

Review Article

Species Distinction and Speciation in Hydrobioid Gastropods (*Mollusca: Caenogastropoda: Truncatelloidea*)

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Abstract

Hydrobioids, known earlier as the family Hydrobiidae, represent a set of truncatelloidean families whose members are minute, world-wide distributed snails inhabiting mostly springs and interstitial waters. More than 1,000 nominal species bear simple plesiomorphic shells, whose variability is high and overlapping between the taxa, and the soft part morphology and anatomy of the group is simplified because of miniaturization, and unified, as a result of necessary adaptations to the life in freshwater habitats (osmoregulation, internal fertilization and eggs rich in yolk and within the capsules). The adaptations arose parallel, thus represent homoplasies. All the above facts make it necessary to use molecular markers in species discrimination, although this should be done carefully, considering genetic distances calibrated at low taxonomic level. There is common believe in crucial place of isolation as a factor shaping speciation in long-lasting completely isolated habitats. However, neither geomorphological facts (springs are rather ephemeral habitats, there is a net of interstitial habitats which may be used as the ways of expansion), nor the actual genetic structure of (Meta) populations of those stygobiont gastropods (not necessarily low intrapopulation polymorphism, not low levels of gene flow) confirm such opinion.

Introduction

Hydrobioids, representing a set of gastropod truncatelloidean families formerly classified as *Hydrobiidae*, include minute world-wide distributed gastropods whose shells are 1-4 mm high. Some of them

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inhabit brackish water habitats, some other rivers and lakes, but vast majority are stygobiont, inhabiting springs, caves and interstitial habitats. Nearly nothing is known about the biology and ecology of those stygobionts. Much more than 1,000 nominal species have been described (Figure 1). However, the real number of species is not known, in fact. Not only because of many species to be discovered in the future, but mostly since there are no reliable criteria, how to distinguish a species within the group.



Figure 1: Shells of some of the European representatives of Truncatelloidea: A - *Ecrobia*, B - *Pyrgula*, C-D - *Dianella*, E - *Adrioinsulana*, F - *Pseudamnicola*, G - *Sadleriana*, H - *Radomaniola*, I - *Anagastina*, J - *Grossuana*, K - *Hauffenia*, L - *Graecorientalia*, M - *Trichonia*, N - *Daphniola*, O - *Boleana*, P - *Graziana*, Q - *Pontobelgrandiella*, R - *Paladilhiopsis*, S - *Lithabitella*, T - *Pseudobithynia*, U - *Bythinella*, W - *Lithoglyphus*, X - *Emmericia*, Y - *Marstoniopsis*, Z - *Heleobia*.

Morphological Characters in Species Distinction

In the Gastropod the shell is the most striking and characteristic structure. The shell remains after the death of animal, thus could be easily studied in old museum materials, or even fossil ones. However, wide ranges of variability of the shells lacking any characteristic feature drastically decrease the usefulness of the shell in species distinction [1-4]. Already, in his classical study on the profundal lymnaeids of the Lake Lemnan, demonstrated that the shell plasticity definitely excludes, in certain cases, species determination based on the shell: curiously looking shells were found in the gastropods, whose anatomy - especially of reproductive organs - was typical of the two species inhabiting the littoral of the lake [5]. Later, anatomy of the reproductive organs became a basis for all the lymnaeid taxonomy [6]. In hydrobioids, the classical papers of Muus on the Baltic Hydrobiinae demonstrated the usefulness of soft parts: morphology of the penis coupled with head pigmentation, in discrimination of species whose shell variability overlapped [7,8].

Anatomical characters, especially of the reproductive system, became a standard in species-level taxonomy in hydrobioids. The anatomy of the female reproductive system as well as the morphology of the penis was considered in species descriptions and diagnoses [9-23]. On the other hand, there are opinions that between the closely related representatives of the same genus, differences in anatomy are not necessarily present, and, in many cases, would not be expected [24]. The 'lock-and-key' mechanism, known mostly in arthropods, is hardly expected in molluscs, whose copulatory organs lack any sclerotized structures, and are more variable than it is usually noted [1,25-28].

In hydrobioids the anatomy does not offer too many characters useful for taxonomy. It is simplified as a result of miniaturisation and made similar because of inevitable adaptations to osmoregulation, internal fertilization, and embryonic development inside a capsule, all necessary in a freshwater habitat, but not plesiomorphic for the Gastropoda. Thus, anatomical similarities are the result of parallelism, or even convergence, at least in many cases, and need not necessarily reflect the common ancestry. In general, homoplasies are common in the *Mollusca* [29-31].

Species Concepts Applied in Hydrobioid; Introduction of Molecular Data

From among the concepts of species, I prefer the cohesive one proposed by Templeton, not the most often accepted biological one [32,33]. The latter defines species as members of populations that actually or potentially interbreed in nature. This works perfectly in clear situations, where nobody doubts in species distinctness, but is hardly applicable in more complex cases and/or if the data are incomplete. Recent studies on DNA clearly has shown that hybridisation is not as rare as had been previously thought. On the other hand, it is hard to prove hybridisation in nature, and in captivity it may be either blocked or promoted by the conditions unusual for the tested animals. This species concept is also absolutely useless in the case of taxa reproducing asexually (e.g., through parthenogenesis), which are still not less distinct and homogenous than the "normal" species. According to the cohesion species concept, on the other hand, a species is a population, or set of populations, that has genetic or demographic (including ecological niche) cohesion of its members.

Unfortunately, we often know too little about the ecology and biology of the hydrobioid taxa to apply this concept. Often a few specimens or only empty shells - sometimes even broken, uncomplete - can be found, thus the taxonomy is based mostly on the shell morphology and geographic distribution. This, coupled with a popular idea that isolation is the first factor shaping divergence and speciation of the spring/cave fauna, resulted in dozens of nominal species in many genera, the species known only as shells at a given locality. Thus, with well-fixed material available, it became necessary to apply molecular data [34]. Especially the relative range of genotypic differentiation, measured as simple p-distance (or, often, K2P distance which is not justified, but the values are only somewhat higher than the ones of p-distance), most often calculated for mitochondrial cytochrome oxidase subunit I (COI, commonly used in phylogenetic studies: Davis et al.), are used [35,36]. It must be stressed, however, that the values of the distances are applicable only within a group of rather closely related species, since there is no general rule, in some genera the interspecies distances are higher, in some other they are smaller [4,37-45].

For example, Bichain et al., reported that the species threshold value of K2P distance in the west European *Bythinella* was 0.015 [36]. Several numerical techniques for species distinction applying the genetic distances were introduced [46,47]. Applying mitochondrial DNA one should be careful since there are cases of introgression, although not often [48].

Morphostatic Mode of Evolution

In hydrobioids it is common that molecular differences are not well reflected in morphology, which confirms the morphostatic model of evolution, with numerous cryptic species within the genus [40,49]. Morphostatic evolution, as defined by Davis, is often a result of non-adaptive radiation marked by the rapid proliferation of species without ecological differentiation [50,51]. This results in a flock of species that are not differentiated morphologically (and ecologically). Although traditionally neglected, non-adaptive radiation seems not to be a rare phenomenon in gastropods [52,53]. Thus the criterion of morphological differences between molecularly distinct taxa may not be useful in the case of morph static evolution. In practice, it is not easy to assess the distinctness of species in more or less different yet allopatric taxa. Where there is sympatry combined with well-marked differences (morphology included) species distinctness is well supported. At this point, however, one should be more than careful in case of morphology - in springs reproduction takes place throughout a year, but the conditions - like amount of food (e.g., algae) varies between summer and winter, which often results in generations strikingly different in morphology at the same spring, which mimics distinct species [54].

Ways of Speciation

The crucial point in distinguishing species is our knowledge - if any - about the ways of speciation in the considered group. And at this point, in hydrobioids we have much more myths and legends than real knowledge. Wide ranges of variability of the shells lacking any characteristic feature, coupled with common belief in extremely high levels of endemism (just a distinct species in each spring/cave, or at least, spring/cave complex:) resulted in enormously long list of presumed species for the Bulgarian stygobiont gastropods) [23,55,56]. There are popular speculations about the founder effect in Hydrobioids, but they are not supported by the genetic structure of local populations, not resembling the one expected as a consequence of founder effect [57-59]. There are also concepts of strictly geographical, but large-scale pattern of vicariant distribution [60].

Undoubtedly the levels of endemism are overestimated, and type specimens stored as empty shells are hardly helpful in solving problems with identification and species boundaries in the hydrobioid snails. In stygobiont hydrobioids living snails can be collected as single specimens, only exceptionally a few specimens can be collected at a place, thus the molecular data, useful in phylogeny as well as in the studies on genetic structure of population, only recently begun to accumulate [61]. It is commonly believed that the springs inhabited by those obligatorily aquatic animals are stable and long lasting habitats. Certainly this cannot be truth: springs are rather ephemeral habitats. Another widely acknowledged idea is that the gene flow among them, if at all present, is very low. In the rich literature covering the phylogeny and population genetic structure and gene flow of the spring fauna, the gastropods are well represented [49,57,58,62-71]. Most of the studies point to low levels of gene flow and high levels of

endemism in spring snails, but on the other hand, some of the species the studies deal with are rather widespread, with much gene flow among their populations [57,58,62,63,67,71].

For long the one-species-at-one-locality view was widely accepted concerning spring-dwelling hydrobioids, like *Bythinella* [1,49]. This argument assumed that: (i) closely phylogenetically related snails have most probably the same or almost the same ecological niche; (ii) there is little or no spatial differentiation inside small and simple habitats like springs. Neither argument need be true. Firstly, the ecological niches of closely related species do not necessarily overlap. Secondly, even the smallest spring may contain more than one microhabitat. On the other hand, one can assume that two species whose ecological niches overlap will coexist if their densities are limited not by their competition, but some other factors (e.g. parasites). Falniowski et al., found an evident case of sympatric occurrence of two *Bythinella* species in Romania: striking morphological differences coupled with the molecular ones [40,49]. Two molecularly distinct sympatric taxa of *Bythinella* were found also in Greece and morphologically different - in Slovenia [24,26,72].

Isolation VS Gene Flow

The available data on the molecular genetics of the stygobiont gastropod did not confirm either the complete isolation of populations or their stability and longevity [1,26,57,58,65,70,73]. For inhabitants of such miniature and changeable habitats survival must depend on dynamic processes of colonization and recolonization events coupled with short- or (in some cases) long-distance dispersal [74,75].

The several cases of presumed long-distance passive transportation (the sea included), reflected by genetic identity/similarity, were reported in several studies [26,74,75]. They confirm that passive dispersal, most probably by birds is an important factor that moulds the geographical distribution of haplotypes [76-79]. There are no observations on the bird transport of spring snails, but the data on snails transported by birds are numerous. Lyell mentioned the possibility of transport by waterfowl to distant islands for a land snail *Succinea putris* through the attachment of eggs to feathers and Darwin observed ducks emerging from a pond with duckweed adhering to their backs [80,81]. For the hydrobioids, Bondesen & Kaiser mentioned a possibility for *Potamopyrgus antipodarum* and other prosobranchs of attaching themselves to feathers by trapping them between operculum and shell. Cadée observed living *Peringia ulvae* emerging from faeces of the shelduck, *Tadorna tadorna*, indicating that they survived the passage of the digestive tract [82-84]. The numbers of *Peringia* observed alive in the shelduck's faeces were considerable: three droppings contained in total 140 living specimens and 960 empty and/or broken *Peringia* shells [83].

Animals adapted to cave environments are also thought to be highly geographically isolated because of their limited dispersal ability, resulting from limited physiological tolerances and, especially in the case of snails, physical limitations of their locomotion [85,86]. However, this isolation is not obvious. In fact, there are many subterranean habitats which are not caves, but also harbour eyeless, depigmented animals, especially unconsolidated sediments bordering and underlying streams and rivers. They are parts of the interstitial habitat, neither rare nor discontinuous, making thus possible migration between caves [87-91].

And, last but not least, nearly all the debate concerns the isolation

as the only factor shaping speciation in stygobiont snails. This need not to be justified: at first, even in isolation, speciation need not to proceed, in a habitat which is stable but not necessarily favourable for an animal, there would be either no mutation or each mutation would be eliminated by strong selection. Extremely low level of genetic diversity in stygobiont *Pontobelgrandiella* throughout Bulgaria may be an example. On the other hand, sympatric speciation must be also considered in the debate on the stygobiont species and speciation [92-94].

Concluding Remarks

In hydrobioid snails simple plesiomorphic shells, whose variability is high and overlapping between the taxa, coupled with the soft part morphology and anatomy, simplified because of miniaturisation, and unified, as a result of necessary adaptations (which often arose parallel, thus represent homoplasies) to the life in freshwater habitats (osmoregulation, internal fertilization and eggs rich in yolk and within the capsules), drastically decrease the usefulness of morphology in taxonomy, also at the species level. Cohesive species concept, most appropriate here, often cannot be applied since we know too little about those snails. It is necessary to use molecular markers in species discrimination, although this should be done carefully, considering genetic distances calibrated at low taxonomic level. Morphostatic mode of evolution seems to dominate in many hydrobioid taxa. There is common belief in crucial place of isolation as a factor shaping speciation in long-lasting and completely isolated habitats. However, springs are rather ephemeral habitats, in fact, and there is a net of interstitial habitats which may be used as the ways of expansion. Also the actual genetic structure of (Meta) populations of those stygobiont gastropods (not necessarily low intrapopulation polymorphism, not always low levels of gene flow) contradicts the crucial role of isolation.

References

- Falniowski A (1987) Hydrobioidea of Poland (*Prosobranchia*: Gastropoda). *Folia Malacol* 1: 11-122.
- Falniowski A (1990) Anatomical characters and SEM structure of radula and shell in the species-level taxonomy of freshwater prosobranchs (*Mollusca*: Gastropoda: *Prosobranchia*): a comparative usefulness study. *Folia Malacol* 4: 53-142.
- Wilke T, Falniowski A (2001) The genus *Adriohydrobia* (*Hydrobiidae*: Gastropoda): Polytypic species or polymorphic populations? *J Zool Syst Evol Res* 39: 227-234.
- Falniowski A, Beran L (2015) *Belgrandiella* A. J. Wagner, 1928 (*Caenogastropoda*: Truncatelloidea: *Hydrobiidae*): how many endemics? *Folia Malacol* 23:187-191.
- Roszkowski W (1914) Contribution à l'étude des Limmées du lac Léman. *Rev Suis Zool* 22: 453-539.
- Hubendick B (1951) Recent Lymnaeidae, their variation, morphology, taxonomy, nomenclature, and distribution. Almqvist publisher, Sweden. 3: 1- 223.
- Muus BJ (1963) Some Danish *Hydrobiidae* with the description of a new species *Hydrobia neglecta*. *Proc Malac Soc Lond* 35: 131-138.
- Muus BJ (1967) The fauna of Danish estuaries and lagoons: distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. University of California, California, USA. 5: 1-316.
- Giusti F, Pezzoli E (1977) Primo contributo alla revisione del genere *Bythinella* in Italia. *Nat Bresc Ann Mus Civ St Nat Brescia* 14: 3-80.

10. Giusti F, Pezzoli E (1980) Gasteropodi, 2 (Gastropoda: *Prosobranchia*; Hydrobioidea, Pyrguloidea). Guide per il riconoscimento delle specie animali delle acque interne, NHBS, UK.
11. Jungbluth JH, Boeters HD (1977) Zur Artabgrenzung bei *Bythinella dunkeri* und *bavarica* (*Prosobranchia*). *Malacologia* 16: 143-147.
12. Boeters HD (1970) Die Gattung *Microna* Clessin, 1890 (*Prosobranchia*, *Hydrobiidae*). *Arch Molluskenk* 100: 113-145.
13. Boeters HD (1998) *Mollusca*: Gastropoda: Superfamilie *Rissooidea*. In: Brauer A, Schwoerbel J, Zwick P (eds.). Süßwasserfauna von Mitteleuropa. Cornell University, Cornell, USA.
14. Bodon M (1988) Note anatomiques “*Belgrandiella*” *hartwigschuetzi* Reischütz e revision della sua posizione sistematica (Gastropoda: *Prosobranchia*: *Hydrobiidae*). *Arch Molluskenk* 119: 55-63.
15. Haase M (1993) *Hauffeniakerschneri* (Zimmermann 1930): zwei Artenzwei Gattungen (*Caenogastropoda*: *Hydrobiidae*). *Arch Molluskenk* 121: 91-109.
16. Haase M (1993) *Belgrandiella ganslmayri*, a new hydrobiid species from Upper Austria (*Caenogastropoda*). *Ann Naturh Mus Wien* 94/95: 181-186.
17. Haase M (1994) Differentiation of selected species of *Belgrandiella* and the redefined genus *Graziana* (Gastropoda: *Hydrobiidae*). *Zool J Linn Soc Lond* 111: 219-246.
18. Haase M (1996) The radiation of spring snails of the genus *Belgrandiella* in Austria (*Mollusca*: *Caenogastropoda*: *Hydrobiidae*). *Hydrobiologia* 319: 119-129.
19. Bernasconi R (1994) Le genre *Moitessieria* BGT, 1863 en France. Revision, inventaire et description de *M. corsica* n. sp. (*Mollusca* Gastropoda *Prosobranchia* *Hydrobiidae*). *Mém Biospéol* 21: 7-20.
20. Bernasconi R (2000) Révision du Genre *Bythinella* (Moquin-Tandon, 1855) (Gastropoda *Prosobranchia* *Hydrobiidae*: Amnicolinae *Bythinellini*) de la France du Centre-Ouest, du Midi et des Pyrénées. University of California, California, USA. 1: 1-126.
21. Haase M, Weigand E, Haseke H (2000) Two new species of the family *Hydrobiidae* (*Mollusca*: *Caenogastropoda*) from Austria. *Veliger* 43: 179-189.
22. Bodon M, Manganello G, Giusti F (2001) A survey of the European valvate hydrobiid genera, with special reference to *Hauffenia* Pollonera, 1898 (Gastropoda: *Hydrobiidae*). *Malacologia* 43: 103-215.
23. Glöer P (2002) Süßwassergastropoden Nord- und Mitteleuropas. Bestimmungsschlüssel, Lebensweise, Verbreitung: Part 73 of Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise (edn2). ConchBooks, Hackenheim, Germany.
24. Radoman P (1983) Hydrobioidea a superfamily of *Prosobranchia* (Gastropoda). Systematics (Vol 1). Srpska akademija nauka i umetnosti, Belgrade, Serbia.
25. Masly JP (2012) 170 Years of “Lock-and-Key”: Genital Morphology and Reproductive Isolation. *Int J Evol Biol* 2012: 247352.
26. Falniowski A, Szarowska M (2011) Radiation and phylogeography in a spring snail *Bythinella* (*Mollusca*: *Rissooidea*) in continental Greece. *Ann Zool Fenn* 48: 67-90.
27. Falniowski A, Szarowska M (2012) Sequence-based species delimitation in the Balkan *Bythinella* Moquin-Tandon, 1856 (Gastropoda: *Rissooidea*) with general mixed Yule coalescent model. *Folia Malacologica* 20: 111-120.
28. Szarowska M, Falniowski A (2008) There is no philosopher’s stone: *coup de grace* for the morphology-based systematics in the *rissooidean* gastropods? 5th Congress of the European Malacological Societies, Ponta Delgada 28.
29. Fretter V, Graham A (1962) British Prosobranch Molluscs. Their functional anatomy and ecology. Ray Society, University of California, California, USA.
30. Haszprunar G (1988) On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *J Moll Stud* 54: 367-441.
31. Szarowska M (2006) Molecular phylogeny, systematics and morphological character evolution in the Balkan *Rissooidea* (*Caenogastropoda*) *Folia Malacol* 14: 99-168.
32. Templeton AR (1989) The meaning of species and speciation: a genetic perspective. In: Otte D, Endler JA (eds.). Speciation and its consequences. Sinauer Associates Inc., Sunderland (MA, USA). Pg No: 3-27.
33. Mayr E (1942) Systematics and the Origin of Species. Columbia University Press, New York, USA.
34. Avise JC (2000) Phylogeography, the history and formation of species. Harvard University Press, Cambridge, USA.
35. Davis GM, Wilke T, Spolsky C, Qiu C-P, Qiu D-C, et al. (1998) Cytochrome Oxidase I-based Phylogenetic Relationships among the *Pomatiopsidae*, *Hydrobiidae*, *Rissoidae* and *Truncatellidae* Gastropoda: *Caenogastropoda*: *Rissooidea*. *Malacologia* 40: 251-266.
36. Bichain JM, Gaubert P, Samadi S, Boisselier-Dubayle MC (2007) A gleam in the dark: phylogenetic species delimitation in the confusing spring-snail genus *Bythinella* Moquin-Tandon, 1856 (Gastropoda: *Rissooidea*: Amnicolidae). *J Mol Phyl Evol*. 45: 927-941.
37. Wilke T, Davis GM (2000) Intraspecific mitochondrial sequence diversity in *Hydrobia ulvae* and *Hydrobia ventrosa* (*Hydrobiidae*: *Rissooidea*: Gastropoda): Do their different life histories affect biogeographic patterns and gene flow? *Biol J Linn Soc* 70: 89-105.
38. Wilke T (2003) *Salenthidrobia* gen. nov. (*Rissooidea*: *Hydrobiidae*): a potential relict of the Messinian salinity crisis. *Zool J Linn Soc* 137: 319-336.
39. Falniowski A, Szarowska M, Grzmil P (2007) *Daphniola* Radoman, 1973 (Gastropoda: *Hydrobiidae*): shell biometry, mtDNA, and the Pliocene flooding. *J Nat Hist* 41: 2301-2311.
40. Falniowski A, Szarowska M, Sirbu I (2009) *Bythinella* Moquin-Tandon, 1856 (Gastropoda: *Rissooidea*: *Bythinellidae*) in Romania: species richness in a glacial refugium. *J Nat Hist* 43: 2955-2973.
41. Szarowska M, Grzmil P, Falniowski A, Sirbu I (2007) *Grossuana codreanui* (Grossu, 1946) and the phylogenetic relationships of the East Balkan genus *Grossuana* (Radoman, 1973) (Gastropoda: *Rissooidea*). *Hydrobiologia* 579: 379-391.
42. Falniowski A, Szarowska M, Glöer P, Pešić V (2012) Molecules vs morphology in the taxonomy of the *Radomaniola*/*Grossuana* group of Balkan *Rissooidea* (*Mollusca*: *Caenogastropoda*). *J Conchol* 41: 19-36.
43. Szarowska M, Falniowski A (2013) Species distinctness of *Sadleriana robici* (Clessin, 1890) (Gastropoda: *Rissooidea*). *Folia Malacol* 21: 127-133.
44. Szarowska M, Falniowski A (2014) *Ventrosia maritima* (Milaschewitsch, 1916) and *V. ventrosa* (Montagu, 1803) in Greece: molecular data as a source of information about species ranges within the Hydrobiinae (*Caenogastropoda*: *Truncatelloidea*). *Folia Malacol* 22: 61-67.
45. Szarowska M, Hofman S, Osikowski A, Falniowski A (2014) *Heleobia malzani* (Westerlund, 1886) (*Caenogastropoda*: *Truncatelloidea*: *Cochliopidae*) from Crete and species-level diversity of *Heleobia* Stimpson, 1865 in Europe. *J Nat Hist* 48: 2487-2500.
46. Falniowski A, Szarowska M, Glöer P, Pešić V, Georgiev D, et al. (2012) Radiation in *Bythinella* Moquin-Tandon, 1856 (*Mollusca*: *Gastropoda*: *Rissooidea*) in the Balkans. *Folia Malacol* 20: 1-10.
47. Falniowski A, Szarowska M (2012) Phylogenetic position of *Boleana umbilicata* (Kuščer, 1932) (*Caenogastropoda*: *Rissooidea*). *Folia Malacol* 20: 265-270.
48. Rysiewska A, Prevorčnik S, Osikowski A, Hofman S, Beran L, et al. (2017) Phylogenetic relationships in *Kerkia* and introgression between *Hauffenia* and *Kerkia* (*Caenogastropoda*: *Hydrobiidae*). *J Zool Syst Evol Res* 55: 106-117.

49. Falniowski A, Szarowska M, Sirbu I (2009) *Bythinella* Moquin-Tandon, 1856 (Gastropoda: *Rissooidea*: Bythinellidae) in Romania: its morphology with description of four new species. *Folia Malacol* 17: 21-36.
50. Davis GM (1992) Evolution of prosobranch snails transmitting Asian *Schistosoma*: coevolution with *Schistosoma*: a review. *Prog Clin Parasitol* 3: 145-204.
51. Gittenberger E (1991) What about non-adaptive radiation? *Biol J Linn Soc* 43: 263-272.
52. Cameron RAD (1992) Land snail faunas of the Napier and Oscar ranges, Western Australia: diversity, distribution and speciation. *Biol J Linn Soc* 45: 271-286.
53. Cameron RAD, Cook LM, Hallows JD (1996) Land snails on Porto-Santo: adaptive and non adaptive radiation. *Phil Trans Roy Soc Lond B* 351: 309-327.
54. Szarowska M (1996) The egg capsules of *Bythinella austriaca* (Frauenfeld, 1856) with observations on the veliger and embryonic shell. *J Moll Stud* 62: 546-549.
55. Boeters HD (1979) Species concept of prosobranch freshwater molluscs in Western Europe, 1. *Malacologia* 18: 57-60.
56. Georgiev D (2013) Catalogue of the stygobiotic and troglophilous freshwater snails (Gastropoda: *Rissooidea*: *Hydrobiidae*) of Bulgaria with descriptions of five new species. *Ruthenica* 23: 59-67.
57. Falniowski A, Szarowska M, Fialkowski W, Mazan K (1998) Unusual geographic pattern of interpopulation variation in a spring snail *Bythinella* (Gastropoda, *Prosobranchia*). *J Nat Hist* 32: 605-616.
58. Falniowski A, Mazan K, Szarowska M (1999) Homozygote excess and gene flow in the spring snail *Bythinella* (Gastropoda: *Prosobranchia*). *J Zool Syst Evol Res* 37: 165-175.
59. Barton NH (1989) Founder effect speciation. In: Otte D, Endler JA (eds.). *Speciation and its consequences*. Sinauer Associates, Sunderland (MA), USA. Pg No: 229-256.
60. Schütt H (1980) Zur Kenntniss griechischer Hydrobiiden. *Arch Molluskenk* 110: 115-149.
61. Richling I, Malkowsky Y, Kuhn Y, Niederhöfer H-J, Boeters HD (2016) A vanishing hotspot-impact of molecular insights on the diversity of Central European *Bythiospeum* Bourguignat, 1882 (*Mollusca*: Gastropoda: Truncatelloidea). *Org Div Evol* 17: 67-85.
62. Colgan DJ, Ponder WF (1994) The evolutionary consequences of restrictions on gene flow: Examples from Hydrobiid snails. *Nautilus* 2: 25-43.
63. Ponder WF, Egger P, Colgan DJ (1995) Genetic differentiation of aquatic snails (Gastropoda: *Hydrobiidae*) from artesian springs in arid Australia. *Biol J Linn Soc* 56: 553-596.
64. Bohonak AJ (1999) Dispersal, gene flow, and population structure. *Q Rev Biol* 74: 21-45.
65. Bilton DT, Freeland J R, Okamura B (2001) Dispersal in freshwater invertebrates. *Ann Rev Ecol Sys* 32: 159-181.
66. Myers MJ, Sperling FAH, Resh VH (2001) Dispersal of two species of Trichoptera from desert springs: Conservation implications for isolated vs connected populations. *J Insect Cons* 5: 207-215.
67. Finston TL, Johnson MS (2004) Geographic patterns of genetic diversity in subterranean amphipods of the Pilbara, Western Australia. *Mar Freshw Res* 55: 619-628.
68. Hershler R, Liu H-P (2004) Taxonomic reappraisal of species assigned to the North American freshwater gastropod subgenus *Natricola* (*Rissooidea*: *Hydrobiidae*). *Veliger* 47: 66-81.
69. Hershler R, Liu H-P (2004) A molecular phylogeny of aquatic gastropods provides a new perspective on biogeographic history of the Snake River region. *Mol Phylogenet Evol* 32: 927-937.
70. Brändle M, Westermann I, Brandl R (2005) Gene flow between populations of two invertebrates in springs. *Freshw Biol* 50: 1-9.
71. Hershler R, Mulvey M, Liu H-P (2005) Genetic variation in the Desert Springsnail (*Tryoniaporrecta*): implications for reproductive mode and dispersal. *Mol Ecol* 14: 1755-1765.
72. Radoman P (1976) Speciation within the family Bythinellidae on the Balkans and Asia Minor. *J Zool Syst Evol Res* 14: 130-152.
73. Falniowski A (1992) The genus *Bythinella* Moquin-Tandon, 1855, in Poland (Gastropoda, *Prosobranchia*, *Hydrobiidae*). In: Gittenberger E & Goud J (eds.), *Proceedings of the 9th International Malacological Congress*: 135-138. Unitas Malacologica, Leiden, Netherland.
74. Szarowska M, Osikowski A, Hofman S, Falniowski A (2016) Do diversity patterns of the spring-inhabiting snail *Bythinella* (Gastropoda, Bythinellidae) on the Aegean Islands reflect geological history? *Hydrobiologia* 765: 225-243.
75. Szarowska M, Osikowski A, Hofman S, Falniowski A (2016) *Pseudamnicola* Paulucci, 1878 (*Caenogastropoda*: Truncatelloidea) from the Aegean Islands: a long or short story? *Org Divers Evol* 16: 121-139.
76. Rees WJ (1965) The aerial dispersal of *Mollusca*. *J Moll Stud* 36: 269-282.
77. Wesselingh FP, Cadée GC, Renema W (1999) Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera *Tryonia* and *Planorbarius*. *Geol Mijnbouw* 78: 165-174.
78. Charalambidou I, Santamaria L (2002) Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. *Acta Oecol* 23: 165-176.
79. Figuerola J, Green AJ (2002) Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biol* 47: 483-494.
80. Lyell C (1832) *Principles of Geology*. John Murray, London UK.
81. Darwin C (1859) *The origin of species*. General Press, Pennsylvania USA.
82. Bondesen P, Kaiser EW (1949) *Hydrobia* (*Potamopyrgus*) *jenkinsi* Smith in Denmark illustrated by its ecology. *Oikos* 1: 252-281.
83. Cadée GC (1988) Levendewadslakjes in bergeend faeces. *Nederl Malacol Vereenig* 243: 443-444.
84. Cadée GC (1994) Eider, shellduck and other predators, the main producers of shellfragments in the Wadden Sea: palaeoecological implications. *Palaeontology* 37: 181-202.
85. Purchon RD (1977) *The Biology of the Mollusca*: International Series of Monographs in Pure and Applied Biology: Division: Zoology (Vol 57). Elsevier Science Limited, Massachusetts, USA. Pg no: 560.
86. Trueman ER (1983) Locomotion in Molluscs. In: Saleuddin ASM, KM Wilbur (eds.). *The Mollusca* (Vol 4). Academic Press Inc., Massachusetts, USA. Pg No: 155-198.
87. Lamoreaux J (2004) Stygobites are more wide-ranging than troglobites. *J Cave Karst Stud* 66: 18-19.
88. Culver DC, Pipan T, Schneider K (2009) Vicariance, dispersal and scale in the aquatic subterranean fauna of karst regions. *Freshwater Biol* 54: 918-929.
89. Culver DC, Sket B (2011) Hotspots of Subterranean Biodiversity in Caves and Wells. *J Cave Karst Stud* 62: 11-17.

90. Culver DC (2012) Mollusks. *Encyclopedia of Caves* (2nd Ed.). In: White WB, Culver DC (eds.). Academic Press, New York. Pg no: 512-517.
91. Osikowski A, Hofman S, Georgiev D, Rysiewska A, Falniowski A (2017) Unique, Ancient Stygobiont Clade of *Hydrobiidae* (Truncatelloidea) in Bulgaria: the Origin of Cave Fauna. *Folia Biol* 65: 79-93.
92. Rysiewska A, Georgiev D, Osikowski A, Hofman S, Falniowski A (2016) *Pontobelgrandiella* Radoman, 1973 (*Caenogastropoda: Hydrobiidae*): a recent invader of subterranean waters. *Journal of Conchology* 42: 1-11.
93. Gittenberger E (1988) Sympatric speciation in snails: a largely neglected model. *Evolution* 42: 826-828.
94. Tauber CA, Tauber MJ (1989) Sympatric speciation in insects: perception and perspective. In: Otte D, Endler JA (eds.). *Speciation and its consequences*. Sinauer Associates Inc., Sunderland (MA), USA. Pg no: 307-344.