ent. Zeitschr.* Submitted in May, 2002.
- Ridley M. *Evolution*. Cambridge, Mass.: Blackwell Science. 1993. 670 p.
- Shaposhnikov G. *Populations and Species in Aphids and the Need for a Universal Species Concept*. Ottawa: Agric. Canada Res. Branch Publication. 1981. 61 p.

33. Shaposhnikov G. Organisation (Structure) of Populations and Species, and Speciation. *Aphids. Their Biology Natural Enemies and Control*, A. Amsterdam: Elsevier. 1987. P. 415–430.
34. Sunnucks P., De Barro P. J., Lushai G., Maclean N., Hales D. Genetic structure of an aphid studied using microsatellites: cyclic parthenogenesis, differentiated lineages and host specialization. *Molecular Ecology*. 1997. Vol. 6. P. 1059–1073.
35. Štepanek J. *Knautia* L. – chrastavec. *Květena České Republiky*, 5. Praha: Academia. 1997. P. 543–554.
36. Вавилов Н. И. Линнеевский вид как система. *Тр. по прикл. бот., ген. и сел.* 1931. Т. 26(3). С. 109–134.
37. Гусынина Л. М. Тли рода *Aphis* L. на смородине и крыжовнике. *Тр. Биол. ин-та Сиб. отд. АН СССР*. 1963. Т. 10. С. 77–81.
38. Завадский К. М. *Вид и видообразование*. Ленинград: Наука. 1968. 396 с.
39. Ракаускас Р. П. *Macrosiphum silvaticum* Meier–новый для СССР вид тлей, обнаруженный в Литовской ССР в 1978–1983 гг. *Новые и редкие для Литовской ССР виды насекомых. Сообщения и описания 1985 года*. 1985. С. 9–13.
40. Ракаускас Р. П., Заянчкаускас П. А. Биологические особенности зеленой розанной тли в Литовской ССР. *Тр. АН ЛитССР. Сер. В*. 1983. Т. 2(82). С. 70–78.
41. Северцов А. С. *Основы теории эволюции*. Москва: Изд-во МГУ. 1987. 320 с.

**Rimantas Rakauskas**

**RŪŠIES KONCEPCIJOS IR PRAKTINĖ SISTEMATIKA: KAS BENDRO?**

**S a n t r a u k a**

Ekologinė mąstysena verčia suvokti biologinę rūšį kaip ekologinį vienetą. Pastaroji rūšies samprata neprieštarauja biologinės rūšies, kaip genetinio ir morfologinio (plačiaja prasme) vieneto, supratimui. Straipsnyje aptariami tokios rūšies koncepcijos teoriniai aspektai ir praktinio taikymo galimybės, remiantis pavyzdžiais iš amarų (Hemiptera, Sternorrhyncha: Aphididae) sistematikos.

**Raktažodžiai:** rūšies koncepcija, sistematika, amarai