Tomáš Ditrich: Ecology of Veliidae and Mesoveliidae (Heteroptera: Gerromorpha) in Central Europe

PhD Thesis by Tomáš Ditrich

External Examiner's Report

The thesis includes 7 papers on ecology, ecophysiology and ecomorphology of Central European Heteroptera: Gerromorpha; 5 published, 1 accepted, 1 submitted; 6 from scientific journals (5 impacted), 1 from proceedings; all with co-authors, all with Tomáš as first author, all in English.

The papers group into sections on Life histories, Cold tolerance and Wing polymorphism, and are interspersed with author's introductions, prefaces and conclusions. The thesis is well organized, formally perfect and reader-friendly. I shall not dwell on enumeration of numerous and often surprising new results and ideas; that is the author's task. Suffice to say, that i regard them as important not only for the gerromorphans in particular and Heteroptera in general, but for all the general entomology. The author combines a time-demanding field studies with those carried in cultures and used both for the experiments and observations, studies under dissecting microscope, and he is well able to generalize his results and to support them by statistical analysis.

The Gerromorpha is a clade especially suitable for any kinds of investigations dependent on complete census of local populations – this is because of life spent mainly in a two-dimensional environment as aptly written by Tomáš in the introduction. This fact jointly with nearly unique way of life of the gerromorphan species on water surface, tendency to form aggregations, ability to colonize ocean marine habitats, accumulation of heavy metals from environment in body tissues, and unique mode of intraspecific ripple-communication have made many of its species popular in research in a variety of branches of biology. It is nowadays a model group for studies such as biomechanics of locomotion, sexual selection, degree of pollution of aquatic biotopes, vibrational communication, and many others. The gerromorphans are really „in" but, nevertheless, Tomáš shows how much is still to be investigated and understood even in well studied Central European fauna. In this respect I should stress the paper on cold tolerance submitted jointly with Vladimír Košťál – it's not only trailblazing and comprehensive but also a first of this kind in the Heteroptera.

Tomáš Ditrich´s research has been carried out in close cooperation with his supervisor, prof. Miroslav Papáček, who also co-authored most of his papers. He is to be thanked for helping Tomáš to find its own path.

I have only very few critical comments and what I am writing in the Appendix is aimed rather to stimulate discussion than to criticize.

Conclusion. The thesis by Tomáš Ditrich is excellent and not only fulfils but exceeds all the requirements called for by the Law and South Bohemian University for awarding the scientific title Doctor of Philosophy (PhD). I ask the dissertation committee to approve the thesis and recommend awarding of the title.

Praha, 2011-01-30

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APPENDIX - COMMENTS, CRITICAL REMARKS AND QUESTIONS

Title

1. Not only species of the Veliidae and Mesoveliidae have been studied but also those of the Gerridae and Hydrometridae. Consequently, the better title would be Ecology of Gerromorpha ... .

General Introduction and Life Histories

2. p. 1 (and elsewhere): The author seems to suggest that most taxa of Gerromorpha are associated with water surface. While this is true for most species, it is highly debatable for clades since many Mesoveliidae, Macroveliidae, Hebridae, Paraphrynoveliidae and Hydrometridae are rather riparial, hygropetric to truly terrestrial. This is true also for many Veliidae and some Gerridae. Can you assess the situation in terms of plesiomorphy and apomorphy?

3. p. 1: The Hebridae are missing in the list of gerromorphan families that live in Europe.

4. p. 3: The statement "all bugs overwinter either in the adult or egg diapause" should be restricted (with caution) only to the temperate Gerromorpha species.

Throughout

5. The term larva is used in introductory parts while nymph in all the papers included. Why? The terms are synonymous but the latter has also a more restricted meaning.

Cold Tolerance

6, p. 33: I have read neither Somme (1989) and Block (1990) but making a mental comparison of true bugs living in tropics and those in temperate and cold zones I fail to see how the latter would be "adapted to the cold environment morphologically (e.g. by body size and wing reduction, extent of melanism)". Taking Heteroptera as a whole, this generalization is not true for clades and species, though it could be valid for conspecific populations. Examples for and against can be easily found, and truly adaptive nature of those supporting the hypothesis could be challenged.

7. p. 34: The authors consider under point (2) whether bet-hedging or low cold tolerance is a plesiomorphic hibernation strategy in *Velia* species. The matter is less clearly explained and less deeply covered than other parts of the thesis. Evolution of present-day areas of species and concomitant ecophysiological changes enabling survival in low temperatures must have been much more complex than to be explainable by a simple march of ancestors northwards.

8. Throughout (incl. Ditrich & Košťál, submitted). The hypothesis on the Mediterranean origin of *Velia* and its impact on the evolution of cold coping strategies have in my opinion one weak point. The winters in the Mediterranean, at least nowadays, are nearly as harsh as in the temperate Europe, and, moreover, the insect inhabiting water surface have to cope (and presumably had have to cope as well) with summer draughts, particularly in streams and pools drying up regularly. Is the adaptation (aptation, exaptation – whatever) to desiccation separable from that of resistance to low temperatures? I presume that nearly nothing would be known on the former.

9. Throughout. It should be worth of attention to discuss why no European Gerromorpha hibernate in larval stage while some species of the Dipsocoromorpha, Nepomorpha, Cimicomorpha and Pentatomomorpha do so (exclusively or including adults as well).

Wing polymorphism

10. p. 75 ff. (a published paper on terrestrial movement of *Velia caprai*) – a comment. There is a distinct parallel between function of macropterous non-flying morph of *V. caprai* to equally non-flying macropterous morph of *Pyrrhocoris apterus*, called "dispersal morph" and investigated in several papers by R. Socha (or Socha & Zemek).

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Review of Ph.D. thesis Ecology of Veliidae and Mesoveliidae (Heteroptera: Gerromorpha) in Central Europe by Tomáš Ditrich

General introduction and introduction to Life histories is a pleasant read, short and intelligible. One family is missing in the list in the last paragraph on page 1. Citations on page 3 follow diverse rules or better no rules, including listing of all three author names, three first author names of a larger team, and only one name accompanied by the abbreviation *et al.* instead of two author names.

The first article published in the Journal of Natural History is a classical study like those that where written tens of years ago and that should continue to be produced. There are some formal errors that should have been corrected by reviewers or editors like unnecessary number of decimal digits in statistical results (last line on page 7) and percentages in tables calculated from less than ten individuals per treatment. Focusing on Figure 2, I have a question [1] how to explain inactivity of bugs in late March, and a recommendation {1} to compute a logistic regression of the data to find the threshold temperature for mass activity.

The second article, although accepted in Entomologica Fennica, seems to need some improvement. Short introduction deals only with *Velia*; information about the two *Gerris* species should be added. Authorships of scientific names (pages 19, 21 and 22) are erroneously written. There is unnecessary precision of geographical coordinates of study sites that obviously included larger areas (pages 21, 22). List of variables in chapter 2.3 Description of statistical analysis is strange, sex ratio is written twice, collecting period is not a variable to analyze but a factor. Comparison of abundance by chi-square in the first paragraph of Results is a unique and not much meaningful method. Sentence on page 26 should be "... relatively high longevity").

Introduction to Cold tolerance chapter should mention more physiological adaptations in the beginning, not just avoiding or tolerating of freezing. The last sentence on page 34 in my copy is not completed, however, I understand what was meant and I appreciate this evolutionary approach. I only regret that I could not see the manuscript D before. Again, small formal errors occur in this manuscript such as wrong usage of authorship of scientific names (page 39). Authors may start to use new valid name for *Drosophila melanogaster*. Logistic analysis of lethal temperature calculates standard error, not deviation (caption of Fig. 3). The term "supercooling capacity" used in caption of Table 1 is not precise. [2] What is the true meaning of this term? Average viability and total number of eggs reported on page 45 would be better replaced by individual species results. Precision of survival calculated to

tenths of percents is unnecessary. Expression of water content in Table 2 is correct but more intuitive water percentage should be added for each species. The data received allow performing multiple regression analysis, e.g. for several factors that may influence SCP. The difference between SCP and LLT in *Microvelia reticulata* is wrong (page 48). The statement that considerable mortality in measured bugs resulted from direct chilling injuries (sensu Lee 2010) is probably wrong. It would require verification at shorter exposure times. Most of the mortality was undoubtedly caused by freezing, and some indirect injury may start to occur. Assumption (page 49) that good survival at zero means lack of indirect chilling injury is wrong (see CryoLetters 19: p. 274). I like the concluding discussion about *Velia* risk-spreading strategy, I would only add a note about a free niche and avoiding competition with other gerromorphans.

There is just opposite term used in the line 2 on page 58 in the introduction to Wing polymorphism (temporary instead of permanent). I appreciate the logical step from observation of wingless bugs in temporal habitats to the discovery of their terrestrial dispersal by means of mark recapture method. The sentence in abstract of article F about commonly shared response is not correct (not present in *Velia*). [3] Is there any evidence for difference in wing polymorphism in males and females of gerromorphan bugs and what is the evolutionary explanation?

Generally I must criticize some formal errors made by the author, such as in zoological nomenclature, in citing literature sources and in presenting numbers in results. He became a teacher and should correct such errors made by students and punish them. Anyway, the set of scientific studies submitted as doctoral dissertation is more than sufficient for awarding the title PhD.

Ceske Budejovice, 21th February 2011

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Ecology of Veliidae and Mesoveliidae (Heteroptera: Gerromorpha) in Central Europe – Ph.D. Thesis by Tomáš Ditrich

External Examiner´s Report by Dr. Berend Aukema, University of Amsterdam, Zoological Museum, Department of Entomoly, Plantage Middenlaan 64, 1018 DH Amsterdam, The Netherlands

Gerromorpha are predatory bugs adapted to the life on the water surface, where they generally spend most of their time. The shore may be used for shelter from enemies, egg depository or overwintering, and the air for flight. Loss of flight by wing reduction or even complete loss of wings is a common phenomenon in Gerromorpha and many species exhibit wing dimorphism or polymorphism and as a consequence los of dispersal power. Dispersal is crucial for species living in unstable or changing environments and has been studied intensively in Gerridae or pondskaters.

This thesis focus on the ecology of three representatives of two other families: the water cricket *Velia caprai* and *Microvelia reticulata*, both of the family Veliidae, and *Mesovelia furcata* of the family Mesoveliidae. All three species are wing dimorphic with either fully winged (macropterous) or wingless (apterous) specimens. Especially life history, overwintering physiology and wing dimorphism are studied.

In the Czech Republic, *Velia caprai* was found to be able to overwinter both as adult and in the egg stage, a possible risk-spreading reproductive strategy, described as "unique" within Gerromorpha and "rare" among insects in general (output A). In output B the same situation was found in Norwegian populations and in both Czech and Norwegian populations adults may even survive two winters. Based on the large climatological differences between the Czech and Norwegian sites it is suggested that populations from all over Europe share this overwintering strategy and life history.

Output C deals with the life history of *Microvelia reticulata* and *Mesovelia furcata*. The first overwinters as adult and *M. furcata* in the egg stage. Field data of nymphs suggest that both species are bivoltine or partly trivoltine in South Bohemia. Laboratory breeding of *M. reticulata*, however, showed that field observations based on the occurrence of young nymphs may be misleading and that the actual number of generations may be lower.

Overwintering strategies of Gerromorpha are evaluated in relation to supercooling and cold tolerance of adults in five species of Gerridae, *Hydrometra stagnorum* (family Hydrometridae), *Microvelia reticulata*, *Velia caprai* and *V. saulii*, and eggs of *V. caprai* (output D). Contrary to the other species examined, the supercooling capacity of adult *V. caprai* (and *V. saulii*) is not sufficient to survive cold winters, but the eggs are winter-proof. The overwintering strategy of *V. caprai* is classified as flexible (plastic, risk-spreading) with overwintering of adults and/or eggs, in contrast to a fixed (strictly programmed) strategy with overwintering of adults only as found in the other examined species.

Spatial distribution and wing-morph frequencies of Gerromorpha in relation to environmental characteristics were established in field populations in the Czech Republic (output E). *Velia caprai* was found on 20 sites and showed a preference for shaded habitats with flowing water, but only one of the 148 specimens caught was macropterous. *M. reticulata* was present on one site only and all four specimens collected were apterous.

Output F treats the effect of population density (crowding) on the development of nymphs of *Mesovelia furcata*, *Microvelia reticulata* and *Velia caprai* with respect to development rate, wing development, body size and rate of oogenesis. The only commonly shared response appeared to be an increase in development rate and body size at high densities. Wing-morph was only affected significantly in *M. furcata*: no macropters among individually reared nymps, a few (5%) at low densities and a significant number (16%) at high densities No long-winged specimens developed in *M. reticulata* and only a few specimens (4%) at high densities in *V. caprai*.

Further experiments with factors that generally favour the development of macropterous morphs in Gerromorpha, i.e. temperature, photoperiod or substrate, were not successful in the case of *Velia caprai* (output G). For dispersal over short distances, however, this species does not depend on winged specimens alone. In mesocosm and mark-recapture experiments in the field they were able to walk on land and cross distances of several tens of meters. In this way apterous individuals can compensate for downstream drift and may even be able to colonize new pools and ditches.

This study clearly reveals the differences in ecology between the well-studied Gerridae and representatives of Mesoveliidae and Veliidae. Whereas Gerridae fly to disperse, to escape adverse conditions, and move between overwintering and reproducing sites, *Velia caprai*

can bridge short distances by walking. The life strategy of *V. caprai* with overwintering of both adults and eggs, is more flexible than in Gerridae with overwintering of adults only. The longer lifespan found in *V. caprai* is exceptional in Gerromorpha as well.

Nymphs of *Microvelia reticulata* and *Mesovelia furcata* show a different reaction towards crowding: whereas nymphs of Gerridae grow faster and produce smaller adults at high densities (a trade-off between developmental rate and body size), those of *M. reticulata* and *M. furcata* grow faster and produce larger adults (a trade-off between developmental rate/body-size and sexual maturation).

This thesis is the result of a balanced combination of field work and experiments, both in the laboratory and in the field, a perfect design! More species - for instance of the families Hebridae and Hydrometridae - should be studied in a similar way to get a more complete picture of the ecology of semiaquatic bugs.

Based on this thesis I recommend to award the Ph.D. title to Tomáš Ditrich.

Renkum, 21 February 2011

Dr. Berend Aukema