Opinion

Is the genus Potamophylax (Trichoptera: Limnephilidae) highly polymorphic?

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Abstract. The present deprived state of taxonomy gives no appropriate resources for taxonomists to apply more sophisticated phenomic tools and to carry out more appropriate population sampling. Without fine structure analysis of large population samples there is no hope to discover speciation traits and there is no chance to delineate young incipient sibling species with subtle but stable shape divergences. Phylogenetic species complexes of these incipient species are frequently mistaken with species polymorphism. However, historical polymorphism is a sympatric phenomenon based on discontinuous variation inside a panmictic population and not between geographically isolated populations. I continue to consider Potamophylax mista (Navas, 1918) a valid species following the evidence given by OLÁH et al. (2013).

Key words. Trichoptera, Potamophylax, polymorphism, polyphenism

In an important paper MARTÍNEZ et al. (2016) described a new species, Potamophylax asturicus Martinez, Martin & González, 2016, a beautiful microendemic of the Spanish Cantabrian Mountains closely related to Potamophylax albergaria Malicky, 1976, described from the nearby Portugal. A secondary byproduct of this paper is their statement that ‘one of the most interesting aspects of this genus is the high polymorphism’. The large number of subspecies described in the Potamophylax cingulatus complex has inspired the authors to make this statement. Secondly, the high polymorphism, as the cause, was also illustrated by not accepting the specific status of Potamophylax mista (Navas, 1918) and keeping it a synonym of Potamophylax nigricornis (Pictet, 1834)*). The specific status of P. mista inhabiting both

*MARTINEZ et al. (2016) wrote: ‘Nevertheless, recently OLÁH et al. (2013) proposed Potamophylax mista (Navás, 1918) as a valid species, but this opinion is not supported by a morphological revision of the type (types are not available). OLÁH et al. (2013) identified and described some Spanish and French specimens as P. mista, but we believe that this association is very confusing and we continue considering it synonymous to P. nigricornis.’ However, this statement does not constitute explicite synonymization but merely authors’ opinion and I continue to consider Potamophylax mista (Navas, 1918) a valid species following the evidence given by OLÁH et al. (2013).
the Spanish and French ranges of the Pyrenees was established recently in a detailed fine structure population study on the large *P. nigricornis* species complex (OLÁH et al. 2013).

The definition of species polymorphism incorporated in their arguments is incorrect. Their statements strongly violate the basic sympathy concept of polymorphism. The widespread sympathy concept of polymorphism is based on discontinuous variation, that requires polymorphic developments inside a panmictic population and not between geographically isolated populations. Although the epistemology of the widely accepted and applied sympathy concept of polymorphism is not well established, it is routinely used by both traditional taxonomy and molecular genetics. In principle the polymorphism could be the very beginning of various speciation processes both in sympathy or allopatry and may represent early stages of speciation combined/coupled or not with reproductive isolation. To correct the incorrect polymorphism concept presented superficially in the paper I repeat some premises and details of the presently accepted sympathy concept of polymorphism below.

**Divergence in isolation is not polymorphism.** Descriptions of polymorphism emphasize the occurrence of more than one kind or form of organisms of the same species that exist together in one locality in contrast to monomorphism with a single form only.

i) Polymorphism, the discontinuous genetic variation, dividing the individuals of a population into two or more sharply distinct forms is the occurrence of two or more different morphs as alternative phenotypes in the same population of a species.

ii) Polymorphism is the coexistence of two or more distinct forms independent of sex.

iii) Sex itself as dimorphism is a form of polymorphism of the same species; the most common example of polymorphism is the sexual dimorphism.

iv) Polymorphic forms of discontinuous variation must occupy the same habitat at the same time in the same panmictic (randomly mating!) population.

v) There are two basic mechanisms in the organisation of polymorphism *sensu lato*. Polyphenism appears, if different morphs arise from the same genotype by environmental interaction. Polymorphism *sensu stricto* is the genetic polymorphism and evolves if different forms are created by certain mutations, alterations and integration in the genotype.

vi) Genetic polymorphism is the occurrence of two or more genetically determined phenotypes together in the same population in such proportion that the rarest cannot be maintained merely by recurrent mutation.

However this distinction between environmental polyphenism and genetic polymorphism is highly artificial, epistemological and often far from reality. Molecular geneticists define frequency of the less common allele in genotype between populations, whilst taxonomists are interested in determining differences in phenotype between individuals. In reality the existence of a species in several forms of phenomics, existence of a gene in several allelic forms of genomics/transcriptomics or the existence of a molecule in several forms of proteomics is rather a rule than an exception, and they are integrated in complex interactive processes. All these -omics are, in emerging systems approach, under the direct or indirect impact of the ecome of ecomics (KIKUCHI et al. 2011) and of the biome of biomics through trans-omics networks by interactome of interactomics (JANGA et al. 2011). As a result of interactome, most polymorphism is transient and governed by the processes of spreading or suppressing in
a population, or balanced by selective agencies. Balanced polymorphism is an equilibrium mixture of homozygotes and heterozygotes maintained by natural selection against both homozygotes through selective advantage.

In routine practice the reference to the phenomenon of polymorphism, similarly to the cryptic species concept, is frequently and unconsciously an epistemological product used to camouflage our limited knowledge, or simply a trial to delineate our narrow horizon. According to the cryptic species concept the species are cryptic because our phenotypic resolution is insufficient and our knowledge on fine structure of phenotype is limited due to the deprived state of taxonomy, the badly depressed science of biodiversity. The so-called highly variable widespread species are frequently composed of populations with large amount of undetected phenotypic divergences. Their morphology or phenotype is only superficially indistinguishable. Many of these polymorphic and cryptic species are pseudo-polymorphic or pseudo-cryptic, they are perfectly diverged incipient siblings simply undetected due to the inadequate study of morphological features, limited knowledge of ecology, unknown behaviour in nonvisual sound, vibration, pheromones and electric mating signals. They are cryptic or polymorphic simply because we are blind. We apply inadequate phenotypic resolution (Ołah et al. 2015).

Species or polymorphism? Allopatric divergences and not sympatric polymorphism have been demonstrated in species complexes of the genus Potamophylax Pictet, 1834 (Ołah & Kovács 2012, 2014; Ołah et al. 2015). Similarly the six subspecies in the Potamophylax cingulatus complex evolved in allopatry of geographical isolation along almost all the European mountain ranges. The diverged taxa in P. cingulatus complex need a detailed population study by fine structure analysis of the speciation traits. Population trait matrices will demonstrate how stable the diverged traits are. In this species complex the phallic organ, especially the paramere divergence, is very pronounced and possibly resulted in contemporary speciation processes producing incipient sibling species of the phylogenetic species concept. Similarly the divergence of Potamophylax mista evolved in isolation in the Pyrenees Mountains far from the present distribution of the ancestral form. Potamophylax nigricornis, the ancestral species of the complex, is not recorded west of the Alps. Two incipient siblings evolved west of the Rhone River, Potamophylax simas Oláh & Coppa, 2013 in the Massif Central and Potamophylax mista in the Pyrenees. In caddisfly taxonomy we used to work with gross structures of neutral, non-adaptive, random traits strongly exposed to both gene flow and genetic drift. The time has come to rely more on the non-neutral, non-random but adaptive traits creating reproductive isolation in contemporary speciation processes and resulting in the rapid formation of subtle and stable speciation traits in incipient sibling species of the phylogenetic species concept.

Minor shape modification. In alpha taxonomy we are frequently faced with unresolved difficulties how to evaluate minor shape modifications. We are frequently forced to decide without real molecular knowledge behind, whether these alterations represent neutral ranges of i) genomic variation; ii) epigenetic variation; iii) phenomic plasticity; or iv) they are sign of developmental instability; v) early signatures of diverging populations; or vi) they are already products of non-neutral, non-random adaptive genomic processes, representing diverged reproductive barriers of closely related incipient sibling taxa; indicating some vii) incomplete lineage sorting or viii) hybrid effects in secondary contact clines under reinforcement.
Rapidly, subtly but stably. In a long series of papers we have documented that species delimitation with subtle, but stable trait divergences seems to be a rule in endemic hotspots of sky-islands in the mountain ranges embracing the Carpathian Basin sensu lato (OLÁH et al. 2015). All the discovered incipient sibling species have exhibited surprisingly rapid, subtle but stable morphological divergences in the shape of the speciation traits, an actor of sexual selection. Traditional phenomics of alpha taxonomy relies on gross structural divergences and suffers from inadequate tradition, experience and knowledge how to detect, visualize and describe these “tiny” divergences. In alpha taxonomy we are even more unprepared to understand the molecular forces, mechanisms and processes underlying the evolution of the “tiny” shape divergences of the speciation traits. The limited knowledge is slowly accumulating, but mostly virtual on the genomic processes of subtle shape divergences and pertains exclusively to some reference elite organisms like *Drosophila* with strong focus of research and funding. Speciation structure defining species boundaries changes rapidly under sexual selection. However, this initial split of speciation divergence appears subtle for our human empirism.

Is it really subtle? It is subtle compared to the inadequate resolution level that traditional taxonomy applies routinely in delimiting species, but robust enough for mate recognition in building the reproductive isolation. Imagine the stimulatory robustness of a rigid sclerotized structure if developed on the phallic organ to operate in human mate! Rapid, stable and subtle shape alterations seem to be a rule, rather than exception in initial lineage splitting evolved under selective, adaptive pressures in non-random, non-neutral phenomic processes of sexual selection. In contemporary taxonomy we used to apply robust genital structural differences of old splitting in determining or differentiating between species. Today the phenomics with hightech and high-throughput procedures, a new research trend, a promising by-product of genomic fiascos in evolution (neutral DNA markers!) and medicine (cancer failure!) research, enlarges our capacity to extract information from phenomes with higher resolution (Houle 2010, Houle et al. 2010, Oláh et al. 2015). Painful failures of modern hybris (Greek: arrogance, pride) force us to learn that phenomics, a comprehensive study of phenotype with high resolution, is essential to understand reality. The time has come to change how we describe biodiversity or how we study the evolution of speciation (Deans et al. 2012).

References


