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Issues in Delimiting Genera in Invertebrates: an Example from the Lepidoptera (Macariini: Geometridae: Ennominae)[1]

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Abstract. Deciding on how inclusive to make genera in Lepidoptera and other invertebrate taxa is scientifically trivial compared with identifying monophyletic groups and building classifications. But the issue is important when making our classifications usable. In this paper, the results of a recent taxonomic review at the genus level of the Geometridae moth tribe Macariini are discussed to highlight some general issues.

1. INTRODUCTION

Professor Clas NAUMANN was a prominent figure, both as the Director of the Museum Alexander Koenig, and as a lepidopterist. This paper is about the importance of taking a global approach to a taxonomic problem that is widely encountered by taxonomists. It was with Clas NAUMANN's strongly international approach to his work in mind that I elected to discuss this general topic. His special interest in Lepidoptera encouraged me to illustrate the generalities by a group of Geometridae moths.

R. A. CROWSON bemoaned the loss of the broad Linnaean concept of the genus (CROWSON 1970). In characteristically waspish mode, he suggested that had systematists admitted intermediate categories between the genus and species they would have shown "a degree of public responsibility and foresight which experience shows is unrealistic to expect of ordinary human beings". A similar approach has been adopted by other authors, who have tried to be more synthetic in their approach (e.g., DAVIS & HEYWOOD 1963, for angiosperms).

With the massive increase in the discovery of species since the time of LINNAEUS, it was inevitable that species would be grouped into ever more clusters. And it was understandable that these clusters would be given generic names, thus splitting the minimal number of genera accepted by LINNAEUS, his contemporaries and slightly later followers. LINNAEUS and his students described species from many parts of the world, not just their native Scandinavia, with many of the specimens collected at trading posts associated with the old shipping lines or the hinterlands of these ports. Nevertheless, their system was founded largely on species encountered in their European surroundings. Division of the genera occurred rather later: for Lepidoptera the process started notably with HÜBNER (1816-[1825]) (EMMET 1991; SCOBLE 1991; HAUSMANN 2001).

1 In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 - 15.02.2004)

Those species of Lepidoptera described by LINNAEUS were assigned to just three genera, *Papilio*, *Sphinx* and *Phalaena*. With the subdivisions of *Phalaena* included, the total number of divisions (call them 'genera') was nine. Today, these divisions are treated mainly as superfamilies (e.g., *Geometra* – Geometroidea; *Noctua* – Noctuoidea). But as large numbers of new species were discovered from outside Europe, those classifications based significantly on European species became unsatisfactory with the consequence that genera became split. New genera were sometimes described for new species with little reference to taxonomic context, particularly where taxonomists were isolated from major European collections. This problem was encountered in a study of the Macariini (SCOBLE & KRÜGER 2002), a tribe of ennomine Geometridae moths distributed worldwide but described originally from Europe, where differences were emphasized at the expense of similarities.

2. THE PROBLEM

The practical problem, which is faced widely by taxonomists working on species-rich groups, is one of how to apply the rank of genus. It is agreed widely among the taxonomic community that each genus should be monophyletic as far as that can be determined. As a scientific problem, the issue of applying rank to the components of a classification is trivial; the more profound question is one of identifying monophyletic groups. But in practical terms applying the rank of genus is not trivial, because the results of taxonomic revision are used not only by taxonomists specialising in areas close to the target taxon, but also by taxonomists working on less closely related taxa, and by a much wider user community with identification and information needs. Taxonomy should be viewed as an information science (GODFRAY 2002), and providing a usable, as well as a formalised, system is a social responsibility. As MABBERLEY (1997) wrote: "... the *Gestalt* of a fig is

Table 1: Major genus-group concepts of the Marcariini

GUENÉE [1858]	PROUT (1915-16) Palaearctic	JANSE (1932) South Africa	WEHRLI (1939-54) Palaearctic	FORBES (1948) New York & Neighbouring States	HOLLOWAY [1994] Borneo	SCOBLE & KRÜGER (2002) Global
Macaria	*Macaria*	*Semiothisa*	*Semiothisa*	*Eumacaria*	*Lampadopteryx*	*Platypepla*
Halia	*Narraga*	**s.l.**	**s.l.**	*Enconista*	*Iridoplecta*	*Milocera*
	Isturgia	(Synonyms	(Subgenera:	*Itame*	*Hypephyra*	*Plateoplia*
	Bichroma	*Macaria, Godonela, Tephrina* (**in part**), *Osteodes, Discalma, Peridela*)	*Semiothisa*	*Semiothisa*	*Oxymacaria*	*Narraga*
	Fidonia		*Godonela*	*Macaria*	*Macaria*	*Heliomata*
	(sensu		*Thyridesia*	*Isturgia*	*Godonela*	*Isturgia*
	Treitschke)		*Neomacaria*	*Mellilla*		*Itame*
	Itame		*Macaria*			*Trigrammia*
	Chiasmia		*Ligdiformia*			*Mellilla*
	Diastictis		*Chiasmia*			*Dissomorphia*
	Osteodes	*Plateoplia*	*Diastictis*			*Paramelora*
		Platypepla	*Asmate*)			*Eumacaria*
		Hyostomodes				*Gnopharmia*
		Milocera	*Bichroma*			*Oxymacaria*
			Narraga			*Semiothisa*
			Isturgia			*Macaria*
			Itame			*Boarmioides*
			Tephrina			*Parosteodes*
			Gnopharmia			*Chiasmia*
						Malgassothisa
						Lampadopteryx
						Digrammia
						Hypephyra

usually unmistakable but to split the genus *Ficus* into several on the basis of characters only revealed by lenses seems academic self-indulgence."

The problem has arisen through a combination of two frequently observed characteristics of taxonomy. First, taxonomy is the product of a long history with a scattered literature. Second, because many taxonomists lack access to comparative material (specimens and literature), a lack of context is often apparent. For about 100 years after LINNAEUS (1758) published the tenth edition of *Systema Naturae*, a relatively small number of species were described (Fig. 1) and by few taxonomists. With the explosion of exploration from the mid 19th Century there was a corresponding increase in collection of specimens and in the description of species. The rate of species description fell around the mid 20th Century and taxonomy entered a more synthetic phase where species were synonymised or recombined with new genera. The emphasis on accepting only monophyletic taxa as valid and worthy of naming, gave an apparent intellectual basis for splitting taxa until all recognised groups were monophyletic. Currently there is a welcome emphasis on the value of taxonomy to a wider user community, which should encourage taxonomists to integrate further their efforts and to be prepared to synthesise.

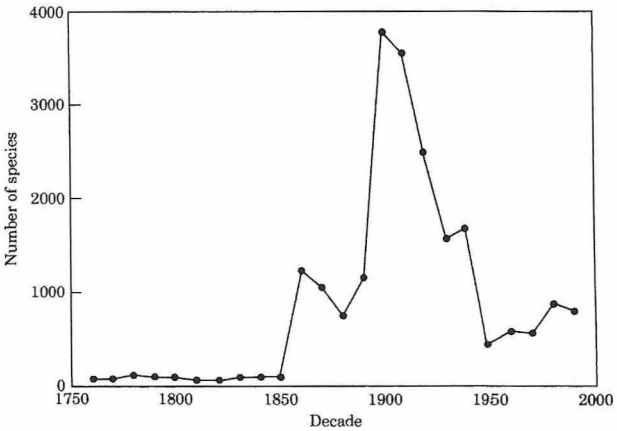

Fig. 1: Graph of number of species of Geometridae described by decade since 1758 (simplified from GASTON et al. 1995).

I use the results of a genus-level study (SCOBLE & KRÜGER 2002) for the geometrid moth tribe Macariini to exemplify some issues faced by taxonomists classify-

ing taxa that are widely distributed. From this basis some general messages are presented.

3. THE TRIBE MACARIINI

There are about 700 species of Macariini, a tribe belonging to the subfamily Ennominae of the Geometridae. The group includes medium-sized geometrid moths and is represented in all biogeographical regions. The larval foodplants of many species belong to Leguminosae (Fabaceae). The moths are encountered frequently in light traps.

The tribe was described (as 'Macaridae') by GUENÉE [1858] for four genera, two of which are now excluded from the tribe. Six prior regional works had a significant influence on the global generic classification proposed by SCOBLE & KRÜGER (2002), the genera accepted in each publication being listed in Table 1. Neither PROUT (1915-16), JANSE (1932), nor WEHRLI (1939-54) united their genera under a tribal division, but they indicated that the genera were associated. JANSE (on the South African species) included all the large macariine genera under *Semiothisa* (including *Macaria*, which has priority), starting a tradition that has been followed to the present day by many lepidopterists understandably confused by the plethora of names and unclear generic concepts. WEHRLI (Palaearctic fauna) recognised more taxonomic structure than did JANSE, treated JANSE's synonyms as subgenera of *Semiothisa*, and added several other subgenera. FORBES (1948), in the few genera treated in his restricted area of New York and neighbouring States, included all genera with the characteristic uncus 'horns' in *Semiothisa*, noting that the genus was enormous and of world-wide distribution. Unfortunately both Janse and Forbes were unaware that the type species of *Semiothisa* lacks 'horns' and has genitalia that are distinctive, the genus being exclusively neotropical and having 18 other members. Thus *Semiothisa* in their sense is equivalent to *Macaria* plus *Chiasmia* in the sense of SCOBLE & KRÜGER (2002).

The genera accepted by SCOBLE & KRÜGER (2002) are also listed in Table 1. These authors concluded that the Macariini are not certainly defined as a monophyletic group – the boundaries are unclear. There appear to be two large, arguably monophyletic genera (*Macaria* and *Chiasmia*), and one large genus (*Isturgia*) that is less convincingly monophyletic. Within these genera occur several well-defined subgroups. Within the other Macariini there are a number of small and probably monophyletic genera.

4. RESULTS OF THE GLOBAL GENERIC REVIEW

Taxonomic treatments of the genera are found in the review (SCOBLE & KRÜGER 2002), but for the purposes of this account a few key results are highlighted.

Macariini are not defined perfectly as a tribe, but the species can be recognised by their expression of one or more of three characters: a divided valva; stout setae ('horns') on the uncus in the male genitalia; and chaetosemata extended across the head. In many species the eighth abdominal sternum is cleft, excavated or emarginated. A further possible character is the presence of a fovea, a raised cuticular patch at the base of the forewing in males largely denuded of scales, but the taxonomic value of this structure is not established. The core genera of the Macariini are properly associated, but the association of certain genera within the Tribe remains questionable.

We treated many generic names as synonyms. Of the three largest genera *Chiasmia* has 12 synomyms, *Macaria* 16 and *Isturgia* three. These were among the earliest to be described for the tribe, and were erected for European species. Discoveries of material from other continents led to the description of new genera without detailed comparisons being made with type species of the European genera.

There are, among Macariini, species with similar wing pattern and colour that fall into quite different genera when genital morphology is compared. This is unsurprising given that the early genera were described on 'facies' alone. Consequently, macariine taxonomy suffered both from a multiplicity of inadequately defined genera and from the erroneous generic assignment of many of the species. As a result of the confusion, many lepidopterists simply, and understandably, used one genus, *Macaria* (or, incorrectly, *Semiothisa*), in which to place most macariine species.

The revised classification proposed was intended to reflect best the considerable amount of taxonomic structure apparent within the Macariini. Most species fall into one of three large genera - *Chiasmia*, *Macaria* or *Isturgia*. Species are included that look quite different in external appearance within the same genus, but morphological similarities suggest their association. Within these genera several species groupings were noted. There are a number of well-defined smaller genera of which the genus *Semiothisa* is one. Thus the revised classification is a compromise between placing most species in a massive single genus '*Semiothisa*' (in the incorrect sense of many authors) and creating numerous genera for small clusters of species or single species. The principle, however, of trying to recognise only monophyletic groups remains.

5. MESSAGES

Taxonomists will be familiar with the issues we encountered in revising the Macariini. The general points that arose are as follows.

1. Much taxonomy is focused on the fauna of a particular region. While it is perfectly reasonable to undertake faunal studies, taxonomists bear a responsibility to exe-

cute their work in a broad context. An excellent contemporary example of how a faunal review can be written within a strongly contextual taxonomic framework is the multi-volume treatment of the *Moths of Borneo* by J. D. HOLLOWAY (e.g., HOLLOWAY [1994], which includes Macariini). Holloway treated the Macrolepidoptera moths of the region to the level of species, but made extensive comparative studies across S E Asia and Australasia and, using the rich collections of the Natural History Museum, London, provided a global context.

A practical problem arises in that many taxonomists work remotely from major comparative reference collections and libraries. If those of us based in such collections expect such a comparative approach from others, we shall need to provide better access to the comparative information by creating cross-institutional infrastructures. The Internet will be the medium through which this infrastructure is delivered.

2. It is preferable not to describe new genera for single species or small groups of species unless they fall demonstrably outside the generic system currently in use. Classifications and names do and should change, within reason, when research shows existing systems are not optimal. However, taxonomists should be sensitive to those who use their results. We must be ever more conscious of that wide community that uses our results and ask ourselves: "will the changes we make to classifications help or hinder those who use the classifications?" With careful thought there should be no reason why we should compromise on scholarship.

Where uncertainty exists as to the generic association of a species, placing inverted commas around the genus name adopted can be a helpful convention to indicate that the species should probably be excluded. This protocol avoids the need to create new genera, but indicates that further study is required. For example, "*Semiothisa*" *nigroalbana* Cassino implies that the generic placement of *nigroalbana* is uncertain. This simple modification avoids the complexity of discarding the binomial system as suggested, for example, by MICHENER (1964), yet protects the integrity of monophyletic groups.

Like MICHENER, many taxonomists (myself included) have probably felt at times that we might be better off cutting the requisite nomenclatural link between genus and species. Such a break would enable species to be described without them having to be assigned to a genus when their associations remained unknown. The advantage of the proposal would obviate the need either to associate each species with an existing genus or to describe a new genus for every unassociated species. However, the cost of abandoning the binomial system of nomenclature would be heavy. Loss of a standard that has served taxonomy so well for 250 years is likely to lead to confusion. Moreover, with increasing computerisation of taxonomic information the established link between genus and species is one that is embedded in many databases.

3. Taxonomists frequently encounter the situation where a large genus includes a number of demonstrably monophyletic subgroups and also many single species unassociated with any others. The use of informal species-groups within a genus can be helpful to indicate taxonomic structure within such a genus without the need to describe a new genus for each subgroup or for each unassociated species. In the macariine exemplar, several subgroups, often closely related species from the same area, are evident in the three large genera, *Macaria*, *Chiasmia* and *Isturgia*, alongside numerous unassociated single species.

4. In nearly all higher taxa we find genera for which the monophyly is convincingly well founded and many genera where it is not. An argument for splitting a genus that is not demonstratively monophyletic into better-established monophyletic genera, and as many further genera as there are unassociated species, is that the situation might best reflect the natural pattern. However, taxonomists would do well to follow this course of action only where the original genus is demonstrably not monophyletic.

5. The taxonomic history of a group helps one understand problems of classification. Bacterial (prokaryote) taxonomy was re-based in 1980 (in effect, a new *Systema Naturae* was created for bacteria) because so many type cultures had been lost that few names could be referenced to specimens (SNEATH 1986). But such is not the case for Lepidoptera taxonomy, where types dating from the time of LINNAEUS still exist. Taxon concepts often have a long history, and there seems little to be gained and much to be lost by discarding the insights and information associated with those concepts (e.g., PULLAN et al. 2000; YTOW et al. 2001; BERENDSOHN 2003). Therefore, any review of genera (or any other taxonomic rank) in Lepidoptera (and most other eukaryote organisms) requires that we examine the different systems through time. Proposing new classifications without understanding how previous taxonomists came to their conclusions leads to poor taxonomy.

6. CONCLUSION

The description of all species of organisms is a worthy goal, but an immense undertaking, particularly when microorganisms are brought into consideration. Indeed description is not a single process, but requires both recognition that a putatively new species is actually undescribed and also its assignment to the appropriate genus - the generic name being a part of the name of the species. To say that a species should not be described in a taxonomic vacuum may sound like stating the obvious, yet the number of new species described within an inadequate generic framework is significant. Material advances in our

understanding of Lepidoptera biodiversity can be made more rapidly by focusing on generic reviews on a global or large regional basis, as has been done over the last decade on Geometridae (e.g., PITKIN 1996, 2002; SCOBLE 1995) including the work on the Macariini discussed in this paper. An advantage of this approach is that it accelerates coverage of Lepidoptera biodiversity while at the same time improving the quality of the taxonomic framework. Such studies will better equip those taxonomists with access to collections that are regional in scope to undertake work on species within their geographical domain.

A further reason for good quality taxonomy of higher taxa was expressed by WILLIAMS & GASTON (1994) who discussed the use of higher taxa as surrogates for biodiversity assessment (for summary see http://www.nhm.ac.uk/science/projects/worldmap/refs/key.htm#key4). They concluded that "With careful choice of higher-taxon rank, it may be possible to re-deploy effort from taxonomically intensive to taxonomically extensive surveys, in order to estimate the global distribution of a much larger proportion of overall biodiversity at the same cost".

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