



Parataxonomy vs. taxonomy in biodiversity studies – pitfalls and applicability of ‘morphospecies’ sorting

FRANK-THORSTEN KRELL

Soil Biodiversity Programme, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK (e-mail: f.krell@nhm.ac.uk; fax: +44-20-7942-5229)

Received 3 October 2002; accepted in revised form 27 February 2003

Key words: Biodiversity, Data quality, Morphospecies, Morphotype, Parataxonomic units, Parataxonomy, RTU, Sorting, Taxonomy

Abstract. Parataxonomic sorting of samples to recognizable taxonomic units (RTUs, morphospecies, morphotypes or, as proposed here: parataxonomic units [PUs]) is generally considered to be a sufficiently reliable and conservative approach in ecological biodiversity studies or conservation biology. It is obviously time-saving because it avoids the burdens of taxonomy. However, evaluations of parataxonomic sorting by taxonomic resorting show many overestimations of species numbers. Hence, RTU sorting is not necessarily conservative. Sorting errors can be more than 100% (median in the present compilation: 22%). Even if the cumulative results for diverse groups like beetles have a very low overall error, the error rate in the single families is generally much higher. This pattern is likely to cause severe problems in multivariate analyses. The presumable error rate in sorting does not depend only on the group to be sorted, but also on the sorter and the sample. Therefore, the sorting error is not predictable. Since PUs are generally neither described nor assigned to existing names, the sorting results are difficult to check and it is mostly not revealed why the samples are sorted as they are. Since parataxonomy does not use existing biological knowledge, creates typological units and does not disclose its sorting criteria, inter-subjective testability and falsifiability of the sorting results are more difficult than of taxonomic identifications (or are even impossible). Parataxonomy does not fulfil the criteria of a scientific method, but is propedeutic and can be a heuristically valuable tool to find out patterns in taxonomically neglected groups. However, it is only the first step in sorting and identifying samples in biodiversity studies. PUs are useless for inventories and area selection in conservation evaluation, biogeographical and autecological studies; they provide only uncertain data for studies in species turnover and overlap, but they can be used quite reliably for global comparisons of gross species richness, non-comparative descriptions of species richness of single sites or for comparisons of sites without species overlap. If results of parataxonomic sorting show clear and biologically meaningful patterns, the sorting is likely to be reliable. Weak or no detectable patterns may easily be caused by erroneous sorting.

Introduction

Species are very much en vogue, both in science and in conservation politics. The Convention on Biological Diversity (Anonymous 1993) included in Agenda 21 (Robinson 1993), which emerged from the 1992 United Nations Conference on Environment and Development in Rio de Janeiro, obliged those nations that ratified the convention to assess and monitor the biological diversity of their territory. A fundamental part of biodiversity assessment deals with species inventories and numbers of species. In environmental sciences, recognizing patterns of species

composition is useful or even crucial for studies of ecosystem functioning, community ecology, biogeography, etc. However, recognizing, naming, and identifying species is not an easy task, requiring experience or at least knowledge of all the taxon-specific pitfalls caused by variation and similarity. The persistent decline of human resources in taxonomy (Anonymous 2000; Hopkins and Freckleton 2002) has confronted community ecologists and applied biodiversity researchers with insuperable problems. Evaluating biodiversity data seemed impossible. But then, some researchers propagated a procedure that avoids all the taxonomic burden: distinguishing and counting species can be done much more rapidly if taxonomic identification and scientific naming are replaced by sorting samples to *recognizable taxonomic units* (RTUs; Oliver and Beattie 1993). Around the same time in Costa Rica the first ‘parataxonomists’ were established to assist taxonomists in collecting and mounting large numbers of specimens (Gámez 1991; Janzen 1991). This was intended to reduce the working burden of taxonomists and to use taxonomic expertise more efficiently. Eventually parataxonomists (or ‘biological diversity technicians’, as they were called in Australia) became involved in preliminary sorting of samples to RTUs (Cranston and Hillman 1992; Basset et al. 2000). All these inventions and developments have been a great benefit for biodiversity studies.

However, the convincing efficiency of parataxonomic sorting was obviously tempting. Data became much more rapidly available than through the taxonomic identification process. Parataxonomic sorting evolved from a preliminary procedure to the data supplying method. RTUs became generally known as ‘morphospecies’, implying status as real biological entities (see Appendix). The implication appeared to be that years of apprenticeship, usual to taxonomy, were no longer necessary. ‘Morphospecies’ sorting with minimum or no involvement of taxonomists has become a widely accepted method in conservation biology and species diversity-based ecology. However, uncertainties still remain. What is the quality of parataxonomic data? How good is the method? Is this technique truly scientific?

The quality of the data

[...] ecologists are often ill informed of both the value and the problems of systematics. That is true even though ecologists have long been parasitic on taxonomists’. Ehrlich 1997, p. 23.

Parataxonomic sorting is, according to the current understanding,¹ sorting of material to ‘species’ on the basis on external morphology without considering taxonomy (i.e., neither taxonomic literature nor specialists of the groups to be sorted are consulted). We find optimistic statements in papers presenting results based on parataxonomic sorting: “Ninety percent agreement has been found between RTU classification by non-specialist technicians and specialist taxonomists (Oliver and

¹ This does not apply to the few projects where parataxonomists do morphospecies sorting, but taxonomists are responsible for the quantitative species data.

Beattie 1993)” (Bolger et al. 2000). “Most species [of the beetles] were clearly different and could easily be separated from each other” (Floren and Linsenmair 1998). Even in the discerning book of New (1998) we find the opinion “The ‘RTU level’ is valuable [. . .] because recognition is a rigorous, consistent process that provides comparable data from different samples and sites”. The general opinion is that parataxonomic classification is a quite reliable and conservative approach resulting mostly in a lower number of units than the real number of species, because similar species are more often not separated into their constituent true species than variable true species are spread into several units (König and Linsenmair 1996; Wagner 1996).

To evaluate these intuitive statements, to judge the method and to estimate the quality of data, I will compare the outcome of parataxonomic sorting with the results of taxonomic identification of the same samples. Some comparative data have been published (Cranston and Hillman 1992; Oliver and Beattie 1993, 1996a, 1996b; Wagner 1996; Trueman and Cranston 1997; Pik et al. 1999; Slotow and Hamer 2000; Derraik et al. 2002), and I added some more from recent projects (Table 1). The common parameter that has been used to judge the quality of sorting is the error, which is defined as number of taxonomically identified species minus number of parataxonomic units (PUs), and this result is divided by the species number (Oliver and Beattie 1993). The highest error was 117%; half of the sortings show an error of 22% or higher. The compilation contains 41 overestimations, 35 underestimations and three correct estimations of the species number. Hence, parataxonomic sorting is *not* necessarily a conservative approach.

The key measure of success of parataxonomic sorting is, however, the accuracy, i.e. the portion of PUs that correspond exactly to one taxonomically identified species (without any lumping or splitting of taxonomic species). Data on the accuracy of parataxonomic sorting are rarely available. I found only 11 values in the literature (Table 1). The accuracy is always lower than the error suggests, because it is diminished by splitting and lumping of species which are compensated in the gross error value. It is, therefore, a more comprehensive parameter to describe the quality of parataxonomic sorting. Oliver and Beattie (1993) had a Bryophyta sorting example with just 1% error, but the accuracy was only 23%. The spider sorting reported by Derraik et al. (2002) resulted in an error of 13%, but the accuracy was only 50%. Hence, the low error rates were only good luck, caused by a similar number of parataxonomic splittings and lumpings.

In cumulative results of parataxonomic sortings (e.g. beetles) we often find a low error rate, which is caused by compensation of underestimates by overestimates within the subgroups (e.g. beetle families), resulting in a low overall accuracy. Overall, the beetle families in Wagner’s (1996) samples have an error of 1%, but the individual families have errors of 43, 33, 33, 33, 25, 25, 17, 15, 14, 14, 11, 11, 10, 10, and 0%. Chung’s beetles (Table 1) show a similar pattern: the overall error is 2%, the errors of the individual families 114, 60, 58, 50, 50, 40, 33, 32, 30, 26, 25, 20, 14, 13, 6, and 0%. It may be seriously questioned if a high level of inaccuracy in a sorting result is acceptable if the gross error is low, because the low overall error is caused only by good luck. The low gross error is not caused by the statistical law of

Table 1. Comparison of results of parataxonomic sortings (PUs) with sortings of the same samples according to taxonomic principles (species).

Taxon	Species (A)	PUs (B)	Gross error $ (A-B)/A $ (%)	Accuracy (%)	Over/under- estimation	Reference
Anthicidae (Coleoptera)	≤12	26	117		+	Uhmman (<i>in litt.</i> 2001)
Alticinae (Coleoptera)	7	15	114		+	Chung (<i>in litt.</i> 2001)
Odonata larvae	3	6 [2×]	100		+	Cranston and Hillman (1992)
Chironomidae larvae (Diptera)	22	1 [3×]	95		-	Cranston and Hillman (1992)
Chironomidae larvae (Diptera)	17	1 [3×]	94		-	Cranston and Hillman (1992)
Chironomidae larvae (Diptera)	18	1 [2×]	94		-	Cranston and Hillman (1992)
<i>Doratogonus</i> (Diplopoda)	30	3	90		-	Slotow and Hamer (2000)
Chironomidae larvae (Diptera)	18	2	89		-	Cranston and Hillman (1992)
Chironomidae pupal exuviae	25	3	88		-	Cranston and Hillman (1992)
Chironomidae pupal exuviae	22	3 [3×]	86		-	Cranston and Hillman (1992)
Chironomidae pupal exuviae	25	4 [2×]	84		-	Cranston and Hillman (1992)
Ephemeroptera larvae	7	2	71		-	Cranston and Hillman (1992)
Curculionidae (Coleoptera)	62	99	60		+	Oliver and Beattie (1996a)
Pselaphinae	57	91	60		+	Chung (<i>in litt.</i> 2001)
Scarabaeidae (Coleoptera)	12	19	58		+	Chung (<i>in litt.</i> 2001)
Carabidae (Coleoptera)	8	12	50		+	Chung (<i>in litt.</i> 2001)
Hydrophilidae (Coleoptera)	6	3	50		-	Chung (<i>in litt.</i> 2001)
Ephemeroptera larvae	4	2 [3×]	50		-	Cranston and Hillman (1992)
Collembola	78	40	49		-	Trueman and Cranston (1997)
Scarabaeidae (Coleoptera)	24	35	46	63	+	de Roode (2000)
Ephemeroptera larvae	7	4	43		-	Cranston and Hillman (1992)
Malachiidae (Coleoptera)	7	4	43		-	Wagner (1996)
Hymenoptera (excl. ants)	113	65	43		-	Trueman and Cranston (1997)
Corylophidae (Coleoptera)	10	6	40		-	Chung (<i>in litt.</i> 2001)
Polychaeta	21	29	38	43	+	Oliver and Beattie (1993)
Malachiidae (Coleoptera)	12	8	33		-	Wagner (1996)
Bruchidae (Coleoptera)	9	12	33		+	Wagner (1996)
Odonata larvae	3	4	33		+	Cranston and Hillman (1992)
Cantharidae (Coleoptera)	6	4	33		-	Wagner (1996)
Scaphidiinae (Coleoptera)	12	16	33		+	Chung (<i>in litt.</i> 2001)
Scydmaenidae (Coleoptera)	28	37	32		+	Chung (<i>in litt.</i> 2001)
Scolytinae (Coleoptera)	40	28	30		-	Chung (<i>in litt.</i> 2001)
Ephemeroptera larvae	7	5	29		-	Cranston and Hillman (1992)
Ptiliidae	27	34	26		+	Chung (<i>in litt.</i> 2001)
Araneae	27	34	26		+	Oliver and Beattie (1996b)
Alticinae pars (Coleoptera)	12	15	25		+	Wagner (1996)
Nitidulidae (Coleoptera)	4	5	25		+	Chung (<i>in litt.</i> 2001)
Cerambycidae (Coleoptera)	12	9	25		-	Wagner (1996)
Staphylinidae (Coleoptera)	74	91	23		+	Oliver and Beattie (1996a)
Araneae	41	50	22		+	Oliver and Beattie (1996b)
Araneae all sites	121	146	21	85	+	Oliver and Beattie (1996b)
Staphylinidae	141	113	20		-	Chung (<i>in litt.</i> 2001)
Lebiinae (Coleoptera)	12	10	17		-	Wagner (1996)
Coleoptera	177	207	17		+	Oliver and Beattie (1996b)

Table 1. (continued)

Taxon	Species (A)	PU's (B)	Gross error $ (A-B)/A $ (%)	Accuracy (%)	Over/under- estimation	Reference
Anthribidae (Coleoptera)	26	22	15		-	Wagner (1996)
Coleoptera all sites	376	431	15	80	+	Oliver and Beattie (1996b)
Bruchidae (Coleoptera)	7	6	14		-	Wagner (1996)
Coccinellidae (Coleoptera)	29	33	14		+	Wagner (1996)
Pselaphidae (Coleoptera)	51	58	14		+	Oliver and Beattie (1996a)
Tenebrionidae (Coleoptera)	7	8	14		+	Chung (<i>in litt.</i> 2001)
Coleoptera	173	197	14		+	Oliver and Beattie (1996b)
Coleoptera	164	186	13		+	Oliver and Beattie (1996b)
Leiodidae (Coleoptera)	16	14	13		-	Chung (<i>in litt.</i> 2001)
Araneae	91	103	13	83	+	Oliver and Beattie (1993)
Araneae	32	36	13	50	-	Derraik et al. (2002)
Lepidoptera	33	37	12	91	-	Derraik et al. (2002)
Alticinae pars	18	20	11		+	Wagner (1996)
Anthicidae	9	8	11		-	Wagner (1996)
Araneae	54	60	11		+	Oliver and Beattie (1996b)
Araneae	59	65	10		+	Oliver and Beattie (1996b)
Carabidae	21	23	10		+	Oliver and Beattie (1996a)
Cerambycidae (Coleoptera)	10	9	10		-	Wagner (1996)
Coccinellidae (Coleoptera)	20	18	10		-	Wagner (1996)
Coleoptera	58	54	7	63	+	Derraik et al. (2002)
Formicidae	85	91	7		+	Pik et al. (1999)
Curculionidae (Coleoptera)	18	19	6		+	Chung (<i>in litt.</i> 2001)
Formicidae	35	33	6	88	-	Oliver and Beattie (1993)
Scarabaeidae (Coleoptera)	22	23	5		+	Oliver and Beattie (1996a)
Formicidae	42	40	5		-	Oliver and Beattie (1996b)
Formicidae	63	66	5		+	Oliver and Beattie (1996b)
Formicidae	28	29	4		+	Oliver and Beattie (1996b)
Coleoptera all families	444	455	2		+	Chung (<i>in litt.</i> 2001)
Coleoptera	117	119	2		+	Oliver and Beattie (1996b)
Formicidae all sites	93	92	1	92	-	Oliver and Beattie (1996b)
Bryophyta	86	87	1	23	+	Oliver and Beattie (1993)
Coleoptera all families	188	180	1		-	Wagner (1996)
Anthicidae (Coleoptera)	8	8	0		=	Chung (<i>in litt.</i> 2001)
Cryptocephalinae (Coleoptera)	14	14	0		=	Wagner (1996)
Formicidae	21	21	0		=	Oliver and Beattie (1996b)

The PUs in the samples of Wagner (1996) and Chung (*in litt.*) were sorted by taxonomically experienced persons (so that calling the results 'PU' is a bit unfair; Chung did his sorting under certain time pressure – therefore, he considered the results to be preliminary). The 'species' in the example given by Chung (*in litt.*) (Winkler samples from Sabah, Borneo) are not identified to nominal species, but checked by one of the most experienced coleopterists (Peter Hammond) according to taxonomic criteria. The example given by Slotow and Hamer (2000) has not been tested by biodiversity technicians but is obviously correct. The Ephemeroptera of Oliver and Beattie (1993) were not identified by a mayfly specialist (Campbell 1995), but by experienced taxonomists. Data of very small samples given in the mentioned references were neglected. If samples were sorted several times to PUs by different sorters with the same result, the number of sortings is given in brackets.

large numbers (which says that a higher number of samples leads to a more accurate estimate on average; Sachs 1982, p. 49) which is often implicitly referred to by remarks like “Over- and underestimates generally level out”. If they do, they do it as luck would have it, because the sorting errors for different groups do not follow stochastic regularities but are systematic errors caused individually by the sorter due to limited knowledge: the same sorter will likely produce systematically the same kind of error (under- or overestimations) with the same taxon in other similar samples and does not produce the errors stochastically. The law of large numbers, however, only works with stochastic errors. A sample with systematic errors is never representative for the entire population. We can never be sure about the reliability of the overall results. We can only hope or believe that the results are good. The low error in cumulative results is an unpredictable pattern, not a predictive tool.

If results from parataxonomic sorting are tested statistically for difference, we have to keep in mind (see Table 1) that the error within the data is probably high and the accuracy is most probably very low (lower than the gross error suggests). This low accuracy of data sets (even if the overall species number is quite reliable) will probably produce misleading patterns in the results of multivariate analyses, if they are analysing the subgroups of the study group (e.g. the families within an order), because for this kind of analysis, the accuracy of the values of the subgroups is crucial for informative results and not a gross overall error of the study group. “The danger of statistical (and general of mathematical) methods in ecology is that their application gives a stamp of extreme exactitude and reliability to conclusions even if derived from faulty, though sufficiently numerous, data.” (Uvarov 1931, p. 174).

The art of sorting

The only way to get reliable and testable results from sorting is by following taxonomic criteria and procedures, because taxonomy is the science of diagnosing biological species² using all available data (morphology, distribution, ecology, molecular data, etc.). All explicitly non-taxonomic ways of sorting result in artificial

² Sometimes in the text I use the term ‘taxonomic species’ in the sense of the operational, approximating equivalent of the ‘biological species’, not as a primary concept. A ‘taxonomic species’ is the species we work with. Ideally a ‘taxonomic species’ (hypothesis of the taxonomist) should be a ‘biological species’ (real entity in nature). Of course, there have been and still are taxonomists who work typologically and do not bother about biological species. However, this is not the place to analyse and criticise bad taxonomic practice. Likewise, this is not the place to discuss the different species concepts which nowadays all approximate to the ‘biological species’ (even if they explicitly oppose). For biodiversity studies, biological species are the tried and tested units. The continuing controversial discussion on species concepts does *not* imply that samples can be sorted to whatever the sorter may think, because there was no agreed standard. The ‘morphospecies’ is out of the biological discourse anyway. “While this concept has served as a traditional method for identifying species [as an operational tool] it is fatally flawed as a primary concept” (Mayden 1997, p. 403; see also Krell 1993).

groupings on principle, which may or may not approach the real species composition. The procedure of taxonomic sorting is usually as follows:

1. sorting to morphologically similar groups (morphospecies, recognized units) to make handling of the samples easier;
2. identification of the specimens using published keys (if available; extensive searching for literature is necessary) and with specimens that were identified by a specialist of the group (if available; museum specimens identified anonymously or by a non-specialist are often misidentified);
3. to make the identification certain or whenever the second step is not feasible (because keys and reliably identified material do not exist) the identified specimens should be compared with original descriptions and types.

Taxonomic identifications lead either to a described, named species or to the result that we have a species that is new to science but whose taxonomic identity is well established in the context of all described species. For the time being, this species may remain formally undescribed and unnamed. Taxonomic descriptions and naming are not an integral part of taxonomic *sorting*, but should follow as soon as possible to make the species-specific facts available to science (i.e. traceable for scientists). Due to inadequate original descriptions or missing revisions, some taxonomically identified species may not be immediately assigned to published names. This does not affect the quality of taxonomic *sorting*, because by considering the taxonomic literature, group specific relevant characters and their variability were considered.

Criteria for the taxonomic value of morphological traits cannot be generalized (cf. Vane-Wright 2003). There are numerous pitfalls of apparent morphological evidence. A character that is useful to diagnose genera in one group may vary intraspecifically in the sister group. Intraspecific variation of a character may be much higher than interspecific variation in one group and the other way round in its sister group. Sexual dimorphism, polymorphism, juvenile forms, different from taxon to taxon lead regularly to an overestimate of species numbers (Beattie and Oliver 1995; Minelli and Foddai 1997). Sibling species cause an underestimate. They are quite a common and well-known phenomenon in different groups of animals (Mayr 1963; White 1978), and for less experienced sorters many more species are siblings. There are no rules about the proportion of polymorphic and sibling species within an assemblage. Therefore, the outcome from under- and overestimations (i.e. the gross error in parataxonomic sortings) is unpredictable on principle. New's (1998, p. 141) view that "recognition is a rigorous, consistent process" is probably true for the same sorter with the same sample, but not for different sorters and different samples.

Giving the sorted entities scientific names does not mean that the sorting is necessarily more reliable. Wrong taxonomic identifications are common in ecological, faunistic and even present in taxonomic publications (cf. Vecchione et al. 2000). Reliable taxonomy-based identification requires reliable keys (which are rather rare), experience and mostly a comprehensive knowledge of the taxon that enables the sorter to judge pervasive variability and similarity.

Hammond (1995) classifies beetle families as 'generally amenable to sorting with

relative ease and accuracy', 'sometimes so' and 'rarely if ever so'. As shown in Table 1, families of the first (easy) group were sorted with errors of 117/11/0% (Anthicidae), 58/46/5% (Scarabaeidae), 50/10% (Carabidae), 33% (Cantharidae), 25/10% (Cerambycidae), 14/10% (Coccinellidae), 14% (Tenebrionidae); those of the second group with 114/25% (Alticinae), 60/6% (Curculionidae), 50% (Hydrophilidae), 30% (Scolytidae), 25% (Nitidulidae), 23/20% (Staphylinidae), 15% (Anthribidae); and those of the last, most difficult group with 60/14% (Pselaphinae), 40% (Corylophidae), 33% (Scaphidiinae), 32% (Scydmaenidae), 26% (Ptiliidae), and 13% (Leiodidae).

We see that the highest errors do *not* occur in the families considered to be the most difficult by a very experienced sorter. On the contrary, they occur in apparently 'easy' families. It is obvious that the sorting errors do not necessarily depend on the group, but on the sorter and the sample. Easy families may be difficult for other sorters or in other habitats. It is highly unlikely that we may find a reasonable 'minimum set' of groups that are reliably sortable by everyone everywhere, as suggested by Beattie et al. (1993). In fact, candidate groups suitable for reliable parataxonomic sorting can only be defined *a posteriori*, after checking the results taxonomically (and at this stage, the sorting is already done). We need many more comparative data on the accuracy of parataxonomic sorting before we may suggest reliable candidate groups.

Practical and epistemological advantages of taxonomy: why is taxonomy science, but parataxonomy is not?

Two main requirements have to be met to classify a research activity as a science: falsifiability, and inter-subjective testability due to reproducibility (Popper 1989). These two criteria have not only theoretical advantages (epistemological stringency), but are also of much practical use: scientific results are not only subjective claims but can be tested or found again by any other person. Hence, their 'truth' does not depend on their authors. In the following I explain why taxonomic identifications are easily checkable whereas testing parataxonomic sorting causes serious problems.

A taxonomic identification to species is the hypothesis that the specimen in question is conspecific with the type³ of the species; that means in practice that it corresponds to the original description of the species.⁴ Such a hypothesis may easily

³ The type is the specimen that the original author (or with older authors a subsequent reviser) has declared to be the relevant specimen representing the species. It is a 'natural document' of the original description and *not*, as it originally was and as the term 'type' still suggests, an essentialist (typological) concept to define the species.

⁴ Sometimes, the underlying hypothesis ('the entity diagnosed, described and named as a taxonomic species is a biological species') might be incorrect, but this is the trivial problem of incomplete knowledge. Taxonomy is a science and not a created (stable) frame of reference. We cannot, because of this instability (i.e. scientific progress) in taxonomy, justify its neglect as a reference system for biodiversity studies.

be wrong, because it depends on the knowledge and experience of the identifier. Many taxonomic identifications, even by renowned specialists, are incorrect. However, they are generally confirmable or falsifiable simply by comparing the specimen with the original description and/or the type (always under consideration of all biological facts on the species such as clinal variation, ecology, etc.). This comparison is possible because (1) a taxonomic identification results in giving a specimen an unequivocal scientific binominal name, and (2) a valid scientific binomen is always accompanied by a description or an indication (i.e. a figure, a reference of a former description, etc.) and, generally – except for species described by some authors of the 18th and 19th century – accompanied by traceable type specimens. Generally, if a specimen is taxonomically identified and named, everybody is able to know or at least to find out what is meant.

PU's are more difficult to handle. A simple nominalistic falsification ('A false name has been given to this unit' = 'The identification of this specimen is wrong') is impossible for PU's because they are not given a scientific name and their diagnostic differences from similar PU's are not known. Parataxonomic identification, i.e. classifying specimens to (recognized) PU's does not disclose its criteria. PU's are generally numbered or only counted and not described. 'Staphylinidae #1' differs from 'Staphylinidae #2' because Frank Krell thinks that 'Staphylinidae #1' differs from 'Staphylinidae #2'. It is not explained by means of which traits (or only by the gestalt [jizz]?) Frank Krell differentiated the two units. Not only do the differences between the units remain unknown, but also the diagnostic (or at least defining) characters of each of the two are unknown. If the material is conserved in a public collection, a reviser may come to another result about Frank Krell's sample, but he cannot falsify his parataxonomic classification, because contrary to the supposed intentions of most sorters, a PU is in fact typological and therefore a tautological system: the PU is defined by morphological criteria (which are generally not disclosed) as an instrumentalistic entity (not diagnosed by using all available biological evidence, as are species by taxonomists). These criteria cannot be used to falsify the hypothesis 'This is a unit' because (if they are given) they are all a part of the definition (the unit exists only through the definition and not beyond). Hence, changing the definition changes the unit. All attempts to falsify such a hypothesis lead to avoidance of falsification on principle by changing the hypothesis. Therefore, a PU does not meet the criteria of a scientific hypothesis and parataxonomic classification does not meet the criteria of a scientific method.

This is quite a formal argumentation, which seems to have only theoretical relevance but apparently does not cause cogent restrictions for the practical work, because obviously we can test the *results* of parataxonomic sorting either by a new parataxonomic sorting or by taxonomic identification. Isn't this a kind of falsification in practice?

As we have seen, a new parataxonomic sorting is a redefinition of units within the sample and not a falsification. Falsification by taxonomic re-sorting requires that we declare all PU's to be biological species and test these hypotheses by all available biological criteria. Although this accepts the intention of the original sorters, it is, strictly speaking, a change of the ontological character of PU's. This is not supported by the method of their making, because parataxonomic sorters do not actually do

what they might think to do: they do not diagnose biological species (falsifiable hypotheses) but create artificial entities (not-falsifiable defined units), if they explicitly ignore the biological framework (i.e. taxonomy) for diagnosing biological species. A procedure that accepts such a change of the ontological character of the units would be a violation of epistemological stringency and logic and would mean that we accept arbitrariness in science.

For the practical biodiversity researcher, these epistemological arguments and problems may admittedly not be relevant to understand the quality problems of parataxonomic sorting. The practical consequence of all this philosophical formalism is that typological classification (e.g. PUs) may lead to erroneous results because typology does not claim to diagnose natural conditions (by even neglecting already known biological information), but is satisfied to define artificial entities and, hence, allows arbitrariness. The only fruitful way to avoid this epistemological and practical dilemma seems to be accepting taxonomic sorting as the adequate procedure for biodiversity studies and considering parataxonomy only as a first helpful, but preliminary and never final step of the sorting process.

Parataxonomy is always either propedeutic (pre-scientific, as it was originally) or, in the worst case, instrumentalistic by complacently neglecting taxonomy (i.e., a whole aspect of evolutionary biology). If the units ('morphospecies') are instrumentalistic means, the whole scientific argument would be based on an idealistic foundation: species are what I recognize and define as such by considering only external morphology and without considering any existing knowledge. Idealism (in taxonomy mostly called typology) should have been abandoned by modern science a long time ago (even from taxonomy; see Mayr 1963, p. 5; Mahner and Bunge 1997, p. 214) and is unequivocally rejected by the critical rationalism (Popper 1972, 1989) as well as by the evolutionary theory of cognition (Vollmer 1990), which represent the two main philosophical theories of knowledge that underpin the methods of modern biology.

However, there are reasonable conditions under which we can accept using PUs (with all their time-saving advantages) as instrumentalistic tools for heuristic purposes.

When and why is such a non-scientific method adequate or even necessary?

“Scientists have been classifying species for over 200 years, and at current rates of progress may take several hundred more years to classify all organisms. However, the speed of loss of natural habitats means that information of which species occur where is needed *now*” (Glowka et al. 1994). Is this a reason to abandon time-consuming taxonomic identification work from inventory programmes? Of course not, because if we cannot name the species, we cannot tell which species occur. Taxonomy is essential for inventories. Taxonomy has admittedly a huge burden of history, resulting in masses of literature, mostly old and of little practical use but unfortunately still relevant anyway, distributed over thousands of unavailable

journals and pamphlets, published in many obscure languages, and generally for the study group neither a revision nor a key exists, but only, say, 373 single descriptions which do not refer to each other. It is hard work to cope with that. This is the day-to-day work of taxonomists, but we cannot expect an ecologist to identify taxonomically all the organisms he is dealing with. However, it is not useful to establish a PU-based parallel parataxonomic world as considered by Kitching (1993, p. 263). Such a parallel (pseudo-)system would avoid the time-consuming burdens of taxonomy, but would create a much more severe burden in a much shorter time: Since the PUs are not described and not named according to rules, comparability of sets of PUs depends only on the 'suitably qualified experts', their experience and powers of recollection. If they have passed away (or are only far away), nobody is able to tell why the units were sorted as they were.⁵

However, there is a need to know species numbers, without necessarily knowing the species names, in some fields of ecology that deal with patterns of biodiversity, functional ecology, or conservation. Can we use parataxonomic sorting for obtaining baseline data for these fields of biology?

There is a severe pitfall for comparison of sites that are spatially close to each other. Presumably sympatric sibling species have different niches (host plants, microhabitats, activity periods). Because of allopatric or ecological speciation, there is a certain probability that morphologically similar species are mutually exclusive (and actually, this is a common pattern in nature). This is even possible at higher taxonomic levels and led, e.g., to highly erroneous results in Ephemeroptera sorting as shown by Cranston and Hillman (1992). If these sibling species (or even sibling genera) are not recognized, an important part of ecological differentiation is neglected. Studies looking at species overlap are generally unreliable if working with PUs. The assertion of Samways et al. (1995) that "RTUs are useful for comparative, localized studies" is certainly erroneous.

If we compare samples from different parts of the world without or with only a negligible species overlap, we avoid having closely related species in the different samples, because the probability of finding sibling species in the different samples is reduced. Convergent characters in distantly related taxa are generally more easily detectable as different than structures that are similar *and* homologous. If processing of such parataxonomic data sets leads to meaningful patterns, which are in accordance with or explainable by our biological knowledge, then we can accept this instrumentalistic procedure as a heuristically fruitful tool. (This is true for clear and meaningful results of all kinds of comparisons, because it is less probable that

⁵ Hundreds of years of experience have unequivocally shown that anarchic naming (each project gives own names according to its own regularities) causes confusion in a very short time. That is why scientific nomenclature and international rules were established. Even if parataxonomic projects document their work properly on websites and coded voucher collections, confusion will be unavoidable if hundreds of projects do this in an uncoordinated way over, say, a hundred years. The solution might be to co-ordinate the parataxonomic naming and to establish binding international rules. This would create a parallel parataxonomic world with all the time-consuming problems of the taxonomic world.

errors cause reasonable patterns.) If no plausible results come out, this instrumentalistic procedure is pointless, because we never know whether there are actually no patterns or whether the patterns are masked by errors. Judging a method by its outcome seems not to be strictly scientific, because it is obviously circular, but this is the only way to decide when an instrumentalistic procedure leads to heuristically valuable results. Rejecting this instrumentalistic procedure for the sake of epistemological stringency as a matter of principle would deprive us of new biological discoveries for only formal reasons.

Conclusions

The following conclusions are derived from the preceding theoretical reflections, literature data (Table 1) and from personal experience (= accumulated anecdotal evidence) in beetle taxonomy and ecology. Empirical tests of these predictions would be highly welcome.

PU's are useless for:

- inventories/faunistics–floristics, since you cannot tell which species you have;
- biogeography at species level, since distribution is a species character and is not generally correlated with morphological similarity;
- autecology, since you never know if you study one or several or only a part of a species;
- area selection in conservation evaluation, since parataxonomic sorting detects only the approximate number of species, but not the 'quality' of the species; the most important results are determined by complementarity, which depends on a knowledge of accurate taxonomic identity across all compared areas (Williams 2001; Vane-Wright 2003).

PU's provide uncertain data for:

- studies of species turnover or overlap, because sibling species generally remain unrecognized;
- comparisons of different habitats within one area (same reason).

(Depending on the skills of the sorters, the quality of parataxonomic sorting may approach the level of good taxonomic sorting, but we can never be sure about that.)

PU's provide limited, but adequately accurate and, therefore, useful data for:

- global comparisons of gross species richness;
- non-comparative descriptions of species richness of single sites or comparisons of species numbers of different habitats within one area without considering species overlap (if the results show reasonable patterns).

In summary, it may be said that the applicability of parataxonomic data is limited, but in those fields where they can be used, they are heuristically valuable, because they are often the only way to get results about highly important questions.

A claim for scientific honesty

(1) Never say 'species' for PUs, even not 'for convenience' or 'for sake of simplicity' (cited from literature). This would imply that the PUs are equivalent to species when they are not (even if some authors may wish this to be so).⁶

Say 'species' only for units sorted according to high taxonomic standards, which means carefully and comprehensively using taxonomic criteria, and with a lot of taxonomic experience in every group to be sorted. The latter can only be done by experienced taxonomists and not by slightly trained ecologists or technicians. The quality of sorting is independent of assigning binomens to taxonomic units. However, only scientifically named units fulfil the scientific criteria of inter-subjective testability and falsifiability and profit from an international frame of reference (the biological nomenclature).

(2) Always mention the kind (quality) of sorting for each group (see Stork (1995) for a possible system of grading the level of reliability of sorting). Statements like 'Some groups were checked by specialists' are pointless if the groups and the specialists are not mentioned. Always give the names of the specialists. A specialist need not be reliable. A very distinguished beetle phylogeneticist may be a bad sorter. If you offer the specialist a coauthorship, he or she may be more careful in sorting. If you do the identifications yourself, mention the literature that you used, so that the basis of your identification is clear (not all keys are reliable or usable by inexperienced persons).

(3) Allow yourself and, if you are a supervisor, your students enough time for sorting or identification. Reliable sorting and identification are not trivial and need, together with the preceding preparation of the material, at least two thirds of the overall time of biodiversity projects, sometimes more than 90%.

(4) When comparing and testing data sets statistically, do always consider the possible error of 10–30% within the data sets (in some difficult groups about 100%, or even more). Clear differences in numbers of PUs or diversities are probably reliable. Small differences, even if statistically significant, or no detectable patterns may easily be caused by erroneous sorting.

(5) Give the name of the institute where the material is deposited. Since some groups can only be sorted if carefully mounted (e.g. beetles), the complete material (not only voucher specimens) should be already prepared to be included in museum collections without requiring much further effort (except for proper labelling). Only if the complete material is available for rechecking, the scientific criterion of inter-subjective testability is met because contrary to the raw data in exact sciences, raw data in biodiversity science are not based on unequivocal measurements but on

⁶ If an author puts parataxonomic sorting on a level with taxonomic identifications, he claims that both are scientific methods. Since the former is not a scientific method, this claim allows us to describe his work as pseudo-science (Radnitzky 1992, p. 404), because such a claim disqualifies a possibly heuristically valuable study by disguising its epistemological character presumptuously.

subjective interpretations (sorting). If the material is destroyed after the end of a study, as is regularly the case with thesis projects at universities, rechecking of these interpretations is impossible and one of the fundamental requirements of science is neglected.

Acknowledgements

I thank Arthur Chung (Sabah Forestry Research Centre, Sepilok, Malaysia) and Gerhard Uhmann (Pressath, Germany) for permission to use unpublished data. Menno Schilthuizen (Universiti Malaysia Sabah, Kota Kinabalu) showed me the thesis of his student J. de Roode. Fieldwork in Borneo was financed by the Darwin Initiative Project 'Tools for Monitoring Soil Biodiversity in the ASEAN Region' (project leader: David Jones). Many discussions with Peter Hammond and Paul Eggleton (The Natural History Museum London) on sorting and handling species data helped me to understand the usefulness of sorting without giving names. Paul Eggleton, David Jones, Dorothy Newman, Dick Vane-Wright (The Natural History Museum), Thomas Wagner (Universität Koblenz-Landau), Peter Cranston (University of California at Davis) and Arthur Chung gave invaluable, sometimes controversial comments on former versions of the manuscript.

Appendix

What should we call the entities sorted in a parataxonomic way?

For the entities resulting from parataxonomic sorting, a number of terms are currently in use: morphospecies, RTU, rarely morphotype and – adopted from the phenetic/cladistic literature – operational taxonomic unit (OTU). All these terms “may represent no more than a tacit admission that taxa are unreliably sorted” (Hammond 1995) and are misleading, because they disguise the possible unreliability of parataxonomic sorting or are preoccupied by other biological meanings. I will discuss the suitability of these terms for parataxonomic units, and since it is very weak in all cases, I propose a simple and adequate term: parataxonomic units (PUs).

Morphospecies is the mostly used term for units sorted by means of morphological differences without considering taxonomic literature or taxonomic standards. However, morphospecies is also a term widely used in evolutionary biology: introduced by Cain (1954, p. 51), it has been in constant use in discussions on taxonomic theory and methodology for taxonomic species founded on morphological characters neglecting or not considering biological evidence (Simpson 1961, pp. 155f; Willmann 1985, pp. 97, 188; Williams 1992; Mayden 1997). The term entered ecological biodiversity literature sometime in the 1980s (e.g. Dudgeon 1988). Adopting it for entities resulting from superficial sorting by obvious differences in external morphology deludes the reader into thinking that these entities are equiva-

lent to biological species. We have seen that the accuracy of this kind of sorting is generally rather low.

Morphotype: Dudgeon (1982, 1984) and later, independently, Wagner (1995, 1996) used this term, which stresses the typological (pre-evolutionary) nature of parataxonomic sorting and is therefore an apt expression for the units resulting from this kind of sorting. However, the term is preoccupied many times: in the sense of bauplan (introduced by Zangerl 1948; Simpson 1961, p. 47), for any distinct morphological form of a given organism (Lincoln et al. 1998, no. 3), for morpho-species in the sense of Cain with explicit or implicit typological background (Willmann 1985, p. 91), grundplan/ground pattern (Lincoln et al. 1998, no. 2), sum of synapomorphies (Patterson 1982, p. 35; Panchen 1992, p. 73), particular variations within populations (Simpson 1961, p. 178) or for a specimen selected to represent such a variation (Lincoln et al. 1998, no. 1). Using the term morphotype for the parataxonomically sorted units results in adding yet another meaning to this overworked word.

OTU (Sokal and Sneath 1963) is sometimes used in this context as well. It means *operational taxonomic unit* and was originally introduced for the entities of unknown phylogenetic status and rank, which are used for a phenetic (or cladistic) analysis. It should remain in its domain.

RTU is the abbreviation for *recognizable taxonomic unit* (Rees 1983; Cranston 1990; Oliver and Beattie 1993). This term is also widely used but does not correctly describe the results of parataxonomic sorting either. Parataxonomic sorting always results in a number of *recognized* rather than *recognizable* units, because the sorting results depend on the subjective sorting ability and experience of the sorter. Different sorters may recognize different numbers of units if they do not use the framework of taxonomy for sorting (and even if they follow taxonomic standards, different [but then falsifiable] opinions may emerge). The term 'recognizable units' gives the wrong impression that the units are recognizable by everyone. Besides, these units are not *taxonomic*, because they were not assigned to a valid species name nor baptised with a proper name, i.e. with a scientific binomen. Giving a biological unit a binomen is always combined with referring to a published description or, in case of a new species, with publishing a description of the unit (to make the binomen valid). However, it is generally agreed that RTUs are not to be described (as this is one of their time-saving advantages). RTUs are, therefore, only subjectively recognized and defined parataxonomic units. To be honest, we should call them *Recognized Parataxonomic Units* or simply PUs (because all PUs are recognized [in fact: created] by somebody). '*Recognizable taxonomic units*' implies a scientific accuracy that is not given and is, therefore, either a sloppy or a rather presumptuous term.

References

- Anonymous 1993. Convention on Biological Diversity opened for signature at Rio de Janeiro 5 June 1992. Miscellaneous Series, Great Britain 3: 26 pp.
- Anonymous 2000. Systematics Agenda 2000: Charting the Biosphere. New York, USA, Technical Report.

- Basset Y., Novotny V., Miller S.E. and Pyle R. 2000. Quantifying biodiversity: experience with parataxonomists and digital photography in Papua New Guinea and Guyana. *BioScience* 50: 899–908.
- Beattie A.J., Majer J.D. and Oliver I. 1993. Rapid biodiversity assessment: a review. In: Beattie A.J. (ed.), *Rapid Biodiversity Assessment*. Macquarie University, Sydney, Australia, pp. 4–14.
- Beattie A.J. and Oliver I. 1995. Reply from A.J. Beattie and I. Oliver. *Trends in Ecology and Evolution* 10: 203–204.
- Bolger D.T., Suarez A.V., Crooks K.R., Morrison S.A. and Case T.J. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. *Ecological Applications* 10: 1230–1248.
- Cain A.J. 1954. *Animal Species and Their Evolution*. Hutchinson's University Library, London.
- Campbell I.C. 1995. Taxonomic minimalism. *Trends in Ecology and Evolution* 10: 203.
- Cranston P.S. 1990. Biomonitoring and invertebrate taxonomy. *Environmental Monitoring and Assessment* 14: 265–273.
- Cranston P. and Hillman T. 1992. Rapid assessment of biodiversity using 'biological diversity technicians'. *Australian Biologist* 5: 144–154.
- Derraik J.G.B., Closs G.P., Dickinson K.J.M., Sirvid P., Barratt B.I.P. and Patrick B.H. 2002. Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. *Conservation Biology* 16: 1015–1023.
- Dudgeon D. 1982. Aspects of the microdistribution of insect macrobenthos in a forest stream in Hong Kong. *Archiv für Hydrobiologie, Supplement* 64: 221–239.
- Dudgeon D. 1984. Longitudinal and temporal changes in functional organization of macroinvertebrate communities in the Lam Tsuen River, Hong Kong. *Hydrobiologia* 111: 207–217.
- Dudgeon D. 1988. The influence of riparian vegetation on macroinvertebrate community structure in four Hong Kong streams. *Journal of Zoology* 216: 609–627.
- Ehrlich P.R. 1997. *A World of Wounds: Ecologists and the Human Dilemma*. Ecology Institute, Oldendorf/Luhe, Germany.
- Floren A. and Linsenmair K.E. 1998. Non-equilibrium communities of Coleoptera in trees in a lowland rain forest of Borneo. *Ecotropica* 4: 55–67.
- Gómez R. 1991. Biodiversity conservation through facilitation of its sustainable use: Costa Rica's National Biodiversity Institute. *Trends in Ecology and Evolution* 6: 377–378.
- Glowka L., Burhenne-Guilmin F., Sygne H., McNeely J.A. and Gründling L. 1994. *A Guide to the Convention on Biological Diversity (Environmental Policy and Law Paper No. 30)*. IUCN, Gland, Switzerland.
- Hammond P.M. 1995. Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society (B)* 345: 119–136.
- Hopkins G.W. and Freckleton R.P. 2002. Declines in the numbers of amateur and professional taxonomists: implications for conservation. *Animal Conservation* 5: 245–249.
- Janzen D.H. 1991. How to save tropical biodiversity. *American Entomologist* 37: 159–171.
- Kitching R.L. 1993. Biodiversity and taxonomy: impediment or opportunity? In: Moritz C. and Kikkawa J. (eds), *Conservation Biology in Australia and Oceania*. Surrey Beatty, Chipping Norton, Australia, pp. 253–268.
- König B. and Linsenmair K.E. 1996. Biologische Diversität – Ein Phänomen und seine Dimensionen. In: König B. and Linsenmair K.E. (eds), *Biologische Vielfalt*. Spektrum Akademischer Verlag, Heidelberg, Germany, pp. 8–15.
- Krell F.-T. 1993. *Taxonomie auf der Grundlage der Evolutionsbiologie*. *Carolinea Beiheft* 8: 53–59.
- Lincoln R., Boxshall G. and Clark P. 1998. *A Dictionary of Ecology, Evolution and Systematics*. Cambridge University Press, Cambridge, UK.
- Mahner M. and Bunge M. 1997. *Foundations of Biophilosophy*. Springer, Berlin, Germany.
- Mayden R.L. 1997. A hierarchy of species concepts: the denouncement in the saga of the species problem. In: Claridge M.F., Dawah H.A. and Wilson M.R. (eds), *Species. The Units of Biodiversity*. Chapman & Hall, London, pp. 381–424.
- Mayr E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, Massachusetts.
- Minelli A. and Foddai D. 1997. The species in terrestrial non-insect invertebrates (earthworms, arachnids,

- myriapods, woodlice and snails). In: Claridge M.F., Dawah H.A. and Wilson M.R. (eds), *Species. The Units of Biodiversity* (The Systematics Association Special Volume 54). Chapman & Hall, London, pp. 309–324.
- New T.R. 1998. *Invertebrate Surveys for Conservation*. Oxford University Press, Oxford, UK.
- Oliver I. and Beattie A.J. 1993. A Possible Method for the Rapid Assessment of Biodiversity. *Conservation Biology* 7: 562–568.
- Oliver I. and Beattie A.J. 1996a. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications* 6: 594–607.
- Oliver I. and Beattie A.J. 1996b. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* 10: 99–109.
- Pik A.J., Oliver I. and Beattie A.J. 1999. Taxonomic sufficiency in ecological studies of terrestrial invertebrates. *Australian Journal of Ecology* 24: 555–562.
- Panchen A.L. 1992. *Classification, Evolution, and the Nature of Biology*. Cambridge University Press, Cambridge, UK.
- Patterson C. 1982. Morphological Characters and Homology. In: Joysey K.A. and Friday A.E. (eds), *Problems of Phylogenetic Reconstruction* (Systematics Association Special Volume 21). Academic Press, London, pp. 21–74.
- Popper R. 1972. *Objective Knowledge*. Clarendon Press, Oxford, UK.
- Popper R. 1989. *Logik der Forschung*. 9th edn. Mohr, Tübingen, Germany.
- Radnitzky G. 1992. Wissenschaftlichkeit. In: Seiffert H. and Radnitzky G. (eds), *Handlexikon zur Wissenschaftstheorie*. Deutscher Taschenbuch Verlag, München, Germany, pp. 399–405.
- Rees C.J.C. 1983. Microclimate and the flying Hemiptera fauna of a primary lowland rain forest in Sulawesi. In: Sutton S.L., Whitmore T.C. and Chadwick A.C. (eds), *Tropical Rainforest: Ecology and Management*. Blackwell, Oxford, UK, pp. 121–136.
- Robinson N.A. (ed.) 1993. *Agenda 21: Earth's Action Plan Annotated* (IUCN Environmental Policy & Law Paper No. 27). Oceana Publications, New York.
- de Roode J. 2000. Testing for Sexual Selection on Male Genitalia in Dung Beetles, M.Sc. Thesis, Wageningen University, The Netherlands, 31 pp. (unpublished).
- Sachs L. 1982. *Applied Statistics. A Handbook of Techniques*. Springer, New York.
- Samways M.J., Stork N.E., Cracraft J., Eeley H.A.C., Foster M., Lund G. et al. 1995. Scales, planning and approaches to inventorying and monitoring. In: Heywood V.H. and Watson R.T. (eds), *Global Biodiversity Assessment*. UNEP and Cambridge University Press, Cambridge, UK, pp. 475–517.
- Simpson G.G. 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York.
- Slotow R. and Hamer M. 2000. Biodiversity research in South Africa: comments on current trends and methods. *South African Journal of Science* 96: 222–224.
- Sokal R.R. and Sneath P.H.A. 1963. *Principles of Numerical Taxonomy*. Freeman, San Francisco, California.
- Stork N.E. 1995. Measuring and inventorying arthropod diversity in temperate and tropical forests. In: Boyle T.J.B. and Boontawee B. (eds), *Measuring and Monitoring Biodiversity in Tropical and Temperate forests*. CIFOR, Bogor, Indonesia, pp. 257–270.
- Trueman J.W.H. and Cranston P.S. 1997. Prospects for the rapid assessment of terrestrial invertebrate biodiversity. *Memoirs of the Museum of Victoria* 56: 349–354.
- Uvarov B.P. 1931. Insects and climate. *Transactions of the Entomological Society of London* 79: 1–247.
- Vane-Wright R.I. 2003. Evidence and identity in butterfly systematics. In: Boggs C.L., Watt W.B. and Ehrlich P.R. (eds), *Butterflies: Ecology and Evolution Taking Flight*. University of Chicago Press, Chicago, Illinois pp. 477–513.
- Vecchione M., Mickevich M.F., Fauchald K., Collette B.B., Williams A.B., Munroe T.A. et al. 2000. Importance of assessing taxonomic adequacy in determining fishing effects on marine biodiversity. *ICES Journal of Marine Science* 57: 677–681.
- Vollmer G. 1990. Against Instrumentalism. In: Weingartner P. and Dorn G.J.W. (eds), *Studies on Mario Bunge's Treatise. Rodopi, Amsterdam, The Netherlands*, pp. 245–259.
- Wagner T. 1995. Verteilungsmuster und Artenvielfalt kronenbewohnender Käfer auf verschiedenen Baumarten in Zentralafrika. *Verhandlungen des Westdeutschen Entomologentages 1994*: 79–87.
- Wagner T. 1996. Zusammensetzung der baumbewohnenden Arthropodenfauna in Wäldern

- Zentralafrikas; mit Anmerkungen zur Nebelmethode und zum Morphotypen-Verfahren. *Mitteilungen des Internationalen Entomologischen Vereins* 21: 25–42.
- White M.J.D. 1978. *Modes of Speciation*. Freeman, San Francisco, California.
- Williams M.B. 1992. Species: current usages. In: Keller E.F. and Lloyd E.A. (eds), *Keywords in Evolutionary Biology*. Harvard University Press, Cambridge, Massachusetts, pp. 318–323.
- Williams P.H. 2001. Complementarity. In: Levin S.A. (ed.), *Encyclopedia of Biodiversity* 1. Academic Press, San Diego, California, pp. 813–829.
- Willmann R. 1985. *Die Art in Raum und Zeit. Das Artkonzept in der Biologie und Paläontologie*. Parey, Berlin, Germany.
- Zangerl R. 1948. The methods of comparative anatomy and its contribution to the study of evolution. *Evolution* 2: 351–374.