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In Murky waters

Swedish demosponges and their genealogies

RAQUEL PEREIRA



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Abstract

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Swedish Sponge fauna last updated happened over 80's years ago. This fact explains, partially, the country's low sponge. In this thesis, I update our knowledge of the Swedish demosponge fauna (**Paper I and II**) and, give an insight to the relationship within one of the most common sponge groups in the country belonging to order Suberitida (**Paper III and IV**), as well as to investigate possible dispersal barriers for freshwater sponges (**Paper I**). I relied on my own sampling, museum specimens and the marine inventory by STI. In total, we found nine new reports for Sweden (one freshwater and eight in sea water) and one new species to science (sea water). In the freshwater survey using *Spongilla lacustris* (**Paper I**) we tested if catchment areas represented dispersal barriers, but with the marker used we could not observe a clear population structure. For the marine environment the collected material contained what appear to be several species *Suberites* (**Paper II**). This genus, and many taxa within the order, is known for a paucity of morphological characters and long taxonomic history. This while being known for not representing a natural group. Thus, in order to know what species of *Suberites* present in Sweden we had to answer: What is the circumscription for the genus? What are its relationships with other suberitids? What are the oldest available names for the genus and the species within?

In **Paper III**, we use phylogenetics to infer the relationships within Suberitida. The trees showed two separate clades for *Suberites* - A and B. Clade B was together with the genus *Aaptos*, a *Homaxinella* species and *Stylocordyla* - family Stylocordylidae and, given that result we argued for expansion of Stylocordylidae. In **Paper IV**, we did an extensive literature review of the senior names for clade A and B. Plus, we presented species delimitation and their names for 30 species found in the Northern Temperate Atlantic realm. We argue for the resurrection of *Syringella* as the name for clade B. While, in clade A (under the name of *Suberites*), we make the case for *S. ficus* proper name to be *S. subereus* and, we solved the homonymy with the name *S. virgultosus* by naming the species found by Bowerbank - *Suberites* sp. "misterbeanii".

Keywords: Porifera, Swedish sponge fauna, *Spongilla lacustris*, population structure, *Suberites*, Suberitida, *Syringella*, Systematics

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Disclaimer. This is not published for purposes of zoological nomenclature, and hence it is not published within the meaning of the International Code of Zoological Nomenclature (chapter 3, article 8.2)

*"But I am very poor today & very stupid hate everybody & everything. One lives only to make blunders" Charles Darwin letter to Charles Lyell, 1861
October 1*

List of papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Robert C., **Pereira R.** & Thollessen M. 2022. Addition to Sweden's freshwater sponge fauna and a phylogeographic study of *Spongilla lacustris* (Spongillida, Porifera) in southern Sweden. European Journal of Taxonomy 828: 138-167-138-167.
<https://doi.org/10.5852/ejt.2022.828.1861>.
- II **Pereira R.**, Larsson M., Cárdenas P. & Thollessen M. Swedish marine demosponge fauna (Porifera: Demospongiae) sampled 80 years later *Manuscript*;
- III **Pereira R.** Thollessen. M. Phylogeny of Suberitida (Demospongiae, Porifera) â from confused to confusing *Manuscript*;
- IV **Pereira R.** Thollessen An initial integrative revision of the genus *Suberites* (Suberitida, Demospongiae) from the Northern Temperate Atlantic realm, with a focus on the Northern European Seas province *Manuscript*;

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Additional Papers

The following papers were published during the course of my doctoral studies but are not part of this thesis.

- I Lino S., Colaço A A., Xavier J.R., Santos R.S., Solé B., Matos V.D.E. **Pereira R.**. 2013. Lipid extractions from marine deep-sea invertebrates: modifications to the Bligh & Dyer method to increase lipid yields. *Arquipelago – Life and Marine Sciences* 31: 9-14.
- II Xavier J.R., Rees D.J., **Pereira R.**, Colaço A., Pham C.K. & Carvalho F.C. 2021. Diversity, Distribution and Phylogenetic Relationships of Deep-Sea Lithistids (Porifera, Heteroscleromorpha) of the Azores Archipelago. *Frontiers in Marine Science* 8: 600087.
<https://doi.org/10.3389/fmars.2021.600087>.

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Contents

List of Tables	xii
List of Figures	xiii
Introduction	14
The Atlantic Ocean	15
Swedish waterscape	16
Freshwater environment	16
Marine Environment	17
Threats	18
What are sponges?	19
Human bias	19
Sponges	20
Demospogiae systematics	22
Suberitidae-Halichondriidae	23
<i>Suberites</i>	24
Molecular markers	24
Sponge Barcoding Project	25
Recent sponge diversity surveys	26
Why study sponge diversity in Sweden?	26
Aims	27
Material and Methods	27
Collection	28
management	28
Morphological identification	29
Results	35
Successful markers	36
Demosponge Fauna in Sweden: an update	36
Freshwater environment	37
Marine environment	37
Suberitida - A Systematic insight	38
How many <i>Suberites</i> species and what are their names	38
Concluding Remarks	39
Plausible or near future perspectives	40
Shenanigans or far future perspectives	40

Svensk sammanfattning	41
Acknowledgements	43
References	46

Abbreviations

AIC	Akaike Information Criterion
BHL	Biodiversity Library of Heritage
BLAST	Basic Local Alignment Search Tool
bp	base pair (DNA)
EEZ	Exclusive Economic Zone
NEA	North East Atlantic
ICZN	International Code of Zoological Nomenclature
ITS	Internal Transcribed Spacer
LIMS	Laboratory Information Management System
MCMCMC	Metropolis-Coupled Markov Chain Monte Carlo
PCR	Polymerase Chain Reaction
RNA	Ribonucleic Acid
rRNA	Ribosomal Ribonucleic Acid
NEA	North East Atlantic
SCUBA	Self-contained Underwater Breathing Apparatus
SP	Systema Porifera
WPD	World Porifera Database
STI	Swedish Taxonomic Initiative

List of Tables

Table 1: List of Primers tested in addition to EPIC primers stated in Supplementary file 1 **Paper II**. Forward direction primers are indicated with "fwr:" and reverse with "rev:"; some primers for 18S (Redmond *et al.*, 2013) we used just for sequencing "[Seq]" while the ones used for both PCR and sequencing are marked with "[PCR & Seq]" 31

List of Figures

Figure 1: North Atlantic map. Bathymetry from ETOPO1 Arc-Minute Global Relief Model (doi:10.7289/V5C8276M). Borders in red represent the Temperate Northern Atlantic and in red-shade the North European Seas, both as defined in Marine Ecoregions of the World (MEOWs) (Spalding <i>et al.</i> , 2007). Swedish EEZ borders in yellow.	16
Figure 2: Plot of the number of valid sponge species described world-wide from 1754 to present day; blue dots indicate the number of species described each year and dashed line species accumulation curve. Data from World Porifera database, 2021-02-03 (Voogd <i>et al.</i> , n.d.)	22
Figure 3: Portax user interface rate (Thollessen, 2017)	29
Figure 4: 28S and 18S structure, with the primers tested and the extention of the predited PCR product. 28S structure predicted using RNAfold web server (Gruber <i>et al.</i> , 2008), using <i>Halichondria okadai</i> full 28S (AB511881); 18S for <i>Halichondria melanodocia</i> (AY737639) structure downloaded from Database for SSU rRNA secondary structures of Porifera (Voigt <i>et al.</i> , 2008). Structure drawn in RNA3draw (Johnson <i>et al.</i> , 2019)	35
Figure 5: <i>In situ</i> photography of some calcareous specimens already collected. Photos by Mats Larsson	41

Introduction

When I started my Ph.D studies at Uppsala University I knew for a fact that Sweden valued, deeply, the natural diversity, especially the names and evolutionary history of the different organisms that inhabit the country. In other words the Taxonomy and Systematics of the Swedish fauna and flora. So in Linnaeus' country, where there is a budget of tens of million SEK (Ronquist, 2010) one can wonder what is still to be known in general or, in my case, in demosponge (class Demospongiae, phylum Porifera) fauna here? I was surprised to learn, shortly after my arrival to Uppsala, that the latest update on sponge diversity overall but, more specifically species diversity, had been at least 80 years ago (Alander, 1942; Arndt, 1932). This is especially concerning to me given the increasingly fast loss of biodiversity around the world (Sweden included) that would mean Sweden was losing demosponge biodiversity without anyone being aware of it. Furthermore, sponges are an important habitat builders e.g., (Hultgren & Duffy, 2010) and an important source of new bio-compounds usable in medicine (e.g., Anjum *et al.* 2016). Thus, losing sponge diversity will mean loose resources that could directly help humanity in a near future. Nonetheless, I personally think that we, humans, are simply critters with curiosity and as such, once a knowledge-gap is found we cannot stop questioning and investigating even without foreseeable benefit. To question without thinking: "why do I need to know that?" is a luxury but also what define us as humans and as in the past revealed fundamental for the advance not only of basic knowledge and technology e.g., Mendel's work on heritable traits (Mendel, 1866). The research I have conducted for this thesis was as well to, just, close the knowledge-gap on what demosponge fauna can be found in Sweden the demosponge fauna which, is aligned with one of the main goals of the Swedish Taxonomic Initiative – to describe all multicellular organisms inhabiting Sweden.

In this thesis I will dwell on the contribution that I have made to close the knowledge-gap in diversity of the demosponge fauna in Sweden in both freshwater **Paper I** and marine environment **Paper II** using both morphological and molecular data. Furthermore in **Paper II** we noticed that many of the collected specimens (16%) belong to the order Suberitida (Chombard & Boury-Esnault, 1999). The order is comprised of three families: Halichondriidae Gray, 1867, Suberitidae Schmidt, 1870 and Stylocordylidae (Topsent, 1892). While Stylocordylidae is a monogeneric deep-sea family encompassing 8 species worldwide, the families Halichondriidae and Suberitidae are much larger and known for intertwining phylogenies. Thus, in order to know what demosponges exist

in Sweden the systematics between these two families will have to be solved. I dwell on that in **Paper III** and ended up by suggesting the expansion of the third family - Stylocordylidae, and dividing the genera *Suberites* Nardo (Suberitidae) and *Halichondria* Fleming (Halichondriidae) two clades, each - Clades A to D, without however reconciling this with the Linnean taxonomy by following International Code of Zoological Nomenclature (ICZN). In **Paper IV**, I then attempted to find a name for Suberites-clade B (the clade without the type species *Suberites domuncula* (Olivi, 1792) in the myriad of forgotten and/or synonymized genus names while discussing species delimitations and their proper names for what *Suberites* (Clade A) species exist in Sweden and the surrounding area.

The Atlantic Ocean

The specimens I used for this thesis are mostly from the North East Atlantic (NEA), with special focus on Sweden. Since sponges are aquatic, their evolutionary history, diversity or changes thereof, are tightly linked to the aquatic environment from where they come from. So in the coming sections I will attempt to give you a very broad overview of the Atlantic and a narrower characterization of the Swedish underwater environment.

The Atlantic Ocean is the second largest ocean in the world covering about 20% of the world's surface and it is roughly S shaped. Its waters have a mean temperature of 3.25°C but with temperatures ranging from 0 to 13.7° C and a salinity between 34.7 and 34.97‰ for 90% of its water (Montgomery 1959). The Atlantic has an average depth of nearly 4000 m but a maximum depth of 8376 m (Bongiovanni *et al.*, 2022). The northernmost area of the Atlantic is at Strait at the coast of Labrador and Greenland while the southmost is at 60 S line parallel to the Antarctic Sea (Rekestraw, 1943). This ocean is divided in the North Atlantic and the South Atlantic by this split in the water masses by the Equatorial counter-current (8° N). These two regions are different in water densities, temperature and each of these divisions has a main gyre. While the South Atlantic is broad and with a relatively straight coastline the North Atlantic narrows and has a coastline fairly irregular which creates several isolated water masses - seas. The North Atlantic counts with: the Caribbean, the Mediterranean and the Black, Norwegian, Baltic, Polar, Labrador, Baffin and Sargasso seas (the only sea enclosed by currents). These different seas are, effectively, barriers for biota dispersal for both lack of water flow among them and also different environmental conditions. Apart from this there is also a meridional division between East and West Atlantic. Despite the appearance of purely political division between East and West, there is a biogeographical reason behind it as this division represents an important barrier for dispersal of biota. The dispersal of a certain species is tightly linked to dispersal capabilities and availability of suitable habitats. Thus shallow water species with

poor dispersal capabilities cannot keep population between East and West of the Atlantic given that there is 1000 km (at least) separating the two coasts. With a basin at 5000 m depth but a mid Atlantic ridge at less than 200 m depth this structure provides an important dispersal barrier for benthic fauna even if the Gulf stream provides a pelagic opportunity to connect East and West. In my thesis I mainly treated sponge fauna from the North East Atlantic (NEA) or the Northern European Seas (Spalding *et al.*, 2007) (Figure 1).

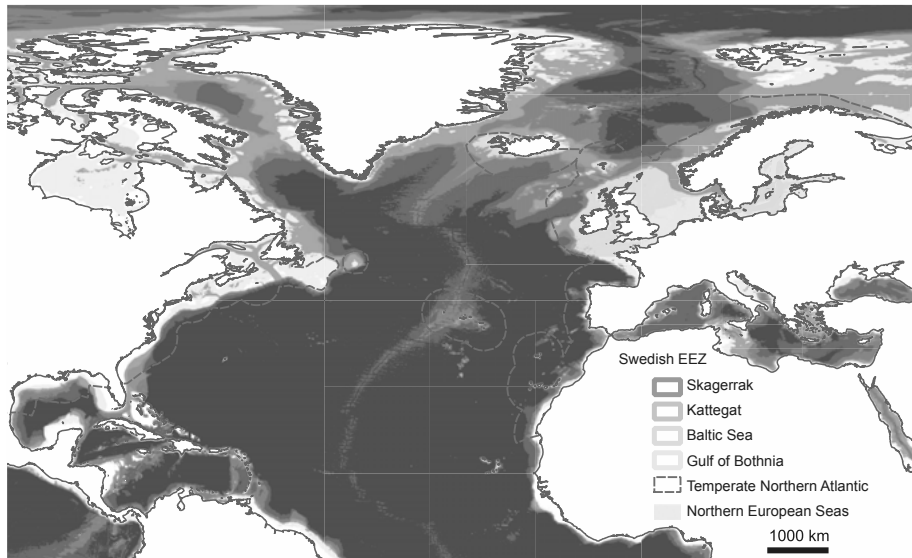


Figure 1. North Atlantic map. Bathymetry from ETOPO1 Arc-Minute Global Relief Model (doi:10.7289/V5C8276M). Borders in red represent the Temperate Northern Atlantic and in red-shade the North European Seas, both as defined in Marine Ecoregions of the World (MEOWs) (Spalding *et al.*, 2007). Swedish EEZ borders in yellow.

Swedish waterscape

Sweden is one of the largest European countries with an area of 528000 km², and a length of 1600 km long from North to South. Much of its land is, however, occupied by innumerable water masses. Apart from that, Sweden has an extensive and intricate coastline throughout Baltic sea and the Kattegat and Skagerrak areas encompassing 11600 km of very different topographies, environments and habitats.

Freshwater environment

There are nowadays 17700 lakes bigger than 104 km² mapped in Sweden (Westman *et al.*, 2017) with twice as many smaller lakes (Håkanson, 1994)

adding to this 136600 rivers and streams (Westman *et al.*, 2017) we obtain and land richly dotted by water. All of these elements are usually assembled into hydrological basins or catchment areas. The water masses among catchment areas do not mix, thus I hypothesised that these catchment areas could contribute to the sponge population variability as it has been shown previously (Dröscher & Waringer, 2007). In Sweden there are 267 main catchment areas (Danielsson & Andersson, 2020) which contain water masses running generally from North West to South East. The existence of well mapped roads helps to delineate the shortest roads to sample as many different catchment areas as possible fast as possible which was preponderant for the sampling in **Paper I**

Marine Environment

The marine environment of Sweden encompasses parts of the Gulf of Bothnia, Baltic Sea, Skagerrak and Kattegat (Figure 1). In total 70000 km² and a maximum depth of 725 m. Most of this area, however, belongs to the Gulf of Bothnia and Baltic Sea which due its brackish waters represents a difficult environment for both freshwater and marine fauna to live in (Berglund, 2015). Hence I will not talk about these areas in my work even though there are some freshwater sponges that can be found in the Baltic (near Stockholm coast).

The majority of my work will focus on the Kattegat/Skagerrak area of the Swedish marine jurisdictions. This area is of higher salinity due North Atlantic water input brought by a number of currents such as Fair Island Current and the European Slope Current. These currents are influenced *i.e.*, weakened or strengthened, by winds but also by the North Atlantic Oscillations (Winther & Johannessen, 2006). Finally, we have the deep current of Norwegian Trench input deep water. In addition to the Atlantic water input, which constitutes 79% of the water in the North Sea, there is still a very significant input from freshwater by the Baltic sea and run offs from nearby rivers (c. 10%).

The coast is topographically rich with a myriad of re-entrances, bays and small islands. However, the Swedish West Coast only possesses two true fjords: Idde fjord and Gullmars fjord. In these two fjords, the inlet is constrained by a shallow sill(s). The sill then creates a deep water area that is isolated from the rest of the ocean. The Idde fjord constitutes a natural border between Sweden and Norway. This fjord extends for 25 km and has four sills: Sponvika, Bjällvarpet, Svinesund and, Brattøya; in depths between 9 and 24 m. Ide fjord is divided into two basins the first being the deepest with 45 m maximum depth and 6.4 km long from Singlefjord in the west to the city of Halden in the Easter part. This fjord has a long industrial history that started in the 1860's but was especially intense in the beginning of the 20th century (Andreassen, 1974; Berge, 1994; Berge *et al.*, 1997) although, condition seemed to have improve considerably since the closure of the paper mill in the 1990's (Asteman *et al.*, 2015; Asteman & Nordberg, 2017). Gullmars fjord on other

hand, is solely Swedish, located roughly 70 km from Gothenburg on the Bohuslän coast and has a long history of fisheries but no heavy industries. Apart from local fisheries this fjord has three biological stations: Klubban Biological Station (Uppsala University), Kristineberg Centre for Research and Innovation (Gothenburg University), and Institute of Marine Research (Swedish Agricultural University). This fjord is 28 km long and 1 to 2 km wide with a maximum depth of 118 m. Gullmaren has a single sill of 42 m depth at the entrance (Filipsson & Nordberg, 2004). Due to its depth there is a strong water stratification in the fjord, which can be divided into three water masses. The deepest, coldest and most saline water mass only found below 50 m depth is the only place where *Suberites* spermatozoon was ever found in Sweden (Alander, 1942). I used some samples from both fjords together with other samples offshore to assess the demosponge species diversity in the Swedish West Coast **Paper II**. These fresh samples together with museum specimens from all over the world would allow me to start revising the Systematic with *Suberitida* **Paper III** and draw some conclusions on what species of *Suberites* existing in Sweden neighbouring countries and what their names are **Paper IV**. All my observations of current fauna are, however, prone to change, if not by my lack of reach then by the current threats/change that all ecosystems are under right now.

Threats

In fact all ecosystems around us are threatened. This is usually translated as loss of biodiversity. One of the major and greatest widespread threats is climate change that has as major consequence the increase of average temperatures. This, in aquatic environments will affect the amount of oxygen in the water thus causing more frequent or at the larger scale hypoxia events (e.g., Golosov *et al.*, 2012; Bendtsen & Hansen, 2013; Hetherington *et al.*, 2015). However, given that climate change happens due, mostly, the increase the CO² in atmosphere, there is a second consequence of climate change - acidification (e.g., Odén, 1976; Eriksson *et al.*, 1983; Ek & Renberg, 2001) which affects the existing biodiversity (e.g., Odén, 1976; Eriksson *et al.*, 1983; Brodin, 1995; Filipsson & Nordberg, 2004). Apart from climate change there are other anthropogenic pressure that are and will continue to affect the ecosystems: a) the contamination with pollutants such as heavy metals Dave & Nilsson, 1994; Kersten *et al.*, 1993; Renberg *et al.*, 2001; b) eutrophication (e.g., Bergstrand, 1990; c) browning of freshwater masses (e.g., Weyhenmeyer *et al.*, 2016; Kritzberg *et al.*, 2020) which affects the phytoplankton communities (Jones, 1992) and the distribution of heat and light at subsurface Ask *et al.*, 2009 and; d) overfishing, which affects mostly the marine areas (e.g., Svedäng, 2010; Baden *et al.*, 2012) and physical disturbance by the use of destructive fishing methods such as bottom trawling and more recently deep-sea mining

(Wedding *et al.*, 2015; Niner *et al.*, 2018) The changes induced by anthropogenic pressures seemed, at least in the marine environment, to remove the rare species from the ecosystem (Obst *et al.*, 2018). At the same time as all this changes and pressure are happening we remain ignorant of the sponges biodiversity that still remains.

What are sponges?

Human bias

When the word "animal" is uttered the vast majority of us will think firstly of a vertebrate - something big and emblematic. The existence of this taxonomic bias has been well reported among STEM (Bonnet *et al.*, 2002; Dunn, 2005; Titley *et al.*, 2017) and it seems to affect all human society including children (Snaddon *et al.*, 2008). In fact vertebrates represent only 4% of the known animal species. However, they do not only represent an unspecious group, they also represent a very restricted body plan and life strategies existing among the kingdom Animalia. Among these other groups (31 Phyla) there are living strategies and body plans that to us seem truly bizarre and alien. Yet the phylum Porifera remains one of the most neglected/understudied of all animal groups. Sponges (phylum Porifera) are usually described as simple, primitive and by what they lack rather than what they have *i.e.*, "lack of organs or tissues, very few of different cells..." (Simpson, 1984; Ereskovsky, 2010; Brusca *et al.*, 2016). While the "primitive" is easily tossed as reminiscent of ladder thinking the term "simple" seems to be a bit more difficult to argue against specially when the group is characterised for what it is not rather than what it is. This view, however, says much about the eyes of the beholder and nearly nothing about the monster itself a fact also pointed out before in Leys, 2003 and; Leys & Riesgo, 2001). In fact, if one was to characterise vertebrates the same way as sponges, the definition would come as something like: "Mobile animals with cells with predestined rigid fates thus, adult cells are incapable to transmute into others, lacking flagellated cells other than sperm cells. Incapable to filter-feed thus resorting to predation and with a very limited amount of commensal or symbiotic bacteria which are only present externally. Their lack of physiological and cellular plasticity means that these species are quite sensitive to environmental change, thus perhaps the reason why they evolved mobility". This vertebrate characterization really tells very little about the group. So in the next section I will give an overview of what a sponge is, rather than what it is not. I will further dwell into the most recent exchanges in the systematic especially regarding the order Suberitida (Chombard & Boury-Esnault, 1999) given that I, myself, attempted to solve some of its systematic problems during my Ph.D (**Paper III**) as well as explain a bit of what exactly a species is and what tools are used to assess species hypothesis given that I

have attempted to answer: How many *Suberites* species exist in Sweden and neighbouring areas and what are their names in **Paper IV**

Sponges

So sponges, phylum Porifera Grant, 1936 have as one of their most prominent characteristics the ability of filter feeding by using an intricate system of pores and canals called the aquiferous system. In fact, the name of the phylum can be literally translated into pore bearing. Their aquiferous system consist: in afferent pores (ostia) and, efferent, usually bigger openings (osculum or oscula, plural) which gives the name to the group; and a system of canals with choanocyte chambers lined with flagellated cells (choanocytes). These choanocytes maintain the unidirectional water flow by beating their flagella of the choanocytes and to lesser extent through contractions called sneezes (Elliott & Leys, 2007; Ludeman *et al.*, 2014). Despite their aquiferous system being their more characteristic feature, some sponges have lost this entire system and have evolved carnivory (Vacelet 2006 and Hestetun *et al.* 2015).

Up until recently, it was thought that, as adults, all sponges were sessile in their adult life. However, this fact was recently contested with photographic evidence of sponge trails (Morganti *et al.*, 2021). So it seems that, in this group, if we look long enough we will find exceptions to all rules. Sponges have two morphologically distinct epithelial cell layers: the pinacoderm composed by flat cells, the pinacocytes, which covers the surface of the sponge and aquiferous system canals and the choanoderm, composed by choanocytes. In between the epithelial layers, pinacoderm and choanoderm, there are a myriad of other cells usual mobile and pluri or totipotent and the skeletal parts which can be organic - collagen fibrils or spongin fibres - or inorganic, called spicules that can be constituted of calcite, aragonite or more commonly silica (Uriz, 2006). These acellular parts of the mesohyl, especially the mineral parts, are used by taxonomists for species identification and description but for the sponges they serve for support and protection. The mineral parts are produced by sclerocytes either internally in case of siliceous spicules (Müller *et al.*, 2006; Uriz, 2006) or externally for calcareous spicules.

The sponge feeding is perhaps one of the most strikingly different from the rest of the animal kingdom. Sponges feed by phagocytosis which usually occur in choanocyte chambers being the choanocytes the main responsible for the intake of particles. However, to a lesser extent, pinacocytes or directly archaeocytes (that enter in contact with the external environment through openings created by porocytes) can also phagocytize of the food particles. The preferred uptaken particles are usual bacteria (Simpson, 1984). Still some studies seem to indicate that dissolved organic material is also absorbed (Goeij *et al.*, 2008, 2013).

The reproduction can be both asexual (e.g. gemmulae in freshwater sponges) or sexual. In sponge sexual reproduction there are really few common elements across the phylum. They can be viviparous or oviparous, hermaphroditic or gonochoristic (Simpson, 1984; Ereskovsky & Tokina, 2007). In any case, the larvae or eggs released into the water column have enough nutrients within themselves to sustain their short free-living stage (Simpson, 1984; Maldonado & Riesgo, 2009).

Sponges are present in a wide geographical and bathymetric range that encompasses marine and freshwater environments, being found from the littoral to the hadal areas. Literally any water mass, regardless of how small it might be, is likely to have a sponge in it. They can even be found in artificial small garden ponds like the one near Blåsenhus (Uppsala University campus). In certain areas, sponges represent the majority of the benthic biomass (e.g., Klitgaard & Tendal 2004 or Murillo *et al.* 2012) providing three dimensional habitats for other fauna Bett *et al.* (1992); Cleary & Voogd (2007); E. *et al.* (2012) and also converting organic matter into more bioavailable forms Goeij *et al.* (2013); Maldonado (2015). Despite all this, we understand very little of how they manage to keep homeostasis and such plasticity. What are the mechanisms behind cell recognition, communication, what dictates cell fate and when are these fates "decided" or initiated? We do know, however, that sponge genomes seem to have some key genes associated with for example neuron signalling and development Riesgo *et al.* (2012) which are perhaps used in a different ways as hypothesised by Leys and collaborators (2015).

Nonetheless, sponges architecture might be a hint on how far back their phylogeny splits from all other animals. In fact, there has been a recent contention on whether sponges are the sister group to all other animals (e.g., Philippe *et al.* 2009; Pick *et al.* 2010; Feuda *et al.* 2017; Redmond & McLysaght 2021). As alternative hypothesis indicating comb jellies Ctenophora (Eschscholtz, 1829) as the most diverged animal phylum (Nosenko *et al.*, 2013; Whelan *et al.*, 2015; Chang *et al.*, 2015; Pandey & Braun, 2020). Sponges present a rich fossil record as far back as 500 Ma (lower cambrian) (Chang *et al.*, 2017; Tang *et al.*, 2019), biomarkers (chemical specific signatures) going as far back in time as 700 Ma (cryogenian period) (Love *et al.*, 2008; Zumberge *et al.*, 2018) seem to also indicate sponges are a earliest diverging animal lineage.

There are currently 9375 accepted/valid species and total species richness is predicted to be between 25800 and 26500 (Soest *et al.*, 2012; Appeltans *et al.*, 2012). However, given that the number of accepted names seems to still increase exponentially and especially accelerating since the end of 1990s (Figure 2), and that it is very difficult to assess the changes in research effort (as the research environment seems to have changed from single author effort to multiple authors consortiums), these estimates are unreliable.

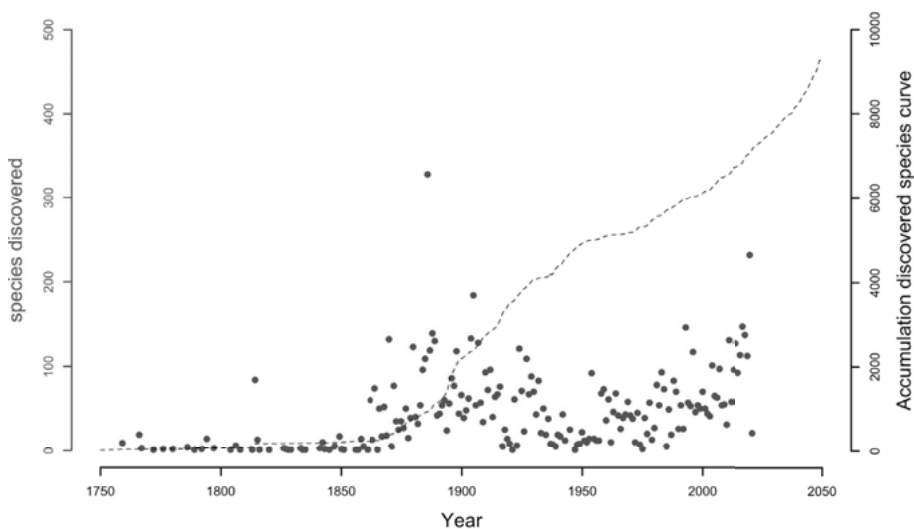


Figure 2. Plot of the number of valid sponge species described world-wide from 1754 to present day; blue dots indicate the number of species described each year and dashed line species accumulation curve. Data from World Porifera database, 2021-02-03 (Voogd *et al.*, n.d.)

Demospogiae systematics

Twenty years later, the classification in SP is quite outdated but, this book remains a good tool for both identification, as well study of the history of sponge taxonomy and classification. This publication made the sponge classification and taxonomy more accessible, being for sure an important milestone to bring sponge systematics to life. At the same time the use of molecular data started to become more common. In fact, the use of molecular data started with allozymes (Solé-Cava & Thorpe, 1987, 1986) but, soon the sequencing techniques caught up and DNA was preferred for it is easier to obtain and interpret than allozymes. Perhaps, one of most influential studies to start revising the class Demospongiae was one by Borchellini and collaborators (2004) where they purposed the removal of the Homoscleromorpha (as order Homosclerophorida) from Demospongiae to a class of its own and. The same study showed a clear evidence that the subclasses Tetractinomorpha and Ceratinomorpha were not monophyletic, and it named four clades well supported by the phylogenies using the Phylocode (Philip *et al.*, 2010) . Keratosa (G1) - Containing orders Dictyoceratida and Dendroceratida (which mostly lack of siliceous spicules); Myxospongiae (G2) - Orders Chondrosida; Halisarcisa and Verongida; Haploscleromorpha (G3) - With marine Haplosclerida; and Heteroscleromorpha (G4) - Agelasida, Handromerida (now split among seven orders), Halichondrida, Tetractinellida, Poecilosclerida and

Spongillina. These four clades were later confirmed by others using other molecular markers (Lavrov *et al.*, 2008; Sperling *et al.*, 2009) and later is implemented in Linnaean nomenclature (Cárdenas *et al.*, 2012). However, in this classification the groups within Heteroscleromopha (G4) represented unnatural classification with, among other issues, Halichondrida and Hadromerida as non-monophyletic (Chombard & Boury-Esnault, 1999; Erpenbeck *et al.*, 2006; Redmond *et al.*, 2013). In fact multiple orders at the time were non-monophyletic (Thacker *et al.*, 2013) and the possible cause being the use of morphological character that were homoplasious thus not suitable to infer the evolutionary history for the groups nor to circumscribe those same groups (Morrow *et al.*, 2013). It was only in 2015 that this problem was solved and a new classification that abandons all proven non-monophyletic "groups" to the family level (Morrow & Cárdenas, 2015). The systematics for the subclasses and orders has been stable since then. However, the same cannot be said for the family and genus level. In my Ph.D I attempted to solve some of the issues for the group Halichondriidae-Suberitidae (Suberitida) group which were known to have intertwining phylogenies.

Suberitidae-Halichondriidae

The family Suberitidae Schmidt, 1870 was created to encompass genera without cortex, confused choanosome and tylotes as spicules. The description, however, counted mostly with negative characters – "lack of cortex", or "lack of microscles", this while using characters that are difficult to infer such as "confused skeleton". So perhaps it comes as no surprise that this family ended up being a taxonomic wastebasket and source of much contention with genera subsequently had been included and excluded from the family. As for examples: Vosmaer, 1887 - includes *Rhizaxinella* Keller, 1880 *Stylocordyla* Thomson, 1873 in the family and excludes some polymastids and, interesting enough remarks that suberitids and halichondrids lookalike. Lendenfeld (1898) - disagrees with Vosmaer and adds back the polymastids previously removed. In 1892 Topsent - removes *Stylocordyla* from Suberitidae and created a new family, Stylocordylidae, Topsent, 1892. In 1900, Topsent lay a supra-family classification which became the most widely accepted until 2000's. In this classification Suberitidae and Stylocordylidae both appear in the same suborder Hadromerina and Halichondriidae is in a different suborder – Halichondrina. Both Halichondrina and Hadromerida were raised to order later (Laubenfels 1936). Still, given that both groups were circumscribed with characters they lack of characters it comes as no surprise that neither represented a natural group, *i.e.*, the classification did not reflect evolutionary history. This was exactly what Chombard & Boury-Esnault concluded in 1999 for the suborder Suberitina. However, the obvious paucity of morphological characters, which is the main culprit in these systematic changes, also resulted in a delay

in the adoption of this suborder. This, in spite of multiple subsequent studies confirming this result. The contention ended in 2015 with proposal for new demosponge classification upgrading Suberitina to order (Suberitida) (Morrow & Cárdenas, 2015).

The order Suberitida comprises of 26 genera in three families: Halichondriidae, Stylocordylidae and, Suberitidae; of which neither Halichondriidae nor Suberitidae are monophyletic with genera of both intertwining with each other. But, in order to solve any of these issues one would have to access type taxa for every genera and be sure that the identification is trustworthy. Neither of these requirements are easy to fulfil because: a) Some of the genera are rare, and have type species that have been sampled very few times (e.g. Halichondriidae: *Ciocalapata* Laubenfels, 1936 - *Ciocalapata amorphosa* (Ridley & Dendy, 1886) with only 7 reports; Halichondriidae: *Cryptax* Laubenfels, 1954- *Cryptax orygni* Laubenfels, 1954 with 1 report); b) the paucity of morphological characters in this group allied with old descriptions, which are often wanting in detail, makes the identification of new specimens complicated even with comparison of type material. Furthermore, the museum material often yields a low success rate in PCR and/or might be lost or in poor preservation conditions which the morphological comparison difficult and often subjective.

Suberites

To assign a specimen to the genus *Suberites* is an easy task. The genus is characterized by a velvety/microhispid surface, often with orange-yellow hue colour. Growing in dense mass, often contractile. Skeleton overall is confused apart from some protruding spicule bouquets at the surface. Spicules are tylostyles, subtylostyles and, often centrotyloted microrhabds. The assignment of a specimen to a particular species within *Suberites*, is, however far from a prosaic task because many of these species seem to have nearly no difference in spicule sizes and their external morphology is plastic. The genus was created to accommodate *Suberites domuncula* Olivi, 1792 and *Suberites ficus* Johnston, 1842. To this date, this genus counts 79 valid species of which 30 can be found within the Northern Temperate Atlantic biogeographic realm. Due to the shallow water nature of many specimens within the species though, there have been numerous authors, sampling, studying and attempting to classify or delimit species within the genus. The result is a vast synonyms list for many of the species presently accepted (e.g., Vosmaer 1933 or Burton 1953). The synonymies or what the correct name for some of these species is, was, already, partially addressed Soest *et al.* 2020, but still much was left to be done since types have not been looked.

Molecular markers

One of the main issues studying sponge diversity is the lack of good markers that are: a) easy to amplify or obtain; b) with a substitution rate that is capable of resolving phylogenies to the family or genus level. This problem is especially frustrating given the amount of animal groups now relying on genomics to tackle the same kind of questions while the use of genomics in sponges is still not very well established due the difficulty to obtain clean data (see Mariani *et al.* 2019).

On the other hand, given the age of some clades it is safe to assume that the fixation rate in different loci is different for different groups hence making it unlikely that the same regions would solve inner clades across groups. Regardless of these annoyances and difficulties, some studies have managed to indeed improve our resolution of the phylogenies within families, as for example: The use of DNA encoding for small and large subunit of ribosomal RNA and partial genes *coxI* (both Folmer fragment and extended) and *alg11* shows monophyly of Cladorhizidae Dendy, 1922 and it is sister to Guitarriidae Dendy, 1924 and Mycalidea Lundbeck, 1905, (Hestetun *et al.*, 2015); or phylogeny based on *coxI* and DNA encoding region for big ribosomal RNA subunit show non-monophyly of the genera within family Polymastidae Gray, 1867 (Plotkin *et al.*, 2017); use of DNA encoding for 18S and 28S (fragment D3-D5), *coxI* gene (M1-M6 partition) shown cryptic species in Hemimycale in the Mediterranean sea and polyphyly for the genera *Hemimycale* and *Crella* (Uriz *et al.*, 2017). In addition some effort have been made in species delimitation using multiple loci as for example; several primers for mitochondrial genes, allegedly more polymorphic than *coxI* (Rua *et al.*, 2011)) were shown useful to access population isolation and existence of cryptic species in barrel sponges (Swierts *et al.*, 2013, 2017), the use of the internal transcribed spacer regions (ITS for populations *Ianthella basta* (Pallas, 1766) (Andreakis *et al.*, 2012) or, the use of *coxI* (fragment I3-M11) in *Phorbas fictitius* (Bowerbank, 1866) and *Cliona celata* (Grant, 1826) allowed to discriminate population structure in the Atlanto-mediterranean region (Xavier *et al.*, 2010). Finally, the use of use of non-targeted sequencing techniques such as RADseq (Leiva *et al.*, 2019; Maas *et al.*, 2020). This and other non-target sequencing techniques have the drawback of sequence whatever is in and on or have been the vicinity of the sponge sample (Mariani *et al.*, 2019), which can be in the end the bulk of one sequences (Steffen, 2022). This fact makes the downstream analysis of the data extremely difficult at least with nowadays bioinformatics.

Sponge Barcoding Project

Molecular data can be used to infer evolutionary history and create a classification that respects (as in above). Alternatively the same data can be used for discrimination and identification or taxa, either in a phylogenetic frame work

or simply by similarity. The DNA barcode started with the idea to standardise species discrimination across big groups by having the same molecular marker and primers across groups. For animals the proposed region was *coxI* (Hebert *et al.*, 2003). Since then, many initiatives have been launched, but maybe the most important was the BOLD system (Ratnasinghan & Herbert, 2007) which aimed to store high quality information of the specimens together with the sequences. For sponges, there has been a Sponge Barcoding project since 2006 (Wörheide & Erpenbeck, 2007) and included several campaigns of sequencing including the attempt to obtain museum specimens sequences (Vargas *et al.*, 2012).

Recent sponge diversity surveys

Despite the promising start for sponge studies of the 2000's, sponge surveys studies still seem a rarity, appearing only sporadically. This fact is in part due the fact that sponges are benthonic and humans do not breathe water (this is an obvious statement) and in part because there is no way to accurately and precisely identify sponges on site. Thus to identify them one will need a lot of space time and resources allocated on collection and preservation of specimens. Plus, the identification in the lab requires trained operator time and resources. To worsen the situation, much of the species described, accepted and common still lack of a published barcode (see examples in **Paper II**), that could be used for faster identification and/or less rigorous surveys. Nowadays, it is common for scientific campaigns to not collect sponges all together or if they do the results often lag behind compared with other biota. Nonetheless, there are some recent good examples of sponge diversity surveys as for example: The survey on demosponges species diversity in South Africa with the creation of a barcode library associated (Ngwakum *et al.*, 2021); Studies on rock sponges in the North East Atlantic (Xavier *et al.*, 2021; Carvalho *et al.*, 2020); The description of species of carnivorous sponges (Demospongiae) in Marina Island (Hestetun *et al.*, 2019), what freshwater sponges can be found UK (Evans, 2017), Mozambique (sea water) (Calcinai *et al.*, 2020) or (sea water) Hawaii (Pons *et al.*, 2017). In **Paper I** and **II**, I too attempted to contribute with demosponge species surveys.

Why study sponge diversity in Sweden?

In 2001, Sweden created the Swedish taxonomic initiative which aims to describe all multi-cellular species in the country and to provide, to the general public, identification keys ("Nationalnyckeln"). For sponges, and many other groups, however, this description could never be complete without a taxonomic and systematic revisions. The description of a species requires a formal name (in this case ICNZ) and, also a circumscriptions with a classification

that reflect the evolutionary history of it. Much of the sponge fauna in Sweden lacks both these requirements. Sponges are highly understudied in Sweden. There has not been an update on the Swedish Sponge Fauna in the last 80 years for neither freshwater nor marine environment. When I started my Ph.D the species richness of this group of animals is low in Sweden when compared to the neighbouring regions counting with only 154 species in total in Sweden in contrast with circa 360 species known for Norway (Oug & Rapp, 2015). It is in this context that both the update for the freshwater sponge fauna **Paper II** and the one marine for marine demosponges fauna are inserted.

Aims

The general aim of my work is to revise the demosponge diversity in Sweden, from species richness to population structure together with the phylogenetic relationships for the taxa found. For **Paper I**, I focuses on the freshwater environment and, not only species richness but, also population structure for one of the species - *Spongilla lacustris* (Linnaeus, 1759) to attempt to answer: Do the catchment areas represent a dispersal barrier for the species?

In **Paper II** we focus on species richness assessment of a broad sampling constituted by dredging by the Swedish Taxonomic Initiative (STI) and SCUBA diving in an attempt to close the knowledge gap on demosponges species diversity. For this we used both molecular data: standard barcoding regions *coxI* Folmer *et al.* (1994) and the DNA encoding region of 28S (D3-D5 fragment) (Morrow *et al.*, 2011) and morphological data. In **Paper III**, I produced a phylogeny for the order Suberitida obtain an overview of the phylogenetic relationships within it (see Introduction) and in **Paper IV**, I attempted to answer: How many *Suberites* species seem to exist in Sweden and in a broader sense Northern European Seas, in and what are their correct names? I conducted these two last studies because a large number (16%) of all specimens collected in **Paper II** happened to be within order Suberitida with several species of *Suberites*. However, clades within the order Suberitida was known for being difficult to classify and discriminate thus in order to know what names to give to the specimens collect one would have to infer their genealogies and to survey the previous descriptions for the group.

Material and Methods

Collection

I wish I could start this section with wondrous tales of places I visited to collect my specimens. However, the vast majority of the material I have examined was already long dead and preserved in spirits when I acquired them. While for faunistic assessment recently collected specimens are best because their better preservation state means that both molecular and morphological data are easier to obtain, to study the systematic of a group, where specific determination is difficult, one would need to visit the historical collections that have the name-bearing specimens (types) or that, at least were identified by the same authors that circumscribed the taxon in the first place. So my sampling mostly looked like a small desk-space at a collection of a museum covered with jars full of spirits and sponges. The bulk of specimens I have collected have been preserved from the 19th and 20th century, the oldest being from 1844. The majority of museum specimens had been collected by bottom trawling.

Besides museum specimens, I also had some specimens collected for me when I arrived at Uppsala, namely the STI collection and some specimens collected by students and staff at Klubban. Without the later contribution I would have never been able to have fresh material for many of the *Suberites* species dealt with in **Paper IV**, especially *Suberites spermatozoon* (Schmidt, 1868). Furthermore, some of the specimens were donated.

Finally, on a whim typical of a Ph.D student I too succumbed to collecting more than I could examine by summer 2017, collecting in the freshwater environment. In total I accumulated c. 1600 specimens at the SystBio cold storage room.

Data management

To take care of such collections and keep track of what has happened or what needs to be done one needs a Laboratory Management System (LIMS). For that our group has created the Porifera Taxonomy Workgroup database (Por-Tax) written as a SpringBoot Java application with a ExtJS javascript front end and a mySQL back end. The same way, in order to keep track of all previous taxonomic work within *Suberites* we had the need to create a tool to manage information on taxon names in the literature and their relationships throughout history, and have the relation between publications. This is how Gossip came

to be useful, by allowing the visualisation of relations of names and opinions in a network or timeline. Another issue handled with Gossip was the amount of previous taxonomic work with genus *Suberites* which, in order to have a thorough taxonomic review, we would have to evaluate *i.e.*, agree or disagree with. Some of these species had several pages of synonymies, thus I would likely get lost in the literature review for the taxonomic work (Figure 3) if I had no aid. Gossip is implemented much like PorTax but with a graphical database (Neo4J) as back end (Thollessen, 2017).

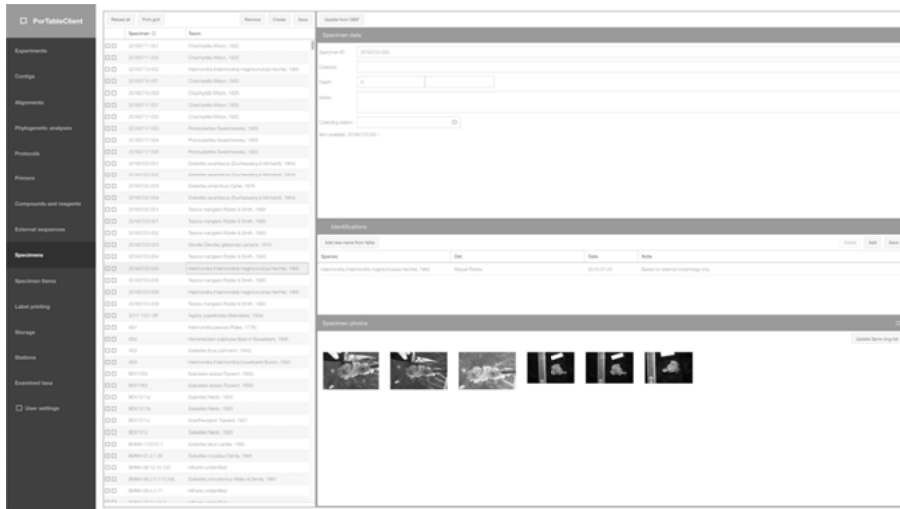


Figure 3. Portax user interface rate (Thollessen, 2017)

Morphological identification

In sponge identifications, the external morphology is usually regarded as uninformative. Although in a small study area with a well curated database some attempts have been made to use external morphology for identification e.g. (McIntyre *et al.*, 2016). In order to identify a demosponge one usually uses microscopical characteristics, namely what type of spicules and their size and what is their skeletal conformation. Like in any other group, each of these elements have a specific name. In my case I followed The Thesaurus of Sponge Morphology (Boury-Esnault & Rützler, 1997) and SP (Hooper *et al.*, 2002) throughout my Ph.D.

To observe these characters one has: a) to make thick sections, by hand. So after having the thick section and the spicule slide (for the demosponges with spicules), one must compare it with the literature. If lucky one can arrive at the genus or family level using the keys in SP (Hooper *et al.*, 2002) and then compare the literature for the region or neighbouring regions. Fortu-

nately, for the marine environment in Sweden there was already a good morphological study from the 1940's (Alander, 1942). Furthermore, good work has already been published for the British Islands (Ackers *et al.*, 2007) and NEA (Soest *et al.*, 2000). However, in case of doubt one should compare the material with the original description which are usually available in World Porifera Database (WPD) (Voogd *et al.*, n.d.) or in Biodiversity Heritage Library (<http://www.biodiversitylibrary.org>) (BHL). In case the textitSuberites and Suberitida(e) the problem was more complex with original description very short or very little information, some of which with spicule names pre-dating what is now used as standard, or without spicules mentioned and with several synonyms so for solving that one will have to go through types of the said taxon, a reason that explains my sampling strategy (see above). For the freshwater environment, we had only one order, with about 200 accepted species of which we already knew of three existing in Sweden (all in a single family: Spongillidae Gray, 1867) (Arndt, 1932). So the identification was relatively simplified. Furthermore, there were other recent studies for neighbouring countries (Tendal, 1967; Richelle-Maurer *et al.*, 1994; Roovere *et al.*, 2006; Evans & Montagnes, 2019) which further narrowed our identification process.

Molecular markers and Phylogenetics

There is a myriad of molecular markers that have shown useful for animal phylogenetics. For demosponges, although less abundant, there are still a considerable amount of molecular makers/primers published throughout the last 30 years. So when looking at literature there is a question that arises: What markers should one use for the study in question? In an ideal world, one could have several independent single copy markers with an amount of variation capable of answering our questions: being species discrimination or resolving deeper nodes in a phylogeny. Unfortunately, to be sure what markers to use, we still resort to trial and error. In Table 1 you can find some of the primers I tested during my Ph.D. However, for a complete overview one must add the supplementary file 1 of **Paper I**. During my Ph.D I have tested for mitochondrial markers: *coxI* (folmer region) (Folmer *et al.*, 1994), the extension I3-M11 (Erpenbeck *et al.*, 2002), which presents bigger variation, in sponges, than the standard barcoding regions (Erpenbeck *et al.*, 2006) and for old samples I employed the mini-barcodes (Meusnier *et al.*, 2008) given that this strategy was shown successful for sponges before (Cárdenas & Moore, 2017). Apart from this I attempted to amplify 16S (Palumbi, 1996) and ATP6 (Rua *et al.*, 2011).

Table 1. List of Primers tested in addition to EPIC primers stated in Supplementary file 1 **Paper II**. Forward direction primers are indicated with "fwr:" and reverse with "rev: "; some primers for 18S (Redmond *et al.*, 2013) we used just for sequencing "[Seq]" while the ones used for both PCR and sequencing are marked with "[PCR & Seq]" .

Marker	Direction : Primer	Publication
coxI Folmer	fwr:LCO1490-GGTCAACAAATCATAAAGATA TTGG rev:HCO1490-TAAACTTCAGGGTGACCAAAAA ATCA fwr:dgLCO1490-GGTCAACAAATGATAAAGA YATYG rev:dgHCO2198-TAAACTTCAGGGTGACCAAA RAAYCA fwr:Uni-MinibarF1-TCCACTAATCACAARGAT ATTGGTAC rev:Uni-MinibarR1-GAAAATCATAATGAAG GCATGAGC	Folmer <i>et al.</i> (1994) Meyer <i>et al.</i> (2005) Meusnier <i>et al.</i> (2008)
I3-M11	fwr:CO1porF1-CCNCANTTNKCNMGMAA AAAAACA rev:CO1porR1-AANTGNTGNGGRAARAANG	Erpenbeck <i>et al.</i> (2006)
16S	fwr:16sar-CGCCTGTTTATCAAAAACAT rev:16sbr-CCGGTCTGAACTCAGATCACGT	Palumbi (1996)
ATP6	fwr:ATP6porF-GTAGTCCAGGATAATTAGG rev:ATP6porR-GTTAATAGACAAAATACATAA GCCTG	Rua <i>et al.</i> (2011)
28S D1-D2	fwr:Por28S-15F-GCGAGATCACCYGCTGAAT rev:Por28S-878R-CACTCCTTGGTCCGTGTTTC	Morrow <i>et al.</i> (2011)
28S D3-D5	fwr:Por28S-830F-CATCCGACCCGTCTTGAA rev:Por28S-1520R-CATCCGACCCGTCTTGAA fwr:RD3a-GACCCGTCTTGAAACACGA rev:RD5B2-ACACACTCCTTAGCGGA	McCormack & Kelly (2010)

28S D6-D8	fwr:Por28S-1490F-AACTCACCTGCCGAATCAAC rev:Por28S-2170R-CCAATCCTTTTCCCAARGTT	Morrow <i>et al.</i> (2011)
18S[PCR & Seq] 18S[Seq]	fwr:1f18S-AACCTGGTTGATCCTGCCAGT rev:1800R18S-GTTCACCTACYGAAACCTTGTT fwr:560F18S-GAGGAACAATTGGAGGGC rev:600R18S-CGAGCTTTTAACTGCAA rev:1350R18S-CGGGACTAGTTAGCAGGTAA	Redmond <i>et al.</i> (2013)
ITS1-5.8S-ITS2	fwr:RA.2-GTCCCTGCCCTTTGTACACA rev:ITS2.2-CCTGGTTAGTTTCTTTTCCTCCGC fwr:Fw13-ACACACCGCCCGTCGCTACTA rev:1278-CTYYGACGTGCCTTTCCAGGT	Wörheide <i>et al.</i> (2004-12) Maikova <i>et al.</i> (2010)
ATPase β	fwr:ATPSbf1-CGTGAGGGHAAYGATTHTACCA TGAGATGAT rev:ATPSbr1-CGGGCACGGGCRCCDGGNGGTT CGTTCAT fwr:ATPS β -F-ATGAGATGATCACATCAGGTG rev:ATPS β -R-GGTTCGTTCATCTGTCC	Jarman <i>et al.</i> (2002) Swierts <i>et al.</i> (2017)
<i>alg11</i>	fwr:ALG11-D1-TTYCAYCCNTAYTGAAAYGCN GGNGG fwr:ALG11-D2-TGYAAYGCNGGNGGNGGN GGNGA rev:ALG11-R1-ATNCCRAARTGYTCRTTCC ACAT rev:ALG11-R2-CCRAARTGYTCRTTCCACAT NGTRTG	Belinky <i>et al.</i> (2012)
Histone 3	fwr:H3F-ATGGCTCGTACCAAGCAGACVGC rev:H3R-ATATCCTTRGGCATRATRGTGAC	Colgan <i>et al.</i> (2000)

The DNA region encoding for rRNA (18S and 28S, also referred as small ribosomal and large ribosomal RNA) which has its amplification success influenced by the possible folding structure that single strands of DNA may create during PCR. Plus, these are multicopy regions which, however, present concerted evolution. The existence of several identical copies render these regions, and nay mitochondrial marker, easy to amplify. Furthermore, some areas of DNA region encoding for rRNA are conserved even from far related

organisms making them attractive for solving deep phylogenies. In my work I have used DNA encoding region for 28S partitions: D1D2, D3D5, and D6D8 (McCormack & Kelly, 2010; Morrow *et al.*, 2011) and encoding for 18S (Redmond *et al.*, 2007) (Figure 4). Furthermore, attempt to use DNA encoding for ITS1-5.8S-ITS2 (Wörheide *et al.*, 2004-12) for potentially being more variable than DNA encoding regions for 18S or 28S.

Apart from these I also tested the following nuclear markers: Exon-Primed-Intron-Crossing (EPIC) markers (Chenuil *et al.*, 2010) (see supplementary file 1 in **Paper I**); ATPase β nuclear intron (Swierts *et al.*, 2017; Jarman *et al.*, 2002); *alg11* (Belinky *et al.*, 2012); Histone 3 (Colgan *et al.*, 2000) (see Table 1). All these nuclear markers have an uncertain position in a sponge genome (but see nuclear positions prediction).

After obtaining sequences I used BLAST (Altschul, 1990), as a method to assess possible contamination with other organisms, namely humans, and select homologous sequences already published. The sequences per maker were aligned creating a matrix with homologies hypothesis per nucleotide position or so-called multi sequence alignment. For **Paper I** we used distance based methods to compute the phylogenies and networks. For the remaining papers we inferred phylogenies using Maximum Likelihood (**Paper II** and **III**) or Bayesian framework (**Paper III** and **IV**). It is important to note that my implementation of Bayesian phylogenetics was done with MrBayes (Ronquist & Huelsenbeck, 2003) which allows for MCMCMC but does not allow to implement all the evolutionary models. This could have been circumvented using (Höhna *et al.*, 2016) RevBayes (Höhna *et al.*, 2016) but, unfortunately that program requires much trial and error to build an effective and convergeable MCMCMC. Furthermore, Bayesian phylogenetic inference seems to perform well in overparameterized models (Lemmon & Moriarty, 2004; Huelsenbeck & Rannala, 2004; Fabreti & Höhna, 2022), which is, effectively, the choice I made when the best model in Akaike information criterion (AIC) was not available in MrBayes.

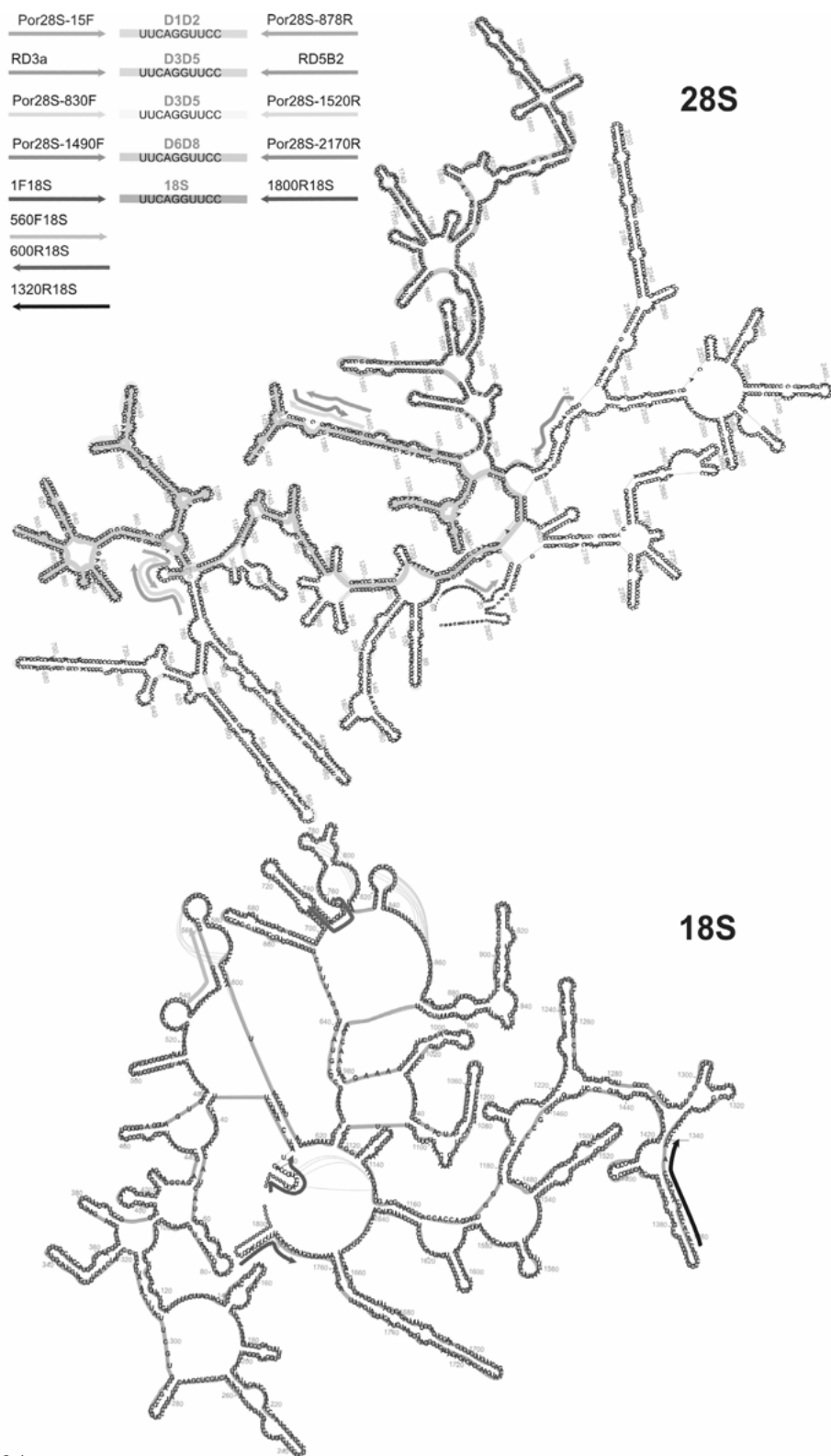


Figure 4. 28S and 18S structure, with the primers tested and the extentation of the predited PCR product. 28S structure predicted using RNAfold web server (Gruber *et al.*, 2008), using *Halichondria okadai* full 28S (AB511881); 18S for *Halichondria melanodocia* (AY737639) structure downloaded from Database for SSU rRNA secondary structures of Porifera (Voigt *et al.*, 2008). Structure drawn in RNA3draw (Johnson *et al.*, 2019)

Results

Successful markers

In this section I will be describing the main results of my thesis. However, because I think it is relevant for any future studies but the results are not publishable elsewhere, I will firstly talk about which primers/markers worked and which did not.

For the mitochondrial genome *coxI* folmer (Folmer *et al.*, 1994) with the standard primers seemed to work very well in all samples except for the samples within the genus *Hymedesmia* (Bowerbank, 1864) **Paper II** so we attempted to use the 16S Palumbi primers (Palumbi, 1996) but equally without success in amplifying. ATP6 (Rua *et al.*, 2011) which presented low variability for *Spongilla lacustris* and did not amplify DNA extracts for specimens of *Suberites*. For the DNA encoding for the ribosomal region the 18 primers (Redmond *et al.*, 2007) present good PCR success. However, the primer 1F18S seems too often yields bad/dirty electropherograms. Furthermore the sequencing requires at least five primers (Table 1) to create a good contig while amplifying only 1800 bp, whereas the 28S requires six primers but results in 2700 bp thus the sequencing for 18S is considerably more expensive than for 28S. For the 28S, the primers for Morrow and collaborators 2011 are successful in amplifying and sequencing any specimens tested. The primers for the region D3D5 worked especially well for amplification and sequencing. This contrasts with the primers from (McCormack & Kelly, 2010) (RD3A and D5B2) that were less successful at amplifying and often had sequences contaminated with dinoflagellates, as previously noted (Morrow *et al.*, 2011). The primers used for ITS were successful in amplifying, however the sequences presented intragenomic variation which makes its use for phylogenetics troublesome. Regarding other nuclear markers: Exon-Primed-Intron-Crossing (EPIC) markers (Chenuil *et al.*, 2010) (see supplementary file 1 **Paper I**) of which only one primer pair worked for the freshwater population study; ATPase β (Swierts *et al.*, 2017) nuclear intron all of the primers failed to amplify for suberitids and shown low variation in *S. lacustris*; Histone 3 (Colgan *et al.*, 2000) are difficult to amplify and shown no differences in the sequences produced for specimens of different *Suberites* species; finally, *alg11* did not amplify easily and, with the current degenerated primers (Table 1) it is impossible to obtain good electropherograms without optimizing the sequencing run conditions.

Demosponge Fauna in Sweden: an update

At the start of my Ph.D, the Swedish sponge fauna had more than 80 years hiatus in both marine and freshwater environments. So one of my contributions is invariably to update the checklist of sponges species for Sweden. For that my collaborators and I used both morphology and *coxI* and 28S D3-D5 (Morrow *et al.*, 2011), in a total of 560 specimens examined (**Paper I** and **II**). These specimens represent a sampling effort of 68 freshwater stations within 12 catchment areas, 124 STI trawling stations and nine SCUBA diving spots in addition to data Gullmars fjord with R/V Belone, within the framework of Uppsala University courses.

Freshwater environment

From our sampling in the freshwater environment we found one new report for the freshwater environment: *Eunapius fragilis* (Leidy, 1851). However, our sampling was restricted to the southern area of Sweden and only shallow water, thus it is possible other species, such as *Trochospongilla horrida* (Weltner, 1894), to be present in Sweden freshwater environment. *Spongilla lacustris* was the most commonly found species in freshwater thus we used specimen of the species for the phylogeography assessment and answer: Do catchment areas represent a dispersal barrier?

From the primers tested, unfortunately only one pair seemed to amplify with moderate success rate. However, when using that marker/primer pair for phylogeography study on *S. lacustris* we found more variation within catchment areas than between catchment areas hence we cannot infer if nor how much catchment areas represent a dispersal barrier for this species **Paper I**.

Marine environment

In the marine environment we found eight new reports for the Swedish west coast: *Aplysilla glacialis* (Merejkowsky, 1878) , *Grambe stillifera* (Goodwin & Picton, 2009), *Hymenaphia elongata* Picton & Goodwin, 2007, *Hymedesmia jecusculum* (Bowerbank, 1866), *Hymedesmia hibernica* Stephens, 1916, *Phorbas dives* (Topsent, 1891), *Mycale macilenta* (Bowerbank, 1866), and *Raspailia aculeata* (Johnston, 1842). Furthermore, from the STI sampling we found a species new to science: *Halisarca* sp. "hansghanssoni". However, 56% of the species had three or less specimens which, together with the disjunction from the demosponge fauna reported in previous studies, might indicate that the description of the Swedish marine demosponge fauna is not yet complete. Furthermore, we found that many of the sponge specimens from Jägerkiöld's campaigns stand unidentified 1938 thus we cannot infer if there has been a shift on demosponge fauna in Sweden. Finally, 16% of all specimens belonged to the family Suberitidae (order Suberitida).

However this family is known for: a) is paucity of morphological characters to enable the identification to the species level; b) do not correspond to a natural group *i.e.*, it is non-monophyletic and in fact species from this family intermingling with halichondriids in several studies (Chombard & Boury-Esnault, 1999; Erpenbeck *et al.*, 2006; Morrow *et al.*, 2011; Thacker *et al.*, 2013; Redmond *et al.*, 2013; Morrow & Cárdenas, 2015). Consequently, in order to know the diversity of marine demosponges in Sweden one would have first to solve some of taxonomic and systematics issues in this group.

Suberitida Systematic insight

So in **Paper III** we used both museum specimens and freshly collected material with nearly DNA encoding regions for 28S, 18S and *coxI*. we concluded that there are two separated clades constituting *Suberites*: One containing *S. domuncula* and *Suberites* species with microrhabds (clade A), and the second one with *Suberites carnosus* (Johnston, 1842), *Suberites massa* Nardo, 1847 and species from e.g., Caribbean sea - *Suberites aurantiacus* (Fonbressin & Michelotti, 1864) and Indonesia - *Suberites diversicolor* Becking & Lim, 2009 that have a radial skeleton near the surface of the sponge (clade B). Clade B appears together with *Aptos* Gray, 1867 and *Homaxinella flagelliformis* Ridley & Dendy, 1887 and with *Stylocordyla* Thomson, 1873 as sister to that clade. Thus we suggested expanding the family Stylocordylidae circumscription to include clade B, *Aptos* and *Homaxinella flagelliformis*. This means that the *Suberites* species of the clade B need to be removed for the genus *Suberites* and the family Suberitidae and the species *H. flagiliformis* too needs to change genus and move from Halichondriidae. Furthermore, *Homaxinella subodola* (Bowerbank, 1866), and *Vosmaeria crustacea* (Fristedt, 1885) appear in a together in a clade sister to the group Halichondriidae-Suberitidae-Stylocordylidae, thus, likely needing to be moved to their own separated family with *H. subodola* in need to be moved from the genus *Homaxinella* and family Suberitidae.

How many *Suberites* species and what are their names

So **Paper III** where we split *Suberites* without finding a proper name for the clade without the type species *i.e.*, clade B, nor did we know what names should be kept for species comprising *Suberites* and which synonymizations were erroneous. This is when Gossip (Thollessen, 2017) comes into play to assist in the network of species hypothesis and names published throughout the 260 years of Linnaean taxonomy. This combined with molecular and morphological data of both fresh and museum material encompassing 18 species all in the Northern Temperate Atlantic biogeographic realm. The Phylogenetic analysis resulting from *coxI* alignment and mitochondrial genomes **Paper IV**

agreed with each other and, with **Paper III**. *Suberites* as it stands with the current circumscription is paraphyletic. Thus, based on that result and the literature review we concluded that clade A (**Paper IV** should remain under the names *Suberites* Nardo, 1833 while the best fitting name for clade B should be *Syringella* Schmidt, 1868 which we propose to resurrect (**Paper IV**). Using morphology reported for recently described species we assigned them to either of the genus. We hypothesise that *Suberites ficus* and *Suberites suberia* (Montagu, 1814) are the same species and given that *Suberites suberia* precedes the name *Subrites ficus* has to change to *Suberites subereus* (epithet changed to be congruent gender of the genus). Furthermore, we find that *Suberites virgultosus sensu* Johnston (Johnston, 1842) and *Suberites virgultosus sensu* Bowerbank (Bowerbank, 1866) are different species. Given the homonym *i.e.*, *Suberites virgultosus* name being already in use when Bowerbank described his species I decided to create a new name for Bowerbank species - *Suberites* sp. "misterbeanii" (**Paper IV**. Some *Suberites* species seem to have cosmopolitan distribution or different external morphologies present in the same area. Therefore, we are inclined to believe this species are in fact, species complexes although such need to be confirmed with molecular data.

Concluding Remarks

This thesis presents an update of demosponges species existing in Sweden. Moreover, it solves some of the systematic issues within Suberitida by circumscribing the genus *Suberites* and assessing what species exist, which species hypothesis can be refuted and what are their correct names (under IZCN). This work is, however, wanting and I truly wish to be considered outdated as soon as possible.

Plausible or near future perspectives

For the freshwater review I would like to do a more thorough sampling in a larger area than what was sampled in **Paper I**. Furthermore, given the existence of chromosome level genome assembly for *E. mulleri* (Kenny & Itskovich, 2020) show how it is possible to obtain good genomic data out of a sponge and create gemmules. Thus, I think by either: a) using *E. mulleri* with the reference genome to obtain more markers suitable for phytogeography and population genetics or; b) by using the same strategy that Kenny to obtain a good reference genome for *Spongilla lacustris* and then make a marker search; is a very much near future (present time even) possibility.

For the marine environment, I would like to examine the sponge specimens collected in the Jägerkiöld survey (1936-1938) in order to assess if there has been any shift in the sponge fauna in the same way it happened with other taxa (Obst *et al.*, 2018).

For my taxonomic and Systematic work with Suberitids, I have not found much morphology to work with, so it would be good to assess if there is any chemical synapomorphy for *Suberites* and closely related clades.

Finally, I think, it is very much feasible to obtain fresh material of *Suberites domuncula* or *Syringella carnosus* from different regions to assess: How many species each group truly constitutes using mitochondrial genomes.

Shenanigans or far future perspectives

Apart from palpable, currently executable, additions there are other works in need to be done but of which I do not know about their feasibility or rather I suspect that they are rather difficult to achieve. Firstly, I have not examined nor identified any calcareous sponges even though Mats Larsson has photographed

and collected some quite beautiful specimens (Figure 5). Then, as you may have noticed, my attempts to find primers that work for my group were, at large, futile. I could have attempted to use RADseq but studies have found massive, contamination problems using this method without a published reference genome. However, Suberitida has some species that grow fast and in shallow water, so perhaps, one could use one of those species growing in a nearby a research station to optimize a protocol for single nuclei sorting which will, likely, bypass the intracellular contamination problem allowing for cleaner sequencing. This would be the first step to obtain a first reference genome for the group and allow for a creation of ultra conservative elements probes which could potential shed a better light over Suberitida systematics either/or *Suberites* species delimitation. Furthermore, these probes would have potential to work with old museum specimens.

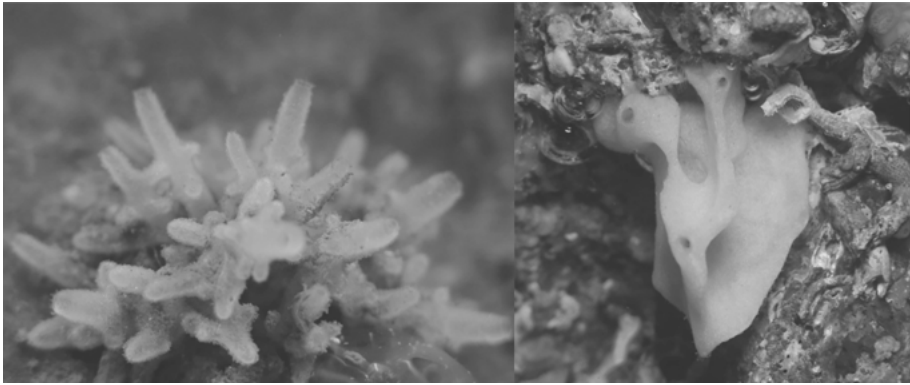


Figure 5. In situ photography of some calcareous specimens already collected. Photos by Mats Larsson

Svensk sammanfattning

Dokumentationen av den svenska svampdjursfaunan har inte uppdaterats på över 80 år. Detta faktum kan till viss del förklara varför diversiteten inom svampdjur har setts som lägre i Sverige än i närliggande länder. I denna avhandling har jag genomfört en uppdatering av Horn- och kiselsvampar (Demospongiae) i svenska vatten (**Artikel II**). Jag har också studerat släktskapsförhållanden inom Suberitida, den vanligaste gruppen svampdjur i Sverige (**Artikel III** och **IV**) och studerat spridningsbarriärer för svampdjur i Svenska sjöar och vattendrag (**Artikel I**). För dessa studier har jag använt svampdjur som vi samlat in speciellt för denna avhandling, tillsammans med material från muséesamlingar och från det Svenska Artprojektets marina inventering (2007-2009), och jag har använt mig av både morfologiska data och fylogenetiska analyser för att dra mina slutsatser. Sammanlagt hittade vi nio arter som tidigare inte beskrivits från Sverige (en i sötvatten och åtta i havsvatten), samt en art som tidigare inte beskrivits i den vetenskapliga litteraturen.

I studien som fokuserar svampdjur i Svenska sjöar och vattendrag (**Artikel I**) använde vi oss av arten *Spongilla lacustris* för att undersöka om vattendelare utgör spridningsbarriärer. Vi använde oss av genetiska markörer, men dessa kunde inte visa på någon populationsstruktur inom arten.

I studien av svampdjur i svenska havsvatten (**Artikel II**) märkte vi att de en stor andel av de identifierade proverna tillhörde ordningen Suberitida, och mer specifikt var släktet *Suberites* välrepresenterat. Detta släkte, liksom många andra taxa inom Suberitida, har en lång och komplicerad taxonomisk historia, något som till stor del har orsakats av en brist på utmärkande morfologiska kännetecken. För att genomföra en utförlig analys av svampdjursdiversiteten i Sverige, var det därför nödvändigt att göra en djupdykning inom systematik och taxonomi för just detta släkte (**Artikel III**). Fylogenetisk släktskapsanalys visade klart att *Suberites* kunde delas in i två undergrupper, som vi kallade A och B. Undergrupp B grupperades tillsammans släktet *Aptos*, samt en art som tillhör släktet *Homaxinella*. Denna grupp var närmast släkt med *Stylocordyla* och utifrån dessa resultat menar vi gruppen bör placeras inom familjen Stylocordylidae.

Släktet *Suberites* har en komplicerad taxonomisk historia och har genom åren ansamlat en mängd alternativa namn och synonymer, och listan med alternativa artnamn sträcker sig över flera sidor. På grund av detta genomförde vi en utförlig litteraturstudie där vi gick igenom de korrekta namnen för de två ovan nämnda undergrupperna, samt för de arter som hittas i den tempererade Nordatlanten (**Artikel IV**). Utifrån denna analys menar vi att *Suberites*

undergrupp B borde ges namnet *Syringella*. I undergrupp A menar vi vidare att *Suberites ficus* ska döpas om till *S. subereus* och vi löste också homonymin för *S. virgultosus* genom att ge arten som studerades av Bowerbank det nya namnet *Suberites* sp. "misterbeanii".

Acknowledgements

Though this thesis is my own making, during my Ph.D, I have not worked alone in a vacuum. Does it come the time to acknowledge those who have helped me in this seven years journey. I would start this section with the two remarks:

1. This document, its mistakes and possible quirkiness is a reflection of my struggle with writing. After reading that self-treatment is highly ineffective (Upper, 1974; Skinner & Perlini, 1995; Hermann, 1984; Didden *et al.*, 2007) I attempted writing in groups, but I found my empirical experience to confirm the later study by McLean and collaborators 2014. All of this to say that I'm thankful to any reader who has come this far in this thesis. If by all means you feel that you didn't enjoy reading it, please consider that I had not enjoyed writing it and I had the further displeasure of having to read it ... multiple times;
2. The acknowledgments of this document will most certainly be lacking and will have a rather chaotic succession though I will try to acknowledge humans firstly.

Firstly I would like to thank **Mikael** for the great supervision, for the error of casting selecting me for this position and especially for never appearing upset for all my bullshitting, inaction or for having to explain things, or correct my English or thought process. Then, I would like to thank **Chloé** for all the methodical processing for paper I and II and, for never quitting on PCRs even when no primers seemed to work. It was fun having you in the lab and going sampling too. To **Hanna** for all the help me to make things move forward. I struggled greatly with seeing things as small published projects rather than stochastic searches and you took your time to hear me and Mikael rumble and then when I noticed I was managing a half time. I will be especially thankful if you stop my identification. Also, big thanks to **Paco** for saving ass with important specimens for (**Paper III** and **IV**) and all important contributions in (**Paper II**. To **Karin** for the Swift help on thesis review some translations from German. I would like to thank Mats for all the specimens and nice photos of specimens and **Nahid** for all the DNA extractions and PCRs for **Paper II** and general support in the lab. To **Martin**, for all the help in this document and all the fun times in the fika room. To **Fabien** for the kind words over the previous version of this kappa and positive attitude in general. A thesis is never appearing out of thin air. In my case, my Ph.D project had two antecedents who started this work with sequencing and sample processing -**Maria** and **Astrid**. You "warmed-up" the seat for me, started this project and though I

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