

Phylogeny and systematics of Caudofoveata (Mollusca, Aplacophora)

Nina Therese Mikkelsen



Avhandling for graden philosophiae doctor (ph.d.)
ved Universitetet i Bergen

2018

Dato for disputas: 07.06.2018

© Copyright Nina Therese Mikkelsen

Materialet i denne publikasjonen er omfattet av åndsverkslovens bestemmelser.

År: 2018

Tittel: Phylogeny and systematics of Caudofoveata (Mollusca, Aplacophora)

Navn: Nina Therese Mikkelsen

Trykk: Skipnes Kommunikasjon / Universitetet i Bergen

Scientific environment

The work for this thesis was carried out at the Natural History collections at the University Museum, University of Bergen. The PhD project was financed through a four-year position at the University of Bergen. Additional funding for laboratory work and travel expenses was provided by grants from the Norwegian Academy of Science and Letters, the Malacological Society of London, a Melbourne R. Carriker Student Research Award from the American Malacological Society, the Natural History Collections at University Museum, and the Joint Fund for the Advancement of Biological Research at the University of Bergen.

For Lars, whose love and support meant the world.

Acknowledgements

First of all, I am grateful to my supervisors Endre Willassen and Christiane Todt. Thank you, Endre, for your never-ending support and encouragement, and for numerous discussions about methodology, phylogenetic software, and taxonomy. Thank you, Christiane, for insightful advice, discussions and our shared exploration of caudofoveate taxonomic mysteries. I am also grateful to Christoffer Schander, who made the project possible, but wasn't here to see the end of it.

I am grateful to the late Amélie Scheltema who provided my first introduction to aplacophoran molluscs. She later welcomed me in her lab where we together took on investigations into the taxonomy of a group of lesser-known caudofoveates, and kept following my work with interest and encouragement. Thanks to Dimitry Ivanov for careful demonstration of morphological methods during my visit to his lab, lengthy taxonomic discussions and knowledgeable advice on many taxonomic matters. Thanks also to the late Luitfried von Salvini-Plawen for providing material and valuable insight into the taxonomy of Caudofoveata.

Many thanks to my two other co-authors for providing very useful material from several cruises, and equally useful comments on several manuscript drafts; to Kenneth Halanych also for the opportunity to visit his lab for sequencing of caudofoveate mitochondrial genomes, and to Kevin Kocot for many hours together in labs working on Aplachs.

Many thanks also to Katrin Linse, Yasunori Kano, Jon-Arne Sneli, Eivind Oug, Saskia Brix-Elsig, Pedro Martinez Arbizu and the late Per Bie Wikander, who provided material that proved valuable to the project. Loans of material that was also essential to the project was facilitated by helpful curators at several museums: NTNU University Museum, the Natural History Museum at the University of Oslo, Gothenburg Museum of Natural History, National Museum of Scotland, American Museum of Natural History and Natural History Museum of Denmark, University of Copenhagen.

Thanks to Louise Lindblom, Kenneth Meland, and Solveig Thorkildsen for help and support, discussions and advice in the molecular lab, on often challenging and uncooperative samples. Thanks to Jon Kongsrud and Katrine Kongshavn for assistance with all practical matters concerning the collections at the University Museum of Bergen. Thanks to Elena Gerasimova and Nataliya Budaeva who helped with translation of papers in Russian. Additional thanks to all my other colleagues, fellow students, and labmates, who have made working on this project more enjoyable.

Finally, I am grateful to my family, first my parents Tove and Øystein, and also Arne, May, and Liv and Iver, who have provided so much support and encouragement and practical help. Thank you, Christoph, for all your support and advice along the way. My own lab-assistant, Eirik Andreas, who has patiently endured my work with the PhD project, interestedly followed my research and helped keep spirits high.

Bergen, March 2018

Nina Therese Mikkelsen

Abstract

Caudofoveata is by far the least known group of molluscs. The shell-less, worm-shaped caudofoveate molluscs are characterized by a mantle covered in calcareous sclerites, giving them a distinctive, shiny appearance. Caudofoveata consists of 141 recognized species found from intertidal habitats to the deep-sea, where they live burrowing in sediments.

Three families are recognized within Caudofoveata; Prochaetodermatidae Salvini-Plawen, 1975, Chaetodermatidae Ihering, 1876, and Limifossoridae Salvini-Plawen, 1970. Evolutionary relationships of the group have been debated, yet studies investigating the phylogeny of the group have been lacking. In this thesis, the phylogenetic relationships within and among the families of Caudofoveata are investigated using molecular phylogenetics and analyses of whole mitochondrial genomes. Special emphasis was put on the fauna of the northern Atlantic Ocean, including the description of a new species, and a thorough investigation of one of the most common species in the area.

In order to investigate relationships among and within families of Caudofoveata, phylogenetic analyses were performed using six sequenced fragments of selected mitochondrial and nuclear genes from 38 species representing all three recognized families of Caudofoveata with species from worldwide sampling locations. In resulting trees, contrary to traditional views, Prochaetodermatidae is sister to a clade containing the other two currently recognized families, Chaetodermatidae and Limifossoridae. The monophyly of Prochaetodermatidae is highly supported, but Limifossoridae and Chaetodermatidae are not recovered as monophyletic. Most of the caudofoveate genera are also not recovered as monophyletic in our analyses. Thus, results from our molecular data suggest that current classification of the group is in need of revision and indicate different evolutionary scenarios than previous hypotheses based on morphology.

Within the family Chaetodermatidae, *Chaetoderma nitidulum* Lovén, 1844 is a common species of caudofoveate with a wide distribution range in the North Atlantic. It was the first species of aplacophoran mollusc to be described, but its species identity has been debated. Here, the molecular and morphological diversity of specimens of *C. nitidulum* from a large geographical area and size range was investigated. Analyses of molecular data revealed two distinct genetic lineages in the eastern Atlantic and one clade sister to these in the western Atlantic Ocean. Morphological analyses revealed significant variation that does not reflect the genetic lineages. In addition, investigation of molecular markers combined with comparative morphological analyses showed that radula characters used to distinguish the genera *Chaetoderma* and *Falcidens* within Chaetodermatidae do not represent apomorphies, but are a result of ontogenetic changes in *C. nitidulum*.

Together Caudofoveata and Solenogastres, the other group of worm-shaped mollusc, constitute the clade Aplacophora. Because many morphological characters of the aplacophoran molluscs have been presumed to be plesiomorphic for Mollusca, Aplacophora has been regarded as early branching within Mollusca. In recent years, Aplacophora has received much attention as part of Aculifera, a clade grouping Caudofoveata and Solenogastres with Polyplacophora (chitons), as sister to the remaining molluscs. In this thesis, mitochondrial genomes of five species of Caudofoveata and one species of Solenogastres were sequenced, in order to shed light on higher-level relationships within Caudofoveata and their placement within Aculifera. Comparison of mitochondrial gene order among different lineages revealed a highly conserved order of protein coding genes, corresponding to the hypothesized ancestral gene order for Mollusca. Unique arrangements of tRNAs were found for the major lineages of Aculifera, as well as for the families of Caudofoveata. Phylogenetic analyses of amino acid sequences for all 13 mitochondrial protein-coding genes recovered Chaetodermatidae, but not Limifossoridae, monophyletic. Aplacophora was recovered as monophyletic and sister to Polyplacophora.

List of publications

PAPER I

Mikkelsen, N. T., Todt, C., 2014. Diversity of Caudofoveata (Mollusca) around Iceland and description of *Psilodens balduri* sp. n. *Polish Polar Research* 35, 279-290. <https://doi.org/10.2478/popore-2014-0014>

PAPER II

Mikkelsen, N. T., Todt, C., 2018. One or many? Molecular versus morphological diversity in the aplacophoran *Chaetoderma nitidulum* Lovén, 1844 (Mollusca: Caudofoveata). *Journal of Molluscan Studies*. <https://doi.org/10.1093/mollus/eyy009>

PAPER III

Mikkelsen, N. T., Kocot, K. M., Halanych, K. M., 2018. Mitogenomics reveals phylogenetic relationships of caudofoveate aplacophoran molluscs. *Molecular Phylogenetics and Evolution*. (Revised and resubmitted.)

PAPER IV

Mikkelsen, N. T., Todt, C., Kocot, K. M., Halanych, K. M., Willassen, E. Molecular phylogeny of Caudofoveata (Mollusca) challenges traditional views on relationships. (Submitted manuscript.)

The published papers are reprinted with permission from De Gruyter (Paper I) and Oxford University Press (Paper II). All rights reserved.

Contents

Scientific environment	3
Acknowledgements	7
Abstract	9
List of publications	11
1. Introduction	15
1.1 Caudofoveata- the burrowing aplacophoran molluscs	15
1.1.1 History of classification of the aplacophoran molluscs.....	17
1.1.2 Caudofoveata and their placement within Mollusca	19
1.2 Systematics of Caudofoveata.....	20
1.2.1 Limifossoridae	20
1.2.2 Chaetodermatidae	24
1.2.3 Prochaetodermatidae	26
1.3 Family level relationships and evolution of Caudofoveata	29
1.3.1 Evolutionary relationships	29
1.3.2 Comparative anatomy and morphology	30
1.4 Distribution and geographical patterns.....	36
2. Aims of the thesis	41
3. Material and Methods.....	43
3.1 Sampling and material.....	43
3.2 Morphological methods.....	45
3.3 Molecular methods	45
4. Results and discussion	49
4.1 Caudofoveata in the North Atlantic	49
4.1.1 New records of Caudofoveata in the North Atlantic.....	49
4.1.2 Species distribution in the North Atlantic.....	49
4.1.3 The identity of <i>Chaetoderma nitidulum</i>	51
4.2 Phylogeny of Caudofoveata	53
4.2.1 The Chaetodermatidae radula	53
4.2.2 Relationships within Chaetodermatidae.....	55
4.2.3 Higher caudofoveate relationships	56

4.2.4	Evolution of Caudofoveata.....	59
4.2.5	Caudofoveata as Aculifera — evidence from mitochondrial genomes.....	62
5.	Future perspectives.....	65
5.1	Undescribed diversity.....	65
5.2	Biogeography and distribution patterns	66
5.3	Systematics of Chaetodermatidae	67
5.4	Higher caudofoveate systematics	67
6.	References	69
7.	Appendices	
	Paper I	
	Paper II	
	Paper III	
	Paper IV	

1. Introduction

1.1 Caudofoveata — the burrowing aplacophoran molluscs

The worm-shaped, shell-less aplacophoran molluscs are classified in two major groups: Caudofoveata and Solenogastres. Caudofoveates are exclusively marine, benthic animals. They are distributed in all the world's oceans, and have a wide bathymetric range, from the subtidal zone down to 9000 meters depth (Scheltema, 1989; Ivanov, 1996a). Caudofoveates are burrowing in sediment, and are deposit feeders, more selective detritivores, or predators of Foraminifera.

The vermiform, cylindrical body has a chitinous cuticle covered in calcium carbonate (aragonite) sclerites (Figure 1a), giving them a shiny appearance. Anteriorly, the characteristic oral shield is partially or completely surrounding the mouth opening (Figure 1b). Posteriorly, the mantle cavity holds a pair of ctenidia, or gills (Figure 1d). A dorsoterminal sense organ is found near the mantle opening (Figure 1c). Caudofoveates are adapted to their burrowing lifestyle by the vermiform body, the presence of an oral shield, which functions both in digging and as a sensory organ; and the terminal position of the mantle cavity, which allows the paired gills to protrude from the surface of the sediment. Caudofoveates range from 1 mm to about 10 cm in adult size, with the exception of a single known species that reaches a length of over 30 cm (Ivanov & Scheltema, 2007).

The morphology of the aplacophoran molluscs is exceptional among the Mollusca. In addition to the lack of a shell, the foot found in other mollusc classes is completely reduced in Caudofoveata, and the mantle edge is fused ventrally. The radula is highly reduced and derived. The gonad is connected to the pericardium, and the excretory system lacks nephridia (Salvini-Plawen, 1985; Scheltema *et al.*, 1994). Solenogastres, the second group of aplacophoran molluscs, are separated from Caudofoveata by a laterally narrowed body where the foot is reduced to a midventral pedal groove, lack

of ctenidia, an undifferentiated midgut, and by being hermaphroditic in contrast to the dioecous Caudofoveata (Salvini-Plawen, 1985; Scheltema *et al.*, 1994).

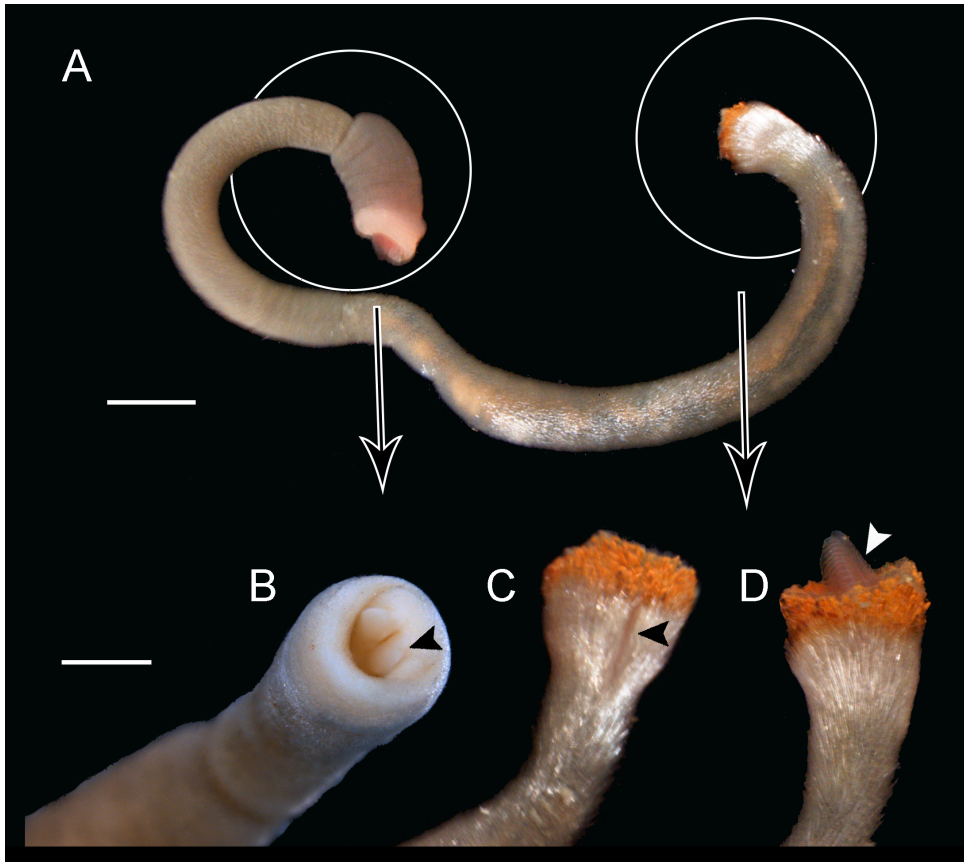


Figure 1. External morphology of Caudofoveata. A. Habitus of *Chaetoderma nitidulum*. B. Anterior end with oral shield (arrowhead). C. Posterior end in dorsal view with dorsoterminal sense organ (arrowhead) visible as a line on the posterium. D. Posterior end with ctenidia (gills; see arrowhead) protruding from the mantle cavity. Scale bar A, 200 μm ; scale bar B-D, 100 μm .

1.1.1 History of classification of the aplacophoran molluscs

The first species of aplacophoran mollusc was described from the Swedish west coast by Sven Lovén in 1844. The small, worm-shaped animal with a shimmering appearance was named *Chaetoderma nitidulum*, from Latinized Greek *chaetos* = spine, bristle; *derma* = skin, hide, and *nitidus* = shining, glistening. Because of the sclerites covering the body it was initially classified as an echinoderm, and was later classified under Gephyrea as both priapulid (Diesing, 1859) and sipunculid (Keferstein, 1865). In 1875, a second shell-less, worm-shaped animal with external spicule-cover was described from the Swedish coast by Tycho Tullberg and named *Neomenia carinata*. These two species also represent the two currently recognized taxa within Aplacophora, *C. nitidulum* represents Caudofoveata and *N. carinata* represents Solenogastres. Only 40 years after the first description were they assigned to the phylum Mollusca (Spengel, 1881), and it would be a century before the discussions about their molluscan nature ceased, and the worm-like, shell-less aplacophorans were universally recognized as molluscs.

Research expeditions around the turn of the 19th century provided samples from previously unavailable localities, and brought on descriptions of more species. Since then, the number of species of aplacophoran molluscs worldwide has reached 283 species of Solenogastres and 141 species of Caudofoveata.

In 1878, Gegenbaur brought *Chaetoderma* and *Neomenia* together in Vermes as Solenogastres, a name that continued to encompass both taxa for nearly a hundred years. Ihering (1876) placed the vermiform molluscs in a new taxon Aplacophora, and joined Aplacophora with "Placophora" (=Polyplacophora) in Amphineura, based on the similarities of the nervous system. Later, Hatschek (1891) synonymized Amphineura to Aculifera based on the ability of the mantle to form spicules; an additional character that sets them apart from the Conchifera, the shell-bearing molluscs. Spengel (1881) performed further investigations of the nervous system of several species, validated Ihering's grouping of chitons and aplacophorans in Amphineura and concluded that both are molluscs. This view, however, was not

universally accepted, and some authors continued to classify the worm-shaped taxa outside of the remaining molluscs; e.g. the prominent malacologist Johannes Thiele (1902, 1913, 1925, 1929), who continued to reject a relationship between the shell-less molluscs, grouping the aplacophoran molluscs in Vermes in an intermediate position, as the ancestors of Mollusca. This view was followed by other authors (e.g. Odhner, 1921; Hoffmann, 1929), but in 1949, Hoffman again raised the question of the molluscan affinities of the Aplacophora and conclusively included them in Mollusca, after thorough investigations of especially the integument. Hoffman recognized two sub-orders Neomenioidea and Chaetodermatoidea in the order Solenogastres (Hoffman, 1949).

The name Solenogastres was used for both classes, until Böttger (1956), who regarded the two groups of aplacophoran molluscs as evolved independently from a vermiform ancestor, used the name Aplacophora for the entire group. He coined the name Ventroplicida for the aplacophoran molluscs with a ventral furrow, and the name Caudofoveata to replace the name Chaetodermatoidea, to avoid using a name based on the genus name *Chaetoderma*, which was believed to be a junior homonym of *Chaetoderma* Swainson, 1839 (Teleostei) and had been replaced by the next available name, *Crystallophrisson* Möbius, 1875.

Salvini-Plawen (1967) argued that the aplacophoran molluscs do not represent a systematic group, but two independent classes, which originated separately. He kept Böttger's name Caudofoveata, and adopted the name Solenogastres Gegenbaur, 1878 as only referring to the group possessing a ventral furrow, regarding Solenogastres and Caudofoveata as two equally ranked classes (Salvini-Plawen, 1980).

Alternatively, the names Chaetodermomorpha and Neomeniomorpha Pelseneer, 1906 have been used for two subclasses under a class Aplacophora (Scheltema, 1978). The names Chaetodermomorpha and Neomeniomorpha were created based on the names of the two known genera at the time, *Chaetoderma* and *Neomenia* (Pelseneer, 1906). As the name *Chaetoderma* had been revalidated after Heppel (1963) showed that Swainson used multiple spellings and obtained validation of *Chaetoderma* Lovén

1844 (Opinion 764, ICZN 1966); Scheltema (1978) argued for preservation these older names for the two subclasses. Today, the simpler names Caudofoveata and Solenogastres are the most widely used for the two groups regardless of view on phylogenetic position.

1.1.2 Caudofoveata and their placement within Mollusca

Although their molluscan affinities are no longer questioned, the position of Caudofoveata and Solenogastres within Mollusca has continued to be debated over the last decades. Whether the two groups constitute a monophyletic taxon, Aplacophora (Scheltema, 1993; Ivanov, 1996b; Scheltema, 1996), or separate classes (Salvini-Plawen, 1985; Salvini-Plawen & Steiner, 1996; Haszprunar, 2000) has been widely debated. Differences in morphological characters between Caudofoveata and Solenogastres have variably been interpreted as evidence for separate origins of the two groups (e.g. Haszprunar, 2000; Salvini-Plawen, 2003); or as secondary adaptations to an epibiontic way of life in Solenogastres and a burrowing lifestyle in Caudofoveata (Scheltema, 1993; Ivanov, 1996b; Scheltema, 1996). Similarly, shared characters (e.g. mantle structure, reduced gonoducts, and a dorsoterminal sense organ) are either interpreted to represent symplesiomorphies or convergences between two separate evolutionary lines; or alternatively to represent synapomorphies that support a common origin and monophyly of Aplacophora.

The Testaria hypothesis places the aplacophoran molluscs basal to all other molluscs, and Polyplacophora as sister to Conchifera (the shelled molluscs). The vermiform spicule-covered aplacophoran morphology is interpreted as representing a plesiomorphic condition within Mollusca (Salvini-Plawen, 1980; Salvini-Plawen, 1985; Salvini-Plawen & Steiner, 1996; Haszprunar, 2000; Salvini-Plawen, 2003; Salvini-Plawen & Steiner, 2014). Morphological characters has variously been interpreted to suggest a basal placement of Caudofoveata (“Scutopoda”) as sister to the remaining mollusc classes (“Adenopoda”) (Salvini-Plawen, 1980; Salvini-Plawen, 1985); or Solenogastres as sister to the remaining molluscs (“Hepagastralia”) (Salvini-Plawen, 1981; Salvini-Plawen & Steiner, 1996; Haszprunar, 2000). Under

the Aculifera hypothesis these characters are instead interpreted as regressively derived from a chiton-like ancestor, potentially as a result of progenesis in the aplacophoran molluscs; meaning that the aplacophorans are paedomorphic, retaining juvenile characters as adults (Scheltema, 1993, 2014). These characters include a distichous radula and fusion of the gonads, characters that can also be observed in the ontogeny of Polyplacophora (Scheltema, 1993; Scheltema *et al.*, 2003; Scheltema, 2014).

The grouping of Aplacophora and Polyplacophora in Aculifera, which was originally proposed on the basis of shared characters of the nervous system, the calcareous sclerites, and epidermal papillae, has later also been supported by ciliary ultrastructure (Lundin & Schander, 2001) and larval development (Nielsen *et al.*, 2007; Scherholz *et al.*, 2015). During recent years, increasing evidence from molecular data (Kocot *et al.*, 2011; Smith *et al.*, 2011; Vinther *et al.*, 2012) and new fossil evidence (Vinther *et al.*, 2017) has also supported the Aculifera hypothesis, also including a grouping of Caudofoveata and Solenogastres in a monophyletic Aplacophora as sister to Polyplacophora.

1.2 Systematics of Caudofoveata

The families of Caudofoveata are defined based on characters of the body shape, the shape of the oral shield flanking the mouth, and most importantly the morphology of the radula. Caudofoveata has been separated into three families, Prochaetodermatidae Salvini-Plawen, 1975, Chaetodermatidae Théel, 1875 and Limifossoridae Salvini-Plawen, 1970 (Figure 2). A fourth family, Scutopidae, was suggested by Ivanov (1981), but has not been generally accepted (Table 1).

1.2.1 Limifossoridae

Representatives of Limifossoridae have a cylindrical body with externally scarcely pronounced body regions (Figure 2g, h). The radula in Limifossoridae is a serial,

distichous radula, a radula bearing transverse rows of two mirror image teeth. In Limifossoridae, radular morphology is also used for defining the genera. Species of *Limifossor* Heath, 1904 have paired teeth, consisting of a plate with two pointed denticles: one larger lateral, and one smaller median denticle (Figure 3c). Species of *Psilodens* Salvini-Plawen, 1977 (Figure 3b) and *Scutopus* Salvini-Plawen, 1968 (Figure 3a), in contrast, have simpler, hook-shaped radular teeth; in *Scutopus* serrated, bearing several small denticles (Salvini-Plawen, 1977). The oral shield is divided into two lateral parts flanking the mouth in *Psilodens* and *Limifossor* and disc-shaped and ventral to the mouth in *Scutopus*. Ivanov (1981) placed *Psilodens* and *Scutopus* in a separate family, Scutopidae, based on their elongated body shape with a defined head, and a radula with thin sickle shaped radular teeth and teeth on opposite sides of the radula interlaced. This would leave *Limifossor* as the only genus in Limifossoridae, with a short cylindrical body without a separated head, and with a bilaterally symmetrical radula. The division into two families has not been generally accepted (Salvini-Plawen, 1992; Saito & Salvini-Plawen, 2014), and the relationships are currently unresolved.

The position of monotypic genus *Metachaetoderma* Thiele, 1913 is uncertain. *Metachaetoderma* is only known from a single specimen collected during the Challenger expedition. Thomson (1878) refers to the collection of the single specimen, and provides an illustration of the animal. Nierstrasz (1903) described the specimen as *Chaetoderma challengerii*, and a new genus, *Metachaetoderma*, was later erected for the species by Thiele (1913). *Metachaetoderma challengerii* was described from what, by the time Nierstrasz received it, was a partial specimen. Most of the holotype specimen was sectioned, but the sections have later been lost. *Metachaetoderma* has been placed in a separate family, Metachaetodermatidae (Ivanov, 1981), and suggested to be most closely related to Prochaetodermatidae (Ivanov, 1981, 1986b), or to be part of Limifossoridae (Salvini-Plawen, 1969b; A. Scheltema, personal communication) based on the digestive system and the radular teeth. The species was described as having a serial radula, similar to the radula found in Limifossoridae, and the description contains a drawing of pair of radula denticles from a section that bear affinities to the simple denticles of *Psilodens*. No animal

from this genus has been collected again, and the affiliation of the species and validity of the genus remain uncertain.

Table 1. Taxonomy of Caudofoveata. Suggested families and genera. Numbers of described species within each taxon as of March 2018.

Taxon	Number of species
Chaetodermatidae Théel 1875	83
<i>Chaetoderma</i> Lovén 1844	45
<i>Caudofoveatus</i> ¹ Ivanov 1981	2
<i>Falcidens</i> Salvini-Plawen 1968	35
(<i>Falcidens Chiastofalcidens</i> ² Corrêa, Fassina & Passos, 2014)	(6)
<i>Furcillidens</i> Scheltema 1998	1
Limifossoridae Salvini-Plawen 1970	16
<i>Limifossor</i> Heath 1904	6
Scutopidae ³ Ivanov 1981	10
<i>Metachaetoderma</i> Thiele 1913	1
<i>Psilodens</i> Salvini-Plawen 1977	3
<i>Scutopus</i> Salvini-Plawen 1968	6
Prochaetodermatidae	42
<i>Chevroderma</i> Scheltema 1985	10
<i>Claviderma</i> Scheltema & Ivanov 2000 ⁴	11
<i>Dacryomica</i> Ivanov & Scheltema 2004	1
<i>Lonchoderma</i> Salvini-Plawen 1992	1
<i>Niteomica</i> Ivanov, 1996 ⁵	4
<i>Prochaetoderma</i> Thiele 1902	9
<i>Spathoderma</i> Scheltema 1985 ⁴	6

¹ Salvini-Plawen, 1984 included species of *Caudofoveatus* in *Chaetoderma*.

² Replaced *Lepoderma* Salvini-Plawen 1992, which is a junior homonym of *Lepoderma* Looss 1899 in Trematoda.

³ Limifossoridae Salvini-Plawen 1970 partim.

⁴ Included in *Prochaetoderma* by Salvini-Plawen, 1992.

⁵ Included in *Prochaetoderma* by Salvini-Plawen, 1999.

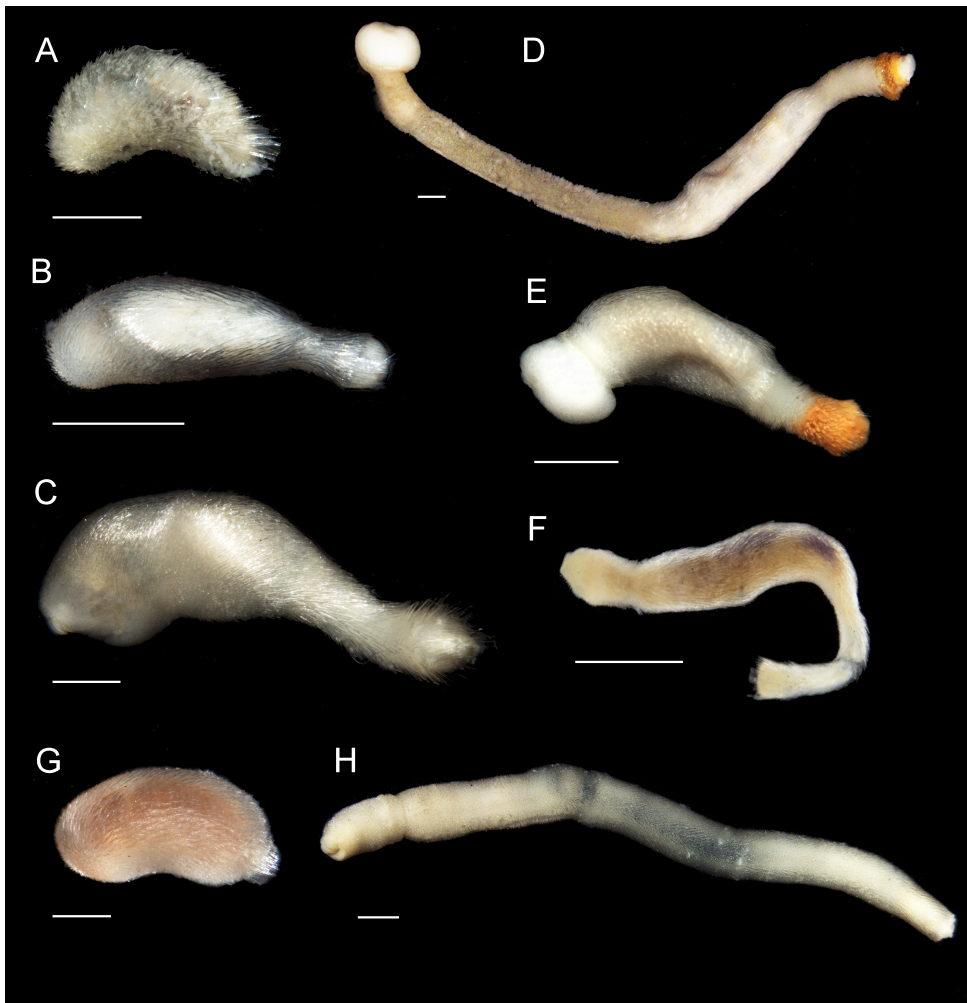


Figure 2. Representatives of taxa of Caudofoveata. A-C: Prochaetodermatidae; D-F: Chaetodermatidae; G-H: Limifossoridae. A. *Niteomica captainkiddae*. B. *Prochaetoderma yongei*. C. *Spathoderma alleni*. D. *Chaetoderma japonicum*. E. *Falcidens caudatus*. F. *Falcidens guttuosus*. G. *Limifossor holopeltatus*. H. *Psilodens* sp. All specimens oriented with anterior end to the left. Scale bars 100 μ m.

1.2.2 Chaetodermatidae

Representatives of Chaetodermatidae have an elongated body clearly divided into three or four body regions (Figure 2d–f). In some species, the posterior region of the body tapers to a tail (Figure 2e, f). The oral shield is circumoral or horseshoe-shaped, and ventral to the mouth opening. Chaetodermatidae is defined by a radula reduced to a single pair of teeth supported by an unpaired cone (Figure 3d, e). Like in Limifossoridae, radula morphology provides the defining characters also on genus level in Chaetodermatidae. The two largest genera, *Chaetoderma* Lovén, 1844 and *Falcidens* Salvini-Plawen, 1968, both have radulae with a single pair of teeth. The pincer-like *Falcidens* radula (Figure 3d), with two sickle-shaped, pointed teeth connected by a proximal symphysis and a central plate between the denticles, differs from the simpler *Chaetoderma* radula (Figure 3e), where the teeth have been reduced to a pair of isolated denticles attached to the dome-shaped membrane which covers the distal end of the radula, and is supported by two lateral projections (Scheltema, 1972, 1981). The chaetodermatid radula was first described by Graff (1876). In 1901, Kowalevsky published detailed illustrations and descriptions, in what was the first description based on a dissection of the radula, earlier descriptions all stemmed from what could be inferred from histological sections. Detailed descriptions of the morphology of the radulae of both *Falcidens* and *Chaetoderma* have later been published by Ivanov (1979) and Scheltema (1972); including a description of the function of the *Falcidens* radula (Ivanov, 1986b). Chaetodermatid caudofoveates are assumed to be selective predators on foraminiferans and other interstitial fauna (Ivanov, 1979).

Chaetodermatidae also includes the small genera *Furcillidens* Scheltema, 1998 and *Caudofoveatus* Ivanov, 1981, which are comprised of one and two species respectively. *Furcillidens* has a radula lacking denticles, and instead only has a forked projection distally (Figure 3f). *Caudofoveatus* is characterized by a radula with four axial denticles, in contrast to the two found in other genera in the family; two main denticles and two additional denticles connected to a plate on the tip of the radular cone with apophyses wrapping around the main teeth. However, Salvini-Plawen

(1984) disputed the validity of the genus, and argued the additional pair of radula denticles is the result of stronger sclerotization of tips of the cuticular lateral supports; something that can also occur in other representatives of the family Chaetodermatidae (e.g. in *Falcidens loveni* Nierstrasz, 1902). Moreover, *Falcidens liosquameus* Salvini-Plawen, 1969 even possess a pair of auxiliary teeth on its radula (Salvini-Plawen, 1969a). Salvini-Plawen (1984) argues that these features therefore do not provide the basis for the establishment of new genera, and can be only used as the distinctions between species. He additionally noted that the shape of the sclerites of the species assigned to *Caudofoveatus* clearly indicates that they belong to the same group of species as *Chaetoderma*.

Falcidens includes species with a wide range of body morphologies and sclerite types. The main body shapes found within the genus include a slender, *Chaetoderma*-like body shape (e.g. *Falcidens sagittiferus* Salvini-Plawen, 1968 and *F. longus* Scheltema, 1998), similar to the members of the other genera within Chaetodermatidae, but also a *Limifossor*-like body shape with externally poorly defined body regions (e.g. *Falcidens halanychi* Schander, Scheltema & Ivanov, 2006 and *Falcidens limifossorides* Salvini-Plawen, 1968), and a tailed body shape (e.g. *Falcidens crossotus* Salvini-Plawen, 1968, *Falcidens caudatus* (Heath, 1918), *Falcidens gutturosus* (Kowalevsky, 1901) and *Falcidens hartmanae* (Schwabl, 1961)).

Included in *Falcidens* is a group of species with a tailed body shape, which are assigned to a separate subgenus, *Chiastofalcidens* Corrêa, Fassina & Passos, 2014 (Salvini-Plawen, 1992; Corrêa *et al.*, 2014). *Chiastofalcidens* are distinguished by a particular type of unique sclerites: thin, delicate scales with a distinctive basal indentation or notch, and ornamentation in the form of fine, radiating lines. Scheltema (1990) first noted the related body shape and shape and ornamentation of the sclerite in this group of species. Scheltema compared the first species with such a morphology that was described, *Falcidens loveni*, from Indonesia to two undescribed species from the Western Atlantic, and to two species from Australia: *Falcidens chiastos* Scheltema, 1989 and an undescribed species. Salvini-Plawen (1992)

assigned the described species to a new subgenus *Lepoderma* together with three additional, newly described species with a similar sclerite morphology. The name *Lepoderma* was later rendered invalid as a junior homonym of *Lepoderma* Looss 1899 in Trematoda, and Corrêa *et al.* (2014) suggested the name *Chiastofalcidens* for the subgenus.

The distinction between species of *Falcidens* with a tailed (e.g. in *F. crossotus*) and a non-tailed (e.g. in *F. halanychi*) body shape (Figure 1) has also been pointed out by some authors, and it has been suggested that *Falcidens* should be split into a tailed and non-tailed group (Salvini-Plawen, 1984). A tailed body shape is also reflected in internal anatomy: in species with a tailed body shape, the midgut sac is short, and does not extend into the tailed posterior body (Salvini-Plawen, 1975; Señaris *et al.*, 2014). All species assigned to *Chiastofalcidens* also have a tailed body-shape, but it is not known if these are more closely related to other *Falcidens* species with this morphology.

1.2.3 Prochaetodermatidae

Representatives of Prochaetodermatidae have a teardrop-shaped body with an abruptly tapering, tail-like posterior end (Figure 2a–c). Prochaetodermatidae, like Limifossoridae, have a serial, distichous radula (Figure 3g). Prochaetodermatidae is in addition characterized by a middle row of central plates between the teeth and the presence of jaws (Figure 3h), both unique within Caudofoveata. The jaws serve to hold the mouth open for protrusion of the radula, which is used in feeding in rasping movements (Scheltema, 1981). Laterally, the radula membrane is drawn out into supports next to each tooth.

While the genera in the other families are defined based on radular morphology, the prochaetodermatid radula differs less among genera, and so far no morphological pattern has been defined. The oral shield also shows little differentiation between species of Prochaetodermatidae. The genera of Prochaetodermatidae are defined based on the morphology of the sclerites and the number of rows of sclerites flanking

the oral shield (e.g. Scheltema & Ivanov, 2000; Ivanov & Scheltema, 2002; Ivanov & Scheltema, 2008), except the genus *Lonchoderma* Salvini-Plawen 1986, which is defined as having two lateral projections of the radular membrane alongside each radula tooth (Salvini-Plawen, 1992). The validity of the genera based on characters of the sclerites have been questioned, and Salvini-Plawen (1992) argues that the shape of the sclerites can at most be used as characters for a subgeneric classification. Variation in shape of the spicules from specimens of the same species from distant populations has also been reported (Scheltema, 1985). No hypothesis has been put forward regarding the internal relationships within Prochaetodermatidae, and the validity of genera and species continues to be debated (e.g. Salvini-Plawen, 1992; Scheltema & Ivanov, 2000; Señarís *et al.*, 2017b).

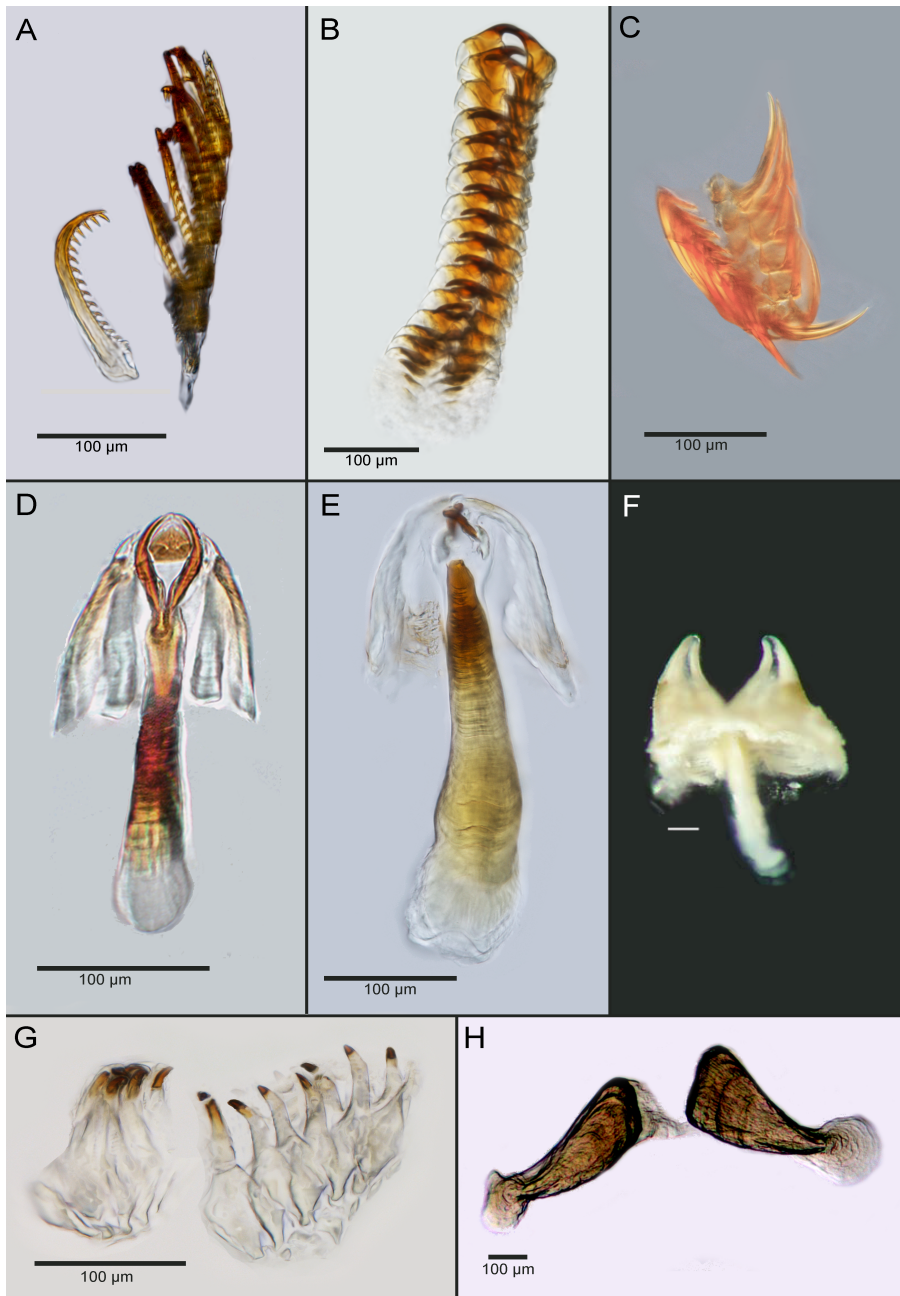


Figure 3. Radulae of selected genera of Caudofoveata. A-C: Limifossoridae; D-F: Chaetodermatidae; G-H: Prochaetodermatidae. A. *Scutopus*. B. *Psilodens*. C. *Limifossor*. D. *Falcidens*. E. *Chaetoderma*. F. *Furcillidens*. G. *Prochaetoderma*. H. Jaws of *Prochaetoderma*. F from Barwick & Cadien, 2005, scale bar 100 µm.

1.3 Family level relationships and evolution of Caudofoveata

1.3.1 Evolutionary relationships

The relationships between the families of Caudofoveata have been debated (e.g. Salvini-Plawen, 1975; Ivanov, 1981; Scheltema, 1981; Ivanov, 1986b), and are still unclear (Todt *et al.*, 2008). Especially the position of the Prochaetodermatidae and its relationship to the other families is unresolved. Limifossoridae has been regarded as basal within Caudofoveata, based on the presence of presumed plesiomorphic characters: the serial distichous radula and a simple, cylindrical body shape with externally scarcely pronounced body regions (Salvini-Plawen, 1977; Ivanov, 1986b). Additionally, the ventral line found in several species of Limifossoridae, has been interpreted as a vestige of a ventral furrow, homologous to the ventral foot groove in Solenogastres (Ivanov, 1986b; Salvini-Plawen, 2003).

Chaetodermatidae has been inferred to be the most derived taxon because of the complex midgut morphology and reduced radula (Salvini-Plawen, 1975; Ivanov, 1979; Scheltema, 1981). The chaetodermatid radula is seen as the most derived, reduced from an ancestral polysegmental state (Salvini-Plawen, 1969b; Ivanov, 1986b), while the radula of Prochaetodermatidae has been interpreted as representing an intermediate state (Salvini-Plawen & Nopp, 1974; Salvini-Plawen, 1975; Salvini-Plawen, 1988). Ivanov (1981) suggested a closer relationship between the taxa with polysegmental radulae, and joined them in one superorder, Limifossorimorpha. This superorder would include two orders, order Limifossorida, with the families Limifossoridae and Scutopidae, and order Prochaetodermatida with Prochaetodermatidae.

The oral shield is divided into two parts flanking the mouth in both Prochaetodermatidae and two of the genera within Limifossoridae (*Limifossor* and *Psilodens*). However, the oral shield is lateral to the mouth in Prochaetodermatidae,

while it has a more ventral position in the two limifossorid genera. The disc-shaped oral shield in *Scutopus*, the third genus within Limifossoridae, is also located in a ventral position (Ivanov, 1986b).

Ivanov (1986b) proposed a progressive evolution from an ancestral form with a *Limifossor*-like habitus; short, with poorly differentiated body regions, into forms with more elongated bodies to allow for penetrating deeper in the sediment. Further, strong anterior musculature, which is visible as constrictions between body regions in some taxa, would have evolved for more effective digging, and tailed forms developed to allow the terminal gills to reach the surface while probing deeper. Tailed body shape and circular constriction between head and body would have evolved independently in Prochaetodermatidae and Chaetodermatidae, according to Ivanov (1986b).

1.3.2 Comparative anatomy and morphology

Early work on aplacophoran molluscs focused on histological sectioning (Wirén, 1892a, 1892b; Nierstrasz, 1903; Heath, 1911), which also forms the basis of our knowledge of internal anatomy (Salvini-Plawen, 1985; Salvini-Plawen, 1988; Scheltema *et al.*, 1994). More recently, the internal anatomy has also been studied using 3D-reconstruction in the chaetodermatid *Falcidens vasconiensis* Salvini-Plawen, 1996 (Señaris *et al.*, 2014). In later years, taxonomic work on caudofoveates has mainly been focused on the morphology of the hard parts, the sclerites and radula (Scheltema & Schander, 2000). Ultrastructural studies have been performed on locomotory cilia (Lundin & Schander, 1999) the osphradial sense organ (Haszprunar, 1987), and the radula (Wolter, 1992). The burrowing caudofoveates are challenging to recover alive and keep in aquaria, and only a few observations on the physiology and behaviour of caudofoveates have been published. These observations of living caudofoveates include descriptions of the animals' burrowing in sediment and respiration by extending the ctenidia (Wirén, 1892a; Heath, 1904). Salvini-Plawen (1968) also examined burrowing behaviour and heart rate. The following section

outlines the morphological and anatomical characters used in classification of Caudofoveata.

Integument

In Caudofoveata, the foot is completely reduced and the mantle edge is fused ventrally. A ventral line can be seen in larval development as putative mantle edges fuse along the ventral midline (Nielsen *et al.*, 2007), and the ventral line that can be seen in certain representatives of Limifossoridae has been hypothesized to represent remnants of a foot (Salvini-Plawen, 1972a; Salvini-Plawen, 1985). In *Scutopus*, the presence of longitudinal ventral muscles, corresponding to the longitudinal-submarginal muscles of other Aculifera, and the presence of dorsoventral or lateroventral pairs of bundles of muscle found in the anterior body, has also been interpreted as a retained plesiomorphy (Salvini-Plawen, 1972b; Haszprunar & Wanninger, 2000). These longitudinal ventral muscles provide the ability to roll up in a spiral, something that is otherwise uncommon in caudofoveates. In other species of Caudofoveata, these muscles are reduced at the expense of the strengthening of the longitudinal body wall musculature for burrowing (Salvini-Plawen, 1985).

Salvini-Plawen hypothesized that the oral shield (pedal shield) of caudofoveates is homologous to the anteriormost part of the ventral fold of Solenogastres, and to the foot found in other classes of molluscs. The presence of glandular mucus cells similar to the ones along the pedal fold of Solenogastres and the innervation of the oral shield have been taken as evidence for a joint origin of the oral shield with the foot in Solenogastres and other molluscs (Salvini-Plawen, 1972b; Salvini-Plawen, 1980; Salvini-Plawen, 1981). However, Scheltema (1978, 1993) argued that the presence of mucus glands cells does not indicate homology. Additionally, the oral shield is cerebrally innervated, and the innervation is more anterior than the innervation of the anteriormost parts of the foot in other molluscs (Scheltema, 1993). Scheltema also argued against a common origin with the foot because the cuticle of the oral shield is continuous with the oral tube (Scheltema, 1981). Salvini-Plawen (1990) however emphasises the differences in the underlying epithelium of the oral shield and the oral

tube, and the fact that the presence of the cuticle is secondary and therefore does not contradict homology. The ontogeny of the oral shield is not known.

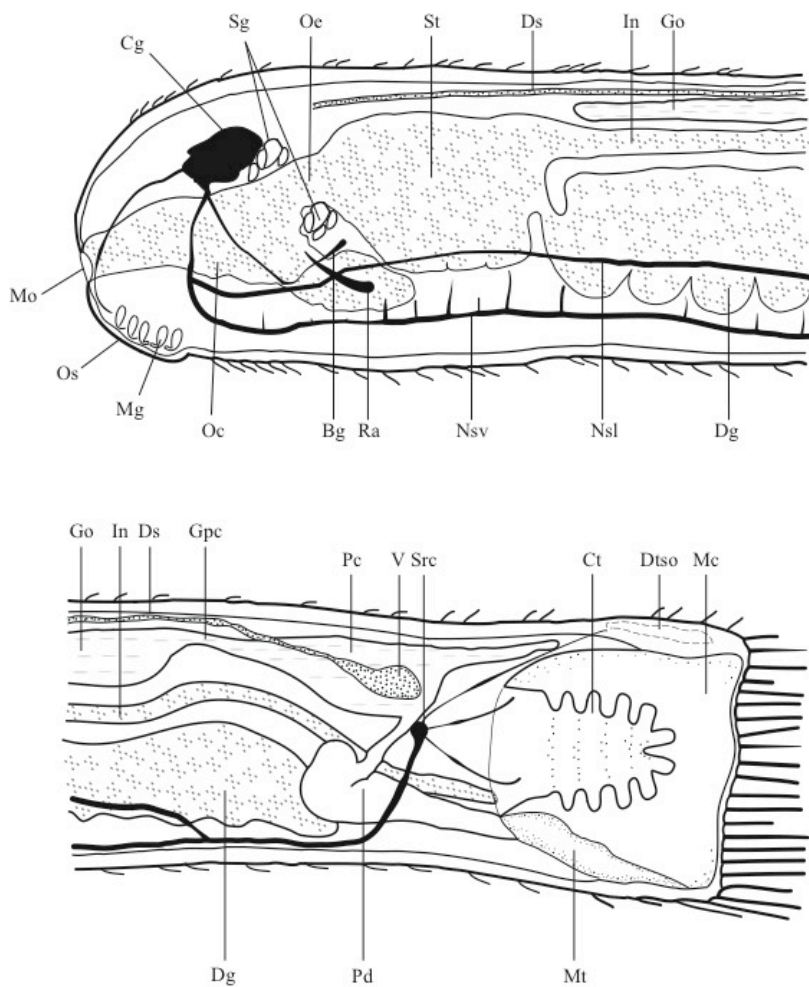


Figure 4. Schematic overview of the anatomy of Caudofoveata. Redrawn and amended after Salvini-Plawen, 1975. Bg–buccal ganglia, Cg–cerebral ganglion, Ct–ctenidia, Dg–digestive diverticulum, Ds–dorsal sinus, Dtso–dorsoterminal sense organ, Go–gonad, Gpc–gonopericardial duct, In–intestine, Mc–mantel cavity, Mg–mucus glands, Mt–mucus tract (spawning duct), Mo–mouth opening, Nsl–lateral nervous cord, Nsv–ventral nervous cord, Oc–oral cavity, Oe–oesophagus, Os–oral shield, Pc–pericardium, Pd–pericardial duct, Ra–radula, Sg–salivary glands, Src–suprarectal commissure, St–stomach, V–ventricle.

Nervous system

Caudofoveates possess a typical molluscan tetra neural nervous system, consisting of cerebral ganglia, an oesophageal nerve ring, paired, medullary lateral and ventral cords, and a suprarectal commissure (Figure 4). The cerebral ganglia are fused in Chaetodermatidae and Limifossoridae, but separate in Prochaetodermatidae (Salvini-Plawen, 1985; Haszprunar, 1987). The oral shield is innervated through frontal swellings located anterior to the cerebral ganglia (Shigeno *et al.*, 2007). The highly innervated oral shield functions both in locomotion when digging, and as a sensory organ (Salvini-Plawen, 1972b; Scheltema, 1981). Buccal ganglia innervate the oral cavity and radula. The suprarectal ganglion innervates the mantle cavity and ctenidia, as well as the dorsoterminal sense organ. The dorsoterminal sense organ forms a longitudinal groove bordered by swellings located dorsal to the mantle cavity (Figure 1c). It is highly developed in Chaetodermatidae, but reduced in Limifossoridae, and vestigial in Prochaetodermatidae (Haszprunar, 1987). The dorsoterminal sense organ is chemoreceptive, and has been suggested to be homologous to osphradia in other mollusc classes (Salvini-Plawen, 1972b; Haszprunar, 1987; Ivanov, 1996b). The dorsoterminal position has been suggested to be a primitive position for the molluscan osphradium (Salvini-Plawen, 1985). However, the structure of the organ differs between the aplacophoran classes, and the ultrastructure as well as the position is considerably divergent from proposed osphradia in other groups; suggesting that at least the position of this sensory organ is an autapomorphy for Aplacophora (Scheltema, 1993; Sigwart & Sumner-Rooney, 2016).

Digestive system

The digestive system has been described in detail for most taxa of Caudofoveata, and differentiation between taxa has been used for taxonomy, as well as evolutionary hypotheses. The radula is located in the buccal cavity, where it is secreted by odontoblasts in a radula sac (Figure 4). The radula has two rows of mirror image teeth attached to a basal radular membrane, which is secreted by membranoblasts. The radular membrane is fused to different degrees in the different taxa. In *Scutopus*, the membrane is in the form of two longitudinal bands connected between each pair of

teeth. In *Limifossor*, the radula membrane forms a continuous sheet posteriorly, but is split further anteriorly. The split radular membrane and presence of a subradular sac makes the *Limifossor* radula capable of more movement than the other genera assigned to Limifossoridae, *Psilodens* and *Scutopus*, which lack the subradular sac (Salvini-Plawen, 1981; Scheltema, 1981). In Prochaetodermatidae, the radular membrane is a unipartite continuous sheet, with lateral tooth-like extensions that are believed to support the radular teeth (Scheltema, 1981). Representatives of Prochaetodermatidae probably feed in a rasping manner, similar to gastropods, and are the only caudofoveates in which wear on the radula teeth has been observed. The unipartite condition of the Prochaetodermatidae radula provides rigor for rasping (Scheltema, 1981), while the jaws serve to open the foregut for protrusion of the radula (Salvini-Plawen, 1988). Bolsters of muscular and connective tissue support the radula and provide a base for attachment of the muscles that are used in movement of the radula. The radula in Limifossoridae has up to 30 pairs of teeth, and in Prochaetodermatidae up to 11 pairs of teeth (Salvini-Plawen, 1988).

In Chaetodermatidae, the radular sheath in which the radula is produced is replaced by a small radular pit and a radular pouch, which produces the cone (Salvini-Plawen, 1981). The cone in the radula in Chaetodermatidae has been suggested to represent a fused radula (Scheltema, 1972), or a thickened radula membrane (Salvini-Plawen, 1972b; Salvini-Plawen, 1981). While the single pair of teeth in Chaetodermatidae are produced only once, the cone is continuously secreted (Scheltema, 2014).

The oral cavity is connected by the oesophagus to a large stomach or midgut, with a midgut sac or digestive diverticulum, followed by a narrow intestine (Figure 4). In the oesophagus, food particles are mixed with secretions to form a mucus strand, which is carried through the midgut. Two types of digestive cells line the caudofoveate midgut; inflated club-shaped cells, that hold a glandular body that is released into the gut, and granula-cells with distal portions that are apocrinely cast off to help with digestion (Scheltema, 1981; Salvini-Plawen, 1988). The presumably most conservative configuration of the digestive system is found in Limifossoridae (Salvini-Plawen, 1972b). In *Psilodens*, the midgut and midgut sac are histologically

undifferentiated. The extended, pouched midgut is lined with club-shaped and granular cells in *Psilodens*, while the shorter midgut in *Scutopus* and *Limifossor* is lined with cubical cells with fine granulation, and the club-shaped and granular cells are restricted to the midgut sac (Salvini-Plawen, 1988).

Two evolutionary lines are suggested from the hypothesized ancestral state of the digestive system, one towards elaboration in Chaetodermatidae, and the other towards reduction in Prochaetodermatidae. In Prochaetodermatidae, the granular cells exist in a modified form, and are only found in the midgut. The shortened midgut sac is lined by a single type of cells, which appear to be modified club-shaped cells (Salvini-Plawen, 1981; Scheltema, 1981). The stomach in Prochaetodermatidae is also unique among the Caudofoveata in lacking a ciliated typhlosole, or groove, running down the stomach to the intestine as found in the remaining taxa (Scheltema, 1981). A mucoid rod or protostyle is formed at the anterior end of the intestine, in all taxa except Prochaetodermatidae. The cell lining in Chaetodermatidae is more similar to that found in Limifossoridae (Salvini-Plawen, 1985), but the midgut has been elaborated to form a gastric shield at the base of the stomach, and a style sac to which the mucoid rod is restricted (Scheltema, 1981).

Reproduction and development

Only few studies have dealt with development and ecology of Caudofoveata, and little is known about reproduction and development. The gonads are paired in juvenile caudofoveates, but become fused in adults, except in *Limifossor* and *Psilodens*. Caudofoveates lack true gonoducts. The gonads empty directly into the pericardial cavity via gonopericardial ducts, from where the gametes pass through the coelomoducts or pericardial ducts to the outside (Figure 4). In Prochaetodermatidae, the gonopericardial ducts are fused (Salvini-Plawen, 1985). Caudofoveates are dioecous and release eggs and sperm into the water column where fertilization occurs (Salvini-Plawen, 1985; Scheltema *et al.*, 1994). The morphology of the ectaqua sperm and unique spermiogenesis have been described for *Chaetoderma* (Buckland-Nicks & Chia, 1989; Buckland-Nicks, 1995). Larval development has also been described for representatives of *Chaetoderma* (Nielsen *et al.*, 2007), which have

lecitotrophic trochophore larvae with a telotroch and prototroch and a pair of protonephridia. In older larval stages, putative fusing mantle edges and seven dorsal rows of spicules can be observed.

Little is known about life histories of caudofoveates, with the exception of the prochaetodermatid *Prochaetoderma yongei* Scheltema, 1985, which has been shown to reach maturity within one year after settlement of larvae in screened experimental deep-sea boxes (Scheltema, 1987).

1.4 Distribution and geographical patterns

Species distribution and bathymetric ranges varies considerably between species within the caudofoveate families. Species of Chaetodermatidae have a predominantly shallow distribution, with several species occurring at depths from about 30 m down to a few hundred meters, although some species can be found down to 2000 m (e.g. *Chaetoderma simplex* Salvini-Plawen, 1971 and *Falcidens caudatus* (Heath, 1918)). The family also includes the only species of Caudofoveata found in the intertidal, *Falcidens poias* Scheltema, 1995, which occur in seagrass beds in Western Australia (Scheltema, 1995). The geographic and bathymetric range of each species within Chaetodermatidae is more limited than e.g. most species of Prochaetodermatidae and of the genus *Scutopus* within Limifossoridae (see below). *Falcidens crossotus* and *Falcidens sagittiferus* Salvini-Plawen, 1968 are for example geographically restricted to the Norwegian coast (Salvini-Plawen, 1975).

Within Limifossoridae, the bathymetric distribution differs between the genera. The limited number of species of *Psilodens* described so far are found at depths from 1600 m down to almost 4000 m, and species of *Limifossor* occur at depths down to 2000 m. Species of *Scutopus* display a similar distribution pattern as found in Chaetodermatidae, with most species having a shallow distribution (<500 m). Deeper records only occur for the two most widespread species in the genus; *Scutopus robustus* Salvini-Plawen, 1970 which is registered from the Norwegian coast to the western Mediterranean, from depths of 50 to 3540 m, and *Scutopus ventrolineatus*

occurring from northern Norway to South Africa, with a depth range of 40 to 1250 m. Species of Limifossoridae, especially *Limifossor* and *Psilodens*, do not seem to occur in large abundances, and more than one or a few specimens are rarely found in a single sample. Some species of *Scutopus*, e.g. *Scutopus ventrolineatus*, have however occasionally been found in larger abundances (Salvini-Plawen, 1975; own unpublished data).

Out of the three recognized families within Caudofoveata, Prochaetodermatidae is the most species-rich and widespread family. Representatives of Prochaetodermatidae are primarily found in the deep-sea, where they can reach high abundances, and have in some areas been reported to exceed even polychaetes in numbers. Densities of up to 350 individuals per m² have been reported (Scheltema, 1997; Scheltema & Ivanov, 2009). The numerous prochaetodermatids might owe their success to the efficient gastropod-like radula and their jaws, which allows them to utilize a larger variety of food sources and have a diet where they are independent of particle size; allowing them to take advantage of a greater amount of food in their deep sea habitat, where food might be a limiting factor (Scheltema, 1981). Several species with deep distributions also have large geographical distribution, e.g. the ampho-Atlantic *Prochaetoderma yongei*, or *Chevroderma turnerae* Scheltema, 1985, which are distributed in large parts of the Atlantic and Indian Oceans.

Prochaetodermatidae have been particularly thoroughly investigated and mapped in many areas (e.g. Scheltema, 1985; Scheltema & Ivanov, 2000; Ivanov & Scheltema, 2001b, 2002; Ivanov & Scheltema, 2008), but the Pacific deep-sea fauna is still largely unknown. No prochaetodermatids are found in the northwest Atlantic (Scandinavia) or in the Arctic (Ivanov and Scheltema 2001). Species of Chaetodermatidae have been recorded from all the world's oceans, and species of Limifossoridae from all oceans except from the polar regions; but records are more scattered for species within these two families than for Prochaetodermatidae in many areas.

Distribution patterns with a disjoint geographical distribution, and distinct, but very similar morphologies, as described by Scheltema (1990) of species of *Falcidens* (*Chiastofalcidens*), can also be observed in other caudofoveate genera. Two distinct morphological groups of species can also be distinguished within *Falcidens*. *Falcidens halanychi* and *Falcidens limifossorides* in the western Atlantic and Eastern Pacific respectively, both share a short and stout body shape, and triangular, thick sclerites. Another group of species has a tailed body shape, and rounded sclerites with concave sides: *Falcidens crossotus* in the North East Atlantic, *Falcidens caudatus* in the North West Atlantic, *Falcidens australocaudatus* Passos, Corrêa & Todt 2016 in the South East Atlantic, *Falcidens guttuosus* (Kowalevsky, 1901) in the Mediterranean Sea, *Falcidens vasconiensis* off of the Iberic peninsula, *Falcidens hartmanae* in the East Pacific and *Falcidens ryokuyomaruae* Saito & Salvini-Plawen, 2014 in the West Pacific. Similarly, two species of *Chaetoderma* with a body shape of even diameter with heavily striated sclerites are found in Scandinavia (*Chaetoderma nitidulum*) and off of the United States east coast (*Chaetoderma canadense* Nierstrasz, 1902).

Few caudofoveate species are known from the Arctic, and all that have been recorded so far belong to the family Chaetodermatidae (Wirén, 1892a; Ivanov, 1981, 1984, 1986a, 1987). The specimens from the Antarctic sequenced in Paper IV represent the first investigation of Caudofoveata from this area, and include species of Prochaetodermatidae and Chaetodermatidae. The North Atlantic, in contrast, represents a particularly well investigated area when it comes to all three caudofoveate families; with sampling from Scandinavia, (Salvini-Plawen, 1975, 1978; Ivanov *et al.*, 2010), Iceland (Ivanov & Scheltema, 2001a), the North West Atlantic (Heath, 1918; Scheltema, 1985; Ivanov & Scheltema, 2008), and the Iberic peninsula (Scheltema & Ivanov, 2000; Señarís *et al.*, 2016a, 2016b; Señarís *et al.*, 2017b). The neighbouring Mediterranean Sea (Salvini-Plawen, 1972a; Scheltema & Ivanov, 2000; Öztürk & Salvini-Plawen, 2006) is also quite well known. The southern Atlantic (Scheltema, 1976; Scheltema & Ivanov, 2000; Ivanov & Scheltema, 2008; Corrêa *et al.*, 2014; Passos *et al.*, 2016; Corrêa *et al.*, 2018) and the Indian

Ocean (Nierstrasz, 1902; Heath, 1911; Ivanov & Scheltema, 2001b, 2002) are less investigated, except for Prochaetodermatidae. The more scattered records from the Pacific Ocean are from the North American west coast (Heath, 1904, 1911; Schwabl, 1963; Salvini-Plawen, 1972a; Scheltema, 1998), the West Pacific (Ivanov, 1996a; Ivanov & Scheltema, 2004; Saito & Salvini-Plawen, 2014) and from Australia (Scheltema, 1989).

Material from sampling in more poorly investigated areas almost exclusively consists of previously undescribed species (e.g. Scheltema, 1989; Passos *et al.*, 2016), and even material from well investigated areas contains undescribed species (e.g. Schander *et al.*, 2006; Señarís *et al.*, 2016a); illustrating that a lot of undescribed diversity still exists within the group.

2. Aims of the thesis

Caudofoveata and Solenogastres are in numbers some of the smallest among the higher taxa of Mollusca, and are still relatively unknown compared to the larger higher molluscs taxa.

Many questions about relationships between and within the two aplacophoran groups remain unanswered, and the internal relationships of both Caudofoveata and Solenogastres are still largely unknown (Todt *et al.*, 2008; Todt, 2013). The aplacophoran molluscs are still seen as obscure and difficult to identify and work with. Material of undescribed species is held in many museums and working collections, and a lot of unrecognized diversity still exists.

Over the last years, the aplacophoran molluscs have received increasing attention as molecular studies have provided evidence for their placement in the clade Aculifera (Kocot *et al.*, 2011; Smith *et al.*, 2011; Vinther *et al.*, 2012). Despite of an increasing number of studies on the phylogenetic position of aplacophorans within Mollusca, the evolutionary relationships of Caudofoveata have never been tested in a proper phylogenetic analysis, neither based on morphological nor molecular data. In the molecular studies that have included sequences of Caudofoveata, only one or few taxa have been included (Passamaneck *et al.*, 2004; Giribet *et al.*, 2006; Meyer *et al.*, 2010; Wilson *et al.*, 2010; Kocot *et al.*, 2011; Smith *et al.*, 2011; Vinther *et al.*, 2012). Except for the sequences from few species of aplacophorans sequenced for the purpose of investigating higher mollusc phylogeny, little molecular data has been available for either of the groups of aplacophoran molluscs. The only previous study focusing on molecular characters in Caudofoveata until now is a publication of the mitochondrial genome of *Scutopus ventrolineatus* (Osca *et al.*, 2014).

Lack of knowledge about polarity and homology of characters in Caudofoveata makes existing information about morphology challenging to interpret in a phylogenetic context. Molecular data has great potential to provide additional

characters, and thereby information that will shed light on the evolutionary relationships within Caudofoveata.

Resolving the phylogenetic relationships within Caudofoveata is also important to inferring the plesiomorphic state of characters within Aplacophora. By providing insight into the evolution of important molluscan characters for which the plesiomorphic state is unknown, resolving caudofoveate relationships can even contribute to our understanding of the evolution of Mollusca as a whole.

The main objective of this thesis was to construct a solid hypothesis for the phylogeny of the Caudofoveata. The aim was to resolve phylogenetic relationships both among and within families (Paper III and Paper IV). Special emphasis was placed on Chaetodermatidae, a family that despite constituting the second largest within Caudofoveata is still poorly understood. For example, within Chaetodermatidae, the genus *Falcidens* consists of species with highly variable morphology, and might not constitute a monophyletic group (Paper II and Paper IV).

The construction of a worldwide phylogeny was coupled with investigations of distribution and occurrence of Caudofoveata in the North Atlantic, particularly Scandinavia (Paper I and Paper II).

3. Material and Methods

Although a fair amount of knowledge exists about morphology and anatomy of Caudofoveata, only very few sequences from caudofoveates were available. Molecular data offers additional sets of characters that can be analysed in a phylogenetic context, and contribute to obtaining a robust phylogeny. Combining knowledge from investigations of morphological characters with molecular data makes it possible to evaluate the characters used to define and identify the taxa within Caudofoveata. Therefore, a large part of the project focused on obtaining molecular data from species of Caudofoveata. Detailed information on the material included, and detailed descriptions of the methodology applied can be found in each of the included papers.

3.1 Sampling and material

Existing material in museum collections is mainly fixed in formalin, which makes it unsuitable for DNA sequencing. It was therefore necessary to acquire freshly sampled material. Samples were obtained from own sampling activities with R/V *Hans Brattström* from western Norway; from the IceAGE I cruise around Iceland; and from the Skagerrak on the BIOSKAG cruises. On these cruises, the material could in part be sorted on board in living condition. Fresh material was also provided by colleagues from the Svalbard archipelago, from Porsangerfjord, Norway, and from cruises along the United States east and west coast, the Gulf of Guinea, the Eastern Pacific, Japan, and Antarctica. In addition to freshly sampled material, material held in museum collections was included. Museum material was made available from the University Museum of Bergen, Natural History Museum in Oslo and NTNU University Museum in Trondheim, Norway; Gothenburg Museum of Natural History, Sweden; National Museums Scotland; and the American Museum of Natural History.

This sampling effort resulted in a global coverage of material, with particularly thorough sampling from the North Atlantic, including material spanning the entire Norwegian coastline, including Svalbard, continuing to Southern Sweden. See Figure 5 for a map of sampling sites for included material.

Material of all three recognized families of Caudofoveata was included in the study. For Chaetodermatidae, material was included from the species rich genera *Chaetoderma* and *Falcidens*, but not the doubtful genus *Caudofoveatus* and the monotypic genus *Furcillidens*. *Falcidens* represents a genus with one of the largest ranges in overall morphology. Species of *Falcidens* covering a wide range of morphotypes were included. Two out of three genera within Limifossoridae, and all genera of Prochaetodermatidae, except the monotypic *Lonchoderma* and *Dacryomica* Ivanov & Scheltema 2004, could be included.

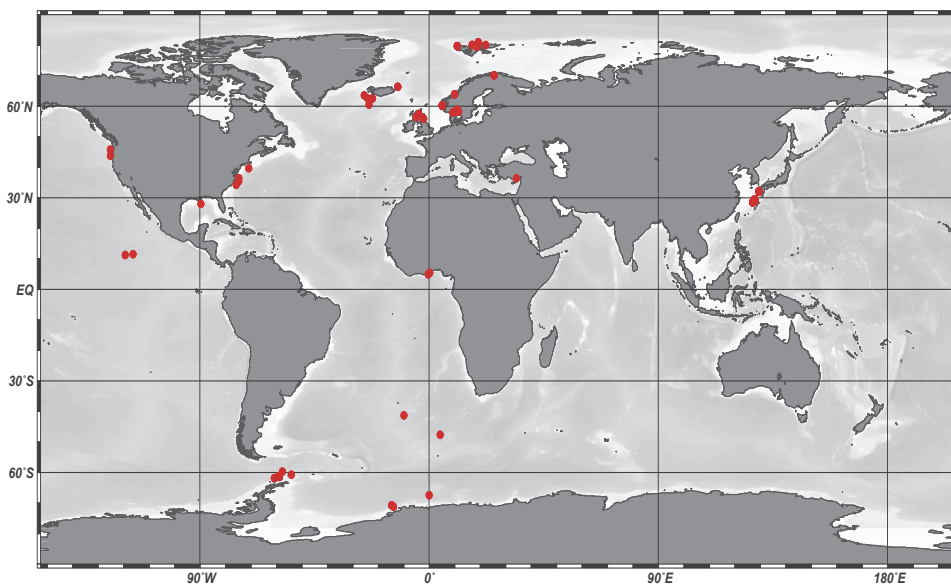


Figure 5. Map of sampling sites for investigated material.

3.2 Morphological methods

In addition to the molecular approach, traditional methods were used to study morphology. All material was studied under a stereomicroscope and photographed prior to sequencing or dissection. The current taxonomy of the aplacophoran molluscs, particularly in Caudofoveata, is largely based on the morphology of hard parts: the radula, and the sclerites covering the body. Radulae and sclerites were prepared using the methods described in Ivanov and Scheltema (2009). Radulae were dissected out and the surrounding tissue dissolved in bleach in order to be studied and mounted permanently on slides. Microscope preparations were also made from sclerites (Paper I, Paper II). These were studied under brightfield lighting and under cross-polarized light, which provides a unique view of the structure and shape of the sclerites (Scheltema & Ivanov, 2004).

Histological sections were made from *Chaetoderma nitidulum* in order to study the anatomy of the radula and surrounding tissues (Paper II).

Description of a new species of *Psilodens* (Limifossoridae) from the North Atlantic was made using standard methods that have been used for species descriptions in the last years (Schander *et al.*, 2006; Ivanov & Scheltema, 2007; Ivanov *et al.*, 2010; Corrêa *et al.*, 2014), and included descriptions of sclerites and radula, and COI barcodes deposited in GenBank (Paper I).

3.3 Molecular methods

As a molecular approach was largely new for Caudofoveata, it posed several challenges. At the onset of this project in 2008, hardly any molecular data was available for aplacophoran molluscs. The use of what little data had been deposited in NCBI GenBank was impaired by many sequences containing sequencing errors (Okusu & Giribet, 2003) or stemming from contamination, and could not be utilized as a trustworthy source of data. As the amount of data in GenBank has been rising, more sequences have become available for comparison with newly acquired

sequences, making it possible to use BLAST searches to verify both the identity of target organisms, and also of prey organisms to reveal contaminated sequences.

Despite efforts to sample new material and obtain material from colleagues, lack of material fixated in a manner suitable for extraction of DNA limited the taxon sampling for molecular phylogenetic analyses. Attempts at extraction of DNA from material fixed in formalin were performed using commercial extraction kits (Qiagen, Mole Genetics) and CTAB extraction, without satisfactory results.

To obtain DNA sequence data, both PCR amplification of individual gene fragments and subsequent Sanger sequencing (Paper IV) and high throughput sequencing on the Illumina platform (Paper III) was used. For Sanger sequencing, universal primers were used for COI, while mollusc-specific primers or primers previously used for molluscs (Okusu & Giribet, 2003; Okusu *et al.*, 2003; Passamaneck *et al.*, 2004; Giribet *et al.*, 2006; Meyer *et al.*, 2010; Wilson *et al.*, 2010) were used for H3 and the ribosomal 16S, 18S and 28S, in addition to own newly designed primers for some fragments.

Species of Prochaetodermatidae proved especially challenging to sequence. Because of the small size of most species in this family, DNA must often be extracted from small amounts of tissue, often leading to little yield of DNA. Also, due to the small size, a larger part of the animal must be used for extraction, leading to a greater chance of contamination from prey organisms, parasites or epibionts. Targeted PCR amplification of the desired markers used in the study proved especially problematic within Prochaetodermatidae. In particular, amplification of mitochondrial genes proved difficult from specimens of Prochaetodermatidae. For the COI gene, universal primers that have been used across the animal kingdom (Folmer *et al.*, 1994) and successfully amplified COI from both of the other sequenced caudofoveate families, as well as two sets of highly degenerate universal primers (Meyer, 2003; Geller *et al.*, 2013) did not yield results. New primers were designed for the Prochaetodermatidae from sequences obtained with non-targeted sequencing from *Spathoderma clenchi* Scheltema, 1985, but even with these specific primers, amplification was

unsuccessful for species outside of the genus. Comparison of the obtained sequences from species of Prochaetodermatidae to other caudofoveate species shows that Prochaetodermatidae are genetically highly differing from other caudofoveates, as well as having a lot of genetic variation among taxa within the family itself. Investigations of full mitochondrial genome sequences (Paper III) showed that both gene order and sequences of the mitochondrial genomes of Prochaetodermatidae is highly disparate from other caudofoveates.

All amplified sequences were verified through a BLAST search against the NCBI nr/nt database and comparison of alignment to other own sequences. Raw data was checked to ensure the quality of sequences. Whenever possible, multiple specimens from each species were sequenced for amplification of individual gene fragments. For a few sequences that were aberrant from the remaining caudofoveate sequences, a new extraction of DNA and new PCRs were performed to rule out contamination and verify the origin of the sequence. Illumina data was used to assemble complete or near-complete mitochondrial genomes of representatives for all families of Caudofoveata, as well as a species of Solenogastres for comparison (Paper III). Individual gene fragments obtained with Sanger sequencing and mined from Illumina data were also used for phylogenetic analyses (Paper III and Paper IV). The increased availability and lower costs of high throughput sequencing has made acquisition of larger amounts of data for lower cost than traditional Sanger sequencing possible. This will greatly aid future studies of aplacophoran molluscs utilizing molecular methods.

4. Results and discussion

4.1 Caudofoveata in the North Atlantic

4.1.1 New records of Caudofoveata in the North Atlantic

The North Atlantic represents a well-investigated area, where the diversity of Caudofoveata has been well mapped (e.g. Salvini-Plawen, 1975; Salvini-Plawen, 1978; Schander *et al.*, 2006; Ivanov & Scheltema, 2008; Scheltema & Ivanov, 2009). Still, new records have been added to the known occurrence and distribution of caudofoveates in this area from the material investigated.

Updated records of occurrence of Caudofoveata around Iceland, which were based on the first records from material sampled during the IceAGE cruise ME85/3 in 2011 (Paper I), include seven species of Caudofoveata with a previously known distribution range in Icelandic waters, and two new records for the area. *Psilodens balduri* Mikkelsen & Todt 2014 is new to science and *Falcidens halanychi*, with a known distribution in the American North Atlantic, is new to Iceland. The records presented in Paper I thus increase the number of known caudofoveate species around Iceland to nine. An undescribed species of *Falcidens* has also been recorded from Iceland (Paper IV).

The description of a new species of *Psilodens* in Paper I increases the total number of species in this genus to three. An additional new species of *Psilodens* (Paper IV) from the United States east coast is awaiting description.

4.1.2 Species distribution in the North Atlantic

The geographical distribution of caudofoveates in the North Atlantic has been mapped to a degree that makes comparison of distribution patterns for the investigated species possible. There is a clear distinction between the caudofoveate

fauna in the North East Atlantic and the North West Atlantic. One example of this is found in the two tailed species of *Falcidens* from this area. *Falcidens crossotus* is found in the North East Atlantic and *F. caudatus* in the North West Atlantic. These two species form a well-supported clade in all analyses (Paper IV), and most likely are sister species with a common origin. Some species in the North West Atlantic have a distribution that extends as far east as to the Mid-Atlantic ridge, e.g. *Falcidens halanychi*, and the prochaetodermatids *Spathoderma clenchi* and *Prochaetoderma yongei*, but it appears that the Mid-Atlantic ridge forms a geographical barrier. These species have a distribution extending south along the United States east coast south to about 35°N. South of 35°N the fauna changes, and species sampled from here include *Falcidens acutargatus*, *Claviderma amplum* Ivanov & Scheltema, 2008, and *Niteomica captainkiddae* Ivanov & Scheltema, 2008.

Chaetoderma nitidulum has previously been recorded from the Svalbard archipelago in the North to the British Isles and Denmark in the South. New molecular data revealed a closely related population off of the United States east coast, extending the distribution of *C. nitidulum* s. l. from the previously known distribution in the East Atlantic to span the entire North Atlantic (Paper II, see also chapter 4.1.3).

In the East Atlantic, *Falcidens sagittiferus* and *F. crossotus* have distributions limited to Scandinavian waters, while the two species of *Scutopus* found in the North Atlantic, *S. ventrolineatus* and *S. robustus*, have distributions that extend further south. These two species of *Scutopus* were not recovered as sister in the analyses. Instead, *S. ventrolineatus* was consistently recovered with a sister relationship with an undescribed species of *Scutopus* from the East Pacific with a similar body shape and sclerite morphology (*Scutopus* sp. A; Paper IV). No species of *Scutopus* have been recorded from the West Atlantic so far.

Two species of *Psilodens*, *P. balduri* and *Psilodens* sp. A (Paper IV) have a distribution in the West Atlantic, but they have a non-overlapping geographic range, and occur at different depths. The two species of *Psilodens* are recovered as sisters with high support in the phylogenetic analyses (Paper IV). A third Atlantic species,

Psilodens tenuis Salvini-Plawen, 1977, has been described from the Strait of Gibraltar, but could not be included in the molecular analyses.

4.1.3 The identity of *Chaetoderma nitidulum*

Chaetoderma nitidulum is a commonly occurring species with a wide distribution range in the North Atlantic (Salvini-Plawen, 1975, 1978), but its species identity has been debated. Investigations combining molecular and morphological data from comprehensive sampling from almost the entire distribution range to investigate the status of this species (Paper II), showed genetic and morphological patterns that were previously unknown.

Analyses of molecular data from material of *Chaetoderma* from the North Atlantic revealed two distinct genetic lineages in the northeastern Atlantic (Clade I) and one clade with equal genetic distance in the northwestern Atlantic (Clade II). The first East Atlantic clade (*C. nitidulum* Ia) includes specimens from all East Atlantic localities (southern Sweden and the entire Norwegian coastline to the Svalbard archipelago), while the second (*C. nitidulum* Ib) comprises specimens from only the southernmost localities, from Sweden and as far north as Bergen, Norway (Paper II, figure 6). Collectively the three clades are here referred to as *Chaetoderma nitidulum* s. l. The division into separate clades is highly supported in the analyses of COI and 16S, but in the 18S gene resolution is lower (Paper II, figures 3–5). Despite the comparable genetic distance in the COI gene, it is evident from the phylogenetic analyses of mitochondrial gene fragments that the two subclades of the *C. nitidulum* s. l. clade I from Scandinavia are more closely related to each other than to the West Atlantic clade, *C. nitidulum* s. l. II. The divergence in gene sequences from both COI and 16S, the fastest evolving genes included in the study, are too low to conclusively support a division into more than one taxon of *C. nitidulum* s. l. in Scandinavia. The division into two genetic subclades can further not be strictly attributed to sediment type, depth, or other abiotic factors.

Morphological analyses showed significant variation between specimens from different geographical areas, and between animals of different sizes, but this variation did not reflect the genetic lineages. Sclerites of *C. nitidulum* s. l. from different geographical regions show a gradual difference in sclerite morphology with changing latitude (Paper II, figures 10–12). The variation in sclerite morphology within *C. nitidulum* s. l. that was found is larger than what has been described previously (Salvini-Plawen, 1978). Comparison of specimens from a larger sampling range than previous studies revealed that specimens of *C. nitidulum* s. l. from the northern part of the distribution range have a relatively consistent sclerite morphology, while specimens from the southern part show larger variations in sclerite morphologies. These morphologies do however not correspond to the two molecular clades found in the area.

Differences in sclerite and radula morphology, morphological characters considered most important for species delimitation in *Chaetoderma*, are not consistent with our molecular results for the two Eastern Atlantic clades. All specimens of the West Atlantic clade II that could be included in the study were juveniles, and therefore do not show the full set of adult sclerites (Paper II, figure 13). Therefore, no new morphological species was defined for this clade. Investigation of morphological characters from fully grown representatives of the *C. nitidulum* s. l. clades II is needed. Comparisons of the hard part morphology (sclerites and radula) between representatives of the two Eastern Atlantic *C. nitidulum* s. l. subclades did not result in any significant differences between specimens of comparable size and similar geographic origins.

Molecular data alone do not justify a splitting of *C. nitidulum* into three separate species. Assignment of species names to the Eastern Atlantic molecular subclades is furthermore complicated by the fact that specimens of both subclades occur at the type locality and that the type material is not viable for molecular analyses. At present, *C. nitidulum* s. l. should therefore be treated as one species, and the name *C. nitidulum* should be used for all Northern Atlantic *Chaetoderma* with striated trunk sclerites.

Molecular data from specimens from the remaining, southernmost part of the distribution range of *C. nitidulum*, in the North Sea and around the British Isles, could possibly aid in clarifying the taxonomic status of the two East Atlantic subclades. In addition, our samples from the Western Atlantic are limited. Genetic data from a larger part of the distribution range of the western Atlantic *C. nitidulum* s. l. II would uncover if genetic patterns similar to those found in Scandinavia are found in the West Atlantic.

Chaetoderma canadense which has a similar morphology to *C. nitidulum* (Salvini-Plawen, 1978) has a registered distribution that overlaps with sampling localities for the West Atlantic *C. nitidulum* s. l. II, but no material of this species was available for molecular investigations. In addition to *C. canadense*, three further *Chaetoderma* species have been described from the North West Atlantic: *Chaetoderma bacillum* Heath, 1918, *Chaetoderma lucidum* Heath, 1918, and *Chaetoderma squamosum* Heath, 1918. Material of these species was not available for investigation, and the description of these species is too brief for adequate morphological comparison. Two other *Chaetoderma* species, *Chaetoderma intermedium* Knipowitsch, 1896 and *Chaetoderma productum* Wirén, 1892, occur in the arctic North East Atlantic. While distinct morphological differences can be pointed out between *C. nitidulum* and these two species (Salvini-Plawen, 1975, 1978), no genetic data is available for these species.

4.2 Phylogeny of Caudofoveata

4.2.1 The Chaetodermatidae radula

The main defining character of Chaetodermatidae as a taxon is a radula reduced to a single pair of denticles attached to a sclerotized cone-shaped structure (Salvini-Plawen, 1968). The main diagnostic characters separating genera within the taxon are also connected to the radula morphology (Salvini-Plawen, 1968; Scheltema, 1972). In *Falcidens* (Figure 3d), the radula consists of a pair of sickle-like teeth connected by a

proximal cuticular symphysis that is attached to the cone, and a central plate with two apophyses that wrap around the teeth. The radula of *Chaetoderma* (Figure 3e) is defined as having a pair of denticles sitting on lateral projections connected to the radular membrane, which forms a dome that surrounds the radula (Scheltema, 1972; Salvini-Plawen, 1975; Ivanov, 1979).

However, investigations using molecular data (Paper II) have revealed that the differences between the radulae of *Chaetoderma* and *Falcidens* at least in the case of *C. nitidulum* represent ontogenetic changes, and are thus not apomorphies for the two genera. A detailed comparison of the radula morphology showed that there is a continuous change from a (juvenile) “*Falcidens*-type” radula morphology, via a (subadult) intermediate stage to the (adult) “*Chaetoderma*-type” radula morphology (Paper II, figure 7). The radula of small *C. nitidulum* s. l. specimens looks very similar to a typical *Falcidens*-type radula (*sensu* Scheltema 1972), except that the symphysis between the teeth of the juvenile *C. nitidulum* s. l. radula is not sclerotized like in the radula of *Falcidens* as described by Scheltema (1972, 1981). The cone and the entire dome appear to grow continuously during ontogeny, while the teeth stay the same size, and the sclerotized central plate is only present in small specimens.

The *Falcidens*-radula is therefore not an apomorphy for the genus *Falcidens* and the diagnosis of *Chaetoderma* needs to be amended. It remains to be investigated whether all species of *Chaetoderma* undergo ontogenetic changes in radula morphology, as found in *C. nitidulum*. Radulae from juveniles of *Caudofoveatus* and *Furcillidens* have not been described, and it is unknown if the radula morphology in these two genera changes during ontogeny. It is possible that the specimens described by Ivanov (1981) as *Caudofoveatus* represent a transitory state. All specimens assigned to this genus were close to 1 cm in length, and based on the average adult size of *Chaetoderma* spp., could be juveniles. Specimens of *Caudofoveatus* were not available for sequencing, and molecular analyses could clarify the status of this genus.

4.2.2 Relationships within Chaetodermatidae

The results from the phylogenetic analyses (Paper, III, IV) strongly contradict traditional classification within Chaetodermatidae. The two sequenced genera within this family, *Falcidens* and *Chaetoderma*, are recovered as intermixed.

Phylogenetic analyses of a complete set of mitochondrial genes (Paper III) gave the same topology as analyses based on fragments of six mitochondrial and nuclear genes (Paper IV). In all the phylogenetic analyses of complete mitochondrial genes (Paper III), Chaetodermatidae is recovered as monophyletic with strong support, but as *Chaetoderma* is nested within *Falcidens*, the latter appears paraphyletic (Paper III, figure 3). In the analyses of nuclear and mitochondrial gene fragments (Paper IV), *Chaetoderma* appears paraphyletic, while *Falcidens* is polyphyletic with two species found at the base of the clade joining both Chaetodermatidae and Limifossoridae (Paper IV, figure 3). The non-monophyly of *Falcidens* and *Chaetoderma* most likely reflect the deficiency of using morphological characters of the radula to define these genera, as shown in Paper II.

Mitochondrial gene order was identical between the two species of *Falcidens* included in the analyses in Paper III, *Falcidens (Chiastofalcidens) acutargatus* and *Falcidens halanychi*. *Chaetoderma nitidulum* shows the same order of protein coding genes and rRNAs as the two *Falcidens* species, but the order of tRNAs differs substantially (Paper III, figure 2). The identical gene order in the two *Falcidens* species, which have very different morphologies, could provide indication that this gene order might be found in the whole taxon, and possibly support the monophyly of at least parts of *Falcidens*.

The suggested split of *Falcidens* into a tailed and non-tailed group (e.g. Salvini-Plawen, 1984) is not recovered in our trees (Paper IV). The non-tailed species of *Falcidens* are not recovered as monophyletic, and two of these are clustering more closely with species of *Chaetoderma*. In our analyses of concatenated gene sequences, the two tailed species of *Falcidens* from the Atlantic Ocean, *Falcidens crossotus* and *Falcidens caudatus*, are consistently recovered as sister species with

high support, while the third tailed species from the West Pacific, *Falcidens* sp. C, is not part of this clade, but rather clusters with *Falcidens* (*Chiastofalcidens*) *acutargatus* (Paper IV, figure 3). *Falcidens* (*Chiastofalcidens*) *acutargatus* does however also have a tailed body shape, as the remaining species assigned to *Falcidens* (*Chiastofalcidens*).

Two species of the subgenus *Chiastofalcidens* (*Falcidens* (*Chiastofalcidens*) *acutargatus* and a yet undescribed species, *Falcidens* (*Chiastofalcidens*) sp. D) could be included in the analyses in Paper IV. These were recovered as sister species in the summarized gene tree, although with moderate support, but not recovered as monophyletic in the analyses of concatenated data (Paper IV, figure 4). The uncertain placement of the species assigned to the subgenus *Chiastofalcidens* leaves the question of the validity of the subgenus open, but the clustering of two of the species in the summarized tree provides some indication towards a closer relationship between the species assigned to *Falcidens* (*Chiastofalcidens*). The sclerites shared by *Falcidens* (*Chiastofalcidens*) species are unique within Caudofoveata in both shape and ornamentation, and support this grouping. Further investigations are however needed to conclusively answer whether they constitute a monophyletic clade.

4.2.3 Higher caudofoveate relationships

The three currently recognized families are well supported on the basis of distinguishing morphological characters, and clearly represent three separate lineages based on morphological evidence. Out of the three recognized families, Prochaetodermatidae is consistently recovered as monophyletic with strong support in the phylogenetic analyses (Paper IV), but neither Chaetodermatidae nor Limifossoridae were recovered as monophyletic in most analyses. In the analyses of six mitochondrial and nuclear gene fragments, both in trees constructed from individual gene fragments (Paper IV, figure 2, figure 4), as well as trees constructed from the concatenated dataset (Paper IV, figure 3), Chaetodermatidae and Limifossoridae are consistently recovered as one clade, sister to a clade comprising Prochaetodermatidae.

In the phylogenetic trees based on complete mitochondrial genes (Paper III), Chaetodermatidae was recovered as monophyletic with high support values in all analyses. Also comparison of mitochondrial gene order in Caudofoveata (Paper III, figure 2) revealed arrangements of rRNAs and tRNAs diagnostic for Chaetodermatidae and for Limifossoridae. Limifossoridae was however recovered as paraphyletic with *P. balduri* sister to Chaetodermatidae in all phylogenetic analyses of complete mitochondrial genes (Paper III), except the Bayesian inference analysis of nucleotide data, which recovered a monophyletic Limifossoridae.

The non-monophyly of both Chaetodermatidae and Limifossoridae, caused by the questionable placement of the three species recovered at the base of the clade joining the remaining Chaetodermatidae and Limifossoridae in the analyses in Paper IV, warrants further investigation and probably does not represent true phylogenetic relationships. The topologies recovered in Paper III and Kocot *et al.* (forthcoming), where Chaetodermatidae is nested within Limifossoridae, however indicate that Chaetodermatidae possibly evolved within a paraphyletic Limifossoridae.

Within Limifossoridae, four out of the five included species, *S. ventrolineatus*, *Scutopus* sp. A, *P. balduri* and *Psilodens* sp. A, were often grouped together in the phylogenetic trees based on both mitochondrial and nuclear gene fragments (Paper IV). The clade is supported by a high posterior probability in the trees resulting from analyses of concatenated data (Paper IV, figure 3). The position of the last limifossorid species, *S. robustus*, is somewhat erratic in the trees from the analyses in Paper IV, but in the analyses of mitochondrial genes (Paper III), *S. robustus* and *S. ventrolineatus* are consistently recovered with a sister group relationship.

Mitochondrial genomes were sequenced from three species within Limifossoridae, *P. balduri*, *S. robustus* and *S. ventrolineatus*. The almost identical mitochondrial gene order indicates a close relationship between the two genera *Scutopus* and *Psilodens* (Paper III, figure 2). Investigation of molecular characters to evaluate a the suggested separation of *Psilodens* and *Scutopus* in a separate family from *Limifossor* has not been possible, as no material suitable for molecular work was available for

Limifossor. Morphological characters suggest that the three genera together form a monophyletic group, in which *Psilodens* and *Scutopus* are more closely related to each other than to *Limifossor*: species of *Psilodens* and *Scutopus* share a similar radular morphology with simple, hook-shaped radular teeth, in *Scutopus* (Figure 3a) bearing several small denticles, while *Limifossor* (Figure 3b) has paired teeth that consist of a plate with two pointed denticles (Salvini-Plawen, 1977). *Psilodens* and *Scutopus* also share a similar body shape, while *Limifossor* has a short, stout body shape that is unusual within Caudofoveata. In addition, *Psilodens* and *Scutopus* share other characteristics of the digestive system: the lack of a subradular sac and the morphology of the midgut sac (Scheltema, 1981; Salvini-Plawen, 1988). *Psilodens* and *Limifossor* do on the other hand share a divided oral shield (Salvini-Plawen, 1977). Molecular data from species of *Limifossor* would aid in further investigations of the relationships within this family.

Within Prochaetodermatidae, none of the genera were recovered as monophyletic in the analyses in Paper IV. Species within the family are separated into two well-defined subclades in the trees resulting from analyses of concatenated data (Paper IV, figure 3) and in most of the trees based on single genes (Paper IV, figure 2). Species of *Chevroderma* Scheltema, 1985, *Claviderma* Scheltema & Ivanov, 2000, and *Spathoderma* Scheltema, 1985 are found in both of the subclades in the tree based on concatenated data. All species of *Prochaetoderma* Thiele, 1902 are recovered in one subclade, however as paraphyletic, as three species of *Spathoderma* and one species of *Chevroderma* are included in this clade. *Prochaetoderma* and *Spathoderma* share features of the sclerites: a broad, flat base and a pointed tip; but while *Prochaetoderma* has flat sclerites with a triangular tip, the tip of the sclerites in *Spathoderma* are rounded and pointed outwards, at an angle to the base. The single species of *Niteomica* Ivanov, 1996 is recovered as sister to *Spathoderma grossum* Scheltema & Ivanov, 2000. *Niteomica* and *Spathoderma* both have sclerites with a broad base and a pointed blade, which is bent outwards from the body. *Chevroderma* is distinguished from all other *Prochaetodermatidae* by distinct chevron-shaped growth pattern and a medial groove on the sclerites. The included species of

Chevroderma are not recovered as monophyletic in our analyses, but spread out in both of the Prochaetodermatidae clades. The topology within Prochaetodermatidae might be affected by the lack of coverage in the data matrix for several species within this family. However, even in the single gene trees most genera were not recovered as monophyletic (Paper III, figure 2).

The validity of several of the genera of Prochaetodermatidae (Scheltema, 1985; Scheltema & Ivanov, 2000; Ivanov & Scheltema, 2004) has been questioned (Salvini-Plawen, 1992; Salvini-Plawen, 1999; Señarís *et al.*, 2017a; Señarís *et al.*, 2017b). Our results suggest that characters of the sclerite cover might be insufficient for classification on genus level within Prochaetodermatidae.

4.2.4 Evolution of Caudofoveata

All results from the analyses of molecular data indicate a closer relationship between Chaetodermatidae and Limifossoridae than that of either to Prochaetodermatidae. In the phylogenetic analyses presented in Paper IV, the data coverage of individual gene fragments for several species of Prochaetodermatidae is limited. However, a topology with Prochaetodermatidae as sister to the two other recognized families was also recovered with the complete set of mitochondrial genes (Paper III), and a topology concurrent with the trees in Paper IV has additionally been recovered with phylogenomic data (Kocot *et al.*, forthcoming). A closer relationship between Chaetodermatidae and Limifossoridae than that of either to Prochaetodermatidae is also seen in the comparison of mitochondrial gene order (Paper III). Our results consequently refute a grouping of the two families with serial radulae as proposed by Ivanov (1986b).

A grouping of Chaetodermatidae and Limifossoridae has however never been suggested earlier, and few morphological characters are shared between these two groups. The basal position of the Prochaetodermatidae within Caudofoveata retrieved in the molecular analyses is unexpected, and has also never been proposed earlier. The basal position of Prochaetodermatidae is contrary to traditional views, as

Limifossoridae has traditionally been viewed as the “basal” clade (e.g. Salvini-Plawen, 1972a; Ivanov, 1986b). Relationships among the caudofoveates sampled here thereby indicate a different evolutionary scenario (Figure 6) than the leading hypotheses based on morphological characters.

Morphologically, Prochaetodermatidae are divergent from Chaetodermatidae and Limifossoridae. The most important characters that distinguish Prochaetodermatidae from the other families are the radula with a central plate and the cuticular jaws, both of which are only present in this family.

Earlier, the simple, distichous radula of Limifossoridae was viewed as the ancestral form in Caudofoveata (Salvini-Plawen, 1975; Scheltema, 1981; Salvini-Plawen, 2003), in concurrence with a hypothetical ancestral aplacophoran radula of the distichous type (Scheltema *et al.*, 2003). A revised view on the morphology of the ancestral aplacophoran radula in the light of recent paleontological findings, however, supports the presence of a rhachidian, or central, tooth between the lateral teeth to represent the ancestral state in Mollusca, and probably also Aplacophora (Scheltema, 2014). Re-examination of the feeding apparatus of the two putative stem-group molluscs and aculiferans, *Wiwaxia* and *Odontogriphus* revealed that they possess a polystichous radula with a central rhachidian tooth (Smith, 2012), instead of a distichous radula as suggested by previous interpretations. Recently, an additional stem-group aculiferan, *Calvapilosa*, was also described with a radula with a central tooth (Vinther *et al.*, 2017). In Caudofoveata, the more complex prochaetodermatid radula has a central plate, which is assumed to be analogous to the rhachidian tooth found in the radulae in other mollusc groups and also in the ancestral molluscan radula (Scheltema, 2014). If, however, the central plate of the prochaetodermatid radula is instead homologous to a rhachidian tooth, this would support the evidence from our molecular data that show an early branching of Prochaetodermatidae within Caudofoveata.

Under this scenario, a reduction of the radula, including the loss of a central row of teeth, would have taken place in the lineage leading to Chaetodermatidae and

Limifossoridae. The ancestral molluscan radula is hypothesized to be unipartite, i.e. with an undivided radula membrane (Smith, 2012), similar to extant Polyplacophora (Scheltema *et al.*, 2003). This is concurrent with the unipartite radula membrane found in Prochaetodermatidae. The undivided radula membrane provides stability for rasping, and could represent an ancestral state in an evolution towards allowing more movement of the radula teeth, in order to increase the ability to manipulate and utilize food sources, as described by Scheltema (1981).

Likely plesiomorphic characters within Aplacophora, including an undifferentiated body shape, and the simple configuration of the digestive system appear to be retained in Limifossoridae, but independently derived in both Chaetodermatidae and Prochaetodermatidae. Several morphological characters that distinguish Prochaetodermatidae from the two remaining families, i.e., characters of the digestive system (simplified digestive tract; Salvini-Plawen, 1981; Scheltema, 1981), nervous system (fused cerebral ganglia, vestigial dorsoterminal sense organ; Salvini-Plawen, 1985; Haszprunar, 1987) and reproductive system (fused gonopericarial ducts; Salvini-Plawen, 1985) have been interpreted as specialized and reduced, and are probably derived. An early split of Prochaetodermatidae within Caudofoveata would have allowed for the evolution of their unique morphology, perhaps combined with a heightened molecular evolutionary rate in this lineage.

Within the lineage leading to Chaetodermatidae and Limifossoridae, Limifossoridae appear to have retained several plesiomorphic characters, while several characters of both body shape (division into externally visible body regions, development of a tailed posterior body) and the digestive system (the highly reduced radula, a style sac and a gastric shield) have evolved within Chaetodermatidae, so that the most derived state for several morphological characters within Caudofoveata is present in Chaetodermatidae, as previously suggested by other authors (Salvini-Plawen & Nopp, 1974; Ivanov, 1986b).

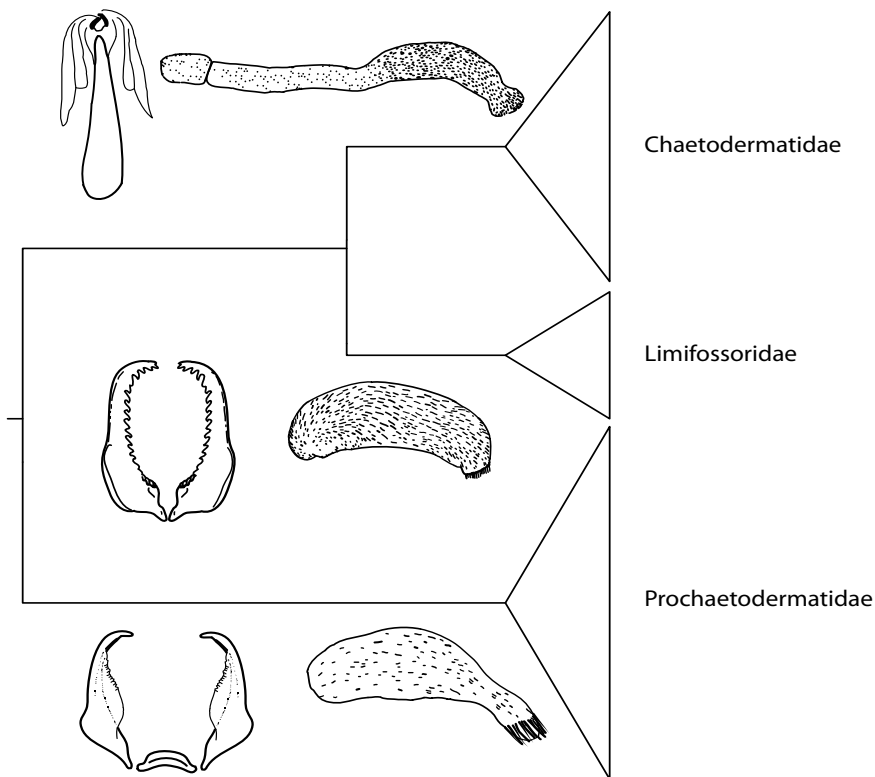


Figure 6. Hypothetical relationships between the caudofoveate families with illustrations of general radula morphology and body shape within each family.

4.2.5 Caudofoveata as Aculifera — evidence from mitochondrial genomes

The order of both protein-coding genes and rRNAs in the mitochondrial genomes is highly conserved within Aculifera as a whole (Paper III, figure 2). Comparison of mitochondrial gene order revealed arrangements of rRNAs and tRNAs diagnostic for Chaetodermatidae and Limifossoridae, while the mitochondrial gene order in the included species of Prochaetodermatidae, *Spathoderma clenchi*, is clearly different with respect to the other sequenced species of Caudofoveata. The *S. clenchi* genome

also differs from other Aculifera genomes in that all genes are encoded on a single strand. This is common in other animal groups (e.g. Annelida; Vallés & Boore, 2006) but has only been described for bivalves within Mollusca (Stöger & Schrödl, 2013).

Some apparent symplesiomorphies are shared by Polyplacophora, the solenogaster *Neomenia carinata* and the prochaetodermatid *S. clenchi*; most notably the position of trnS1 between nad3 and nad2, and the relative positions of rrnS and rrnL. The relative positions of the rRNAs appear to be conserved in Polyplacophora, Solenogastres, and Prochaetodermatidae as rrnL-rrnS, but interchanged to rrnS-rrnL in Chaetodermatidae and Limifossoridae. In addition, the tRNA complex trnM-trnC-trnY-trnW-trnQ-trnG (without trnE) is shared by *N. carinata* and Polyplacophora. In the remaining caudofoveates (Chaetodermatidae and Limifossoridae), these complexes appear to have been modified from the plesiomorphic state retained in Polyplacophora, to form new complexes that are shared in Chaetodermatidae and Limifossoridae (trnM-trnC-trnQ-trnY and the position of rrnS and rrnL); and others that are diagnostic for each of the two groups (trnK-trnA-trnR-trnI-trnS1-trnN and trnV-trnG-trnW-trnE in Limifossoridae, trnK-trnS1-trnN in Chaetodermatidae, trnV-trnW-trnA-trnR-trnI-trnF-trnG-trnE in *Falcidens* and trnV-trnA-trnR-trnI-trnE in *Chaetoderma*). The order of tRNAs found in Chaetodermatidae appears to be further modified from the arrangement in Limifossoridae.

The aculiferan mollusc mitochondrial genomes investigated are relatively conserved in terms of gene order when compared to other mollusc groups (Stöger & Schrödl, 2013; Irisarri *et al.*, 2014; Osca *et al.*, 2014). The order of protein-coding genes found in all investigated aculiferan mitochondrial genomes (except Prochaetodermatidae) has been proposed as the ancestral gene order for Mollusca (Osca *et al.*, 2014). This order of protein-coding genes is shared by basal lineages in Cephalopoda, Gastropoda and Bivalvia and is close to the gene order of other lophotrochozoans (Stöger & Schrödl, 2013; Osca *et al.*, 2014).

The conservation and correspondence of the gene order to taxonomic lineages in the mitochondrial genomes of aculiferan molluscs shows that mitochondrial genome data

is useful for investigating phylogenetic relationships within this group. Although the order of protein coding genes is highly conserved within the mitochondrial genomes of aplacophoran molluscs sequenced here, the arrangements of tRNAs and rRNAs still contribute phylogenetic characters. Mitochondrial genome data thus provides valuable information and can be a useful tool to investigate relationships among the aplacophoran molluscs.

5. Future perspectives

5.1 Undescribed diversity

The work with this thesis has resulted in the recognition of a number of undescribed species. Material of undescribed species has been registered of *Falcidens* from Iceland and Japan (Paper IV), of *Psilodens* from Iceland (Paper I) and the United States east coast (Paper IV), of *Scutopus* from the United States west coast (Paper IV), and of Prochaetodermatidae from Japan, the East Pacific and from Antarctic waters (Paper IV).

A lot of undescribed diversity still exists within Caudofoveata. Samples from poorly explored areas bring up almost exclusively new species, as exemplified by collections from recent years from Japan (Saito & Salvini-Plawen, 2014, Paper IV), Antarctica (Paper IV), New Zealand (K. Kocot, personal communication), and Brazil (Corrêa *et al.*, 2014; Passos *et al.*, 2016). Even regions where extensive sampling has been carried out and the aplacophoran fauna has been studied for years include species that remain to be described. The North Atlantic is a well-investigated area, from which most species have been described, and their distribution has been mapped. But even so, the North Atlantic caudofoveate fauna is most likely richer than what is presently known. Material of Caudofoveata has been sampled from Icelandic waters in both the BIOICE project and the IceAGE project (Ivanov & Scheltema, 2001a, Paper I) and the material still includes several undescribed species. Undescribed species are for example also registered from the United States east coast (own unpublished data, Paper IV) and the Iberian Peninsula (Señaris *et al.*, 2016a). Large areas where the caudofoveate fauna remains largely unexplored, e.g. the deep Pacific and the Indian Ocean, are also expected to harbour unrecognized diversity. Various published records of unidentified Caudofoveates might also represent yet undescribed species, e.g. Singapore (Ang & Tan, 2013), Columbia (Gracia *et al.*, 2013), and Brazil (Cruz *et al.*, 1998).

Material of undescribed species from all over the globe is held in private or institutional collections (Todt 2013; K. Kocot, A. Scheltema, L. v. Salvini-Plawen, and C. Todt personal communication), and large amounts of undescribed material is also held in museum collections (Glaubrecht *et al.*, 2005; Todt, 2013). The number of species awaiting description in museum collections alone has for some regions been estimated to be ten times higher than the number of currently known species (Todt, 2013).

5.2 Biogeography and distribution patterns

Within several of the genera of Caudofoveata, groups of species with similar morphologies can be found in different biogeographical regions. Species of *Falcidens* from different regions sharing distinct morphotypes were included in the analyses in Paper IV, and similar morphological sister species have been described within *Prochaetoderma* (Scheltema, 1990), in *Claviderma* (Corrêa *et al.*, 2018) and in *Scutopus* (Salvini-Plawen, 1972a). Species of *Falcidens* with similar morphotypes were, however, in most cases not recovered as monophyletic (Paper IV). Further studies are necessary to explore mechanisms that have lead to these patterns of species distribution. Biogeographical studies would show if similar morphotypes evolved independently as an adaption to habitat, or are a result of radiation on a larger geographical scale without major morphological changes. Studies of the processes that have lead to these distribution patterns will also provide important clues for developing further hypotheses about the evolution of morphological characters in Caudofoveata in general.

The very large distribution ranges of several species of Prochaetodermatidae (e.g. the amphi-Atlantic *Prochaetoderma yongei*) leads to questions if more than one evolutionary unit could be present in these species. Similarly, *Scutopus ventrolineatus*, which represents a well-defined species, has the largest distribution within Limifossoridae, occurring in the East Atlantic from Scandinavia to South Africa, and has been registered from 40 to 1250 m (Salvini-Plawen, 1985).

Intraspecific genetic variation could be expected to be large within many of these species due to extensive distribution ranges. Molecular investigations of these widespread species could uncover potential cryptic species or geographical population structures, comparable to the patterns found in the North Atlantic in *Chaetoderma nitidulum* (Paper II).

5.3 Systematics of Chaetodermatidae

Our molecular analyses suggest that the radula characters presently used for classification within Chaetodermatidae are ambiguous. The validity of the characters of the radula that define the genera within Chaetodermatidae is in need of further scrutiny, as characters of the *Falcidens* radula have been shown to be present in juveniles of *Chaetoderma*, the differences in radula morphology in part represent ontogenetic changes (Paper II).

It is likely that some species assigned to *Falcidens* in fact are juveniles of a *Chaetoderma* species. Among these is *Falcidens sterreri* (Salvini-Plawen, 1967), which was described from Gullmarsfjord, Sweden, and later also recorded from localities close to Bergen, Norway, geographic areas also included in our study. It is possible that *F. sterreri* was based on *C. nitidulum* juveniles and should be considered a synonym of *C. nitidulum*.

A revision of the Chaetodermatidae is necessary to evaluate whether the currently recognized genera are valid, and to investigate other potential morphological characters that could be used to differentiate between the genera, especially at the juvenile stages.

5.4 Higher caudofoveate systematics

The use of molecular methods has provided new knowledge and outlooks on the evolution of the aplacophoran molluscs and their phylogenetic position within Mollusca. The molecular studies presented in this thesis have strengthened the

framework for building phylogenies, and provided insight into possible evolutionary pathways in this group. Several open questions remain; the investigation of many of these was limited by the availability of material for sequencing. The paraphyly of Chaetodermatidae and Limifossoridae recovered based on molecular data, warrants further investigation. A denser taxon sampling, in particular the inclusion of the genus *Limifossor* might further give better estimates of family relationships. Further studies including more markers and more taxa and will undoubtedly further illuminate the phylogenetic relationships of Caudofoveata in the future.

6. References

- Ang, H. P. & Tan, S. K. (2013). New records of the molluscan classes Caudofoveata and Solenogastres in Singapore. *Nature in Singapore*, 6, 143–148.
- Barwick, K. & Cadien, D. (2005). Aplacophore mollusks of the 2003 Regional Monitoring Survey of the Southern California Bight. *SCAMIT Newsletter*, Supplement volume 23.
- Buckland-Nicks, J. & Chia, F. S. (1989). Spermiogenesis in *Chaetoderma* sp. (Aplacophora). *Journal of Experimental Zoology*, 252, 308–317.
- Buckland-Nicks, J. A. (1995). Ultrastructure of sperm and sperm-egg interaction in Aculifera: implications for molluscan phylogeny. In: Jamieson, B. G. M., Ausio, J. & Justine, J.-L. (Eds.), *Advances in spermatozoal phylogeny and taxonomy*, 166. pp. 129–153. Mémoires du Museum national d'histoire naturelle Paris.
- Böttger, C. R. (1956). Beiträge zur Systematik der Urmollusken (Amphineura). *Zoologischer Anzeiger*, 19, 223–256.
- Corrêa, P. V. F., Fassina, P. V. & Passos, F. D. (2014). *Falcidens targatus* and *F. acutargatus*: two species of Caudofoveata (Mollusca, Aplacophora) new for Brazil. *Journal of Natural History*, 48, 2947–2963.
- Corrêa, P. V. F., Miranda, M. S. & Passos, F. D. (2018). South America-Africa missing links revealed by the taxonomy of deep-sea molluscs: examples from prochaetodermatid aplacophorans. *Deep-Sea Research Part I*, 132, 16–28.
- Cruz, R., Lins, U. & Farina, M. (1998). Minerals of the radular apparatus of *Falcidens* sp. (Caudofoveata) and the evolutionary implications for the phylum Mollusca. *The Biological Bulletin*, 194, 224–230.
- Diesing, K. M. (1859). Revision der Rhyngodeen. *Sitzungsberichte der Akademie der Wissenschaften in Wien*, 37, 719–782.
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.
- Gegenbaur, C. (1878). *Grundriss der vergleichenden Anatomie*. 2nd ed. Wilhelm Engelmann, Leipzig.
- Geller, J., Meyer, C., Parker, M. & Hawk, H. (2013). Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. *Molecular Ecology Resources*, 13, 851–861.
- Giribet, G., Okusu, A., Lindgren, A. R., Huff, S. W., Schrödl, M. & Nishiguchi, M. K. (2006). Evidence for a clade composed of molluscs with serially repeated structures: Monoplacophorans are related to chitons. *Proceedings of the National Academy of Sciences*, 103, 7723–7728.
- Glaubrecht, M., Maitas, L. & Salvini-Plawen, L. v. (2005). Aplacophoran Mollusca in the Natural History Museum Berlin. An annotated catalogue of Thiele's type specimens, with a brief review of “Aplacophora” classification. *Zoosystematics and Evolution*, 81, 145–166.

- Gracia, C., Fontalvo, A., Gámez, E. & Carlos, L. (2013). La clase Caudofoveata (Mollusca) en el mar Caribe Colombiano. *Boletín de Investigaciones Marinas y Costeras*, 42, 421–424.
- Graff, L. v. (1876). Anatomie des *Chaetoderma nitidulum*. *Zeitschrift für wissenschaftliche Zoologie*, 26, 166–192.
- Haszprunar, G. (1987). The fine morphology of the osphradial organs of the Mollusca. IV. Caudofoveata and Solenogastres. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 315, 37–73.
- Haszprunar, G. (2000). Is the Aplacophora monophyletic? A cladistic point of view. *American Malacological Bulletin*, 15, 115–130.
- Haszprunar, G. & Wanninger, A. (2000). Molluscan muscle systems in development and evolution. *Journal of Zoological Systematics and Evolutionary Research*, 38, 157–163.
- Hatschek, B. (1891). Aculifera. In: Blumrich, J. Das Integument der Chitonen. *Zeitschrift für wissenschaftliche Zoologie*, 52, 404–406.
- Heath, H. (1904). The Habits of a few Solenogastres. *Zoologischer Anzeiger*, 27, 457–461.
- Heath, H. (1911). The Solenogastres. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 45 no. 1, 1–182.
- Heath, H. (1918). Solenogastres from the eastern coast of North America. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 45 no. 2, 187–260.
- Heppel, D. (1963). *Chaetoderma* Lovén, 1844 (Mollusca), and *Chaetodermis* Swainson, 1839 (Pisces): Proposed addition to the official list of generic names. Z.N.(S.) 1250. *Bulletin of Zoological Nomenclature*, 20, 429–431.
- Hoffman, S. (1949). Studien über das Integument der Solenogastren nebst Bemerkungen über die Verwandtschaft zwischen den Solenogastren und Placophoren. *Zoologiska Bidrag från Uppsala*, 27, 293–427.
- Hoffmann, H. (1929). Amphineura und Scaphopoda. Bronns Klassen und Ordnungen des Tierreichs wissenschaftlich dargestellt in Wort und Bild. Mollusca, I. Abtl. Suppl., Nachträge. Vol. 3, pp. 1–368. Akademische Verlagsgesellschaft, Leipzig.
- Ihering, H. (1876). Versuch eines natürlichen Systemes der Mollusken. *Jahrbuch der Deutschen Malakozoologischen Gesellschaft*, 3, 97–148.
- Irisarri, I., Eernisse, D. J. & Zardoya, R. (2014). Molecular phylogeny of Acanthochitonina (Mollusca: Polyplacophora: Chitonida): three new mitochondrial genomes, rearranged gene orders and systematics. *Journal of Natural History*, 48, 2825–2853.
- Ivanov, D. L. (1979). Structure and functional morphology of radula apparatus in *Chaetoderma* (Mollusca, Caudofoveata). *Zoologicheskii Zhurnal*, 58, 1302–1306.
- Ivanov, D. L. (1981). *Caudofoveatus tetradens* gen. et sp. n. and diagnosis of taxa in the subclass Caudofoveata (Mollusca, Aplacophora). *Zoologicheskii Zhurnal*, 60, 18–28.
- Ivanov, D. L. (1984). Caudofoveates (Mollusca, Caudofoveata) from Peter the Great Bay. In: Kafanov, A. I. (Ed.), Hydrobiological investigations of basins and bays of Primorje. pp. 28–41. USSR Academy of Sciences, Vladivostok.

-
- Ivanov, D. L. (1986a). New species of Caudofoveata from the Chukchi Sea. *Proceedings of the Zoological Museum of Moscow State University*, 24, 84–96.
- Ivanov, D. L. (1986b). Phylogeny of the subclass Caudofoveata. *Proceedings of the Zoological Institute of the USSR Academy of Sciences*, 148, 12–32.
- Ivanov, D. L. (1987). Class Aplacophora Ihering 1876. Molluscs of the White Sea. pp. 28–35. Zoological Institute of the USSR Academy of Sciences, Leningrad.
- Ivanov, D. L. (1996a). *Chevroderma hadalis*, a new species of Prochaetodermatidae (Caudofoveata, Aplacophora) from the North-West Pacific. *Ruthenica*, 6, 83–84.
- Ivanov, D. L. (1996b). Origin of Aculifera and problems of monophyly of higher taxa in molluscs. In: Taylor, J. D. (Ed.), Origin and evolutionary radiation of the Mollusca. Centenary Symposium of the Malacological Society of London. pp. 59–65. Oxford University Press, Oxford.
- Ivanov, D. L., Mikkelsen, N. T. & Schander, C. (2010). *Falcidens sagittiferus* Salvini-Plawen, 1968: additional data on morphology and distribution (Mollusca, Aplacophora, Caudofoveata). *Fauna norvegica*, 29, 3–9.
- Ivanov, D. L. & Scheltema, A. H. (2001a). Distribution of known caudofoveate species (Mollusca, Aplacophora) around Iceland. *Ruthenica*, 11, 1–6.
- Ivanov, D. L. & Scheltema, A. H. (2001b). Prochaetodermatidae of the Western Indian Ocean and Arabian Sea (Mollusca: Aplacophora). *Mémoires du Muséum national d'histoire naturelle*, 185, 9–38.
- Ivanov, D. L. & Scheltema, A. H. (2002). Prochaetodermatidae of the Indian Ocean collected during Soviet VITYAZ cruises 1959–1964 (Mollusca: Aplacophora). *Molluscan Research*, 22, 183–202.
- Ivanov, D. L. & Scheltema, A. H. (2004). *Dacryomica plana*, gen. et sp. nov., a prochaetodermatid Aplacophora from a Pacific seamount. *The veliger*, 47, 1–5.
- Ivanov, D. L. & Scheltema, A. H. (2007). *Chaetoderma felderi* — a new giant caudofoveate species from the Gulf of Mexico (Mollusca: Aplacophora). *Ruthenica*, 17, 7–12.
- Ivanov, D. L. & Scheltema, A. H. (2008). Western Atlantic Prochaetodermatidae from 35°N south to the Argentine Basin including the Gulf of Mexico (Mollusca: Aplacophora). *Zootaxa*, 1885, 2–60.
- Ivanov, D. L. & Scheltema, A. H. (2009). Aplacophora (Mollusca) of the Gulf of Mexico. In: Felder, D. L. & Camp, D., K. (Eds.), Gulf of Mexico origin, waters, and biota. Vol. 1 Biodiversity, pp. 565–568. Texas A&M University Press.
- Keferstein, W. (1865). Beiträgen zur anatomischen und systematischen Kenntnis der Sipunculiden. *Zeitschrift für wissenschaftliche Zoologie*, 15, 404–449.
- Kocot, K. M., Cannon, J. T., Todt, C., Citarella, M. R., Kohn, A. B., Meyer, A., Santos, S. R., Schander, C., Moroz, L. L., Lieb, B. & Halanych, K. M. (2011). Phylogenomics reveals deep molluscan relationships. *Nature*, 477, 452–456.
- Kocot, K. M., Todt, C., Mikkelsen, N. T. & Halanych, K. M. (forthcoming). Phylogenomics of Aplacophora (Mollusca, Aculifera) and a solenogaster without a foot.

- Kowalevsky, A. O. (1901). Sur le genre *Chaetoderma*. *Archives de zoologie expérimentale et générale.*, 3, 261–284.
- Lundin, K. & Schander, C. (1999). Ultrastructure of gill cilia and ciliary rootlets of *Chaetoderma nitidulum* Lovén 1844 (Mollusca, Chaetodermomorpha). *Acta Zoologica*, 80, 185–191.
- Lundin, K. & Schander, C. (2001). Ciliary ultrastructure of neomeniomorphs (Mollusca, Neomeniomorpha = Solenogastres). *Invertebrate Biology*, 120, 342–349.
- Meyer, A., Todt, C., Mikkelsen, N. T. & Lieb, B. (2010). Fast evolving 18 S rRNA sequences from Solenogastres (Mollusca) resist standard PCR amplification and give new insights into mollusk substitution rate heterogeneity. *BMC Evolutionary Biology* 10, 70.
- Meyer, C. P. (2003). Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society*, 79, 401–459.
- Nielsen, C., Haszprunar, G., Ruthensteiner, B. & Wanninger, A. (2007). Early development of the aplacophoran mollusc *Chaetoderma*. *Acta Zoologica*, 88, 231–247.
- Nierstrasz, H. F. (1902). The Solenogastres of the Siboga Expedition. Siboga-Expeditie. 47. E. J. Brill, Leyden.
- Nierstrasz, H. F. (1903). Neue Solenogastren. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*, 18, 359–386.
- Odhner, N. H. (1921). Norwegian Solenogastres. *Bergens Museums Aarbok 1918-1919*, 3, 1–86.
- Okusu, A. & Giribet, G. (2003). New 18S rRNA sequences from neomenioid aplacophorans and the possible origin of persistent exogenous contamination. *Journal of Molluscan Studies*, 69, 385–387.
- Okusu, A., Schwabe, E., Eernisse, D. J. & Giribet, G. (2003). Towards a phylogeny of chitons (Mollusca, Polyplacophora) based on combined analysis of five molecular loci. *Organisms Diversity & Evolution*, 3, 281–302.
- Osca, D., Irisarri, I., Todt, C., Grande, C. & Zardoya, R. (2014). The complete mitochondrial genome of *Scutopus ventrolineatus* (Mollusca: Chaetodermomorpha) supports the Aculifera hypothesis. *BMC Evolutionary Biology* 14, 197.
- Passamaneck, Y. J., Schander, C. & Halanych, K. M. (2004). Investigation of molluscan phylogeny using large-subunit and small-subunit nuclear rRNA sequences. *Molecular Phylogenetics and Evolution*, 32, 25–38.
- Passos, F. D., Corrêa, P. V. F. & Todt, C. (2016). A new species of *Falcidens* (Mollusca, Aplacophora, Caudofoveata) from the southeastern Brazilian coast: external anatomy, distribution, and comparison with *Falcidens caudatus* (Heath, 1918) from the USA. *Marine Biodiversity*, 1, 1–12.
- Pelseneer, P. (1906). Mollusca. In: Lankester, E. R. (Ed.), *A treatise on zoology*. Vol. 5. Black, London.
- Saito, H. & Salvini-Plawen, L. v. (2014). Four new species of the aplacophoran class Caudofoveata (Mollusca) from the southern Sea of Japan. *Journal of Natural History*, 48, 2965–2983.

-
- Salvini-Plawen, L. v. (1967). Über die Beziehungen zwischen den Merkmalen von Standort, Nahrung und Verdauungstrakt bei Solenogastres (Aculifera, Aplacophora). *Zeitschrift für Morphologie und Ökologie der Tiere*, 59, 318–340.
- Salvini-Plawen, L. v. (1968). Über Lebendebeobachtungen an Caudofoveata (Mollusca, Aculifera), nebst Bemerkungen zum System der Klasse. *Sarsia*, 31, 105–126.
- Salvini-Plawen, L. v. (1969a). Faunistische Studien am Roten Meer im Winter 1961/62: V. Caudofoveata und Solenogastres (Mollusca, Aculifera). *Zoologische Jahrbucher. Abteilung für Systematik, Ökologie und Geographie der Tiere*, 96, 52–68.
- Salvini-Plawen, L. v. (1969b). Solenogastres und Caudofoveata (Mollusca, Aculifera): Organisation und phylogenetische Bedeutung. In: Proceedings of the Third European Malacological Congress. *Malacologia*, 9, 191–216.
- Salvini-Plawen, L. v. (1972a). Die Caudofoveata des Mittelmeeres und das Genus *Scutopus* (Mollusca, Aculifera). In: Battaglia, B. (Ed.), Fifth European Marine Biology Symposium. pp. 27–51.
- Salvini-Plawen, L. v. (1972b). Zur Morphologie und Phylogenie der Mollusken: Die Beziehungen der Caudofoveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia. *Zeitschrift für wissenschaftliche Zoologie*, 184, 205–394.
- Salvini-Plawen, L. v. (1975). Mollusca Caudofoveata. Marine Invertebrates of Scandinavia. Universitetsforlaget, Oslo.
- Salvini-Plawen, L. v. (1977). Caudofoveata (Mollusca) des Forschungsprojektes Polymède. *Bulletin du Museum national d'histoire naturelle*, 3, 413–421.
- Salvini-Plawen, L. v. (1978). The species problem in Caudofoveata Mollusca. *Zoologischer Anzeiger*, 200, 18–26.
- Salvini-Plawen, L. v. (1980). A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia*, 19, 249–278.
- Salvini-Plawen, L. v. (1981). The molluscan digestive system in evolution. *Malacologia*, 21, 1–33.
- Salvini-Plawen, L. v. (1984). Comments on *Chaetoderma* and *Crystallophrisson* (Mollusca, Caudofoveata). *Zoologicheskii Zhurnal*, 63, 171–175.
- Salvini-Plawen, L. v. (1985). Early evolution and the primitive groups. In: Trueman, E. R. & Clarke, M. R. (Eds.), *The Mollusca. Evolution*. Vol. 10, pp. 59–150. Academic Press, London.
- Salvini-Plawen, L. v. (1988). The structure and function of molluscan digestive systems. In: Trueman, E. R. & Clarke, M. R. (Eds.), *The Mollusca. Form and Function*. Vol. 11, pp. 301–379. Academic Press, Orlando.
- Salvini-Plawen, L. v. (1990). Origin, phylogeny and classification of the phylum Mollusca. *Iberus*, 9, 1–33.
- Salvini-Plawen, L. v. (1992). On certain Caudofoveata from the Vema expedition. In: Gittenberger, E. & Gould, J. (Eds.), *Proceedings of the 9th International Malacological Congress*. pp. 317–333.
- Salvini-Plawen, L. v. (1999). Caudofoveata (Mollusca) from off the northern coast of the Iberian Peninsula. *Iberus*, 17, 77–84.

- Salvini-Plawen, L. v. (2003). On the phylogenetic significance of the aplacophoran Mollusca. *Iberus*, 21, 67–97.
- Salvini-Plawen, L. v. & Nopp, H. (1974). Chitin bei Caudofoveata (Mollusca) und die Ableitung ihres Radulaapparates. *Zeitschrift für Morphologie und Ökologie der Tiere*, 77, 77–86.
- Salvini-Plawen, L. v. & Steiner, G. (1996). Synapomorphies and plesiomorphies in higher classification of Mollusca. In: Taylor, J. D. (Ed.), *Origin and evolutionary radiation of the Mollusca*. pp. 29–51. Oxford University Press, Oxford.
- Salvini-Plawen, L. v. & Steiner, G. (2014). The Testaria concept (Polyplacophora + Conchifera) updated. *Journal of Natural History*, 48, 2751–2772.
- Schander, C., Scheltema, A. H. & Ivanov, D. L. (2006). *Falcidens halanychi*, a new species of Chaetodermomorpha (= Caudofoveata) (Mollusca) from the northwest Atlantic Ocean. *Marine Biology Research*, 2, 303–315.
- Scheltema, A. H. (1972). The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere*, 72, 361–370.
- Scheltema, A. H. (1976). Two new species of *Chaetoderma* from off West Africa (Aplacophora, Chaetodermatidae). *Journal of Molluscan Studies*, 42, 223–234.
- Scheltema, A. H. (1978). Position of the class Aplacophora in the phylum Mollusca. *Malacologia*, 17, 99–109.
- Scheltema, A. H. (1981). Comparative morphology of the radula and alimentary tracts in the Aplacophora. *Malacologia*, 20, 361–383.
- Scheltema, A. H. (1985). The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma* n.g. and *Spathoderma* n.g. (Mollusca; Chaetodermomorpha). *The Biological Bulletin*, 169, 484–529.
- Scheltema, A. H. (1987). Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yongei*. *Marine Ecology Progress Series*, 37, 171–180.
- Scheltema, A. H. (1989). Australian aplacophoran molluscs: I. Chaetodermomorpha from Bass Strait and the continental slope off south-eastern Australia. *Records of the Australian Museum*, 41, 43–62.
- Scheltema, A. H. (1990). Aplacophora as a Tethyan slope taxon: evidence from the Pacific. *Bulletin of Marine Science*, 47, 50–61.
- Scheltema, A. H. (1993). Aplacophora as progenetic aculiferans and the coelomate origin of mollusks as the sister taxon of Sipuncula. *The Biological Bulletin*, 184, 57–78.
- Scheltema, A. H. (1995). *Falcidens poias*, a new species of chaetoderm Aplacophora from Rottnest Island, Western Australia (Chaetodermomorpha, Chaetodermatidae). *Molluscan Research*, 16, 45–49.
- Scheltema, A. H. (1996). Phylogenetic position of Sipuncula, Mollusca and the progenetic Aplacophora. In: Taylor, J. D. (Ed.), *Origin and Evolutionary Radiation of the Mollusca*. pp. 53–58. Oxford University Press, Oxford.
- Scheltema, A. H. (1997). Aplacophoran molluscs: deep-sea analogs to polychaetes. *Bulletin of Marine Science*, 60, 575–583.
- Scheltema, A. H. (1998). Class Aplacophora. In: Scott, P. V. & Blake, J. A. (Eds.), *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the western*

-
- Santa Barbara Channel. Vol. 8. The Mollusca Part 1, The Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda, pp. 1–49. Santa Barbara Museum of Natural History.
- Scheltema, A. H. (2014). The original molluscan radula and progenesis in Aplacophora revisited. *Journal of Natural History*, 48, 2855–2869.
- Scheltema, A. H., Herth, K. & Kuzirian, A. M. (2003). Original molluscan radula: comparisons among Aplacophora, Polyplacophora, Gastropoda and the Cambrian fossil *Wiwaxia corrugata*. *Journal of Morphology*, 257, 219–245.
- Scheltema, A. H. & Ivanov, D. L. (2000). Prochaetodermatidae of the eastern Atlantic Ocean and Mediterranean Sea (Mollusca: Aplacophora). *Journal of Molluscan Studies*, 66, 313–362.
- Scheltema, A. H. & Ivanov, D. L. (2004). Use of birefringence to characterize Aplacophora sclerites. *The Veliger*, 47, 153–160.
- Scheltema, A. H. & Ivanov, D. L. (2009). A natural history of the deep-sea aplacophoran *Prochaetoderma yongei* and its confamilials (Mollusca, Prochaetodermatidae). *Deep Sea Research Part II: Topical Studies in Oceanography*, 56, 1856–1864.
- Scheltema, A. H. & Schander, C. (2000). Discrimination and phylogeny of solenogaster species through the morphology of hard parts (Mollusca, Aplacophora, Neomeniomorpha). *The Biological Bulletin*, 198, 121–151.
- Scheltema, A. H., Tscherkassky M & Kuzirian, A. M. (1994). Aplacophora. In: Harrison, F. & Kohn, A. (Eds.), *Microscopic anatomy of invertebrates*. Vol. 5. Mollusca I: Aplacophora, Polyplacophora, and Gastropoda, pp. 1–36. Wiley-Liss Inc., New York.
- Scherholz, M., Redl, E., Wollesen, T., Todt, C. & Wanninger, A. (2015). From complex to simple: myogenesis in an aplacophoran mollusk reveals key traits in aculiferan evolution. *BMC Evolutionary Biology*, 15, 201.
- Schwabl, M. (1963). Solenogaster mollusks from Southern California. *Pacific Science*, 17, 261–281.
- Señarís, M. P., García-Álvarez, O. & Urgorri, V. (2014). Morphology of *Falcidens vasconiensis* (Mollusca, Caudofoveata, Chaetodermatidae), including a 3D reconstruction of the internal anatomy. *Journal of Natural History*, 48, 2871–2884.
- Señarís, M. P., García-Álvarez, O. & Urgorri, V. (2016a). Four new species of Chaetodermatidae (Mollusca, Caudofoveata) from bathyal bottoms of the NW Iberian Peninsula. *Helgoland Marine Research*, 70, 28.
- Señarís, M. P., García-Álvarez, O. & Urgorri, V. (2016b). The habitus of *Scutopus robustus* Salvini-Plawen, 1970 (Caudofoveata, Limifossoridae), a rare mollusc from the NW Iberian Peninsula. *Marine Biodiversity*, 47, 377–378.
- Señarís, M. P., García-Álvarez, O. & Urgorri, V. (2017a). Two new records of *Prochaetoderma* Thiele, 1902 (Mollusca, Caudofoveata, Prochaetodermatidae) on bathyal and abyssal bottoms of Galicia, NW Iberian Peninsula. *Nova Acta Científica Compostelana (Biología)*, 24, 91–103.
- Señarís, M. P., García-Álvarez, O., Urgorri, V. & Pedrouzo, L. (2017b). Morphology of *Prochaetoderma iberogallicum* Salvini-Plawen, 1999 and its validity vs *Prochaetoderma boucheti* Scheltema & Ivanov, 2000. *Thalassas*, 33, 117–132.

- Shigeno, S., Sasaki, T. & Haszprunar, G. (2007). Central nervous system of *Chaetoderma japonicum* (Caudofoveata, Aplacophora): implications for diversified ganglionic plans in early molluscan evolution. *The Biological Bulletin*, 213, 122–134.
- Sigwart, J. D. & Sumner-Rooney, L. H. (2016). Mollusca: Caudofoveata, Monoplacophora, Polyplacophora, Scaphopoda, Solenogastres. In: Schmidt-Rhaesa, A., Harzsch, S. & Purschke, G. (Eds.), *Structure and evolution of invertebrate nervous systems*. pp. 172–189. Oxford University Press, Oxford.
- Smith, M. R. (2012). Mouthparts of the Burgess Shale fossils *Odontogriphus* and *Wiwaxia*: implications for the ancestral molluscan radula. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4287–4295.
- Smith, S. A., Wilson, N. G., Goetz, F. E., Feehely, C., Andrade, S. C. S., Rouse, G. W., Giribet, G. & Dunn, C. W. (2011). Resolving the evolutionary relationships of molluscs with phylogenomic tools. *Nature*, 480, 364–367.
- Spengel, J. W. (1881). Die Geruchsorgane und das Nervensystem der Mollusken. Ein Beitrag zur Erkenntnis der Einheit des Mollusken typus. *Zeitschrift für wissenschaftliche Zoologie*, 35, 333–383.
- Stöger, I. & Schrödl, M. (2013). Mitogenomics does not resolve deep molluscan relationships (yet?). *Molecular Phylogenetics and Evolution*, 69, 376–392.
- Thiele, J. (1902). Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken. *Zeitschrift für wissenschaftliche Zoologie*, 72, 249–466.
- Thiele, J. (1913). Solenogastres. In: Schulze, F. E. (Ed.), *Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen*. Vol. 38, pp. 1–57. R. Friedlander & Sohn, Berlin.
- Thiele, J. (1925). Solenogastres. In: Kükenthal, W. & Krumbach, T. (Eds.), *Handbuch der Zoologie. Eine Naturgeschichte der Stämme des Tierreiches*. Vol. 5, pp. 1–14. Walter de Gruyter & Co., Berlin, Leipzig.
- Thiele, J. (1929). *Handbuch der systematischen Weichtierkunde*. Vol. 1–2. G. Fischer, Jena.
- Thomson, C. W. (1878). *The voyage of the "Challenger". The Atlantic. A preliminary account of the general results of the exploring voyage of H.M.S. "Challenger" during the year 1873 and the early part of the year 1876*. Vol. 1. Harper, New York.
- Todt, C. (2013). Aplacophoran mollusks – still obscure and difficult? *American Malacological Bulletin*, 31, 181–187.
- Todt, C., Okusu, A., Schander, C. & Schwabe, E. (2008). Phylogeny of Solenogastres, Caudofoveata and Polyplacophora. In: Ponder, W. & Lindberg, D. (Eds.), *Phylogeny and Evolution of the Mollusca*. pp. 71–96. University of California Press, Berkeley, Los Angeles, London.
- Vallés, Y. & Boore, J. L. (2006). Lophotrochozoan mitochondrial genomes. *Integrative and Comparative Biology*, 46, 544–557.
- Vinther, J., Parry, L., Briggs, D. E. G. & Van Roy, P. (2017). Ancestral morphology of crown-group molluscs revealed by a new Ordovician stem aculiferan. *Nature*, 542, 471–474.
- Vinther, J., Sperling, E. A., Briggs, D. E. G. & Peterson, K. J. (2012). A molecular palaeobiological hypothesis for the origin of aplacophoran molluscs and their

-
- derivation from chiton-like ancestors. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1259–1268.
- Wilson, N. G., Rouse, G. W. & Giribet, G. (2010). Assessing the molluscan hypothesis Serialia (Monoplacophora + Polyplacophora) using novel molecular data. *Molecular Phylogenetics and Evolution*, 54, 187–193.
- Wirén, A. (1892a). Studien über die Solenogastren II. *Chaetoderma productum*, *Neomenia*, *Proneomenia acuminata*. *Kongliga Svenska Vetenskaps-Akademiens handlingar*, 25.
- Wirén, A. (1892b). Studien über die Solenogastres. Monographie des *Chaetoderma nitdulum* Lovén. *Kongliga Svenska Vetenskaps-Akademiens handlingar*, 24.
- Wolter, K. (1992). Ultrastructure of the radula apparatus in some species of aplacophoran molluscs. *Journal of Molluscan Studies*, 58, 245–256.
- Öztürk, B. & Salvini-Plawen, L. v. (2006). New records of Caudofoveata (*Falcidens guttuosus*, *Prochaetoderma raduliferum*) and of Solenogastres (*Eleutheromenia carinata*, spec. nov.) from the eastern Mediterranean Sea. *Spixiana*, 29, 217–224.