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# What is taxonomy? - An overview with myriapodological examples

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#### Abstract

Taxonomy is presented in a very broad sense. It is suggested to abandon the concept 'systematics'. Seven types of taxonomic activities and five types of taxonomists are defined. The seven types of activities are illustrated with examples drawn from the myriapodological literature. Several international/regional initiatives and projects related to taxonomy are mentioned.

Keywords: systematics, millipede, centipede, Diplopoda, Chilopoda

#### Introduction

Meetings like the international congresses of myriapodology focus on a particular group of organisms, in our case the Myriapoda (plus the 'honorary myriapods' Onychophora). At the meetings, taxonomists, ecologists, anatomists, cytologists, palaeontologists etc. come together to talk and hear about the focal taxon. In other words, the rationale for our meetings is of a **taxonomic** nature.

But what is actually taxonomy, is it interesting and important? Whatever it is, it cannot be neglected, as it has become quite visible on what might be called 'the biodiversity agenda'. Concepts like *the Taxonomic Impediment* and *the Global Taxonomic Initiative* or GTI (http://www.cbd.int/gti/) are often cited products of the Convention on Biological Diversity (http://www.cbd.int/). On a less than global scale, there are such large-scale initiatives as the North American *Partnerships for Enhancing Expertise in taxonomy* or PEET (http://www.nhm.ku.edu/peet/), the *European Distributed Institute of Taxonomy*, or EDIT (www.e-taxonomy.eu/), and several others, not all of which have taxonomy in their name although their scope is clearly taxonomic.

In the present paper I will present a brief overview of how I understand taxonomy. In order to illustrate the different 'subspecies' of taxonomy, a number of examples from the myriapodological literature (mostly from the last few decades) will be given. I am aware that there is a lot of papers which might equally well have been chosen, and which some readers may think better illustrate certain points.

### Taxonomy - the general concept

Etymologically, the word taxonomy is derived from Greek *taxis*, meaning 'arrangement or division', and *nomos*, meaning 'law'. Taxonomy can thus be understood as meaning 'laws of arrangement and division'. A host of other definitions of the word can be found on the web, e.g.:

- the science of classification according to a pre-determined system (www.whatis.com)
- the practice and science of classification (Wikipedia)
- The science of categorisation, or classification, of things based on a predetermined system (www.webopedia.com)

One can also speak of 'the taxonomy of something' (e.g., millipedes), meaning the result of taxonomic work (on millipedes). Such taxonomies are composed of taxonomic units known as *taxa* (singular: *taxon*), frequently arranged in a hierarchical structure and related to one another by supertype-subtype relationships ('parent-child' relationships).

Taxonomy as a concept is not restricted to the biological world. A quick web search gave, among many others, these examples:

- 'Scholars have been laboring to develop a taxonomy of young killers' (www.thefreedictionary.com)
- 'The term 'military taxonomy' encompasses the domains of weapons, equipment, organizations, strategies, and tactics' (Wikipedia)

### **Biological taxonomy**

Here we are concerned with taxonomy as applied to living organisms, biological taxonomy. The nature of biological taxonomy (henceforward: taxonomy) may perhaps be visualised as 'the language of biology'. Like any language, taxonomy consists of more than the words per se. The equivalent of words would be the Latin/Greek or at least latinised /hellenised names that taxonomists attach to species, genera and so forth (taxa). However, taxonomy also consists of the interpretation of the names, the so-called taxonomic concepts (Franz et al. 2008), and of the way we believe that the taxa are phylogenetically related to one another. And like any language, taxonomy evolves: new taxa are discovered and are given names; taxonomic concepts change, as do phylogenetic hypotheses.

#### **Taxonomy vs systematics**

Peoples' (including biologists') understanding of taxonomy has been hampered by confusion vis-a-vis *systematics* (Wheeler 2008). In a very influential textbook, Mayr (1969) characterised taxonomy as 'the theory and practice of classifying organisms' whereas he regarded systematics as 'the science of the diversity of organisms'. Systematics was science, taxonomy mere 'theory and pratice' like plumbing, haircutting and other respectable but clearly non-scientific activities. In another much-read book Simpson (1961) wrote in the introductory chapter 'A main purpose of this chapter, therefore, is to establish precisely what is meant by taxonomy in this book. That also involves consideration of systematics, which is

broader than taxonomy and includes it, and of classification and nomenclature, which are narrower than taxonomy and ... included in it'. These definitions probably have played a major role in pushing taxonomy into the disrespect from which it has only recently started to recover (Wheeler 2008). The disrespect may be epitomised by a statement of a high-ranking European science administrator (ecologist), who at a conference on the role of natural history museums a few years ago stated that 'in the natural history museums, there are scientists as well as taxonomists'.

For Mayr, Simpson and many others, taxonomy is thus clearly inferior to systematics when measured with an academic yardstick. The opposite view also exists, however: For Wheeler (2008), systematics is a subdiscipline of taxonomy concerned with reconstructing phylogeny.

The simplest way of avoiding this rather futile discussion is to abandon the term 'systematics' and instead adopt a broad definition of taxonomy as was done of the abovementioned Global Taxonomy Initiative: 'Broadly understood, taxonomy is the classification of life, though it is most often focused on describing species, their genetic variability, and their relationships to one another. For the purposes of the Convention taxonomy is taken in its broadest sense and is inclusive of systematics and biosystematics at the genetic, species and ecosystem levels.' (Decision VI/8 of the 6th Conference of Parties to the Convention on Biological Diversity, http://www.cbd.int/decisions/?m=COP-06&id=7182&lg=0).

#### Taxonomy in a very broad sense

An even broader definition of taxonomy was proposed by Enghoff & Seberg (2006). According to these authors, taxonomy consists of seven types of activities:

- 1. Recognition, description and naming of taxa (species, genera, families etc., also revision of older descriptions, synonymisations, etc.) ( $\approx \alpha$ -taxonomy).
- 2. Comparison of taxa, including studies of relationship (phylogeny) ( $\approx$  part of β-taxonomy).
- 3. Classification of taxa (preferably based on phylogenetic analyses) ( $\approx$  part of  $\beta$ -taxonomy).
- 4. Study of (genetic) variation within species ( $\approx \gamma$ -taxonomy)
- 5. Construction of tools for identification (keys, DNA barcodes).
- 6. Identification of specimens (referring them to taxa, using the tools).
- 7. Inventories of taxa in specific areas or ecosystems (using the tools for identification)

This 'taxonomy of taxonomy' is an elaboration and widening of a long-existing division of taxonomy into

α-taxonomy: description of species – 'descriptive taxonomy'

β-taxonomy: classification

γ-taxonomy: study of intraspecific variation

where the subdisciplines formerly assigned to systematics have been incorporated.

#### What are taxonomists?

The various types of taxonomic activities are carried out by taxonomists. Enghoff & Seberg (2006) presented a 'taxonomy of taxonomists':

- 1. α-taxonomists: describe, name, revise and synonymise taxa
- 2. β-taxonomists: compare and classify taxa, make phylogenies
- 3. γ-taxonomists: study intraspecific variation
- 4. tool-makers: construct keys and other identification tools
- 5. tool-users: identify specimens, make inventories

Unlike a biological taxonomy, in this one an individual (a person) may belong to several co-ordinate 'taxa': Most taxonomists engage in several different types of taxonomic activities, and some taxonomists engage in all of them.

Who are these individuals who may belong to one or several types of taxonomists? Here one must realise that a very large amount of taxonomic work is carried out by people who are not paid to do so. This category includes amateurs, retired professional taxonomists as well as some categories of students. The other category includes the 'professional taxonomists' who are paid to do taxonomy, at least during part of their working hours. Professional taxonomists are typically found in natural history museums, where they often are at the same time curators of scientific collections, in university departments, and in institutions for applied science, e.g., the French 'Centre de Biologie et de Gestion des Populations' (http://www1.montpellier.inra.fr/CBGP/englishvers06.htm).

#### Pure α-taxonomy

In our days, purely  $\alpha$ -taxonomic papers are rare. Even when the title of a paper like, e.g., '*Pectinunguis roigi* n. sp., from the Amazonian rainforest of Ecuador' (Pereira et al. 2001) promises no more than the description of a new species, the reader will actually find a careful comparison with other species sharing a set of diagnostic characters with the new species.

But this is not always the case. Especially in the older literature, we find descriptions of new species without any comparison with others. R. V. Chamberlin was a particularly 'puristic'  $\alpha$ -taxonomist. For example his original description of *Tylobolus castaneus* (Chamberlin, 1918) is clinically devoid of any comparison with other species, although the original description of *T. claremontus* in the same paper does at least include a little bit of comparison with other species.

Whereas purely  $\alpha$ -taxonomic descriptions like the one cited above are difficult to use, if not entirely useless, and not at all to be recommended,  $\alpha$ -taxonomy remains an extremely important component of taxonomy, providing the very basic information needed for a wide variety (if not all?) types of biological research.

Ideally,  $\alpha$ -taxonomy should, and nowadays usually does, form part of a broader approach which also includes other types of taxonomic activities. A typical contemporary, mainly  $\alpha$ -taxonomic paper may have a title like '*Ommatoiulus malleatus* n. sp., a new Tunisian millipede, with notes on the *punicus* species group of *Ommatoiulus*' (Akkari & Voigtländer 2007). Here,  $\alpha$ , in the form of the recognition and description of the new species, meets  $\beta$ , in the form of a comparison of the species in the *punicus* group.

In any case, the description of a new species can be seen as a scientific hypothesis: The author hypothesises that a species exists with the characteristics given in the description, and that this species is different from other species. The hypothesis is open to testing: others may find additional specimens and check if they agree with the description, or they may look at other characters than those included in the first author's description. Seen this way,  $\alpha$ -taxonomy is science in the Popperian sense.

### β-taxonomy: classification and names

β-taxonomy is quite a broad category (classification, comparison, phylogeny). Classification pervades all taxonomy but in its purest form can be exemplified by the recent re-classification of the Pauropoda by Scheller (2008), the global catalogue of the millipede order Callipodida by Stoev et al. (2008), and by Chilobase – the online classification of the Chilopoda (http://chilobase.bio.unipd.it/).

The physical expression of a biological classification basically consists of a number of *names* arranged in a hierarchical system. The system introduced by Carl von Linné a quarter of a millennium ago, with its binomials for species (e.g., *Julus terrestris* L., 1758) and its nested set of genera, families, orders etc., has proven amazingly sustainable. The Linnean system, with several necessary modifications added through the years, remains a top-class means of communication about organisms: a true biodiversity informatics tool.

Anybody working with taxonomy of millipedes will agree that the monumental compilation of millipede names in C. A. W. Jeekel's 'Nomenclator generum et familiarum Diplopodorum' (Jeekel 1970, supplemented by Shelley et al. 2000) is an indispensible treasure-trove of well-organised information. Centipede taxonomists will have similar feelings for Jeekel's later 'Nomenclator generum et familiarum Chilopodorum' (Jeekel 2005, supplemented by Shelley 2006) although they also have access to centipede names through the abovementioned Chilobase.

Although, as mentioned above, the Linnean binomens are universally accepted as the best vehicle for communication about species, many biologists view the Latin/Greek, sometimes quite tongue-breaking names of organisms as a burden. As fewer and fewer taxonomists have any knowledge of Latin and/or classical Greek, it is no wonder that feelings of alienation towards these names prevail. For many, the names are little more than 'an arbitrary combination of letters' (which is fully legal according to the current International Code of Zoological Nomenclature [International Commission on Zoological Nomenclature 1999]) It used to be recommended that the names should say something about the species. Taking Linnean examples, Polydesmus complanatus (L., 1761) is indeed flattened (complanatus), Ommatoiulus sabulosus (L., 1758) is indeed often found on sandy soil (sabulosus), and although Geophilus electricus (L., 1758), is apparently not luminescent (electricus), some Geophilus species are – Linnaeus made a mistake here. With the decline of Latin and Greek, and the international rise of English, it is perhaps not surprising that we can now find names like Bicoxidens nasti and Bicoxidens friendi, coined by Mwabvu (2000) for two species of millipedes, one of which produces large amounts of a rather nasty defensive secretion when disturbed, whereas the other is more friendly in this respect. These names look Latin, satisfy the code, and tell something about the species in what is currently the dominant scientific language!

With regard to oral communication, some names are more or less impossible to pronounce, depending on how Latin/Greek is pronounced in your own language. For instance, an American colleague once complained about the name *Australobius tenuiunguis* (Eason, 1980), because 'tenuiunguis' appears to be close to unpronounceable in American English Latin, whereas in the present author's Latin (Danish Latin) it is no problem to speak about this centipede.

## β-taxonomy: revisions and monographs

The 'holy grail' of taxonomy is a *revision*, or even better, a *monograph*. In a revision, all taxonomic information about a genus, a family, or another taxon, is reviewed, type specimens are studied, new species are described, an identification key to the species is presented, and there may be a phylogenetic analysis and discussions about characters, relationships, distribution etc. A monograph is essentially a big revision.

Outstanding, large, recent myriapodological revisions/monographs are R. L. Hoffman's two brick-size books about the African millipede families Oxydesmidae and Gomphodesmidae (Hoffman 1990, 2005). If you want to work taxonomically on a certain group, the first thing to do is to look for such publications. If you are lucky and they exist, you have a valuable basis for your research – if not, you will have to compile the necessary information from a number of dispersed sources.

## β-taxonomy: phylogenetic analysis

Comparison of taxa is, as mentioned above, a necessary part of all descriptive taxonomy. Pure comparison has in recent decades, following the formulation of the cladistic principles by Hennig (1950, 1966), experienced quite a boost in the form of phylogenetic analysis based on strict analysis and comparison of characters. Myriapods were one of the first groups to be considered from a cladistic point of view, thanks to the work of Kraus (1966), who, being German, had the advantage of being able to read the original version of Hennig's book – not exactly an easy bit of reading for others than born germanophones.

The first phylogenetic analyses were based on morphological characters. Molecular characters, mostly DNA sequences, now play a huge and still increasing role in phylogenetic reconstructions, see, e.g., Regier et al. (2005). Combined analyses of morphological and molecular characters are, of course, preferable: the more evidence you can get, the better. The analysis of scutigeromorph centipede relationships by Edgecombe & Giribet (2006) is an outstanding example of such a combined analysis.

### γ-taxonomy: the infraspecific level

Like  $\beta$ -taxonomy, this is quite a broad category, and often  $\gamma$  elements can be found in publications with an  $\alpha$  or  $\beta$  focus. For example, in the aforementioned monograph of Gomphodesmidae by Hoffman (2005), the treatment of *Astrodesmus laxus* (Gerstäcker, 1893) recognises six subspecies, three of which are downgraded from full species status, and three are described as new.

Some of the 'purest'  $\gamma$ -taxonomic papers on myriapods are those by Pedroli-Christen & Scholl (1990, 1996) on the chordeumatidan genus *Rhymogona*. Pedroli-Christen & Scholl

addressed the complicated taxonomy of this genus with a variety of approaches, including detailed field studies, study of morphological variation in male and female genitalia, as well as allozyme analysis.

#### Tools for identification

As mentioned above, the 'classical' identification tool, the dichotomous key, often forms part of  $\beta$ -taxonomic papers. Some publications, however, are more directly focused on identification. One may mention a classic such as Eason's book on British centipedes (Eason 1964, numerous copies of which have been worn to pieces by their users), the key to Neotropical millipede orders by Golovatch et al. (1995) in which the couplets are shown on a dichotomous, cladogram-like tree, or the recent magnificent key to North European myriapods by Andersson et al. (2005). Although identification keys are very often illustrated, the latter is so to an extent that it borders on another type of identification tool more typical of groups such as birds and butterflies: the pictorial key.

Other types of identification tools, such as DNA barcodes (see Meier 2008 for a critical review), and automated identification based on image recognition (e.g., McLeod 2007) have still not been applied to myriapods, although DNA sequences (Bond & Sierwald 2003) as well as advanced morphometric methods (Tanabe et al. 2001, see also Bolton et al. 2008) have been used for recognition of species.

## Using the tools: identification of specimens

Identification of a specimen may be regarded as the most basic taxonomic activity. The results of identification are used for a wide scope of purposes, in the purest form for lists of species from particular areas: inventories. Among numerous examples one may mention the online inventory of the European fauna of non-marine multicellular animals, Fauna Europaea (www.faunaeur.org). Fauna Europaea covers a huge area, but an inventory is more often limited to one or a few particular countries – the aforementioned identification keys by Eason (1964) and Andersson et al. (2005) are thus also inventories, a part of a country, or just a single site. The inventory may also focus on a particular habitat type such as caves (e.g., Shear 1969), montane rain forests (e. g., Hoffman 1993), or suburban gardens and parks (e.g., Enghoff 1973).

If identification is the most basic type of taxonomic activity, failure to identify a specimen is no less important. It is failure to identify a specimen at hand that leads to the recognition of new species.

One might argue against inclusion of identification as a taxonomic activity. For instance, if I see a bird, say, a great tit (*Parus major*) in my garden and recognise which species it is because I have studied the local illustrated field guide, is this a taxonomic activity?

On the other hand, identification of individuals (which, if they are preserved, become specimens) constitutes a test of an existing hypothesis, *in casu* the hypothesis that the species *Parus major* consists of individuals some of which look like the one I saw. Under this view, my identification of the great tit *is* a taxonomic activity. And if instead of the bird example, it was a question of finding a centipede in my garden and identifying it as *Stigmatogaster subterranea* using the keys in Andersson et al. (2005), fewer people would doubt that I had performed a taxonomic activity.

#### The future of taxonomy

In Linné's time, biology was virtually identical with taxonomy. In the quarter of a millennium elapsed since then, biology has undergone a huge amount of evolution and diversification. Taxonomy is now only part of biology, and it is a part under pressure. The Convention on Biological Diversity (http://www.cbd.int/). has launched a Global Taxonomy Initiative http://www.cbd.int/gti/ to ameliorate the existing taxonomic impediment. Large international/regional initiatives like Encyclopedia of Life (http://www.eol.org/), Fauna Europaea (http://www.faunaeur.org/), Global Biodiversity Information Facility (www.gbif.org), and Species 2000 (http://www.sp2000.org/) help to make biodiversity information, including taxonomic information, more readily available, using the internet. In the United States of America, large projects like Assembling the Tree of Life (http://atol.sdsc.edu/) and Planetary Biodiversity Inventories (http://www.nsf.gov/news /news summ.jsp?cntn id=103065) generate lots of new taxonomic information. And worldwide, taxonomists continue their work, which has been going on for centuries. Nevertheless, it is a long way till we can claim sufficient knowledge of Earth's species. A multitude of papers, reports and meeting address the plight of taxonomy, e. g., Bourgoin & Silvain (2008), Godfray (2002), House of Lords (2008), Wheeler (2008). The consensus seems to be that if taxonomy is ever going to come just reasonably close to its ultimate but asymptotic goal: description and analysis of all species on Earth, drastic changes in the way taxonomists work are necessary, see, e.g. EDIT (2008).

To finish on a positive note, a nice initiative was launched in 2008: 'Top 10 New Species' (http://www.species.asu.edu/index.php). Ten 'charismatic' species were selected among the thousands of new species described in 2007 (and a new list is planned for each coming year). The ten species on the 2008 list include a ray, a dinosaur, a frog, a snake, a fruit bat, a mushroom, a jellyfish, a beetle, a plant, and a millipede (Fig. 1). Myriapodologists can be content that a myriapod made it to a list on which vertebrates dominate.

Let us hope that this 'media stunt' bodes well for the future for myriapod taxonomy.



Fig. 1 The shocking pink dragon millipede, *Desmoxytes purpurosea* Enghoff et al. (2008), one of the 'Top 10 New Species' described in 2007, see text. Paratypes courting. Photograph by S. Panha.

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#### References

Akkari, N. & K.Voigtländer (2007): *Ommatoiulus malleatus* n.sp., a new Tunisian millipede, with notes on the *punicus* species group of *Ommatoiulus* (Diplopoda, Julidae). – Zootaxa **1400**: 59–68.

Andersson, G., B. Meidell, U. Scheller, J.-Å. Winquist, M. Osterkamp Madsen, P. Djursvoll, G. Budd, & U. Gärdenfors (2005): Nationalnyckeln till Sveriges flora och fauna. Mångfotingar. Myriapoda. – ArtDatabanken, SLU, Uppsala: 351 pp.

Bolton, S., G. Edgecombe & N. McLeod (2008): Variability in female gonopods of scutigeromorph centipedes (Chilopoda): a geometric morphometric approach. – Peckiana 6: 97.

- Bond, J. E. & P. Sierwald (2003): Molecular taxonomy of the *Anadenobolus excisus* (Diplopoda: Spirobolida: Rhinocricidae) species-group on the Caribbean island of Jamaica. Invertebrate Systematics 17: 515–528.
- Bourgoin, T. & J.-F. Silvain (2008): Systématique et taxinomie. Commision scientifique de l'IFB. Réflexion stratégique: 41–50. [http://www.gis-ifb.org/content/download/2067/10761/version/1/file/IFB+FR+BD.pdf].
- Chamberlin, R. V. (1918): New spiroboloid diplopods. Proceedings of the Biological Society of Washington 31: 165–170.
- Eason, E. H. (1964): Centipedes of the British Isles. Frederick Warne & Co., London and New York: 294 pp.
- Edgecombe, G. D. & G. Giribet (2006): A century later a total evidence re-evaluation of the phylogeny of scutigeromorph centipedes (Myriapoda:Chilopoda). Invertebrate Systematics **20**: 503–525.
- EDIT (2008): Taxonomy in Europe in the 21st century, report to the Board of Directors, [http://ww2.bgbm.org/EditDocumentRepository/Taxonomy21report.pdf].
- Enghoff, H. (1973): Diplopoda and Chilopoda from suburban localities around Copenhagen. Videnskabelige Meddelelser fra dansk naturhistorisk Forening **136**: 43–48.
- Enghoff, H. & O. Seberg (2006): A taxonomy of taxonomy and taxonomists. The Systematist, Newsletter of the Systematics Association 27: 13–15. – [http://www.systass.org/newsletter/ TheSystematist27.pdf].
- Enghoff, H., C. Sutcharit & S. Panha (2008): The shocking pink dragon millipede, *Desmoxytes purpurosea*, a colourful new species from Thailand (Diplopoda: Polydesmida: Paradoxosomatidae). Zootaxa 1563: 31–36.
- Franz, N. M., R. K. Peet & A. S. Weakley (2008): On the use of taxonomic concepts in support of biodiversity research and taxonomy. In Wheeler, Q. D. (ed.): The new taxonomy. The Systematics Association Special Volume Series 76, CSC Press: 63–86.
- Godfray, H. C. J. (2002): Challenges for taxonomy. Nature 417: 17-19.
- Golovatch, S. I., R. L. Hoffman, J. Adis & J. W. de Morais (1995): Identification plate for the millipede orders populating the Neotropical region south of central Mexico (Myriapoda, Diplopoda). – Studies on the Neotropical Fauna and Environment 30: 159–164.
- Hennig, W. (1950): Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin: 370 pp.
- Hennig, W. (1966): Phylogenetic systematics (translated by D. D. Davies & R. Zangerl). University of Illinois Press, Urbana: xiii + 263 pp.
- Hoffman, R. L. (1990): Myriapoda 4. Polydesmida: Oxydesmidae. Das Tierreich 107: i–xv + 1–512.
- Hoffman, R. L. (1993): Biogeography of East African montanee forest millipedes. In Lovett, J. C. & S. K. Wasser (eds): Biogeography and ecology of the rain forests of eastern Africa. – Cambridge University Press: 103–114.
- Hoffman, R. L. (2005): Monograph of the Gomphodesmidae, a family of African polydesmoid millipeds. Verlag des Naturhistorischen Museums Wien: 537 pp.
- House of Lords (2008): Systematics and Taxonomy: Follow-up. Report with Evidence. House of Lords, London: 330 pp.
- International Commission on Zoological Nomenclature (1999): International code of zoological nomenclature. [http://www.iczn.org/iczn/index.jsp].
- Jeekel, C. A. W. (1970): Nomenclator generum et familiarum Diplopodorum: A list of the genus and family-group names in the class Diplopoda from the 10th edition of Linnaeus, 1958, to the end of 1957. Monografieën van de Nederlandse Entomologische Vereniging 5: i–xii + 1–412.
- Jeekel, C. A. W. (2005): Nomenclator generum et familiarum Chilopodorum: A list of the genus and

- family-group names in the Class Chilopoda from the 10th edition of Linnaeus, 1758, to the end of 1957. Myriapod Memoranda Supplement I: 1–130 + i–viii.
- Kraus, O. (1966): Phylogenie, Chorologie und Systematik der Odontopygoideen (Diplopoda, Spirostreptomorpha). – Abhandlungen der senckenbergischen naturforschenden Gesellschaft 512: 1–143.
- Mayr, E. (1969): Principles of systematic zoology. McGraw-Hill Book Company, New York etc.: xi + 428 pp.
- McLeod, N. (ed.) (2007): Automated taxon identification in systematics. Theory, approaches and applications. – CRC Press: 339 pp.
- Meier, R. (2008): DNA sequences in taxonomy, opportunities and challenges. –In Wheeler, Q. D. (ed.): The new taxonomy. The Systematics Association Special Volume Series 76, CSC Press: 95–127.
- Mwabvu, T. (2000): Two new species of *Bicoxidens* Attems, 1928, from Zimbabwe (Diplopoda: Spirostreptida: Spirostreptidae). African Zoology 115: 115–119.
- Pedroli-Christen, A. & A. Scholl (1990): Ecological and genetic studies on parapatric *Rhymogona sylvatica* Roth. and *R. cervina* Verh. Diplopoda Craspedosomatidae) with special reference to hybrid populations in a zone of contact. Revue suisse de zoologie **97**: 349–359.
- Pedroli-Christen, A. & A. Scholl (1996): Rhymogona (Diplopoda: Craspedosomatidae) un genre monospécifique. Deuxième partie: Révision basée sur les résultats morphologiques, génétriques et faunistiques. – Mémoires du Museum National d'Histoire Naturelle 169: 53–60.
- Pereira, L., D. Foddai & A. Minelli (2001): Pectinunguis roigi n.sp., from the Amazonian rainforest of Ecuador (Chilopoda: Geophilomorpha: Schendylidae). – Studies on the Neotropical Fauna and Environment 36: 143–150.
- Regier, J. C., H. M. Wilson, & J. W. Shultz (2005): Phylogenetic analysis of Myriapoda using three nuclear protein-coding genes. – Molecular Phylogeneteics and Evolution 34: 147–158.
- Scheller, U. (2008): A re-classification of the Pauropoda. International Journal of Myriapodology 1: 1–38.
- Shear, W. A. (1969): A synopsis of the cave millipeds of the United States, with an illustrated key to genera. Psyche 76: 126–143.
- Shelley, R. M. (2006): Nomenclator generum et familiarum Chilopodorum II: A list of the genus- and family-group names in the Class Chilopoda from 1958 through 2005. Zootaxa 1198: 1–20.
- Shelley, R. M., P. Sierwald, S. B. Kiser & S. I. Golovatch (2000): Nomenclator generum et familiarum Diplopodorum II, A list of genus and family-group names in the class Diplopoda from 1958 through 1999. – Pensoft Series Faunistica 20: 200 pp.
- Simpson, G. G. (1961): Principles of animal taxonomy. Columbia University Press, New York: xii+247 pp.
- Stoev, P., P. Sierwald, & A. Billey (2008): An annotated world catalogue of the millipede order Callipodida (Arthropoda: Diplopoda). – Zootaxa 1706: 1–50.
- Tanabe, T., H. Katakura & S. F. Mawatari (2001): Morphological difference and reproductive isolation: morphometrics in the millipede *Parafontaria tonominea* and its allied forms. – Biological Journal of the Linnean Society 72: 249–264.
- Wheeler, Q. D. (2008): Introductory. Toward the new taxonomy. In Wheeler, Q. D. (ed.): The new taxonomy. The Systematics Association Special Volume Series 76, CSC Press: 1–17.

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