

Studies on the amphipod genus *Metopa* (Stenothoidae):

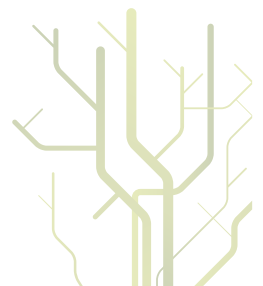
Taxonomy, Ecology, Phylogeny



Anne Helene Solberg Tandberg

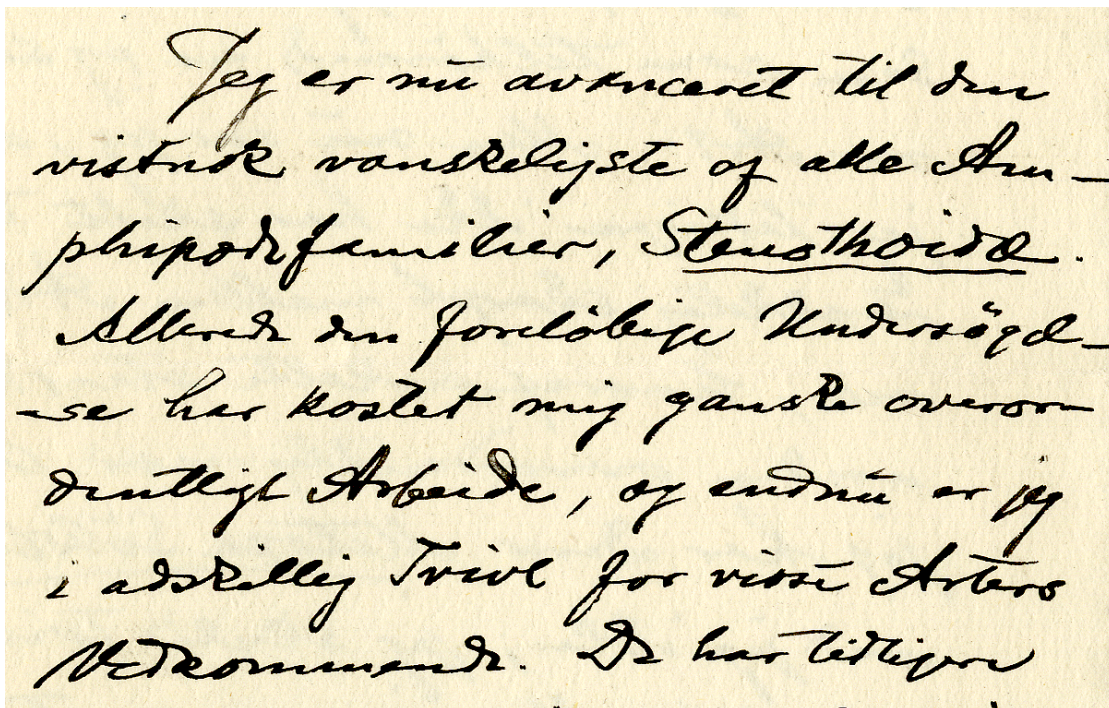
A dissertation for the degree of Philosophiae Doctor

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**Studies on the amphipod genus *Metopa*
(Stenothoidae):
taxonomy, ecology, phylogeny**

Anne Helene S. Tandberg



Jeg er nu avanceret til den
vistnok vanskeligste of alle Am-
phipodfamilier, Stenothoidae.
Allerede den foreløbige Undersøgelse
har kostet mig ganske overordentligt
Arbejde, og endnu er jeg
i adskillig Tvivl for visse Arters
Bestemmelse. De har tidligere

Figure 1: Facsimile of letter from G.O. Sars to Sparre-Schneider Oct 15th, 1891

Translation:

I have now advanced to the supposedly most difficult of all Amphipod-families, *Stenothoidae*. Already the preliminary examination has cost me extremely much work, and I am still in considerable doubt concerning some of the species. (...)

Preludium

This thesis is the result of several years of studies on the taxonomy and biology of the amphipod genus *Metopa*. The funding was kindly provided by the Norwegian Research Council, through a grant in the programme "Havet og Kysten".

The driving force behind this thesis has been to elucidate taxonomy and phylogeny of *Metopa*, and thus also make a contribution to the phylogeny of the family Stenothoidae. The genus *Metopa* has long been considered polyphyletic (Barnard and Karaman 1991b), and it was thus an interesting and important group to study.

Early in the process it became clear that it would not be possible to collect enough fresh material of enough described species of *Metopa* for a thorough molecular study of the genus to be carried out. The original plans were, of course, to make both molecular and morphological phylogenies, and then to find the common denominator of these. Given the limited access to fresh material, and with much of the historic material having at one time or another been stored in formaldehyde, I decided to go for a morphological approach only. I have visited the collections of the Zoological Museum of Copenhagen, the National Museum of Natural History of the United States (Smithsonian) and the Natural History Museum of the University of Oslo. These three museums cover in their type-collections approximately 40% of the valid *Metopa* species. No new species have been described as part of this thesis, but introductory examinations of material from deeper parts (deeper than 1500m) of the Norwegian Sea and from Greenland have indicated several new species that will be described outside of this thesis. (Tandberg et al, in *early prep*).

The study has been limited to what was considered *Metopa* at the start of this study, with the addition of the species that have been described as *Metopa* during the process of writing this thesis (Krapp-Schickel 2009). For the phylogenetic analysis (Paper 6) we have added the genus *Stenula*; this is discussed further in that paper and in the chapter on Phylogenetic analysis.

Why has it been so important that an amphipod genus - albeit consisting of a fairly large number of described species - should be examined for so many years? Many answers can be given here, some of these will be elucidated below. The diversity of life is still very little known to us, figures range between 1/5 and 1/10 of the possible biodiversity of the world being even rudimentarily described, depending of what number of species we think are present in the world (for a discussion on this, see Mora et al. (2011) and references therein). Knowing the biodiversity is the minimum requirement for being able to know what biodiversity-losses we suffer, and hopefully knowing a bit more about the different taxa will enable us to stop (or at least slow down) the present rate of losses. Monitoring possible effects of changes (both climate- and other) on ecosystems also requires knowledge of the taxa being part of the systems. As mentioned later, *Metopa* is one of the very few genera of Crustacea that is represented in the Norwegian Red List for Species with more than one taxon, indicating that this is a group of organisms we know

very little about. Last, but not least, honouring the natural curiosity about the world around us trying to understand one group of life must be admitted as one of the major driving forces for me. The puzzle of trying to find out how the evolution of this group might have happened, to discover minute details of beauty in these little creatures, and finding out new things has for me been a true joy.

Acknowledgements

Nobody ever said writing a PhD thesis would be easy. In fact, most people told me it would be four years of hard work, a continuously bad consciousness and a feeling of always being inadequate and mostly stupid. Add some extra years to that timeframe, and the description fits my "PhD-years" to a large degree.

There have, however, also been many moments when I have seen the possibility that I might manage to finish, and moments when understanding a little more have brightened the week, not to say month. Most of the time I have felt the luckiest person on earth being allowed to spend my days learning more and digging deeper into the problems I have wanted to understand more about. These moments would never have come if it were not for the unfailing support and encouragement from my mentor Wim Vader, and from my team of supervisors; Jørgen Berge, Traudl Krapp-Schickel and Willy Hemmingsen. You have opened your homes, offices and ears for me and continued to push all the times I have wanted to stop. Wim introduced me to taxonomy and not least to amphipods when he supervised my master-thesis many years ago, and I now see that this love for crustaceans might be more than a short fling also for me. Wim, Jørgen and Traudl - most of all thank you for being friends in addition to supervisors and teachers! Willy - thank you for never forgetting to remind me that your officedoor was open whenever I should need it, and for continuing to ask for updates.

Christoffer Schander and Fredrik Pleijel saw that our findings in Hinlopen and Rjipfjorden could become a short note, and pushed me to write it. Fredrik also introduced me to macrophotography of benthic animals, and took the beautiful pictures of *Metopa alderii* in paper 4 (my bank-account is not quite as happy as I am with this wonderful photographic world and its technical necessities). For photographs and inspiration to use photographic documentation my thanks also go to Geir Johnsen, and to Karsten Sund at the NHM Oslo, who photographed all the Oslo type material for me (his pictures do not really come to their right in Paper 3, and I am sorry for that) so I could pick the specimens to pieces and mount them on microscopic slides.

Tromsø Museum - Universitetsmuseet has welcomed me and included me during my "official years" as a PhD student, as well as the time I spent as a master student earlier. Being part of a multidisciplinary community of dedicated scientists and communicators has been inspirational, and being part of the museum has given me a much welcomed opportunity to vent all my needs for sharing science with others - thank you! A special thank goes to the Zoological department/Section for Natural History, who welcomed me patiently and stood up for me whenever I needed support. Ellen and Astrid - your smiling support has helped me more than you would know! Being able to visit UNIS almost whenever I felt the need, and to stay for long periods, granted both much of the fieldwork I needed and wanted, and a workplace I very much needed. The Norwegian Research Fund (NFR) and the Programme "Havet og Kysten" provided the money for this PhD-project: "Hurrah!", and thank you!

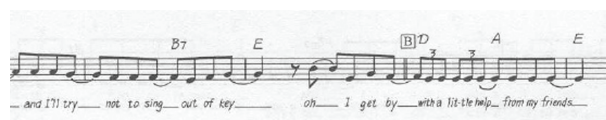
My "other workplace" - IRIS - gave me leave for several years to pursue my dream of Amphipods - I don't think many other employers would have done the same. My newest employer Havforskningssinstituttet has been much more patient and understanding than they need be with an employee that should have finished her PhD before starting the new project.

My visit to Zoologisk Museum in Copenhagen was funded through a grant from Synthesys. The time in Copenhagen became both productive and friendly, thanks to Jørgen Olesen and his staff at 2. afdeling, and to Ole, who provided coffee and discussions every day of my stay. I was very nervous before going to my two weeks visit to the NMNH (Smithsonian) in Washington DC. I should not have wasted energy being nervous had I known beforehand how welcoming and helpful William Moser and his staff at Invertebrates would be, and how well Kelly would look after me when I was in town. My many weeks in the attic at Tøyen at the Natural History Museum in Oslo would never have been possible if not Åse Wilhelmsen and Lutz Bachman had welcomed me and given me full access to all the type specimens from Sars and Boeck.

The thing I have understood more than anything during these last years, is how important friends are. The "PhD-group" at the museum has been a daily support for me during the whole PhD-time - both while having an office at the museum and after. Especially the "Extended Phylogeny-group" - with our montly journal-clubs and the scientific support and "blow-out sessions" when things did not follow the plans. Kirstin Janssen gave much of her time to help me trying to understand molecular methods, and she sequenced and analyzed my sampled amphipods patiently. Jesper has always read whatever I have tried to formulate, and has helped to put my fledging thoughts into shape. Cédric is a true friend who always tells me his thoughts - and is never afraid of being honest when I need correction.

Outside of my field of science have been all my friends who have suffered my many talks about amphipods, science in general, and who have wanted to share in life outside of biology. My friends in Tromsø, Bergen, Stavanger, Longyearbyen, Oslo and Trondheim: I will not promise to stop talking about amphipods, but I will try to talk about other things as well. Thank you for taking my head away from science ever so often! To the university choir mimas - thank you for letting me be part of making music!

To my family: thank you for supporting me (both with love and money). Håvard: thank you for "letting me" be the big sister long enough to submit before you. Tormod: thank you for always staying calm whenever I did not, and for always telling me I could finish this.



List of Papers

Paper 1: Tandberg, A.H.S. and Vader, W. (2009) A redescription of *Metopa* species (Amphipoda, Stenothoidae) based on the type material. 1. Zoological Museum, Copenhagen (ZMUC). *Zootaxa*, 2093:1-36.

This paper deals with the types of *Metopa* from Copenhagen: *M. clypeata*, *M. glacialis*, *M. groenlandica* and *M. abyssalis*. The paper also discusses the mandible palp as a character and includes a historic overview of the genus *Metopa*.

Paper 2: Tandberg, A.H.S. (2009) A redescription of *Metopa* species (Amphipoda, Stenothoidae) based on the type material. 2. The United States National Museum of Natural History (NMNH). *Zootaxa*, 2309:43-68.

This paper deals with the types of *Metopa* in the collections of the Smithsonian: *M. spinicoxa* and *M. stelleri*. It also includes redescrptions of *M. dawsoni*, *M. cristata* and *M. majuscula*, as these species are represented in the collections with specimens identified by the original authors.

Paper 3: Tandberg, A.H.S. (2010) A redescription of *Metopa* species (Amphipoda, Stenothoidae) based on the type material. 2. The Natural History Museum Oslo (NHM). *Zootaxa*, 2465:1-94.

This paper deals with the types of *Metopa* in the collections of the Natural History Museum in Oslo; this museum houses the types from Sars and Boeck. Altogether 14 species are redescribed in this paper, including 11 from Sars and 2 from Boeck. The paper also includes a list of species present in the Oslo type collections originally described as *Metopa* and later moved to other genera.

Paper 4: Tandberg, A.H.S., Schander, C. and Pleijel, F. (2010) First record of the association between the amphipod *Metopa alderii* and the bivalve *Musculus*. *Marine Biodiversity Records*, 3, e5 doi:10.1017/S1755267209991102

This short note concerns the findings of *Metopa alderii* inside the mollusks *Musculus discors* and *Musculus niger* collected north of Spitsbergen. This both presented a new northerly record for *M. alderii* and new information on its ecology.

Paper 5: Tandberg, A.H.S., Vader, W. and Berge, J. (2010) *Metopa glacialis*: an analy-

sis of its ecology and its association with *Musculus discors*. Polar Biology, 33:1407-1418.

This paper deals with the association between *Metopa glacialis* and the mollusk *Musculus discors*. The material for the study is from Spitsbergen, and included samples from 279 *M. discors*. A discussion of the possible life-history strategies that can be supported by the material concluded in two opposing possibilities: multiple broods during one year, or 3 or more seasons of single broods. Extended parental care seems to be a part of either strategy.

Paper 6: Tandberg, A.H.S. and Vader, W. Phylogenetic analysis of the stenothoid genera *Metopa* and *Stenula* (Crustacea, Amphipoda, Stenothoidae). Manuscript.

This manuscript gives a phylogenetic analysis based on the morphology on the genera *Metopa* and *Stenula*. 45 species are included and the result is two large groups of species (A and B) both containing *Metopa* and *Stenula* species, with the type species of both in group B. The manuscript does not formally name these two groups, mainly because not all nominal species could be included in the analysis, while a formal naming will have very extensive nomenclatorial consequences.

Errata

Paper 1 (Tandberg and Vader 2009)

In the synonymy-list for *Metopa clypeata* (p 3, line 2 of the list) the synonym *Leucothoe norvegica* Liljeborg, 1850 should be removed.

Abstract

The Amphipod-genus *Metopa* is a relatively large genus, with currently 55 accepted species. This PhD thesis consists of redescrptions of 23 of these species based on type-specimens or specimens collected and identified by the original authors; this has been done to create consistent descriptions that could form a basis for a phylogenetic analysis of *Metopa*. For some species Scanning Electron Microscopy has been used to look for characters that have been overlooked by the original authors. The redescrptions are presented in 3 papers (Papers 1-3), with a phylogenetic analysis of 37 *Metopa* species (mostly based on personal examinations, but 6 based on literature-information) together with 6 *Stenula* species (partly based on literature, but most from examinations performed by Dr. Traudl Krapp-Schickel) presented in a manuscript (Paper 6). The result of the phylogenetic analysis is two clear clades (A and B), both including species from both original genera. This result could suggest a thorough change in stenothoid systematics, with the possible synonymization of *Stenula* into the older *Metopa* and erection of one or more new genera to include the species of clade A, but we have argued against doing this before further investigations have been undertaken. The stability of the resulting phylogeny is discussed, and in our opinion further studies are necessary to strengthen the conclusions reached here, before we formally make the necessarily very extensive nomenclatorial changes. However, the indications that *Metopa* and *Stenula* are paraphyletic are strong.

Two papers (Papers 4-5) examine the ecology of *Metopa* species associated with mollusks. Paper 4 is a short note about findings of *Metopa alderii* inside the mussel *Musculus* spp., whereas Paper 5 is a more thorough discussion on the possible life history strategies for *Metopa glacialis* in its well known association with the mussel *Musculus discors* based on data collected by Svalbard. We show the presence of more than one broods in several examined mussels, and from the brood sizes and cohort compositions we suggest two possible scenarios: 3 or more seasons of single broods and parental care over more than 1 year after hatching, or multiple broods in one season and extended parental care.

The introductory synthesis to the papers gives a short discussion of the papers, in addition to a historical introduction to both taxonomy and the amphipod-genus *Metopa*. A complete list of taxa that at some time have been included in *Metopa* is presented, this includes synonymies and references to the auctors and different authors who have moved the different taxa. There is also a table with biogeographical information about the genus, and the ecology of *Metopa* is discussed. A short discussion on molecular methods and the possible ways to ensure more data for a better phylogenetic analysis is also included.

Introduction

Biology rests on the basis of taxonomy. Without knowing exactly which taxon we work with/on, much of the information we collect and find out and end up with has limited value. Taxonomy is also the "oldest" part of biology: naming and structuring life around us came before the science of biology. In our western mythology Adam got the naming of plants and animals as his first task - in general most cultures have a quite sophisticated system of naming for the plants and animals they come in contact with. Aristotle classified all animals into a ladder of organization of Life in "A History of Animals"; this may be considered a first attempt at creating a scientific framework for the world we live in.

Even during the first decades of "modern" biology taxonomy and faunistics and floristics were at the basis - the Naturalist described and systematicised what he saw. These works are often the basis of what we work with today - in Scandinavian crustacean taxonomy some of the most prominent early names include Axel Boeck, Georg O. Sars (and his father Michael Sars) and Henrik Krøyer. Of early naturalists in Scandinavia in general are often also counted the clergymen Gunnerus and Fabricius, who both did much to initiate the natural sciences but whose work today no longer is quite so visible. Then the specialized scientific journeys and multiyear expeditions began - the most famous today is perhaps the Beagle-expedition in which Darwin participated, but of more importance to the study of amphipods were perhaps the Challenger expedition (Stebbing 1888) and for the arctic realm the Norwegian North-Atlantic Expeditions (1876-1878) (Sars 1885). For the first scientific knowledge of *Metopa*, the trip of the vessel *La Recherche* (1834-1840) was of importance, even though the results were poorly published (Knutsen and Posti 2002). Several of these expeditions mapped for the first time the oceans as more than vast blue patches on the map, with examinations of both oceanography and fauna and flora (an excellent example for this is Mohn and Wille (1882) and the subsequent volumes of the Norwegian North-Atlantic Expedition). Today's taxonomists are much more specialized and work on much smaller subgroups than what the earlier scientists worked with (Pliny and Linnaeus started out with "Life"), and newcomers like me often start with a single genus.

The science of taxonomy is today considered the "practical" work of discovering and describing taxa, to classify these taxa and to give them a name that follows the accepted codes (Bakken and Stensøien 2009). Systematics is very close to this discipline, but if one separates systematics and taxonomy (in Norway these two combined are often named "biosystematics" (Norges Forskningsråd 2005)), systematics considers work with phylogenies, evolutionary theories, speciation/species delimitation and phylogeography

(Bakken and Stensøien 2009). The definition of "species" (the most common taxon-level to consider for both taxonomy and systematics) thus becomes central, this is also reflected in the long and sometimes heated debates this concept has spurred not only during the last years (see ex. Ghiselin 2004; Hey 2006; Naomi 2011), but in effect since Darwin (1859), who wrote: 'Nor shall I here discuss the various definitions which have been given to the term species. No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species.' The biological species concept that Mayr (1942) introduced is probably the definition most biology-students have been faced with, and that most non-systematicists still use. The basis of this is that a species is "a group of interbreeding natural populations, which is reproductively isolated from other such groups" (Mayr 1942). This has in the later years been developed into a species-concept where the species is an evolutionary lineage (Mayden 1997; Queiroz, K. de 2007), but for many scientists there are still problems with this concept. These are mainly that there is no separation between groups (taxa) and rank (categories) (Donoghue 1985), but also the possibly more obvious that for many species there is no good way to check for reproductive isolation, whereas some reproductive isolated units consist of several known "species" (many examples of this are given from botany, e.g. *Quercus* (see Donoghue (1985) and references therein)). As a possible answer to these problems the phylogenetic species concept has been proposed (Donoghue 1985; Cracraft 1983, 1987; Mishler and Brandon 1987). The basis of this concept is that a species is a monophyletic unit, and that the species is defined by its (unique set of) derived (apomorphic) characters. A practical result of using a phylogenetic species concept instead of a biological species concept is that reproductive isolation is no longer examined (but may very well still be a trait), and ranks like subspecies (used within a biological species concept) are no longer necessary, but might result in becoming two different phylogenetic species (given apomorphic characters for each of the phylogenetic species).

The different taxa (groups, eg. Crustacea, Amphipoda or *Metopa*) have since Linnaeus (1758) been hierarchically organized in categories (for animals this goes from (most inclusive) Kingdom [Animalia] to (least inclusive) species [e.g. *Metopa clypeata*]), this system is regulated by the International Commission on Zoological Nomenclature (1999). This system is presently under discussion, and some scientists have proposed a new code, the PhyloCode (Cantino and de Queiroz 2010). Their argument against the 'classical' Linnean (hierarchical) system is the strict hierarchy it necessitates; even if a family only consists of one genus with only one species, all these categories have to be constructed and defined, using the strict set of rules in International Commission on Zoological Nomenclature (1999). The basis of the argument for PhyloCode rests on the protest that such a strict hierarchical system does not fully accept the fact that from accepting the theory of evolution, by definition all taxa must change over time. The claim is that that this is not clear enough in the hierarchical system, and rather than considering a set hierarchy of taxa we should consider the phylogenetic trees, and from these discuss the taxon-groups (clades) that are necessary to discuss - without considering their rank. Some of the clades under discussion could then easily be what under Linnean systematics

is a given category, but not necessarily. The many name-changes often resulting from new analyses of different taxa under the Linnean system (examples of this can be seen in Table 2) would not necessarily come if using PhyloCode, as the name is suggested to have no phylogenetic information. Some of the proponents of the PhyloCode suggest to stop using "species" altogether, and start using "Least Inclusive Taxonomic Unit" (LITU) - a concept that will reflect the ever ongoing puzzle-solving of a living science. It will possibly also reflect the intrinsic uncertainty for many systematists whether their "species" really is reproductively isolated. This is in many ways an extreme representation of the phylogenetic species concept, but not all users of a phylogenetic species concept will use LITU.

I have, as most other biologists, been taught the biological species concept first. It is therefore my first thought when asked "What is a species?". I do, however, see many of the problems that have been proposed for the biological species concept, and I must admit I am sympathetic to many of the proposals of the phylogenetic species concept. For many of the problems systematics face today I also think PhyloCode might have many good suggestions, if we have stable phylogenies for the groups we discuss. For this thesis, however, I have chosen to stay with the hierarchical Linnean system, as the regulations still support this (International Commission on Zoological Nomenclature 1999) and as the results of a hierarchical taxonomy combined with a phylogenetic analysis still can be utilized by and transferred to phylogenetic systematics with relative ease. I have therefore used all the "normal" grades of genus and family and species throughout this thesis.

Main Objectives

The main objective of this thesis is to study the phylogeny of the amphipod genus *Metopa*. First, a re-description of the morphology of 23 species was performed to give consistent descriptions that can form a basis for a morphologically based phylogeny. Second, the ecology of *Metopa glacialis* is studied closely, with resulting information about life history strategies and feeding. Indications that there might be similarities to these strategies in *Metopa alderii* are also presented. Third, a phylogeny of the two genera *Metopa* and *Stenula* based on morphology is presented; this gives two distinct clades (A and B), both including species from both genera. Finally, a discussion on how this analysis can be strengthened is included.

Metopa

The genus *Metopa* - the subject of this thesis - consists of small gammarid amphipods (adult size ranging from 2-8mm) in the family Stenothoidae. Figure 2 shows a photograph of a typical *Metopa*, with the morphological features of a large triangular coxa 4 and prominent gnathopods 2 clearly visible. As is shown in Fig 3, the records of *Metopa* are mainly from northern waters: mostly from the arctic and boreal; in the few cases where they have been found further south, there is a connection to cold water currents or deep waters (ex: *Metopa dawsoni* from the coast of (California), *Metopa majuscula* from the Japan sea and *Metopa spinicoxa* from the Kurile islands). The one exception to this is *Metopa torbeni* Krapp-Schickel, 2009; there is still a certain uncertainty about the generic placement of this taxon (Krapp-Schickel, pers. comm.).



Figure 2: Live *Metopa boeckii* Sars, 1892 sampled in Svalbard waters August 2005. This specimen is approximately 4 mm long.

Most of the species we know something about ecologically are found on hard bottoms,

and a few species are known to associate with other animals such as bivalves (this includes *Metopa glacialis* (Just 1983; Vader and Beehler 1983; Tandberg and Vader 2009; Tandberg et al. 2010a), *Metopa groenlandica* (Stephensen 1936) and *Metopa alderii* (Tandberg et al. 2010b)), hydromedusae (*Metopa alderii* (Vader 1972)) hydroids (several species including *Metopa pusilla*, pers obs) and sea anemones (*Metopa solsbergi* (Vader 1972)). It must, however, be noted that for the majority of species we have no other ecological information than where they have been collected, and this has for many species been only once or twice including the original sampling that lead to the initial description. Possible exceptions are the species *Metopa glacialis* and *M. pusilla*, and to a certain degree *M. alderii*, that have been sampled extensively compared to the rest of the genus.



Figure 3: *Metopa* recordings.

Zoogeographic region	spp present	<i>Metopa</i> sp
North of Siberia	13 (17?)	<i>Metopa alderii</i> , <i>Metopa clypeata</i> , <i>Metopa glacialis</i> , <i>Metopa gurjanovae</i> , <i>Metopa leptocarpa</i> , <i>Metopa longicornis</i> , <i>Metopa nordmanni</i> , <i>Metopa robusta</i> , <i>Metopa shoemakeri</i> , <i>Metopa spitzbergensis</i> , <i>Metopa submajuscula</i> , <i>Metopa propinqua</i> , <i>Metopa wiesei</i> , ? <i>Metopa bulychevae</i> , ? <i>Metopa kobjakovae</i> , ? <i>Metopa mirifica</i> , ? <i>Metopa timonovi</i>
Bering Sea	10	(<i>Metopa beringiensis</i>), <i>Metopa colliei</i> , <i>Metopa derjugini</i> , <i>Metopa layi</i> , <i>Metopa majuscula</i> , <i>Metopa norvegica</i> , <i>Metopa spitzbergensis</i> , <i>Metopa submajuscula</i> , <i>Metopa ushakovi</i> , <i>Metopa wiesei</i>
North East Atlantic	25	<i>Metopa abyssalis</i> , <i>Metopa aequicornis</i> , <i>Metopa affinis</i> , <i>Metopa alderii</i> , <i>Metopa boeckii</i> , <i>Metopa borealis</i> , <i>Metopa bruzelii</i> , <i>Metopa clypeata</i> , <i>Metopa glacialis</i> , <i>Metopa groenlandica</i> , <i>Metopa hearni</i> , <i>Metopa invalida</i> , <i>Metopa latimana</i> , <i>Metopa leptocarpa</i> , <i>Metopa longicornis</i> , <i>Metopa norvegica</i> , <i>Metopa palmata</i> , <i>Metopa propinqua</i> , <i>Metopa pusilla</i> , <i>Metopa quadrangula</i> , <i>Metopa robusta</i> , <i>Metopa sinuata</i> , <i>Metopa solsbergi</i> , <i>Metopa spitzbergensis</i> , <i>Metopa tenuimana</i>
North West Atlantic	22	<i>Metopa abyssalis</i> , <i>Metopa alderii</i> , <i>Metopa boeckii</i> , <i>Metopa borealis</i> , <i>Metopa bruzelii</i> , <i>Metopa clypeata</i> , <i>Metopa glacialis</i> , <i>Metopa groenlandica</i> , <i>Metopa hearni</i> , <i>Metopa invalida</i> , <i>Metopa latimana</i> , <i>Metopa leptocarpa</i> , <i>Metopa longicornis</i> , <i>Metopa longirama</i> , <i>Metopa nordmanni</i> , <i>Metopa norvegica</i> , <i>Metopa pusilla</i> , <i>Metopa propinqua</i> , <i>Metopa robusta</i> , <i>Metopa sinuata</i> , <i>Metopa solsbergi</i> , <i>Metopa tenuimana</i>

North of Canada/ Alaska	9	<i>Metopa boeckii</i> , <i>Metopa clypeata</i> , <i>Metopa glacialis</i> , <i>Metopa leptocarpa</i> , <i>Metopa longicornis</i> , <i>Metopa propinqua</i> , <i>Metopa robusta</i> , <i>Metopa spinicoxa</i> , <i>Metopa tenuimana</i>
Pacific Ocean	13 (14)	<i>Metopa angustimana</i> , <i>Metopa cistella</i> , <i>Metopa cristata</i> , <i>Metopa dawsoni</i> , <i>Metopa eupraxiae</i> , <i>Metopa exigua</i> , <i>Metopa glacialis</i> , <i>Metopa japonica</i> , <i>Metopa koreana</i> , <i>Metopa majuscula</i> , <i>Metopa samsiluna</i> , (<i>Metopa stelleri</i>), <i>Metopa spitzbergensis</i>
Other areas	1	<i>Metopa torbeni</i> (Indian Ocean)

Table 1: Zoogeographic overview of *Metopa*

As can be seen both in fig 3 and in table 1, the colder waters and northerly latitudes are overrepresented habitats/finding places for *Metopa*. If we split the Pacific Ocean into east ("American side") and west ("Asian side"), the west has 11 species represented, while the east has 3. The lack of findings both north of Siberia, north of Canada/Alaska and in the Pacific (both east and west) might be due to the smaller amounts of sampling that has occurred there, combined with a probable sorting of Stenothoidae or *Metopa* to bulk from many of the collections that have been undertaken in these regions. Also, for much of the material from the east Pacific, there might be a lag in the registrations and recordings due to the fact that other scientists work on the material (or plan to work on it and keep it on safe shelves in their labs). As this material has not been worked up, it has been impossible to include it in this work. It is striking that all of the latest published species for *Metopa* have been from these more "inaccessible" areas (Tzvetkova and Golikov 1990; Krapp-Schickel 2009). Material from the east Pacific (Oregon to north of Alaska) has been collected, but is awaiting proper examination.

As noted earlier, *Metopa torbeni* seems to live in a much differing water-mass from all other *Metopa* - in that the Indian Ocean is much warmer than the Arctic/Boreal water masses the genus normally occurs in. This species needs further study, if and when more material will be available.

The present Norwegian red list chapter for Crustacea (Oug et al. 2010) has 38 amphipod species mentioned. Of these, 6 species are *Metopa*. All *Metopa*-species are listed through the category DD (Data Deficiency), and include *Metopa affinis*, *M. invalida*, *M. leptocarpa*, *M. longicornis*, *M. palmata* and *M. propinqua*, all species originally described by Sars, and since then very seldom, or not at all, found again. Discovering more about these species (such as the ecology, the distribution today, populations etc) would help removing them from the DD-category and hopefully out of the red list. Discovering

more about species will of course also be good for finding indicators for nature types or habitats that should be protected.

History

The systematics of Amphipoda started very sparingly with Linnaeus (1758) who described scientifically *Cancer pulex* L. 1758 (literally "flea crab") and *Cancer locusta* L. 1758 ("grasshopper crab") with descriptions that could have fit almost any species we today recognize as amphipods. Leach (1814) established the amphipod family Gammaridae based on *Cancer Gammarus* (Fabricius, 1775) (Krapp-Schickel 2009), and since that time, several carcinologists have worked on refining this system, both making it more comprehensive and attempting to better its reflection of the phylogeny of the Amphipoda. Today the amphipods count approximately 9300 species (Vader 2005).

Even though Amphipoda is easily shown to be a monophyletic taxon using the structure and arrangement of the uropoda as the defining synapomorphy (Browne et al. 2007), it has proven extremely difficult to resolve the internal phylogeny of the taxon, and since Barnard and Karaman (1991a) many researchers have resigned to using an alphabetical listing of the families as a way around this. Bulycheva (1957) was the first to introduce superfamilies, when she erected Talitroidea, and this phylogenetic work has during many years been followed up by Bousfield in his many works (see eg. Bousfield 1977, 1978, 1983; Bousfield and Shih 1994), even though the highest level phylogeny of the Amphipoda remained untouched. The last decade has given some interesting indications that the traditional four suborders of the Amphipoda (Caprellidea, Gammaridea, Hyperiidea and Ingolfiellidea) should be reduced to three with the Caprellidae now placed as a gammaroid family (Myers and Lowry 2003). Using molecular methods either exclusively or jointly with morphological methods Englisch et al. (2003); Serejo (2004); Lörz and Held (2004); Davolos and Maclean (2005); Macdonald et al. (2005) and Browne et al. (2007) have produced phylogenies for parts of the Amphipoda.

The history of the amphipod genus *Metopa* is schematically represented in figure 4, with the major events being: A) Krøyer (1842) described the two species *Leucothoe clypeata* and *L. glacialis*, Liljeborg (1850) described *Leucothoe norvegica*. B) Sp.Bate (1862) described *Montagua alderii* and Goës (1866) described *Montagua bruzelii* while *Leucothoe clypeata*, *L. glacialis* and *L. norvegica* were moved to the genus *Montagua* C) Boeck (1871b) claimed *Montagua* to be synonymous with the genus *Stenothoe* (since the diagnosis for *Montagua* and *Stenothoe* were both without a mandibular palp) D) Boeck (1871b) created the new genus *Metopa* to contain the *Montagua* species with a mandible palp, and moved *Montagua clypeata*, *M. glacialis*, *M. norvegica*, *M. alderii* and *M. bruzelii* from *Montagua* (*Stenothoe*) to his new genus, while he also described 5 new species. The history of *Metopa* is described more extensively in Paper 1 (pages 2-3).

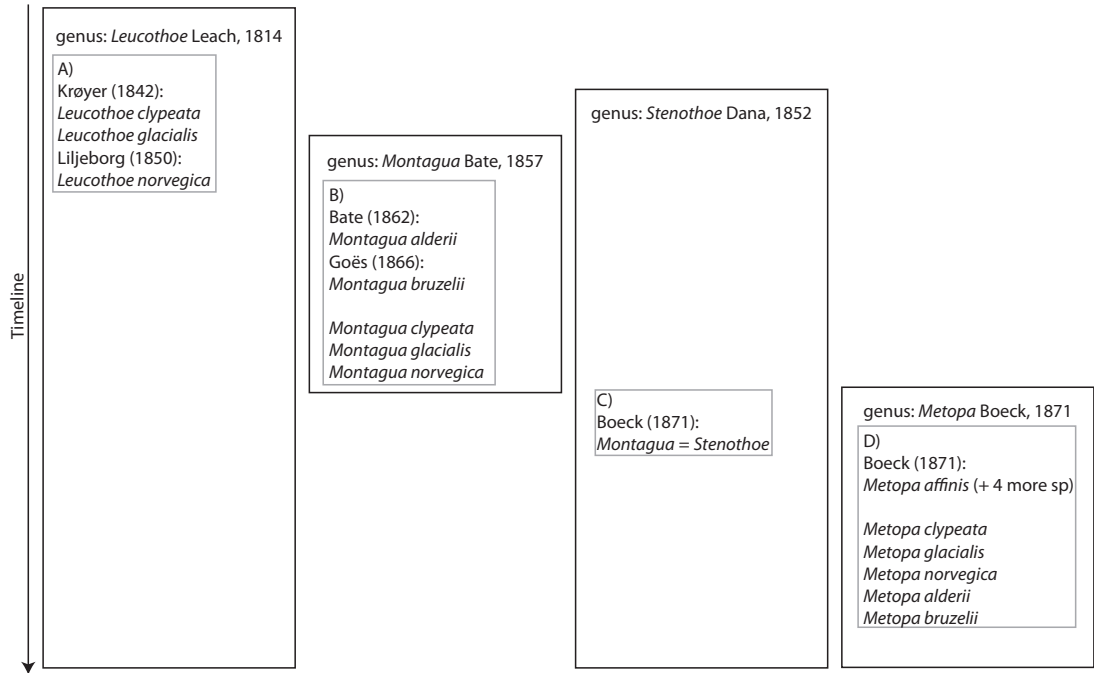


Figure 4: The systematic history of the early species in the genus *Metopa*: A) Krøyer placed in 1842 and Lilljeborg in 1850 their new species in *Leucothoe*. B) these were moved to *Montagua* in 1862 by Bate when he described *Montagua alderii*. C) In 1871 Boeck synonymized *Montagua* with *Stenothoe* D) at the same time he erected the genus *Metopa* for the species with a mandibular palp earlier found in *Montagua*.

Altogether 75 species have at some time been described as *Metopa*; a chronological listing with the present names and a list of synonyms is presented in table 2. At the start of this thesis 52 valid *Metopa* were acknowledged, more recently Krapp-Schickel (2009) has presented 3 more (*Metopa eupraxiae*, *M. exigua* and *M. torbeni*), making a total of 55 valid species (before the phylogenetic analysis presented below).

Original description author/year	original name	valid name	citation for valid name	synonyms (author)	exam. spec.
Krøyer 1842	<i>Leucothoe clypeata</i>	<i>Metopa clypeata</i>	Boeck (1871b)	<i>Montagua clypeata</i> (Krøyer) (Goës, 1866), ? <i>Metopa beringiensis</i> Oldevig, 1959	X
Krøyer 1842	<i>Leucothoe glacialis</i>	<i>Metopa glacialis</i>	Boeck (1871b)	<i>Proboloides glacialis</i> (Krøyer) (Stebbing, 1906), ? <i>Metopa cariana</i> Gurjanova, 1929	X
Liljeborg 1850	<i>Leucothoe norvegica</i>	<i>Metopa norvegica</i>	Boeck (1871b)	<i>Montagua pollexiana</i> Sp.Bate, 1857, <i>Montagua norvegica</i> (Liljeborg) (Sp.Bate, 1862), <i>Probolium pollexianum</i> Norman, 1869, <i>Metopa pollexiana</i> (Bate) (Sars, 1892)	X
Sp.Bate 1857	<i>Montagua Alderii</i>	<i>Metopa alderii</i>	Boeck (1871b)	<i>Metopa spectabilis</i> Sars, 1892	X
Goës 1866	<i>Montagua Bruzelii</i>	<i>Metopa bruzelii</i>	Boeck (1871b)		
Boeck 1871b	<i>Metopa affinis</i>	<i>Metopa affinis</i>			X
Boeck 1871b	<i>Metopa longicornis</i>	<i>Metopa longicornis</i>			X
Boeck 1871b	<i>Metopa longimana</i>	<i>Metopella longimana</i>	Sars (1892)		
Boeck 1871b	<i>Metopa nasuta</i>	<i>Hardametopa nasuta</i>	Barnard and Karman (1991b)		
Boeck 1871a	<i>Metopa Esmarki</i>	<i>Mesometopa esmarki</i>	Gurjanova (1938)		
Sars 1879	<i>Metopa aequicornis</i>	<i>Metopa aequicornis</i>			X
Stuxberg 1879	<i>Metopa gigas</i>		nomen nudum (Barnard and Karman, 1991b)		

Sars 1883	<i>Metopa borealis</i>	<i>Metopa borealis</i>				X
Sars 1883	<i>Metopa gregaria</i>	<i>Probolooides gregaria</i>	Della Valle (1893)		<i>Probolium gregarium</i> (Sars, 1892)	
Sars 1883	<i>Metopa leptocarpa</i>	<i>Metopa leptocarpa</i>				X
Sars 1883	<i>Metopa rubrovittata</i>	<i>Stenula rubrovittata</i>	Lincoln (1979)		<i>Stenothoides latipes</i> Chevreux and Fage, 1925	
Schneider 1884	<i>Metopa Sölsbergi</i>	<i>Metopa solsbergi</i>			? <i>Stenothoe clypeata</i> s. Stimpson 1853,	
Hansen 1888	<i>Metopa groenlandica</i>	<i>Metopa groenlandica</i>			<i>Probolooides groenlandicus</i> (Stebbing, 1906), <i>Metopa hirsutimana</i> Blake, 1929, <i>Probolooides clypeatus</i> s. Stephensen (1931)	X
Hansen 1888	<i>Metopa latimana</i>	<i>Metopa latimana</i>			<i>Metopa abscisa</i> Norman, 1902	
Hansen 1888	<i>Metopa carinata</i>	<i>Hardametopa carinata</i>	Barnard and Karman (1991b)			
Hansen 1888	<i>Metopa neglecta</i>	<i>Mesometopa neglecta</i>	Shoemaker (1955)			
Pfeffer 1888	<i>Metopa sarsii</i>	<i>Metopoides sarsii</i>	Chevreux (1906)		<i>Metopa walkeri</i> Chevreux, 1906	
Stebbing 1888	<i>Metopa crenatipalmata</i>	<i>Torometopa crenatipalmata</i>				
Stebbing 1888	<i>Metopa magellanica</i>	<i>Metopoides magellanica</i>	Stebbing (1906)			
Stebbing 1888	<i>Metopa ovata</i>	<i>Probolisca ovata</i>	Gurjanova (1938)			
Hoek 1889	<i>Metopa Normani</i>	<i>Stenula rubrovittata</i>	Schellenberg (1942)			
Sars 1892	<i>Metopa Boeckii</i>	<i>Metopa boeckii</i>			<i>Metopa norvegica</i> s. Sp.Bate and Westwood (1868)	X
Sars 1892	<i>Metopa invalida</i>	<i>Metopa invalida</i>				X
Sars 1892	<i>Metopa palmata</i>	<i>Metopa palmata</i>				X
Sars 1892	<i>Metopa propinqua</i>	<i>Metopa propinqua</i>				X

Sars 1892	<i>Metopa pusilla</i>	<i>Metopa pusilla</i>			X
Sars 1892	<i>Metopa robusta</i>	<i>Metopa robusta</i>			X
Sars 1892	<i>Metopa sinuata</i>	<i>Metopa sinuata</i>			X
Sars 1892	<i>Metopa tenuimana</i>	<i>Metopa tenuimana</i>			X
Norman 1902	<i>Metopa abscisa</i>	<i>Metopa latimana</i>	Lincoln (1979)	<i>Metopa latimana</i> Hansen, 1888	X
Reibisch 1905	<i>Metopa quadrangula</i>	<i>Metopa quadrangula</i>			
Chevreaux 1906	<i>Metopa walkeri</i>	<i>Metopoides sarsii</i>	Thurston (1974)	<i>Metopoides sarsii</i> (Pfeffer, 1888)	
Brüggen 1907	<i>Metopa spitzbergensis</i>	<i>Metopa spitzbergensis</i>			
Norman 1907	<i>Metopa sarniensis</i>	<i>Parametopa kervillei</i>	Lincoln (1979)	<i>Parametopa kervillei</i> Chevreaux, 1901	X
Holmes 1908	<i>Metopa pacifica</i>	<i>Probolooides pacifica</i>			
Stebbing 1917	<i>Metopa rotunda</i>	<i>Probolooides rotunda</i>	Barnard (1940)		
Blake 1929	<i>Metopa hirsutumana</i>	<i>Metopa groenlandica</i>	Stephensen (1936)		
Gurjanova 1929	<i>Metopa cariana</i>	? <i>Metopa glacialis</i>	Dunbar (1954)		
Stephensen 1931	<i>Metopa nordmanni</i>	<i>Stenula nordmanni</i>	Just (1980)		X
Stephensen 1931	<i>Metopa abyssalis</i>	<i>Metopa abyssalis</i>			
Pirlot 1933	<i>Metopa abyssi</i>	<i>Metopa abyssi</i>			X
Gurjanova 1933	<i>Metopa wiesei</i>	<i>Metopa wiesei</i>			
Dunbar 1942	<i>Metopa longirama</i>	<i>Metopa longirama</i>			
Gurjanova 1948	<i>Metopa angustimana</i>	<i>Metopa angustimana</i>			
Gurjanova 1948	<i>Metopa collicii</i>	<i>Metopa collicii</i>			
Gurjanova 1948	<i>Metopa derjugini</i>	<i>Metopa derjugini</i>			
Gurjanova 1948	<i>Metopa layi</i>	<i>Metopa layi</i>			
Gurjanova 1948	<i>Metopa majuscula</i>	<i>Metopa majuscula</i>			
Gurjanova 1948	<i>Metopa submajuscula</i>	<i>Metopa submajuscula</i>			
Gurjanova 1951	<i>Metopa uschakovi</i>	<i>Metopa uschakovi</i>			
Gurjanova 1952	<i>Metopa japonica</i>	<i>Metopa japonica</i>			
Gurjanova 1952	<i>Metopa koreana</i>	<i>Metopa koreana</i>			

Gurjanova 1952	<i>Metopa mirifica</i>	<i>Metopa mirifica</i>		
Dunbar 1954	<i>Metopa hearni</i>	<i>Metopa hearni</i>		
Gurjanova 1955	<i>Metopa kobjakovae</i>	<i>Metopa kobjakovae</i>		
Gurjanova 1955	<i>Metopa timonovi</i>	<i>Metopa timonovi</i>		
Gurjanova 1955	<i>Metopa bulychevae</i>	<i>Metopa bulychevae</i>		
Gurjanova 1955	<i>Metopa cristata</i>	<i>Metopa cristata</i>	? <i>Metopa stelleri</i> (Shoemaker, 1964) (see paper 6)	X
Shoemaker 1955	<i>Metopa spinicoxa</i>	<i>Metopa spinicoxa</i>		X
Oldevig 1959	<i>Metopa beringiensis</i>	<i>Metopa beringiensis</i>	? <i>Metopa clypeata</i> (Krøyer, 1842) (see paper 1)	
Barnard 1962	<i>Metopa dawsoni</i>	<i>Metopa dawsoni</i>		X
Shoemaker 1964	<i>Metopa stelleri</i>	<i>Metopa stelleri</i>	? <i>Metopa cristata</i> (Gurjanova, 1955) (see paper 6)	X
Barnard 1966	<i>Metopa samsiluna</i>	<i>Metopa samsiluna</i>		
Barnard 1969	<i>Metopa cistella</i>	<i>Metopa cistella</i>		
Tzvetkova and Golikov 1990	<i>Metopa gurjanovae</i>	<i>Metopa gurjanovae</i>		
Tzvetkova and Golikov 1990	<i>Metopa shoemakeri</i>	<i>Metopa shoemakeri</i>		
Ren (in Ren and Huang 1991)	<i>Metopa longipalma</i>	<i>Scaphodactylus longipalma</i>	<i>Scaphodactylus elephantensis</i> (Andres and Rauschert, 1992)	
Krapp-Schickel 2009	<i>Metopa eupraxiae</i>	<i>Metopa eupraxiae</i>		
Krapp-Schickel 2009	<i>Metopa erigua</i>	<i>Metopa erigua</i>		
Krapp-Schickel 2009	<i>Metopa torbeni</i>	? <i>Metopa torbeni</i>		

Table 2: Chronological listing of *Metopa* with valid names and synonyms. Senior synonyms in bold face.

The first two species to be described of what is now *Metopa* were found during the expedition with the corvette La Recherche, and should have been published together with the vast material of natural and cultural findings that came out from this several years long trip, but the zoological findings were never published (Knutsen and Posti 2002). The examination of the Arctic and boreal waters has been most intense in the Atlantic, and this has probably given the bias we see in fig 3.

Five genera (*Hardametopa*, *Mesometopa*, *Metopella*, *Metopoides* and *Torometopa*) have been erected based on species described originally as *Metopa*; other species originally described within *Metopa* have been moved to already existing stenothoid genera. This is summarized in Paper 1 (p.2); see also Table 2.

Norman (1900) erected the genus *Metopina*, with *Metopa palmata* Sars, 1892 as type species, in addition to *M. clypeata* (Krøyer, 1842) (sic! the type species of *Metopa*) and *M. robusta* Sars, 1892, on the basis on the shape of P1, which in all these species is simple and elongate. In 1902 he changed the name to *Sthenometopa*, since he discovered the name *Metopina* had already been occupied. *Sthenometopa* was merged back into *Metopa* by Stebbing (1906). For more details, see Paper 6.

d'Udekem d'Acoz (2010) has pointed out, and discussed, that following the rules of the International Commission on Zoological Nomenclature (1999, articles 32.2 and 32.5), original spellings for latin species names should be used if they are not clearly misspelled in the original publication. He concluded that the original spelling by Sars for species epithets such as *aeqvicornis* (corrected from *æqvicornis*) and *propinquus* should retain this spelling, and not, as usually has been done, be 'corrected' to the modern *qui*. Following his suggestions, I have therefore here, but not in the earlier papers in this thesis, reverted to the original spelling in these cases.

Taxonomy

(Papers 1, 2 and 3)

As the main result of this thesis was proposed to be a morphologically based phylogeny, a thorough re-description of as many species as possible was seen as the best starting point. As the style and tradition for species-descriptions has changed over the years since *Metopa clypeata* was first described, this was necessary, to be able to have comparable material to build a matrix for a phylogenetic analysis.

Some of the oldest of the species in *Metopa* were described at a time when any figure would be considered unnecessary and luxurious (see fig 5). The original descriptions from Krøyer (some of which were supposedly produced by Boeck!) have been impossible to find, as the zoology-volume of the La Recherche expedition must never have been published (Knutsen and Posti 2002). The financial problems for science must have started earlier than most of us like to acknowledge... Sars (1892) is still famous for his beautiful and detailed illustrations, but also his illustrations lack for all but one *Metopa*-species the mouthparts that are of diagnostic importance (see fig 6). Several of the later descriptions have included varying levels of illustration; the absence of illustrations in Bate and the fine artwork of Sars mark the extremes. The modern descriptions are more focused on minute details of mouthparts in addition to the larger characters (see figures in Krapp-Schickel (2009) for a very good example), and include several techniques of illustrations. Modern digital drawing-techniques have been developed and described by Coleman (2003, 2009), and are now used throughout the community. Other methods of illustration includes today Scanning Electron Microscopy and computer stacked and enhanced light microscopy photos.

3. *M. Alderii* (mihi). Hand square, furnished with a small thumb; palm denticulated.
Coast of Northumberland, *J. Alder, Esq.*

Figure 5: Original description of *Montagua Alderii* Sp. Bate (1857)

As the work progressed, it has become pressing to find new characters that could be used for a phylogeny, as there seem to be very minute details separating the different species. Also, for some of the defining characters in *Metopa* we have demonstrated that they seem to be plastic (ex. the articulation of the mandible-palp, see p.14 in Paper 1), and other commonly used characters (ex. the shape of propodus in pereopod 2 (Gnathopod 2)) have been shown to vary with size and age. An example of this is the synonymisation

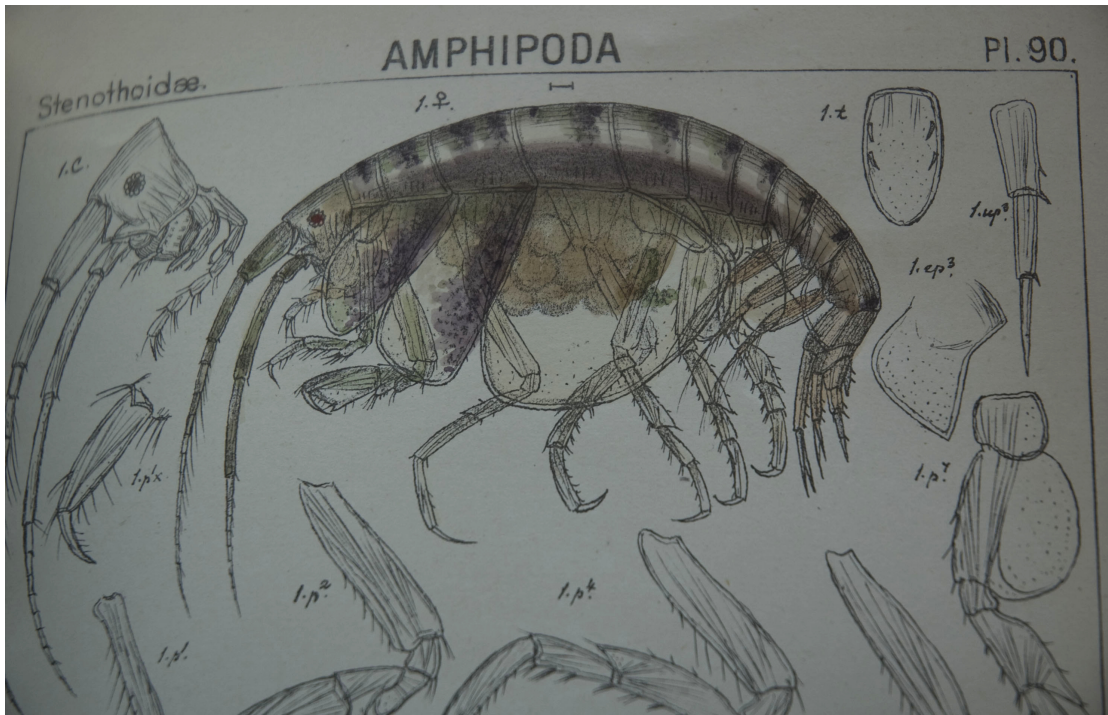


Figure 6: Photo of hand-coloured version of Sars' illustration of *Metopa pusilla*, Sars (1892)

of *Metopa alderii* and *M. spectabilis* by Dahl (1946) (see p. 10 in Paper 3 and table 2 here). This synonymisation has been tested out in our phylogenetic analysis (Paper 6). The usability of different characters is discussed further under Phylogeny.

The redescriptions are based on type material, and are organised according to the type-collections of different musea (Papers 1, 2 and 3). Obviously missing in this are the types of Gurjanova (Gurjanova 1948, 1951, 1952, 1955) - but here again are problems of tradition - Gurjanova herself did very often not designate types for her species, she rather knew where to go if she needed to collect later. It is therefore also unfortunate that several of her many species are only described, often quite briefly, in her papers - many of whom are in Russian - a language I sadly do not master. Some of her specimens are stored in USNMNH, and these were examined together with this type-collection; other specimens (not types) are in a quite bad shape in the collections of the Academy of Sciences in St Petersburg. This material I received for examination, but it has not been possible to summarize this in a manuscript worthy of publication due to the state of the specimens and the very few species represented in the loaned material. There are also "single" types in different musea that have not been examined. Even with kind help from several friends with the translation of Gurjanovas descriptions, the tradition of her time and school of not keeping more specimens than needed for the original work has limited the full analysis I would have liked to give her species for this thesis.

Even though the mouthparts, especially the mandible and the maxilla 1, traditionally have been used as diagnostic characters for several genera of the Stenothoidae, very many species were originally described without descriptions of mouthparts. For this thesis one of the objectives was to give descriptions of the mouthparts of as many species as possible - using type material or material identified by the original author and from areas close to the type locality. The possibility to examine the mouthparts in closer detail than a normal light microscope allows using a scanning electron microscope at the museum in Copenhagen (Paper 1), helped identify new and possibly useful characters for phylogenetic analysis.

After redescribing 23 species, it was clear that several of these would no longer fall under the genus *Metopa* using the classic definition from Krøyer that the mandible palp should be 2- to 3-articulate, but rather should be moved to *Stenula*, which should have a 1-articulate mandible palp, see Paper 3. Due to this, we decided to include *Stenula* in the phylogenetic analysis (Paper 6), this will be discussed further under Phylogeny. Also the shape of gnathopod 1 (pereopod 1) shows so much variation – from very long and slender/simple via a boatshaped paddle-form to the broad subchelate almost transverse palm – that we had hopes this might be used as a character that might help with the understanding of this group. Also this character will be discussed under Phylogeny.

Abbreviations used in the papers in this thesis:

A 1,2 = antenna 1,2

acc = accessory

ant = anterior

art = article

b = breadth

C = coxa

Ep = epimeral

fem = female

flag = flagellum

Gn 1,2 = gnathopod 1,2

ip = inner plate

lbi = labium

lbr = labrum

Md = mandible

Mx 1,2 = maxilla 1,2

Mxp = maxilliped

op = outer plate

P 3-7 = pereopod 3-7

ped = peduncle

post = posterior

T = telson

U 1-3 = uropod 1-3

Ecology

(Papers 4 and 5)

The family Stenothoidae is easily recognized due to the large and triangular coxa 4, which together with the relatively simple urosome and head enables the animals to roll up and hide all legs and other small or vulnerable appendages and look almost like a small ostracod, a feature that fits well with the fact that several species are associated with or live close to other fauna (Krapp-Schickel and Koenemann 2006; Krapp-Schickel and Vader 2009). Several species of Stenothoidae are obligate symbionts on sea anemones (Vader and Krapp-Schickel 1996; Krapp-Schickel and Vader 2009), in tunicates (Pirlot 1933; Stephensen and Thorson 1936; Vader 1984) and on other Crustacea (Thomas and Cairns 1984). The morphology of the species that are associated with other species is not much different from the species we think are free-living. This, in addition to the fact that associated species are spread around the whole family points to the probability that these associations are not evolutionary very old.

Metopa species often seem to live associated with other epifauna, and they are thus usually found on hard bottoms. For most species there is no ecological information available, and no doubt many surprises are still awaiting us, once we learn about the biology of the various *Metopa* species. For some species (eg. the B-group species in Paper 6, see under Phylogeny), the morphology (of eg. Gn1) points to the possibility of a specialized way of life, but for other species (e.g. the species known from a mollusk-dwelling life) the general morphology does not give any immediate hints to such specialized lifestyle. It is, however, quite common that we do not know much about the biology of a species, and when this is the case, we often believe the species to be free-living.

Compared with other Stenothoidae *Metopa* seems to have a more restricted set of associates; only one species is associated with sea anemones (Krapp-Schickel and Vader 2009), one other with hydroids, and a few species are associated with mollusks. No *Metopa* have so far been found associated with other crustaceans (whereas eg. *Stenothoe symbiotica* is found on spider crabs (Shoemaker 1956)), also none is found in or on sponges - contrary to several other Stenothoids (see Vader (1984)), nor directly in or on tunicates (maybe except *M. groenlandica* (Stephensen and Thorson 1936)), animals where several other stenothoids have been collected from (Pirlot 1933; Vader 1984). It should, however, be noted that the mollusk *Musculus discors*, where *Metopa glacialis* and *M. alderii* have been found (see Papers 4 and 5) is often found inside tunicates in the southern Barents sea and in the Norwegian Sea (J.A. Sneli, pers. comm.), so there is a possible indirect association of *Metopa* and tunicates there.

Metopa associated with mollusks

This type of association has been what we have observed and studied in the papers presented in this thesis. Finding *Metopa* associated with mollusks was not a novel discovery, Stephensen and Thorson (1936) have shown this for *Metopa groenlandica* (see fig 7) and Just (1983) and Vader and Beehler (1983) for *M. glacialis*. The findings of Paper 5 are novel to the extent that *M. alderii* had not been found so far north nor associated with mollusks before. Both species of mollusk (*Musculus discors* and *M. niger*) had been found to have *M. glacialis* associated with them earlier (Vader and Beehler 1983). There seem to be no large sexual differences in the species associated with mollusks.

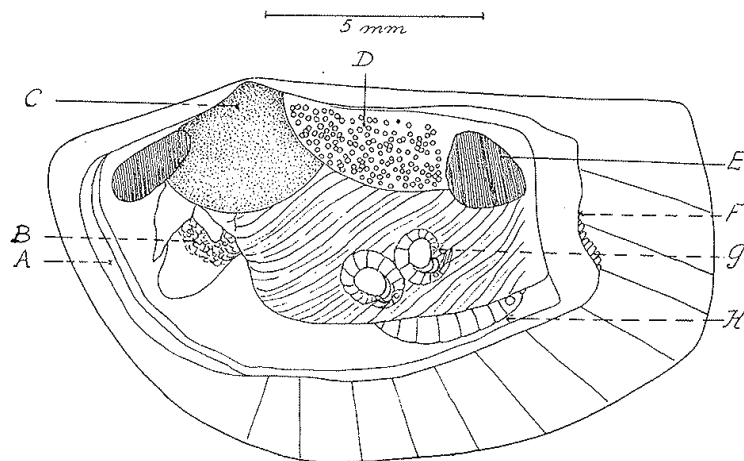


Fig. 2. *Pandora glacialis* LEACH. Left shell removed; with 3 specimens of *Metopa groenlandica* H. J. HANSEN in the mantle-cavity. A. slit for the foot, B. Testis, C. Liver, D. Ovary, E. Adductor posterior, F. Siphon, G. Young specimens of *Metopa* attached to the gills, H. Adult *Metopa* lying free between the gills. Off Cape Stosch, depth 15 m, August, 4, 1930 (B. Löppenthin leg.).

Figure 7: Facsimile from Stephensen and Thorson (1936) of *Metopa groenlandica* living inside *Pandora glacialis*.

The association with bivalves and not (as far as we know) with other mollusks, and the apparent specificity in host-choice (see Paper 4) leads to the possible conclusion that this association allows the amphipods to have specific life-history strategies. This thought is also supported by the many finds of juveniles either alone or together with one or two adults of *Metopa glacialis* associated with *Musculus discors* (see fig 8); this is presented and discussed further in Paper 4.

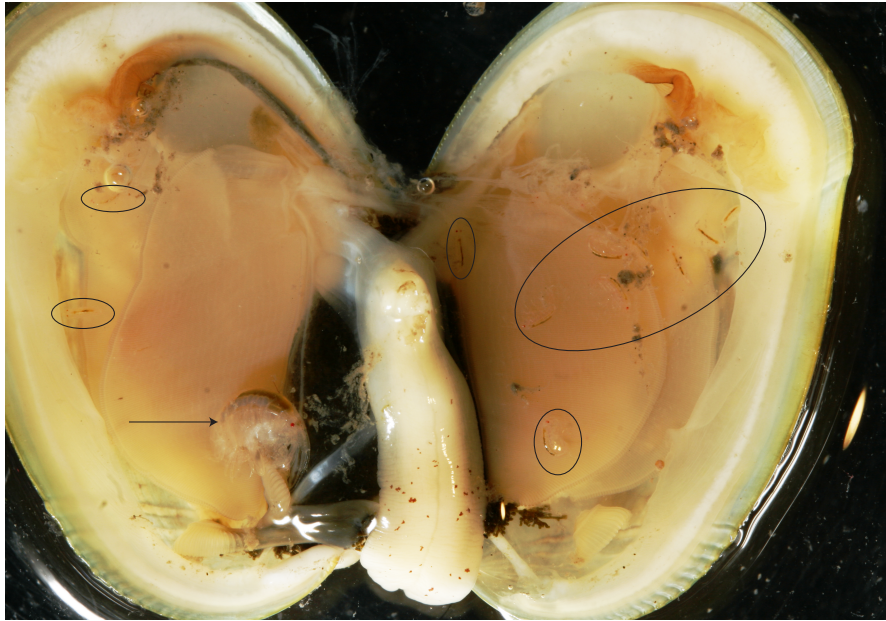


Figure 8: Photo of adult *Metopa glacialis* (arrow) with juveniles (circled) found inside *Musculus discors*.

***Metopa* associated with cnidaria**

Metopa solsbergi Schneider (1926) is an obligate associate of *Metridium* species (Elmhirst 1925; Vader 1983; Fenwick and Steele 1983). *Stenothoe brevicornis* is also always found on sea anemones (Vader and Krapp-Schickel 1996; Auster et al. 2011), as is *Parametopella antholoba* (Krapp-Schickel and Vader 2009). *Metopa pusilla* has been observed by me and the amphipod group at the Tromsø Museum as sitting on hydroids when collecting along the Finnmark coast and in Svalbard waters.

***Metopa* associated with other specific environments**

Hydrothermal vents

Metopa samsiluna has been found in small numbers on hydrothermal vents in the Guaymas Basin in the Gulf of California (Vinogradov 1993, 1995). These are hypothesized to be "common" mobile epibenthic animals appearing at the vent by chance, and not as specialized vent-amphipods. The original description (and only other find of this species) is from Baja California (at 1620 m depth) by Barnard (1966, 1967).

Phylogeny

(Paper 6)

As mentioned above (see under Taxonomy), the morphological examinations of the mouthparts of several of the nominal *Metopa* species (Papers 1-3) revealed that these species did not in all cases agree with the diagnosis of *Metopa*. This was especially apparent in the palp of the mandibles and maxilla 1. Barnard and Karaman (1991b) state the diagnosis of the genus *Metopa* as:

Antenna 1 lacking nasiform process on article 1. Accessory flagellum absent or vestigial. Palp of mandible 2 to 3-articulate; palp of maxilla 1-articulate. Inner plate of maxilla 2 ordinary. Inner plates of maxillipeds mostly fused together or well separated (type). Gnathopods 1-2 subchelate, different from each other in size and shape: gnathopod 1 small, almost simple (variable), article 4 incipiently chelate; article 5 elongate, barely lobed; article 6 scarcely expanded, almost linear. Gnathopod 2 enlarged, palm oblique; articles 4-5 short, 5 lobed. Pereopod 5 with rectilinear article 2, pereopods 6-7 with expanded, lobate article 2. Pereonite 4 short. Pleonites 4-6 free; pleonite 3 lacking dorsal process; pleonite 4 not extended posterodorsally. Telson ordinary, flat.

Having found that several of the species described as *Metopa* by the morphology of their mouthparts rather should have been moved to *Stenula* (Paper 3), we decided to include this genus in our phylogenetic analysis of *Metopa*. Initially working together with Dr Traudl Krapp-Schickel, who has worked extensively with the stenothoid genera, we put together a matrix of 64 characters scored for 74 taxa from both genera. The scoring was based on data from the literature, where possible the original descriptions, in addition to papers 1, 2 and 3 (see appendix B in paper 6), and examinations of non-type material of several species. After evaluation of how much information we had for each taxon, this list was reduced to 45 taxa including two outgroup-taxa.

The characters were all kept unweighted, both because we did not want to presuppose any character more important to the evolution of the different species than any other characters, and because we wanted the resulting phylogeny to reflect the complete organisms and not special parts of the organisms. As some details of the organisms were favoured with more characters than other parts, a certain focus (especially on the mouthparts - given their historic importance in the genus-definitions) will inadvertently have been given to the resulting trees. We did try to keep the characters independent; this

is not always possible because so many characters are more or less interdependent. The matrix should, if possible, have more characters than taxa.

The focus on mouthparts (and especially palps of mouthparts) in the character-list can be discussed. This has, as mentioned above, come from the historic focus on palps, a character that has been shown in Paper 1 (p. 14) to be plastic and probably should not have had such a strong focus. Many of the other characters are allometric, and for some species (eg. in the synonymy proposed by Dahl (1946) for *Metopa alderii* and *M. spectabilis*) it has been shown that the allometric relations change with the age of the specimens. For some *Metopa* species there are strong allometric differences between the sexes. The presence of more or longer setae and even articles of eg. the flagella of the antennae may also change with age or sex, this may have further clouded the coding of the matrix and the resulting phylogenies. Reductions of the number of articles in eg. palps might have happened independently on several occasions during evolution, and thus we also kept all characters unordered as well as unweighted. The resulting matrix is the result of the combined suggestions by both authors of Paper 6 together with Dr Krapp-Schickel.

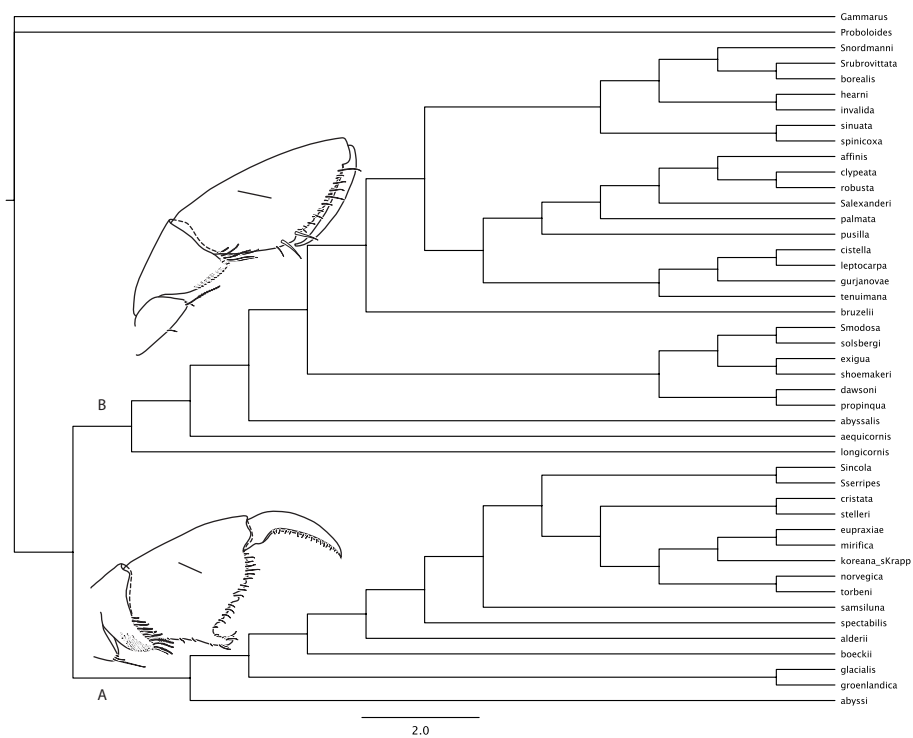


Figure 9: Figure 3 from Paper 6 with representations of character 41 (palmar corner, propodus Gn2, female) for clades A (with strong tooth) and B (with small tooth/only spines)

The main result of the phylogenetic analysis is that the two genera *Metopa* and *Stenula* mix thoroughly. The joint clade of *Metopa* plus *Stenula* is split into two clades. These we have not yet wanted to name more formally than clades A and B, as doing so would cause an enormous upheaval in the nomenclature, while we feel that further analyses are necessary before formalizing the results. Paper 6 does indeed show that the trees are somewhat unstable, but we have also shown that the separation into groups A and B was mainly retained even before we excluded several taxa due to the lack of information.

Another result of this initial phylogeny is that very few of the morphological characters follow a clear pattern in the tree - the example of the three characters we used for the mandible is shown in Paper 6 (figure 6). The characters that seem to follow the tree-topology best, are characters of pereopod 2 (Gn2), most regarding features of the propodus (proportions and palmar corner), see Figures 9 and 10. This is also discussed in Paper 6.

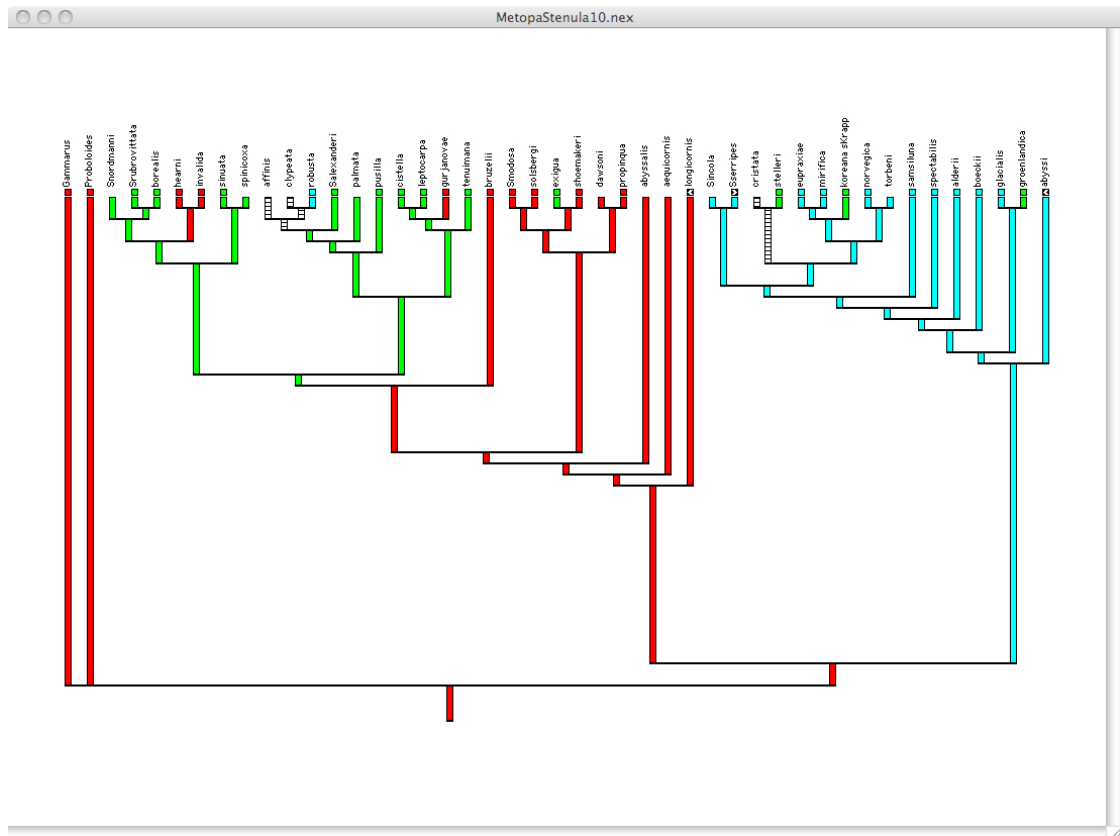


Figure 10: Mapping of character 41 (palmar corner, propodus Gn2, female) on tree shown in Fig 9

Discussion

All the work presented in this thesis has been performed in order to produce the best possible phylogeny of the genus *Metopa*. One may wonder if this has been totally successful, but under the constraints of a purely morphological analysis, I feel the phylogenies presented are sound. Nevertheless, these analyses should not be viewed as the final word on this complex of taxa.

The matrix was heavily influenced by allometric characters, and for most taxa scored from literature it was impossible to score several of the characters. Also, it was not always possible to know if the specimens described in the literature were fully adult males or females. The strong focus on mouthparts both in the taxonomic and the phylogenetic work is historically dictated through the early genus definitions, and might be too strong. Dunbar (1954) commented "It is doubtful whether the sturdy reliance on the mouthparts shown by the classical amphipod systematists gives a true natural classification" (p.727). This doubt is also shown in Paper 1, where we demonstrated the plasticity of the number of articles in the mandibular palp. It is also highly possible from an evolutionary point of view that the mouthparts undergo strong selection - they are after all instrumental in the food-uptake, and thus survival, of the animal.

A thorough examination of the taxa I have not examined for the phylogenetic analysis, will no doubt contribute a fuller picture and hopefully a more stable phylogeny than what has been presented here. Possibly, more genera should be examined, as the proposed outgroup-representative *Proboloides gregarius* needed a restraint to remain an outgroup taxon. The only character supporting this rooting is character 15 (Maxilla 1 palp number of articles). Krapp-Schickel and Koenemann (2006) have suggested that *Metopa* is not very far from *Proboloides* and other basal genera such as *Scaphodactylus* and *Torometopa* (they are all represented in Clade 1 - the most basal clade of their analysis), but I have to admit I do not fully agree with their analyses. That said, the family Stenothoidae has for a long time been considered an unwieldy complex, and its generic divisions have been viewed as possibly weak. Even Barnard and Karaman (1991b) said about the family Stenothoidae:

The genera are artificially separated on the basis of the 1- to 2-articulate palp of maxilla 1, the 0- to 3-articulate condition of the mandibular palp, occasionally the presence or absence of accessory flagellum (which is often badly observed), and the breadth of article 2 on pereopods 6 to 7 (which is relatively workable but occasionally transformational species and genera have intermediate degrees of expansion which cause minor confusion). These

are very poor characters because fusion or loss of articles is undoubtedly polyphyletic. Virtually no attention has been paid to gnathopods and other possible characters although we have isolated a few new genera herein where separation is fairly clear. Because many species are poorly described, the stenothoids await a monographer who can give them synoptic treatment.

In view of the few supporting and stable characters in the phylogeny presented in Paper 6 it might be pleasing to know that so many esteemed amphipodologists have found this amphipod-family difficult and the possible characters messy. This does give support to our results in Paper 6 that the genus *Metopa* should be split, and that it should be analyzed together with other stenothoid genera such as *Stenula*. Our phylogeny no doubt has its weaknesses as well, not least the aforementioned low support. What this does point to, is the still present need for a thorough phylogenetic analysis of the taxa of this group, as well as the need to continue the search for characters that may be phylogenetically more informative.

One of the characters that does show in the phylogeny is a character that is not used in the matrix - one of ecological traits. There is a sub-group within clade A, close to the basis, but with *Metopa abyssi* placed more basally, that contains all the species we have knowledge of living inside bivalves (in the final analysis these were *M. glacialis* and *M. groenlandica*, but in the earlier and more enlarged analyses (before we cut out several taxa from the analysis) the clade also included *M. colliei*, *M. japonica*, *M. timonovi* and *M. submajuscula* (see fig 1 in Paper 6) - all taxa that were removed from the final matrix due to lack of morphological information, -we also do not have any information whether these taxa may live inside mollusks. We did for some time think about separating this clade out as a new genus, but with the decision of not making any formal changes now also this has been laid to rest. The morphological traits that are the apomorphies for this clade are the size of coxa 4 and the shape and setation of pereopod 1 (Gn1) (see example of coxa-size mapping in fig 11).

This is to some extent a quite curious result - and again also somewhat logical. The large C4 of most stenothoids allows the animals to curl up and hide all the appendages (very much like an ostracod) - and this might be a good thing for an animal living amongst epifauna on hard substrates, and the possibility of retracting into a "shell" is known from the species that are not good swimmers. Living completely inside another species (and Paper 5 gives indications that *Metopa glacialis* lives inside *Musculus discors* all its life) this trait may not be as necessary. The shape and especially setation of the first pairs of pereopods (Gn1 and Gn2) will possibly help the animals positioning themselves inside the mussels (Stephensen and Thorson's illustration (see fig. 7) shows that *M. groenlandica* uses the antennae to hold on to the gills of *Pandora glacialis*), and Paper 1 gives indications of several highly specialized types of setae (both on the mouthparts and on Gn1 and Gn2) [Paper 1: Fig 21, p. 30] and show a setation of Gn1 and Gn2 that is not shown on any of the other taxa redescribed (Papers 1, 2 and 3).

The fact that some species have been synonymized with the argument that they were juvenile and adult (or young and old adult) of the same species (as with *Metopa alderii*

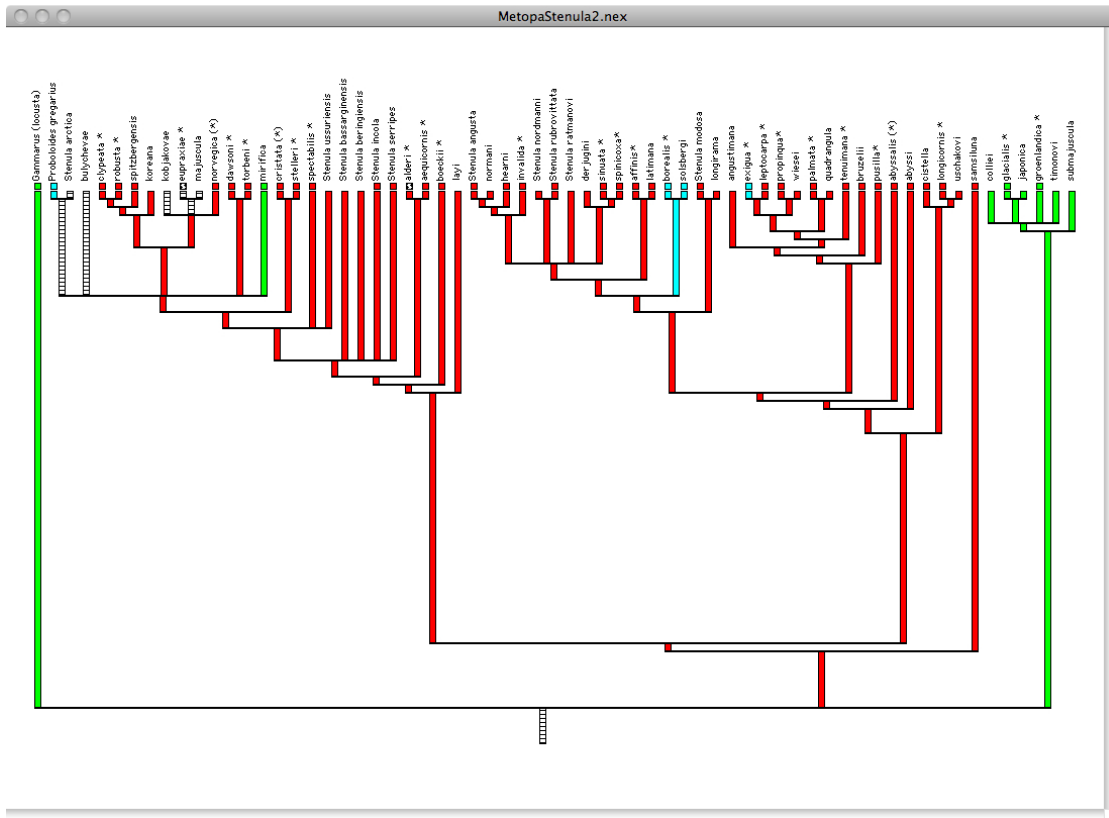


Figure 11: Mapping of character 17 (ratio of C4 : (C2+C3)) on original consensus tree

and *M. spectabilis*, see Paper 3) is clouded in our phylogeny since the matrix is heavily based on allometry. An additional problem for all the species that have been scored for the analysis from literature only is that it is not always known if the illustrations and descriptions are made from completely adult males or females, and often descriptions are made only from one sex.

Because of all the above presented shortcomings in the analyses I do not want to formalize the clades resulting from our morphological analysis. I do, however, think this work has pointed to several possible ways to continue the work on finding a good phylogeny for *Metopa*, *Stenula* and possibly several other nominal genera of Stenothoidae, and I hope this work will continue.

Molecular approach

I have attempted to produce molecular examinations of *Metopa* specimens. Two main problems were associated with this; both availability of specimens to extract DNA from, and adjustment of primers. These trials should not be viewed as a finished work on

molecular markers for *Metopa*, and no conclusions can be drawn from them. They should, however, be viewed as a pilot for what we might be able to expand on in later examinations of the genus.

The molecular tests were performed in close cooperation with Dr. Kirstin Janssen, who represented both the knowledge of techniques and methods, and did most of the lab work. Two genes were sequenced and tested: the mitochondrial *CO1* and the nuclear *28S*. Standard primers for both genes and PCR settings for commonly available kits were used. A series of *Metopa* were tested for possible isolation of DNA; from freshly sampled specimens to older museum-specimens. It was evident that several of the older samples have been stored unsatisfactorily for DNA-preservation, sadly this seems to be the case also for some of the newer samples. The main reason for this is the tradition for fixing samples in formaldehyde instead of ethanol, thus reducing the possible amount of specimens we could sequence DNA from.

Not all samples we managed to sequence worked with both genes, and so it is a bit difficult to compare the resulting trees, but both trees show one clear result: a clade consisting of *Metopa bruzelii*, *M. pusilla*, *M. borealis* and *M. tenuimana*. This clade does come out at different positions in the two gene trees, but it is consistent with the findings of the morphological phylogeny where all these four taxa are found in Clade A. Therefore there could be some molecular support for the morphological phylogeny presented earlier in this thesis. I do think that molecular examinations very well might be one of the possible next places to look for good characters to examine the phylogeny further, especially as we seem to have trouble finding enough morphological characters to give a stable phylogeny for the family.

Postludium

I clearly think that this is not the end of finding a phylogeny for *Metopa* - or for *Stenula*. Producing a stronger matrix with more data for more taxa is one obvious way to proceed, another is looking at molecular characters. Both the mitochondrial gene *COI* and the nuclear genes 18S and 28S have been used by others to elucidate phylogenetic relationships at species level for amphipods (see eg. Englisch et al. 2003; Lörz and Held 2004; Fiser et al. 2008; Hou et al. 2007), and to get proper results here fresh samples of several of the species are needed. Personally, I would in addition love to look more closely both at how morphological characters might trace on a molecular tree, and to look at the genetic variation within some of the wider spread species (ex. *Metopa glacialis*). Describing the life-history of more species and discovering more about the ecology would no doubt be helpful - these are traits that we have almost no information on for most amphipods, but mapping ecological traits on phylogenetic trees would be interesting.

Every year several new species of amphipods are described, mostly by a quite small community of amphipodologists. This should be an indication of how much work is left in this beautiful and exciting group of animals. Even easily accessible habitats such as shallow temperate waters have new species described almost every year, not to talk about the more inaccessible deep and cold waters and special habitats such as caves, vents or wood- and whalefalls. To end where I started: it is of great importance that we spend time and money to find out what is "out there" of our biodiversity. Both to discover what is here before it might disappear, to be able to make informed decisions about the environment, and to know what we work with and look at when we do try to make assumptions about the environment and the ecology. All this need for knowledge rests upon the knowledge of systematics, and the need for more systematic knowledge.

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